The Role of Behavioural Changes in Biological Invasions

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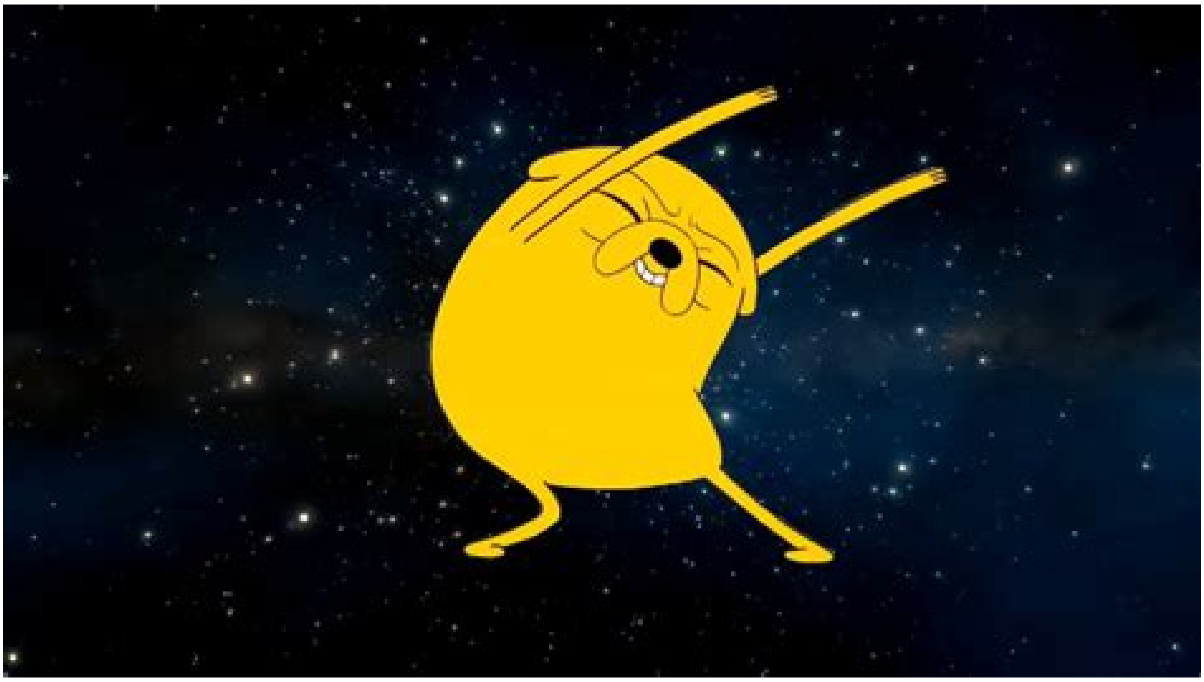

"There are reasons to believe, behavioural shifts have been involved in most evolutionary innovations, hence the saying that behaviour is the pacemaker of evolution."

Ernst Mayr (What Evolution is. 2001)

SUMMARY

All ecosystems on Earth are undergoing rapid human-induced changes. One important component of these changes is the transport of species to new ecosystems, where they often establish and spread, and cause ecological disruption as invasive species. Behaviour plays a major role in this process, not only by enabling species to spread or establish, but also in the native species' response to invasion. These behavioural changes drive population dynamics, and the speed at which they happen are crucial. The shared evolutionary history between two species influences how fast or effective these changes happen. To study these complicated interactions, this thesis combines a comparative study of the existing literature with novel concepts and metadata, as well as analyses of laboratory experiments and field data.

For Chapter 1, a large cross-taxonomical dataset on behavioural changes in biological invasions was gathered and analysed. It is the first to include native and non-native species, to identify types of behaviour and mechanisms of change and to quantify the speed of the behavioural change. This gave us the opportunity to test hypotheses in invasion ecology, but also to explore the distribution of learning across types of behaviour and its implications for the speed of behavioural change. All analyses were conducted considering the biases in the data and differences in the ecology of native and invasive species.

In Chapter 2, the behavioural differences between an established non-native crayfish species, the spiny-cheek crayfish *Faxonius limosus*, and the novel non-native marbled crayfish (*Procambarus virginalis*) were experimentally quantified, and findings were used to predict the invasion success of the latter species. Experiments were designed to show the outcome of inter-specific agonistic interactions, activity and exploration. Finally, not only inter-specific differences were tested but also between both sexes of the spiny-cheek crayfish, and between lab-reared and wild-caught individuals of the marbled crayfish. Apart from predicting invasion success, these analyses help to better understand behavioural plasticity in this special clonal species.

Chapter 3 contains the application of two classification schemes - of animal innovation and eco-evolutionary experience - to the dataset of Chapter 1. I encourage the use of this general quantification scheme of animal innovation to mine a broader range of behavioural changes. The scheme was applied in this study to specifically investigate if big changes in behaviour help native species to cope with invasion. It was also tested if high eco-evolutionary experience with that species buffers negative population consequences for native species. We reject the first hypothesis and accept the latter and found as well a negative relationship between both parameters, as lower experience necessitates bigger change. Therefore, these classifications can help a priori predictions of invasion impact on specific native species.

In Chapter 4, the population dynamics and nesting behaviour of the common eider (*Somateria mollissima*) in West Iceland was analysed from field data. The dataset encompasses yearly nest count data on

134 islands over up to 123 years. Therefore, we were able to investigate how long-term climate dynamics affect the eider colonies and how that changed with the invasion of the American mink (*Neovison vison*) into the region in 1948. Similarly, the arctic fox (*Vulpes lagopus*), the only native terrestrial nest predator, was absent from the study area for decades and we compared the behavioural response to both predators. The differences between the effects of specific predators help to direct targeted conservation efforts to protect the common eider.

Finally, Chapter 5 presents population dynamics of the American mink in Iceland, Denmark, Germany and its native range in the USA estimated from hunting bag data using a novel method. Effects of anthropogenic factors on the hunting bag were quantified, namely the global price of American mink fur, the production of fur in the respective country, and hunting effort and legislation connected to hunting and fur production. While we were able to test several hypotheses on American mink population dynamics in Europe - for example, if it follows a boom-bust dynamic - the utility of this method stretches beyond this system and can be applied whenever population numbers are estimated from hunting bag data.

My thesis explores a novel dataset on behavioural changes in biological invasions (Chapter 1). It includes experimental results on the role of behaviour in an over-invasion scenario of crayfish in Europe (Chapter 2) and expands the horizon of behavioural studies in invasions by introducing classification schemes for eco-evolutionary experience and animal innovation (Chapter 3). Finally, the introduction of the American mink in Europe is studied, by its consequences for the Icelandic avifauna (Chapter 4) and the estimation of its population dynamics through hunting bag data in several countries (Chapter 5).

Keywords: Behaviour, biological invasions, eco-evolutionary experience, innovation, naïveté, population dynamics

ZUSAMMENFASSUNG

Sämtliche Ökosysteme der Erde sind rapidem menschengemachten Wandel unterworfen, unter anderem durch Arten, die in neue Ökosysteme transportiert wurden, sich dort ansiedeln und dann verbreiten, um dabei oft erheblichen ökologischen Schaden anzurichten: invasive Arten. In diesen biologischen Invasionen spielt Verhalten eine wichtige Rolle: Verhaltensänderungen können Invasionen ermöglichen, können es heimischen Arten aber umgekehrt auch erlauben, adäquat auf invasive Arten zu reagieren. Verhaltensveränderungen können Populationsdynamiken beeinflussen; dabei ist die Geschwindigkeit, in der sie passieren, von großer Bedeutung. Diese ist wiederum davon abhängig, ob die Arten an ökologisch ählniche Arten evolutionär angepasst sind. Um diese Zusammenhänge zu erforschen, wurden in vorliegender Dissertation eine Literaturstudie mit einer konzeptionellen Studie und Analysen von Experimenten und Freilanddaten kombiniert.

Für die Analysen im ersten Kapitel wurde eine neue Datenbank zu Verhaltensänderungen in heimischen und nicht heimischen Arten angelegt. Diese vereinigt zum ersten Mal Daten zu verschiedenen Verhaltensänderungen sowie den zugrunde liegenden Mechanismen, wie z.B. genetische Selektion oder Lernen, und erfasst zudem die jeweilige Geschwindigkeit, mit der Verhaltensänderungen passieren. Dadurch konnte die Häufigkeit von Lernverhalten über verschiedene Verhaltenskategorien verglichen werden, immer mit den Unterschieden zwischen heimischen und invasiven Arten im Fokus. Es wurde diskutiert, welche Bedeutung diese Unterschiede für die Auswirkungen von Invasionen haben.

In Kapitel 2 wurden Verhaltensunterschiede zwischen einer etablierten nicht heimischen Art, dem Kamberkrebs (*Faxonius limosus*), und einer neu eingewanderten Art, dem Marmorkrebs (*Procambarus virginalis*), experimentell untersucht, mit Blick auf den potentiellen Invasionserfolg des Marmorkrebses. Die Experimente sollten den Ausgang zwischenartlicher feindlicher Interaktionen quantifizieren. Schlussendlich wurde nicht nur auf Unterschiede zwischen den Arten, sondern auch zwischen den Geschlechtern des Kamberkrebses und zwischen den Marmorkrebsen aus dem Labor gegen die aus der Wildnis getestet. Abgesehen von der Vorhersage des Invasionserfolgs hilft diese Studie, die beeindruckende Plastizität im Verhalten des klonalen Marmorkrebses besser zu verstehen.

Das dritte Kapitel enthält die Anwendung zweier neuer Klassifikationsschemata - von Innovation in einzelnem Tierverhalten und öko-evolutionärer Erfahrung einer Art mit einer anderen - auf einen Teil des Datensatzes von Kapitel 1. Während das Innovationsschema auch erstellt wurde, um eine größere Vielfalt an Verhaltensweisen quantitativ untersuchen zu können als bisherige Schemata, wurde es hier zusätzlich verwendet um zu testen, ob innovative Verhaltensänderungen negative Folgen für heimische Arten abwenden können. Weiterhin wurde analysiert, ob eine hohe öko-evolutionäre Erfahrung Populationsdynamiken positiv beeinflusst. Ersteres konnte nicht bestätigt werden, zweiteres schon, zusätzlich wurde ein negativer Zusammenhang zwischen Innovation und öko-evolutionärer Erfahrung herausgefunden. Wir konnten zeigen, dass diese Klassifikationen für Vorhersagen der Auswirkungen von Invasionen auf bestimmte heimische Arten benutzt werden können.

Im vierten Kapitel wurden Felddaten zur Analyse von Populationsdynamiken und Nistverhalten der Eiderente (*Somateria mollissima*) in Westisland analysiert. Die Daten sind jährliche Nestzahlen von 134 Inseln, über einen Zeitraum von bis zu 123 Jahren. Daher konnten wir nicht nur die Effekte von langfristiger Klimaveränderungen auf die Entenkolonien untersuchen, sondern auch Veränderungen durch mit der Invasion des Amerikanischen Nerzes (*Neovison vison*) im Jahr 1948. In ähnlicher Weise ist der über mehrere Jahrzehnte abwesende heimische Nesträuber, der Polarfuchs (*Vulpes lagopus*), 1998 zurückgekehrt, und wir haben die Verhaltensanpassungen an beide Räuber verglichen. Diese Unterschiede sind bedeutsam für präzise Schutzmaßnahmen für die bedrohte Eiderente in der Region.

Das fünfte und letzte Kapitel der Doktorarbeit zeigt die Populationsdynamiken des Amerikanischen Nerzes in Island, Dänemark, Deutschland und in einem seiner Ursprungsländer, den USA, abgeschätzt aus den jährlichen Abschussraten. Die Effekte anthropogener Faktoren - globaler Nerzfellpreis, die Produktionszahlen des jeweiligen Landes, Jagdaufwand und Gesetze in Bezug auf Jagd und Haltung - auf die Abschusszahlen wurden quantifiziert. Mit den so korrigierten Daten konnten wir testen, ob die Nerzzahlen in Europa dem Boom-Bust Schema folgen. Die Anwendbarkeit der hier entwickelten Korrekturmethode erstreckt sich aber über dieses System hinaus und kann immer benutzt werden, wenn Populationszahlen aus Jagddaten approximiert werden.

Meine Doktorarbeit erforscht einen neuen Datensatz zu Verhaltensänderungen in biologischen Invasionen (Kapitel 1). Sie enthält eine experimentelle Studie zur Rolle des Verhaltens in einer Überinvasion von Flusskrebsen in Europa (Kapitel 2) und erweitert den Horizont von Verhaltensstudien in der Invasionsökologie durch Klassifikationsschemata von Innovation und öko-evolutionärer Erfahrung (Kapitel 3). Abschließend wurde die Invasion des Amerikanischen Nerzes in Europa untersucht, einmal in Bezug auf die Konsequenzen für Vogelarten in Island (Kapitel 4) und durch die Analyse der Populationsdaten des Nerzes aus Jagddaten in mehreren Ländern (Kapitel 5).

Schlagwörter: Biologische Invasionen, Innovation, öko- evolutionäre Erfahrung, Naivität, Verhalten, Populationsdynamiken

THESIS OUTLINE

The dissertation consists of a General Introduction, five separate chapters and a General Discussion. The General Introduction describes the background and purpose of the studies, and defines the research objectives. Each of the following chapters represents an independent manuscript and follows the conventional structure of research papers, with subsections for the Introduction, Material and Methods, Results and Discussion. All manuscripts have either been published (Chapter 2) or submitted (Chapters 1, 3 and 4) to a peer-reviewed journal or are in preparation for submission (Chapter 5). In the last section, the thesis' findings are synthesised, evaluated and discussed with respect to other research in the field, and an outlook to possible future research is provided as well.

LIST OF PUBLICATIONS WITH AUTHOR CONTRIBUTIONS

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The following publications derived from this thesis:

Ruland F, Jeschke JM. How biological invasions affect animal behaviour: A global, cross-taxonomic analysis.

FR and JMJ conceived the idea and design of the study. FR gathered the data, conducted the analyses and drafted the manuscript. Both authors reviewed and revised the manuscript.

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SML and JMJ conceived the idea of the study and designed the experiments. SML and LSG performed the experiments. SML gathered the data. FR developed and performed the statistical models. SML drafted the manuscript. All authors reviewed and revised the manuscript.

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FR and JMJ conceived the idea of the study and developed the classifications. AAM and MSN revised and expanded the classification and gathered the data. FR analysed the data and drafted the manuscript. All authors reviewed and revised the manuscript.

Jónsson JE, Ásgeirsson Á, Ruland F. Climate and predation driving population dynamics and nest site choice of the common eider in West Iceland.

JEJ and ÁÁ gathered the data and formulated the original research questions. FR analysed the data and drafted the respective sections of the paper. JEJ drafted the introduction and the discussion and JEJ and FR reviewed and revised the manuscript.

Stille D, Ruland F, Stefánsson RA, Jeschke JM. Of mink and men: socio-economic factors influence the hunting bag of American mink in Europe and North America.

JMJ, DS and FR conceived the study. DS and RAS collected the data. DS and FR performed the statistical analyses. All authors jointly discussed and interpreted the results. DS drafted the manuscript, and all authors contributed to revisions.

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General Introduction

Life on Earth has undergone several massive phases of reorganization (Jablonski and Chaloner 1994). The origins lie in microbial mats in anoxic ecosystems (Nisbet and Fowler 1999), while the oxygenation of the atmosphere led to the Cambrian explosion of biodiversity (Chen et al. 2015). It can be argued that these transitions happened through organisms finding ways to exploit novel energy sources, from geochemical energy over sunlight and oxygen to flesh; the spread of new life forms was accompanied with the mass extinction of others (Judson 2017). A lot more recently, modern humans started to use fire (Gowlett and Wrangham 2013) for cooking, heating, tool building or locomotion and were subsequently able to colonize the entire planet. Many more inventions followed like the Haber-Bosch cycle for fixing nitrogen or the internal combustion engine and facilitated further accelerating population growth and productivity (Lenton et al. 2016). Humans are now in the exceptional position of simultaneously being observers and drivers of the reorganization of life on Earth.

And drivers they are: humans change the composition of soils (Tilman and Lehman 2001), the flow dynamics of rivers (Zarfl et al. 2014), increase the atmospheric temperature due to emitting greenhouse gases (Cook et al. 2016) etc. In concert, these processes cause catastrophic population declines in most wild species (Ceballos et al. 2017), and there is evidence, that we are witnessing the sixth mass extinction event on Earth (Wake and Vredenburg 2008). With only an estimated 25-39% of the global landmass considered "wild" (Perring and Ellis 2013), the field of ecology shifted its attention from natural ecosystems to habitats with differing degrees of disturbance, called Anthromes (Ellis et al. 2010). The study of novel ecosystems (Morse et al. 2014) - within the general framework of ecological novelty (Jeschke et al. 2013, Heger et al. 2019) - brought about new challenges and the fields of urban ecology and invasion ecology. They can be seen as modern ecology under human disturbance. While urban ecology has the habitat in focus, exploring how species adapt to human settlement, the altered nutrient and light availability, noise levels, pollution and dangers like traffic (Dowding et al. 2010; Slabbekoorn 2013; Potvin 2017; Proppe et al. 2017; Fleming and Bateman 2018). Invasion ecology has a focus on the species interactions, how species arrived at the new habitat and what impacts they have on the native species community (Lockwood et al. 2013).

Invasion Ecology

While colonizing the entire planet, humans brought with them a host of other species - some unintentional parasites or crop pests, others crop or ornamental plants and domesticated farm animals (Zeder 2015). Many of them are now considered invasive species in various locations around the globe. An invasive species is in this thesis considered a species that i) was - intentionally or unintentionally - introduced into a new habitat by humans, ii) escaped from confinement or was released into the wild, iii) established a self-sustaining population there and iv) spread beyond the area it was introduced; these are the four stages of the invasion process (Blackburn et al. 2011). Invasive species can drastically change the recipient ecosystems and have received considerable attention over the last decades, evident in the exponential increase of literature in the field of Invasion Ecology (Richardson and Pyšek 2008, Enders et al. 2019). There has been much discussion about the definition of "invasive species" (see e.g. Heger et al. 2013), and many synonyms exist for "non-native" species, i.e. those species that have reached stage ii of the above-mentioned four stages of the invasion process: "alien", "exotic" or "introduced" are common alternative terms. In this thesis, I use the probably most neutral term "non-native" species.

This field of research is called invasion ecology and aims at answering questions like: Are there general features, i.e. life-history traits, taxonomy or physiological features making a successful invasive species? The evidence is mixed, despite some strong results for specific taxonomic groups. Ornamental plants are common invaders (Dehnen-Schmutz et al. 2007), fast life-history traits are beneficial for amphibian and reptile invaders (Allen et al. 2017) and clever birds more commonly become invasive than other bird species (Sol and Lefebvre 2000). This is explained by the challenges a species is facing in the new ecosystem: abiotic changes in for example salinity, temperature or humidity; but also biotic changes, which means finding new food, evading new predators or coping with new competitors. More generally, biotic changes are changes in biotic interaction partners. This can be for example a new interaction partner (a new species in the system) or changes in abundance of local species; something that can be difficult for specialists that are

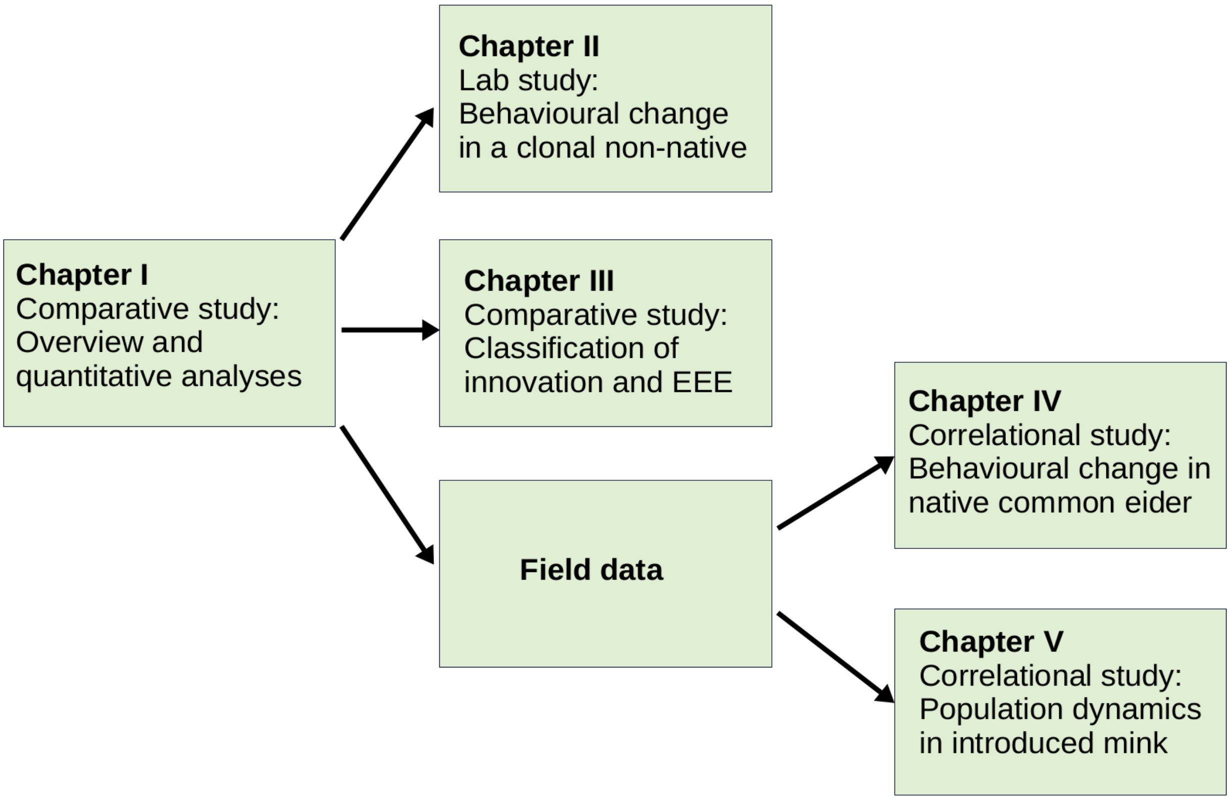

Figure 1 - Flow chart of the chapters in this thesis. Arrow indicate chronological flow.

dependent on one or few interaction partners or specific food to complete their life cycle. Generalists, however, are equipped to feed on a wider range of prey phenotypes and therefore can more easily shift to other species when their preferred prey species is not present in the invaded range. Empirical evidence suggests that indeed generalists are better invaders (Sol et al. 2012), most importantly due to dietary flexibility (Harms and Turingan 2012). Higher aggression to the new potential competitors in the invaded range can further facilitate invasion (Hudina et al. 2014).

Another central aim of invasion ecology is to predict the impact of the non-native species on the native species community (Severns 2008; Moroń et al. 2009; Eisenhauer 2010). As the prediction of invasion success, the impact of a non-native species on native species is dependent on the dynamics of their interaction. The non-native species may have escaped predation or parasitism by settling in the invaded range (as the enemy-release hypothesis predicts; Keane and Crawley 2002) and can, therefore, invest more energy in reproduction. In the opposite case, the non-native species may be readily exploited as a food source by a native predator (Pintor and Byers 2015). More generally, the evolutionary adaptation to similar past biotic interactions - or the eco-evolutionary experience one species has with the other - is predicted to shape the outcome of the interaction (Saul and Jeschke 2015). A way to cope with the challenges in the new interactions is shifted in behaviour (Sih et al. 2016). Before we will look more closely at the role of behaviour in species invasions (and its rising significance since the early key paper by Holway and Suarez 1999), it is worth looking at different concepts in behavioural ecology.

Behavioural Ecology

The behaviour of an animal is part of its observable phenotype, but there are several problems with the subjectivity in this observation. First, there are problematic interpretations made in terms of the meaning of a behaviour, especially in animal communication (Scott-Phillips 2015). While the mechanistic definition of a communication signal, or "information", does not have to contain "meaning" (Shannon & Weaver 1949), “information” and “meaning” are still often conflated conceptually (Owren et al. 2010). There are a plethora of concepts about information in animal communication and its implications for observational studies which are beyond the scope of this introduction (but see Stegmann 2013 for a comprehensive and critical overview). Secondly, it is hard to define what is special about behaviour in comparison to other aspects of the phenotype (Duckworth 2009). How is behaviour drastically different from physiological changes in the animal that are similarly induced by the environment? For clarity, let us look at several definitions of behaviour and specify which is used for this work. This is especially important because of the interdisciplinary nature of the field of behaviour (Levitis et al. 2009).

There are many different definitions of behaviour which significantly changed over time. The early influential ecologist Tinbergen defined behaviour as "The total movements made by the intact animal" (1955, page 2). This restriction to movement and to animals as a taxonomic group was later lifted with Davis' definition that behaviour is "*[w]hat an animal (or plant) does*" (1966, pages 4-5). It is sometimes defined as the response to stimulation (Raven & Johnsson 1989, page 1119), in other cases the mechanisms like genetic selection or learning are clearly highlighted (Starr & Taggart 1992, Glossary) or responses are including the lack of a response and all observable physiological changes like blood flow and pigmentation (Grier & Burk 1992 page 4). I used the synthesis of Levitis et al. (2009) where all above definitions were included as well as the empirical analysis of 174 expert questionnaire responses. The definition of behaviour consistently used throughout this thesis therefore is:

"*behaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes*" (Levitis et al. 2009, p. 103).

It is important to note that this explicitly does not exclude plants as subjects of behaviour. There is a growing body of literature supporting the notion that plants too behave and that the distinction between animal and bird behaviour is not as strict as historically assumed (Trewavas 2014). The definition used in this thesis allows for the classification of plant reaction to stimuli as behaviour, as for example shown in touch sensitivity of Arabidopsis (Braam and Davis 1990). In this thesis, however, I exclusively focused on animal behaviour, as the taxonomic breadth and the differences contained therein were already challenging across invertebrates and vertebrates, spanning from sponges to primates.

The notion that behaviour is a reaction to a stimulus makes it intuitively seem a fast, plastic phenotypical response of an organism. The behaviour evolved in a certain context, however, and can be quite fixed for a certain individual/species/developmental stage. It is therefore important to know what mechanism is behind the behaviour: Is it genetically fixed, formed in development or plastically changed by learning at an infant or adult stage? This diversity of mechanisms is reflected in the above definition of behaviour and is important for the purpose of the work in this thesis. As to other symptoms of human-induced rapid environmental change (HIREC, Sih 2013), behavioural changes can mitigate the effects of species invasions (Hoare et al. 2007). These interactions are therefore good model systems to look for rapid evolutionary changes (Moran and Alexander 2014), as species introductions happen at in Earth's history unprecedented short timescales (Carlton 2016).

Native species can face selection pressures through non-native species that vastly differ from their eco-evolutionary history. They, therefore, lack eco-evolutionary experience; they are naive to a certain degree. In the framework of Banks and Dickman (2007) investigates naiveté in interactions between native prey and novel predators. They describe three levels of naiveté: Level I naiveté is the native species not recognizing the non-native species as a threat at all. Level II naiveté is the native species recognizing a threat, but reacting with an inappropriate response. Finally, level III naiveté is the native species recognizing the threat, reacting with an appropriate defence mechanism but being "outgunned" by the non-native species due to lack of specific adaptation.

Level I and II naiveté are mostly caused by differences in signals. If the native prey species do not recognize the cues emitted by the non-native predator, may it be odour (Banks et al. 2003) or kairomones (Grason and Miner 2012) in the water, colouration (Théry and Casas 2002) or sounds (Moiseff et al. 1978), there will be a level I naiveté. The native prey species, however, can correctly interpret the signal but block out the wrong signal towards the non-native predator to effectively hide for example. The cryptic pose taken by native New Zealandian birds is ineffective, as the introduced predators like cats and dogs hunt by visual cues and smell (Karl and Best 1982). A level III naiveté is not a problem of communication but of the eco-evolutionary history that the two species share and who wins the arms race (Saul and Jeschke 2015). This sets off new evolutionary dynamics which subjects the native species to change (Strayer et al. 2006).

The non-native species can genetically diverge from the source population by two distinct paths: The dispersal filter (Myles-Gonzalez et al. 2015), where the individuals fitting better into the invasive range arrive there in greater numbers or the local adaptation to the new environments through selection on the whole population in the invasive range (Brown et al. 2014). Behavioural differences between the populations in the home- and the invasive range do not necesseralily correspond to genetic differences, though. While it has been demonstrated how innovation aids species to cope with environmental change (Sol et al. 2016), it is not entirely clear if the ability to cope with diverse environments evolved in these environments (Sayol et al. 2016) or were a precondition for colonization (Lefebvre et al. 2016). Studies to resolve this question are usually only focusing on one type of behaviour or behavioural challenge in one taxon (see for example Quinn et al. 2016 who did not find evidence for heritability in problem-solving ability in great tits (*Parus major*)).

A general framework for experimental studies on innovation was proposed (Tebbich et al. 2016), but animal innovation research still is focused on a narrow range of taxa, mostly primates (Ramsey et al. 2007) and birds (Overington et al. 2009), and some specific tasks (Griffin and Guez 2014). It is more promising to search for innovation across a broader range of taxa and contexts, to make more informed statements about, for example, the relationship with group size. Despite some evidence for a positive relationship (Muthukrishna and Henrich 2016) due to dispersal by social learning (Aplin 2016), conformity effects can hinder behavioural shifts on the population level (Day et al. 2001). Non-random dispersal of information due to age, sex and status can further slow the dispersal of new behaviour in a population (Itani 1958). In a novel ecological interaction with high extinction risk, innovations will be more crucial to behaviourally cope with the selection pressure fast. Without innovation in the threatened population at the necessary pace, human intervention and protection has to happen.

Conservation Ecology

As a strategy to help species threatened by non-native predators, researchers train individuals to recognize and appropriately respond to cues (Moseby et al. 2012; Steindler et al. 2018). The cases where these training measures are feasible and make sense to protect threatened native species are rare, however, more commonly non-native species are controlled by direct killing or poisoning. As it is notoriously difficult to remove non-native species from places where they established or even halt their spread, the most effective measure against negative effects of species invasions is to hinder their introduction (Leung et al. 2002). Non-native species that are of commercial interest are a special case in that context: their trade can be banned which is a handy tool not available for cryptic invaders, but criminal actions are still commercially incentivised.

Trade bans and other legislation to suppress further spread are used against two species in this thesis: The first is the marbled crayfish (*Procambarus virginalis*), the only known parthenogenetically reproducing decapod (Scholtz et al. 2003). It appeared in 2003 in a lake near Freiburg, Germany (Marten et al. 2004), and is now distributed across Europe, Madagascar and Japan. Its reproduction strategy - all individuals are genetically identical (Vogt et al. 2015; Gutekunst et al. 2018) - makes it a dangerous invader as one female can populate any water-body given enough resources and low predation pressure. To prevent further spread, it has been classified as invasive alien species of European Union concern under the Regulation 1143/2014, but is likely still released by hobbyists keeping them in aquaria.

The American mink (*Neovison vison*) was introduced into several European countries for the fur trade in the first half of the 20th century (MacDonald and Harrington 2003). It is now distributed across at least 16 countries (Bonesi and Palazon 2007) and considered one of the worst invasive species in Europe (Nentwig et al. 2018), while it is still commercially bred in many countries. As of 2016, Europe held 27% of the global production of mink fur (14 mio. of 52 mio., Kopenhagen Fur 2016). Mink are shot in most countries where it is spreading but the fur quality of feral mink is lower than of farmed mink, so while the hunting pressure on mink is not high enough for its eradication, it is meanwhile behaviourally adapting to the human control measures (Bodey et al. 2010).

The mink's spread and current behaviour are particularly well studied in Iceland (Stefansson et al. 2016), where bounties for shot mink are paid. Iceland with its fish-rich waters is an important breeding spot for many seabird species, which were breeding safely from arctic fox (*Vulpes lagopus*) nest predation on islands along the shore. But as the American mink is a good swimmer, these bird species suffer massive declines from the mink invasion (Magnusdottir et al. 2014). The commercially important common eider (*Somateria mollissima*), whose down are harvested, is declining despite protection efforts (VU, IUCN Red List of Endangered Species of Iceland, Schmalensee 2010). It will be important to know if behavioural shifts - for example shifts to islands further from the shore - will be sufficient to buffer predation effects or if species will be lost without further intervention.

Animal Behaviour in Biological Invasions - Thesis Objectives

Changes in the behaviour of non-native individuals have to happen fast after their arrival in the new ecosystem in order for them to successfully establish. A high degree of innovation in the early stages of invasion is predicted, followed by social learning by which the new behavioural traits disperse in the founder population (Wright et al. 2010). Vice versa, an asymmetrical ecological mismatch of the native species community not being adapted to the non-native species with a non-native species thriving in the new habitat causes disruptions in the ecosystem. In fact, we have seen that invasive species are one of the most serious threats to global biodiversity, and animal behaviour serves as a double-edged sword in that context. Behavioural predispositions enable invasions and correlate with invasion success, while behavioural shifts help both non-native and native species to strive in the new species communities. It is crucial to know how fast the behaviours will change in these interactions and how the population dynamics will be after the shift. Figure 1 is a flow chart illustrating how these questions were tackled in this thesis.

In Chapter 1, a broad number of studies was scanned and searched through for instances of changes in behaviour during or following an invasion. Changes in both native and non-native species across all animal taxa were recorded and classified in terms of i) type of behaviour, ii) mechanism underlying the behavioural change and iii) speed of change. We aimed to get an overview of the field and see what cases of behavioural change were commonly investigated. Are there biases in taxonomy? How diverse are the kinds of behavioural interactions? Are the frameworks to understand behavioural interactions between native and non-native species sufficient to contain the diversity in the literature?

Chapter 2 investigates behavioural differences between two non-native crayfish species in Europe, the spiny-cheek crayfish (Faxonius limosus) that was introduced in the 1890s and the marbled crayfish (Procambarus virginalis) which originated in the aquarium trade and was first found in European water-bodies in 2003 (Marten et al. 2004). In this study, we tested for behavioural differences between the old and the new non-indigenous crayfish species (NICs). We were looking for potential competitive advantages of one species over the other by aggression in direct competition, activity (higher foraging potential) or response to aggression. The extent of these differences are helpful to inform statements of a potential over-invasion by the marbled crayfish.

In Chapter 3, we conducted empirical analyses on the outcome of novel species interactions depending on the eco-evolutionary experience the native species has with the non-native species and the degree of innovation in the new behaviour. The cases of behavioural shifts of native mammals, birds and amphibians from Chapter 1 were classified along a gradient of innovation (innovation gradient, IG) and the eco-evolutionary experience (EEE) the native species had with the non-native species. Population dynamics after the onset of the interaction is correlated with IG as well as EEE. We argue for searching for innovative behaviour in the context of these novel species interactions, as well as quantifying the degree of innovation in the behaviour. This can not only help studying the evolution of cognition and culture in a broader range of animals (Arbilly and Laland 2017), but show if drastic behavioural changes can mitigate negative effects of invasion.

Chapter 4 looks at the specific case of nest-site choice in the native common eider in Iceland (Somateria mollissima), where we studied if EEE shaped the population dynamics consequences of behavioural shifts towards the return of the known predator, the arctic fox, and the invasion of the non-native mink. In the bay of Breiðafjörður in West Iceland, there are islands inaccessible to the fox, while the mink is able to reach all islands. We looked at the overall nest number dynamics in the Purkey and the Brokey archipelago in Breiðafjörður to know the overall population-level impacts before and after the arrival of the respective predator. Then we investigated the migration patterns between the islands to see if an effective shift in breeding grounds has taken place in either or both of the archipelagos.

In the last chapter, we performed similar analyses of mink numbers in Iceland, Germany and Denmark, in which countries the mink is invasive, plus in the USA where the mink is native. Control measures differ and all available data are hunting bag data. We corrected these data for the anthropogenic factors production, hunting effort and legislation to get a better estimate of population numbers from the hunting bag data.

In the last section of this thesis, I discuss implications of my research on estimating extinction risk for native species as well as invasion potential of non-native species. I suggest using the broad innovation scheme to scan through more broad literature in the search for innovative non-human animal behaviour. Species invasions can be seen as large-scale natural experiments, and before-after comparisons as well as temporal dynamics in behaviour and population dynamics can inform us about plasticity, adaptations and general evolutionary dynamics. The relatively young and trophically simple ecosystem of Iceland constitutes a special example. I will make a case about what was learned from the dynamics following the mink invasion and point to future directions and ongoing projects.

References

Allen WL, Street SE, Capellini I. 2017. Fast life history traits promote invasion success in amphibians and reptiles. Ecol Lett. 20(2):222–230. doi:10.1111/ele.12728.

Aplin L. 2016. Understanding the multiple factors governing social learning and the diffusion of innovations. Curr Opin Behav Sci. 12:59–65. doi:10.1016/j.cobeha.2016.09.003.

Arbilly M, Laland KN. 2017. The magnitude of innovation and its evolution in social animals. Proc R Soc B Biol Sci. 284(1848). doi:10.1098/rspb.2016.2385.

Banks PB, Dickman CR. 2007. Alien predation and the effects of multiple levels of prey naiveté. Trends Ecol Evol. 22(5):229–230. doi:10.1016/j.tree.2007.02.006.

Banks PB, Hughes NK, Rose TA. 2003. Do native Australian small mammals avoid faeces of domestic dogs? Responses of *Rattus fuscipes* and *Antechinus stuartii*. Aust Zool. 32(3):406–409. doi:10.7882/AZ.2002.018.

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM. 2011. A proposed unified framework for biological invasions.

Bodey TW, Bearhop S, Roy SS, Newton J, McDonald R a. 2010. Behavioural responses of invasive american mink neovison vison to an eradication campaign, revealed by stable isotope analysis. J Appl Ecol. 47(1):114–120. doi:10.1111/j.1365-2664.2009.01739.x.

Bonesi L, Palazon S. 2007. The American mink in Europe: Status, impacts, and control. Biol Conserv. 134(4):470–483. doi:10.1016/j.biocon.2006.09.006.

Braam J, Davis RW. 1990. Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in Arabidopsis. Cell. 60(3):357–364. doi:10.1016/0092-8674(90)90587-5.

Brown, C. "Experience and learning in changing environments." Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press, 2012. 46-62.

Brown GP, Phillips BL, Shine R. 2014. The straight and narrow path: The evolution of straight-line dispersal at a cane toad invasion front. Proc R Soc B Biol Sci. 281(1795):1–7. doi:10.1098/rspb.2014.1385.

Carlton JT. 2016. The non-mystery of non-native species. Human-Wildlife Interact. 10(1):137–139.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc Natl Acad Sci U S A. 114(30):E6089–E6096. doi:10.1073/pnas.1704949114.

Chen X, Ling HF, Vance D, Shields-Zhou GA, Zhu M, Poulton SW, Och LM, Jiang SY, Li D, Cremonese L, et al. 2015. Rise to modern levels of ocean oxygenation coincided with the Cambrian radiation of animals. Nat Commun. 6(May). doi:10.1038/ncomms8142.

Cook J, Oreskes N, Doran PT, Anderegg WRL, Verheggen B, Maibach EW, Carlton JS, Lewandowsky S, Skuce AG, Green SA, et al. 2016. Consensus on consensus: A synthesis of consensus estimates on human-caused global warming. Environ Res Lett. 11(4). doi:10.1088/1748-9326/11/4/048002.

Day RL, MacDonald T, Brown C, Laland KN, Reader SM. 2001. Interactions between shoal size and conformity in guppy social foraging. Anim Behav. 62(5):917–925. doi:10.1006/anbe.2001.1820.

Dehnen-Schmutz K, Touza J, Perrings C, Williamson M. 2007. The horticultural trade and ornamental plant invasions in Britain. Conserv Biol. 21(1):224–231. doi:10.1111/j.1523-1739.2006.00538.x.

Dowding C V., Harris S, Poulton S, Baker PJ. 2010. Nocturnal ranging behaviour of urban hedgehogs, Erinaceus europaeus, in relation to risk and reward. Anim Behav. 80(1):13–21. doi:10.1016/j.anbehav.2010.04.007.

Duckworth RA. 2009. The role of behavior in evolution: A search for mechanism. Evol Ecol. 23(4):513–531. doi:10.1007/s10682-008-9252-6.

Eisenhauer N. 2010. The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. Pedobiologia (Jena). 53(6):343–352. doi:10.1016/j.pedobi.2010.04.003.

Ellis EC, Goldewijk KK, Siebert S, Lightman D, Ramankutty N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Glob Ecol Biogeogr. 19(5):589–606. doi:10.1111/j.1466-8238.2010.00540.x.

Elton, CS. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Enders M, Havemann F, Jeschke JM. 2019. A citation-based map of concepts in invasion biology. NeoBiota. 42(47):23–42. doi:10.3897/neobiota.47.32608.

Fleming PA, Bateman PW. 2018. Novel predation opportunities in anthropogenic landscapes. Anim Behav. 138:145–155. doi:10.1016/j.anbehav.2018.02.011.

Gowlett JAJ, Wrangham RW. 2013. Earliest fire in Africa: Towards the convergence of archaeological evidence and the cooking hypothesis. Azania. 48(1):5–30. doi:10.1080/0067270X.2012.756754.

Grason EW, Miner BG. 2012. Behavioral plasticity in an invaded system: Non-native whelks recognize risk from native crabs. Oecologia. 169(1):105–115. doi:10.1007/s00442-011-2188-5.

Grier, J. W. & Burk, T. 1992. Biology ofAnimal Behavior. 2nd edn. St Louis, Missouri: Times Mirror/Mosby College.

Griffin AS, Guez D. 2014. Innovation and problem solving: A review of common mechanisms. Behav Processes. 109(PB):121–134. doi:10.1016/j.beproc.2014.08.027.

Gutekunst J, Andriantsoa R, Falckenhayn C, Hanna K, Stein W, Rasamy J, Lyko F. 2018. Clonal genome evolution and rapid invasive spread of the marbled crayfish. Nat Ecol Evol. 2(3):567–573. doi:10.1038/s41559-018-0467-9.

Harms C a., Turingan RG. 2012. Dietary flexibility despite behavioral stereotypy contributes to successful invasion of the pike killifish, *Belonesox belizanus*, in Florida, USA. Aquat Invasions. 7(4):547–553. doi:10.3391/ai.2012.7.4.011.

Heger T, Bernard-Verdier M, Gessler A, Greenwood AD, Grossart H-P, Hilker M, Keinath S, Kowarik I, Kueffer C, Marquard E, et al. 2019. Towards an Integrative, Eco-Evolutionary Understanding of Ecological Novelty: Studying and Communicating Interlinked Effects of Global Change. Bioscience. XX(X):1–12. doi:10.1093/biosci/biz095.

Heger T, Pahl AT, Botta-Dukát Z, Gherardi F, Hoppe C, Hoste I, Jax K, Lindström L, Boets P, Haider S, et al. 2013. Conceptual frameworks and methods for advancing invasion ecology. Ambio. 42(5):527–540. doi:10.1007/s13280-012-0379-x.

Hoare JM, Pledger S, Nelson NJ, Daugherty CH. 2007. Avoiding aliens: Behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv. 136(4):510–519. doi:10.1016/j.biocon.2006.12.022.

Hochberg ME, Marquet PA, Boyd R, Wagner A. 2017. Innovation: An emerging focus from cells to societies. Philos Trans R Soc B Biol Sci. 372(1735). doi:10.1098/rstb.2016.0414.

Holway D a., Suarez A V. 1999. Animal behavior: An essential component of invasion biology. Trends Ecol Evol. 14(99):328–330. doi:10.1016/S0169-5347(99)01636-5.

Hudina S, Hock K, Žganec K. 2014. The role of aggression in range expansion and biological invasions. Curr Zool. 60(3):401–409.

Itani J. 1958. On the acquisition and propagation of a new food habit in the natural group of the Japanese monkey at Takasaki - Yama. Primates. 1(2):84–98. doi:10.1007/BF01813697.

Jablonski D, Chaloner WG. 1994. Extinctions in the Fossil Record [and Discussion]. Philos Trans R Soc B Biol Sci. 344(1307):11–17. doi:10.1098/rstb.1994.0045.

Jeschke JM, Keesing F, Ostfeld RS. 2013. Novel organisms: Comparing invasive species, GMOs, and emerging pathogens. Ambio. 42(5):541–548. doi:10.1007/s13280-013-0387-5.

Judson OP. 2017. The energy expansions of evolution. Nat Ecol Evol. 1(6). doi:10.1038/s41559-017-0138.

Karl BJ, Best HA. 1982. Feral cats on stewart island; their foods, and their effects on kakapo. New Zeal J Zool. 9(2):287–293. doi:10.1080/03014223.1982.10423857.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. 17(4):164–170.

Kopenhagen Fur (2016) World production of mink drops. https://www.kopenhagenfur.com/en/news/2016/june/world-production-of-mink-drops/ Accessed 9 October 2019

Lefebvre L, Ducatez S, Audet JN. 2016. Feeding innovations in a nested phylogeny of Neotropical passerines. Philos Trans R Soc B Biol Sci. 371(1690):20150188. doi:10.1098/rstb.2015.0188.

Lenton TM, Pichler P-P, Weisz H. 2016. Revolutions in energy input and material cycling in Earth history and human history. Earth Syst Dyn. 7:353–370. doi:10.1056/NEJMe0902377.

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. Proc R Soc B Biol Sci. 269(1508):2407–2413. doi:10.1098/rspb.2002.2179.

Levitis DA, Lidicker WZ, Freund G. 2009. Behavioural biologists do not agree on what constitutes behaviour. Anim Behav. 78(1):103–110. doi:10.1016/j.anbehav.2009.03.018.

Lockwood, J. L., Hoopes, M. F., & Marchetti, M. P. (2013). Invasion ecology. John Wiley & Sons.

MacDonald DW, Harrington LA. 2003. The american mink: The triumph and tragedy of adaptation out of context. New Zeal J Zool. 30(4):421–441. doi:10.1080/03014223.2003.9518350.

Magnusdottir R, von Schmalensee M, Stefansson R a., Macdonald DW, Hersteinsson P. 2014. A foe in woe: American mink (*Neovison vison*) diet changes during a population decrease. Mamm Biol. 79(1):58–63. doi:10.1016/j.mambio.2013.08.002.

Marten M, Werth C, Marten D. 2004. Der Marmorkrebs (Cambaridae, Decapoda) in Deutschland-ein weiteres Neozoon im Einzugsgebiet des Rheins. Lauterbornia. 50:17–23.

Mayr, E. 2001. What evolution is. Science Masters Series. Basic Books, New York.

Moiseff A, Pollack GS, Hoy RR. 1978. Steering responses of flying crickets to sound and ultrasound. Mate attraction and predator avoidance. Proc Natl Acad Sci U S A. 75(8):4052–4056. doi:10.1073/pnas.75.8.4052.

Moran E V., Alexander JM. 2014. Evolutionary responses to global change: Lessons from invasive species. Ecol Lett. 17(5):637–649. doi:10.1111/ele.12262.

Moroń D, Lenda M, Skórka P, Szentgyörgyi H, Settele J, Woyciechowski M. 2009. Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. Biol Conserv. 142(7):1322–1332. doi:10.1016/j.biocon.2008.12.036.

Morse NB, Pellissier PA, Cianciola EN, Brereton RL, Sullivan MM, Shonka NK, Wheeler TB, McDowell WH. 2014. Novel ecosystems in the Anthropocene: A revision of the novel ecosystem concept for pragmatic applications. Ecol Soc. 19(2). doi:10.5751/ES-06192-190212.

Moseby KE, Cameron A, Crisp H a. 2012. Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? Anim Behav. 83(4):1011–1021. doi:10.1016/j.anbehav.2012.01.023.

Muthukrishna M, Henrich J. 2016. Innovation in the collective brain. Philos Trans R Soc B Biol Sci. 371(1690):20150192. doi:10.1098/rstb.2015.0192.

Myles-Gonzalez E, Burness G, Yavno S, Rooke A, Fox MG. 2015. To boldly go where no goby has gone before: Boldness, dispersal tendency, and metabolism at the invasion front. Behav Ecol. 26(4):1083–1090. doi:10.1093/beheco/arv050.

Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilà M. 2018. More than “100 worst” alien species in Europe. Biol Invasions. 20(6):1611–1621. doi:10.1007/s10530-017-1651-6.

Nisbet EG, Fowler CMR. 1999. Archaean metabolic evolution of microbial mats. Proc R Soc B Biol Sci. 266(1436):2375–2382. doi:10.1098/rspb.1999.0934.

Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav. 78(4):1001–1010. doi:10.1016/j.anbehav.2009.06.033.

Owren MJ, Rendall D, Ryan MJ. 2010. Redefining animal signaling: Influence versus information in communication. Biol Philos. 25(5):755–780. doi:10.1007/s10539-010-9224-4.

Perring MP, Ellis EC. 2013. The Extent of Novel Ecosystems: Long in Time and Broad in Space. Nov Ecosyst Interv New Ecol World Order.:66–80. doi:10.1002/9781118354186.ch8.

Pigliucci, M. 2001. Phenotypic plasticity: beyond nature and nurture. JHU Press.

Pintor LM, Byers JE. 2015. Do native predators benefit from non-native prey? Ecol Lett. 18(11):1174–1180. doi:10.1111/ele.12496.

Potvin DA. 2017. Coping with a changing soundscape: avoidance, adjustments and adaptations. Anim Cogn. 20(1):9–18. doi:10.1007/s10071-016-0999-9.

Proppe DS, McMillan N, Congdon J V., Sturdy CB. 2017. Mitigating road impacts on animals through learning principles. Anim Cogn. 20(1):19–31. doi:10.1007/s10071-016-0989-y.

Quinn JL, Cole EF, Reed TE, Morand-Ferron J. 2016. Environmental and genetic determinants of innovativeness in a natural population of birds. Philos Trans R Soc B Biol Sci. 371(1690). doi:10.1098/rstb.2015.0184.

Ramsey G, Bastian ML, van Schaik C. 2007. Animal innovation defined and operationalized. Behav Brain Sci. 30(4):393–407; discussion 407-32. doi:10.1017/S0140525X07002373.

Raven, P. H. & Johnson, G. G. 1989. Biology. 2nd edn. St Louis, Missouri: Times Mirror/Mosby College.

Richardson DM, Pyšek P. 2008. Fifty years of invasion 7ecology – the legacy of Charles Elton. Divers Distrib. 14:161–168. doi:10.1111/j.1472-4642.2008.00464.x.

Saul W-CC, Jeschke JM. 2015. Eco-evolutionary experience in novel species interactions. Ecol Lett. 18(3):236–245. doi:10.1111/ele.12408.

Sayol F, Maspons J, Lapiedra O, Iwaniuk AN, Székely T, Sol D. 2016. Environmental variation and the evolution of large brains in birds. Nat Commun. 7. doi:10.1038/ncomms13971.

Schmalensee M von. 2010. Vagestir i vistkerfum - fyrri hluti. Náttúrufræðingurinn. 80:15–26.

Scholtz G, Braband A, Tolley L, Reimann A, Mittmann B, Lukhaup C, Steuerwald F, Vogt G. 2003. Parthenogenesis in an outsider crayfish. Nature. 421(6925):806. doi:10.1038/421806a.

Scott-Phillips TC. 2015. Meaning in animal and human communication. Anim Cogn. 18(3):801–805. doi:10.1007/s10071-015-0845-5.

Severns PM. 2008. Exotic grass invasion impacts fitness of an endangered prairie butterfly, Icaricia icarioides fenderi. J Insect Conserv. 12(6):651–661. doi:10.1007/s10841-007-9101-x.

Shannon, CE, Weaver, W. 1949. A mathematical model of communication. Urbana, IL: University of Illinois Press, 11.

Sih A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Anim Behav. 85(5):1077–1088. doi:10.1016/j.anbehav.2013.02.017.

Sih A, Trimmer PC, Ehlman SM. 2016. A conceptual framework for understanding behavioral responses to HIREC. Curr Opin Behav Sci. 12:109–114. doi:10.1016/j.cobeha.2016.09.014.

Slabbekoorn H. 2013. Songs of the city: Noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim Behav. 85(5):1089–1099. doi:10.1016/j.anbehav.2013.01.021.

Smil, V. (2003). The Earth's biosphere: Evolution, dynamics, and change. Mit Press.

Sol D, Lefebvre L. 2000. Behavioural Flexibility Predicts Invasion Success in Birds Introduced to New Zealand. Oikos. 90(3):599–605.

Sol D, Maspons J, Vall-llosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP. 2012. Unraveling the life history of successful invaders. Science 337(6094):580–583. doi:10.1126/science.1221523.

Sol D, Sayol F, Ducatez S, Lefebvre L. 2016. The life history basis of behavioural innovations. Philos Trans R Soc B Biol Sci. doi:10.1098/rstb.2015.0187.

Starr, C. & Taggart, R. 1992. Biology: the Unity and Diversity ofLife. 6th edn. Belmont, California: Wadsworth.

Stefansson RA, von Schmalensee M, Skorupski J. 2016. A tale of conquest and crisis: invasion history and status of the American mink (*Neovison vison*) in Iceland. Acta Biol. 23:87–100. doi:10.18276/ab.2016.23-08.

Stegmann, U. (Ed.). 2013. Animal communication theory: information and influence. Cambridge University Press.

Steindler LA, Blumstein DT, West R, Moseby KE, Letnic M. 2018. Discrimination of introduced predators by ontogenetically naïve prey scales with duration of shared evolutionary history. Anim Behav. 137:133–139. doi:10.1016/j.anbehav.2018.01.013.

Strayer DL, Eviner VT, Jeschke JM, Pace ML. 2006. Understanding the long-term effects of species invasions. Trends Ecol Evol. 21(11):645–651. doi:10.1016/j.tree.2006.07.007. [accessed 2014 Jul 13].

Tebbich S, Griffin AS, Peschl MF, Sterelny K. 2016. From mechanisms to function: An integrated framework of animal innovation. Philos Trans R Soc B Biol Sci. 371(1690). doi:10.1098/rstb.2015.0195.

Ten Cate, C, Healy, S, and Healy, SD (Eds.). 2017. Avian cognition. Cambridge University Press.

Théry M, Casas J. 2002. Predator and prey views of spider camouflage. Nature. 415(6868):133–133. doi:10.1038/415133a.

Tilman D, Lehman C. 2001. Human-caused environmental change: Impacts on plant diversity and evolution. Proc Natl Acad Sci U S A. 98(10):5433–5440. doi:10.1073/pnas.091093198.

Trewavas A. 2014. Plant Behaviour and Intelligence. Oxford University Press, Oxford, UK.

Vogt G, Falckenhayn C, Schrimpf A, Schmid K, Hanna K, Panteleit J, Helm M, Schulz R, Lyko F. 2015. The marbled crayfish as a paradigm for saltational speciation by autopolyploidy and parthenogenesis in animals. Biol Open. 4(11):1583–1594. doi:10.1242/bio.014241.

Wake DB, Vredenburg VT. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proc Natl Acad Sci U S A. 105 Suppl:11466–73. doi:10.1073/pnas.0801921105.

West-Eberhard, MJ. 2003. Developmental plasticity and evolution. Oxford University Press.

Wright TFF, Eberhard JRR, Hobson E a. A, Avery MLL, Russello M a. A. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethol Ecol Evol. 22(4):393–404. doi:10.1080/03949370.2010.505580.

Zarfl C, Lumsdon AE, Berlekamp J, Tydecks L, Tockner K. 2014. A global boom in hydropower dam construction. Aquat Sci. 77(1):161–170. doi:10.1007/s00027-014-0377-0.

Zeder MA. 2015. Core questions in domestication research. Proc Natl Acad Sci U S A. 112(11):3191–3198. doi:10.1073/pnas.1501711112.

Chapter 1: How Biological Invasions Affect Animal Behaviour: A Global, Cross-Taxonomic Analysis

Resubmitted to the *Journal of Animal Ecology* as:

Ruland F, Jeschke JM. How biological invasions affect animal behaviour: A global, cross-taxonomic analysis.

Abstract

1. In the Anthropocene, species are faced with drastic challenges due to rapid, human-induced changes, such as habitat destruction, pollution and biological invasions. In the case of species invasion, native species potentially change their behaviour to cope with invaders, but invaders also need to be flexible in their behaviour to be successful in their new environment.

2. We aimed at giving an overview of which changes in behaviour are studied in invasions, and what is known about the types of behaviour, mechanisms and speed.

3. Based on a review of the literature, we identified 191 studies and 360 records (some studies reported multiple records) documenting behavioural change caused by biological invasions in native (236 records from 148 species) or invasive animals (124 records from 50 species). We investigated both the underlying mechanisms and the speed of behavioural changes. This global dataset - which we make openly available - is not restricted to particular taxonomic groups.

4. However, we did find a taxonomic bias in the literature: most records were reported for mammals, birds and insects. We also found that native species changed their anti-predator behaviour more frequently than invasive species, which is in line with the enemy release hypothesis. Types of behaviour changed at different speeds. Mechanisms such as learning and genetic adaptation were surprisingly evenly distributed across taxa and allowed for faster or slower change, respectively.

5. Our findings may help to better understand the role of behaviour in biological invasions as well as temporal changes in both population densities and traits of invasive species, and of native species affected by them.

Keywords: behavioural flexibility, biological invasions, ecological novelty, global change, HIREC, invasive alien species, phenotypic plasticity, temporal dynamics

1 Introduction

Invasive species profoundly affect native species, communities and ecosystems (Bellard, Genovesi, & Jeschke, 2016; Vilà and Hulme 2017). They are defined as species that have been intentionally or unintentionally (i) transported and (ii) introduced to a new habitat by humans, have (iii) established in the wild and (iv) substantially spread beyond their point(s) of introduction (Blackburn et al., 2011; Jeschke, Keesing, & Ostfeld, 2013). Behaviour can affect all of these four steps of the invasion process. For example, ship rats (*Rattus rattus*) need to enter a ship and, after it has crossed the sea, leave it at a distant location. They will have to find food, cope with potential competitors and evade predators and parasites in order to establish themselves and spread there. At the same time, climatic conditions in the new environment may differ from those in the home range or fluctuate more strongly, necessitating immediate behavioural adjustments.

Studies investigating the role of behaviour in biological invasions either look at the invasive or native species. On the one hand, some, but not all, found animal personality (Brodin & Drotz, 2014) or behavioural flexibility (Sol & Lefebvre, 2000; Weis and Sol 2016) to be related to invasion success. On the other hand, behavioural flexibility is also beneficial for native species interacting with invaders (Berthon, 2015; Sih, Trimmer, & Ehlman, 2016). It makes sense not to generalize over invasive and native species, as both groups face a different ecological situation: Invasive species find themselves in a sometimes drastically different environment with almost all ecological aspects changed at once. Native species, on the contrary, will have to cope with the arrival of the focal invasive species, but the other characteristics of their environment will initially be rather unaffected.

This ecological difference should be reflected in how the behaviour of invasive vs native species changes, yet case studies can only focus on one type of behaviour. For example, the invasive species can be a new parasite (Dunn et al., 2012) or a predator (Carthey & Banks, 2014), and native species have to cope with this new stress; or the focus lies on prey choice of invaders (Chabaane, Laplanche, Turlings, & Desurmont, 2015), changes in sociality (Fogarty, Cote, & Sih, 2011) or aggression and dispersal (Michelangeli, Smith, Wong, & Chapple, 2017). Case studies cannot offer comparisons of, for example, the speed by which different behavioural changes manifest. At the intersection of conservation ecology and animal behaviour, there have been efforts for overarching theory (Sih, 2013, Berger-Tal & Saltz 2016) which found biases in the studied types of behaviour. Most studies focus on foraging and dispersal, fewer on mating and competition, and fewest on anti-predator behaviour (Berger-Tal et al., 2016).

It is important to know the speed of behavioural change to predict lags in invader impacts (Epanchin-Niell & Liebhold, 2015) and potential boom-and-bust dynamics (Strayer et al., 2017; Strayer, Eviner, Jeschke, & Pace, 2006 and references therein). This may be especially important in novel ecological settings when species that have not previously interacted come into contact (cf. Saul & Jeschke, 2015) and also differ between invasive and native species. For example, if a delayed behavioural innovation allows an invasive species to feed on an abundant prey species in its new environment, this will likely lead to a delayed increase in the population density of the invasive species. Vice versa, a delayed innovation in a native species allowing it to effectively reduce predation by an invader may reduce the invader's population density with a time delay. Similarly, the recognition of the invader as prey can lead to an increase in native species and increased predation pressure on the invader. This effect was observed in the Jeziorsko Reservoir in central Poland, where native mute swans (*Cygnus olor*) started to feed on invasive zebra mussels (*Dreissena polymorpha*). Swans began to exploit the zebra mussel as a food source from the winter 1998/1999 on, when they became hugely abundant a few years after their introduction (Wlodarczyk & Janiszewski, 2014). Whether or not the population of a high-impact invader will crash without targeted management action is of high practical value, but at the moment we cannot predict which native or invasive species will change their behaviour quickly or with a delay.

There is a mechanism behind each behavioural change, specifically learning or adaptation, and it is important to have information about this mechanism, for example because it determines the speed of change. For the invasive species, the new environment poses new challenges that serve as a barrier or select on the species traits after establishment. When the golden apple snail (*Pomacea canaliculata*), native to regions with a tropical climate, arrived in South Korea, it was subjected to selection for increased activity to reduce thermal stress in its invaded range (Bae, Chon, & Park, 2015). A mechanism that acts within one generation is learning. For instance, the common planigale, a native predator of Australia, has learned to avoid the cane toad as toxic prey over a few days of experiments with staged encounters (Llewelyn, Webb, Schwarzkopf, Alford, & Shine, 2010). In this example, the planigales learned through individually acquired cues, which is a fast but risky way to interact with the environment. Social learning is using the experience of others which is safer, especially when ingesting potentially toxic prey, but this may fail if the environment changes too rapidly (Brown, 2012). Other mechanisms behind behavioural changes that were observed in invasions are epigenetics (Ardura, Zaiko, Morán, Planes, & Garcia-Vazquez, 2017) and maternal effects (Badyaev, 2005).

There is a difference in the potential for rapid genetic adaptation and the need for learning between native and invasive species. While the native species has a regular population size at the onset of the interaction between the native and invasive species, the invader may arrive to the new system in low numbers. Invasive species are therefore predicted to typically learn at the first step of the invasion process; they innovate more individually in the early stages of invasion and then disperse the new behavioural traits across the population via social learning (Wright, Eberhard, Hobson, Avery, & Russello, 2010). Generation time and the number of reproductive events differ vastly among taxa, as do fecundity and parental care. Investing in learning and the potential for selection to act will therefore differ among taxa. Understanding this taxonomic range of behavioural changes and their underlying mechanisms thus requires comparative studies across taxa (Griffin, 2016).

Although behavioural changes in a dynamic environment are generally well investigated (Wong & Candolin, 2015), and biological invasions have been recognized as drivers of behavioural change (Holway & Suarez, 1999), a synthesis of the literature that combines all these data is currently lacking. Instead, data and hypotheses have been linked to a particular perspective. For example, starting from a conservation perspective, some studies have explored the evolutionary capacity of native species responding to invasion (Strauss, Lau, & Carroll, 2006), the naiveté of natives towards invaders (Carthey & Banks, 2014) and - along similar lines - the danger of ecological traps in interactions with invaders (Robertson, Rehage, & Sih, 2013). Similarly, studies with a behavioural focus have proposed concepts about the specific mechanisms underlying behavioural change of native (Berthon, 2015) or invasive species (Wagner, 2017), but not both in parallel.

We therefore aimed to combine and compare data about behavioural changes caused by biological invasions, bridging research in invasion biology, conservation and animal behaviour across taxonomic groups. While we are aware of a growing literature on plant behaviour, we restrict our study to animal behaviour (Trewaras, 2014). We gathered records of behavioural change in native and invasive species across a wide range of taxa, all types of behaviour, the speed at which the behaviour changed and the mechanism by which the data changed.

The following research questions were addressed: (1) Do different types of behaviour change in native as compared to invasive species? According to the enemy release hypothesis, invasive species can be relatively safe from (specialist) predators in the invaded range and thereby under less stress to innovate defence strategies (Heger & Jeschke, 2014, 2018; Keane & Crawley, 2002). (2) Do some types of behaviour change faster than others? We expect behavioural changes that are either not complex or linked to immediate survival to happen faster than complex or less vital changes. (3) Does learning allow for faster behavioural changes than other mechanisms in an invasion context, and is it more commonly studied in vertebrates than invertebrates (Rosenthal, Gertler, Hamilton, Prasad, & Andrade, 2017)? (4) Are specific types of behavioural change associated with specific underlying mechanisms of behavioural change? In all these comparisons, we distinguish between invasive and native species, as they are subjected to very different ecological settings, and also consider biases in published studies, especially towards high-impact invaders.

2 Material and Methods

2.1 Literature Search

We used a general search algorithm following the PRISMA statement (Moher, Liberati, Tetzlaff, & Altman, 2009). Specifically, we searched the Web of Science on 30 June 2015, from the institution Freie Universität Berlin in Germany. We searched “All databases”, but selected the research areas "Behavioural Sciences", "Genetics Heredity", "Environmental Sciences Ecology", "Plant Sciences", "Biodiversity Conservation", "Zoology" and "Evolutionary Biology", using the general search string: Behavio* AND (shift* OR change* OR transition*) AND (alien OR exotic OR introduc* OR invas* OR naturali?ed OR nonindigenous OR non-indigenous OR nonnative OR non-native).

This initial search yielded 6463 studies before and 5948 studies after duplicate removal (see Appendix S1 for PRISMA flow chart). In the next step, we scanned the titles and abstracts of these studies to exclude obvious false hits, for example studies from other research fields. The remaining 524 studies were read to identify those that fit our criteria of eligibility: (i) One or more specific behaviours were observed to have changed. The definition of behaviour we use in this study is that “*[B]ehaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes*” (Levitis, Lidicker, & Freund, 2009, p. 103). (ii) The change in behaviour had to be observed either in an invasive species or in a native species now interacting with an invasive species. We found 191 studies from 1990 to 2015 that were eligible according to these criteria. It was not uncommon that a study documented more than one record of a species' behavioural change or different types of behaviour that changed for one species. As a results, our dataset includes a total number of 360 records.

2.2 Data on individual records of behavioural change

General Data

Each record of behavioural change focused on exactly one native or invasive species that changed its behaviour. All records were subsequently scanned for information on the respective study system. First, we extracted background information reported in the study, i.e. year of publication, title, journal, the location where the behavioural observations were made, the type of study (laboratory, field or enclosure), type of evidence (experimental or observational/correlational), type of habitat (aquatic, terrestrial, marine or any combination) and the focal species as well as – if any – the species that the focal species interacted with. The focal species in each record of behavioural change was classified into its respective higher taxonomic group. We used five vertebrate (mammals, birds, reptiles, amphibians, fish) and four invertebrate groups (insects, crustaceans, molluscs, other invertebrates).

Types of Behaviour

While most studies that compare drivers and taxonomic bias in behavioural shifts focus on feeding innovations, e.g. a shift of prey items or technical innovations (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005), we aimed to capture the full range of behaviours that can change during invasions in native or invasive species. We noted the observation of behavioural change in each record, for example gut content analysis showing that a predator species ingested a new prey species. This can be understood as the means of the animal species to change its ecological interaction with the environment. As we were more interested in the ecological context of the behaviour and not the actual motor activity performed, we then classified the ends of the behavioural shift in one of these six, mutually exclusive categories: (1) "Feeding", i.e. behavioural changes of the focal species to feed on a new prey species and/or development of a new feeding technique by the focal species. (2) "Defence" describes records where the focal species changed its behaviour to defend itself against a new predator or parasite. (3) Behavioural changes allowing species to better cope with abiotic stress were classified in the category "climate". (4) Changes that allowed for better dispersal or migration were classified as "dispersal". (5) "Mating" describes behavioural changes to enable any stages of the reproduction, including courtship. Finally, (6) changes allowing to better cope with a competitor in direct interaction were labelled as "competition".

This way we ended up with the exact behaviour that changed in the respective species, but also with its ecological ends. For example, the change in nest height of native Hawaiian Oahu Elepaio (*Chasiempis ibidis*) after the introduction of ship rats (*Rattus rattus*) fits the "defence" category. Birds are choosing higher trees to move their nest as a defence against nest predation by rats (Vanderwerf, 2012). From the 360 records of behavioural change we found in total, only 4 were impossible to classify in (only) one of the above categories; these were excluded from analyses using the type of behaviour.

Speed of Behavioural Change

Some records in our dataset were reported to be instant, flexible behavioural changes, whereas others were plastic changes over a certain time span, for example over an individual’s lifetime or adaptations over generations. We calculated the speed of such plastic behavioural changes by using the estimated time span of the interaction between the focal species and the new stimulus (either abiotic or interacting species).

This estimated interaction time came from different sources. In some studies, sites with different, known invasion histories were compared, such as for native fence lizards *Sceloporus undulatus* in the southern USA predated by the invasive red imported fire ant *Solenopsis invicta*. The antipredator response of the lizards was compared between uninvaded sites and sites invaded 23, 54 and 68 years prior to the data collection (Langkilde, 2009). In other cases, species that have never interacted in the wild were experimentally brought together, like the native European mirid bug *Macrolophus pygmaeus* feeding on the invasive tomato leafminer *Tuta absoluta* in a laboratory setting (Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013). As in habituation to anthropogenic stimuli, a behavioural response can only be triggered at a certain degree of repeated stimulation (Blumstein, 2016). This stimulation by interaction necessitates a substantial population size or spatial proximity. Thus if available, we also noted the point in time when the species was spreading in the introduced range when interactions with the native species became far more common. An example for this scenario is the more frequent egg rejection of native village weavers (*Ploceus cucculatus*) in Hispaniola in the West Indies with a growing population of invasive shiny cowbirds (*Molothrus bonariensis*), documented over the course of 16 years (Robert & Sorci, 1999).

In some cases, it was appropriate to use the difference between the time of introduction and the first documentation of the behavioural change. While this time span can be very long, as for example in case of the introductions of several mammal species to Australia with the first Europeans, we only used this time span if the author(s) give evidence for the respective behaviour changing over that time span. Where ongoing genetic changes are documented, as in the cane toad population in Australia for instance, the time span can realistically be several decades long.

We performed two types of analysis with these data: First, we used the categorical data of instant (i.e. flexible) vs non-instant (i.e. plastic or adaptive) behavioural changes to compare the relative number of instant changes between types of behaviour, native and invasive species and among taxa, using Chi-Square tests with 100'000 simulations. To compare the speed of behavioural change between learning and rapid genetic adaptation, we used the estimates of interaction time over which the change occurred and compared them by calculating Hedge's g effect sizes. We only used the time records of behavioural change where there was evidence of the change happening over a known interaction time as described in the previous two paragraphs. The time span of the behavioural change was corrected for differences in life history by dividing by the age at sexual maturity (ASM) of the focal species. We chose ASM as it was more commonly available than generation time or age at first reproduction. We also performed analyses based on the absolute time span of behavioural changes, as these can also be relevant, for example for species conservation, and provide the results in the Supplement S1.

Mechanisms of Behavioural Change

Another major goal of this study was to document the different mechanisms of behavioural change, compare their speed of change and look at their distribution across taxa. To categorize the mechanisms behind behavioural changes in our dataset, we used an explorative approach. We took down each mechanism of behavioural change proposed by the author(s) and checked if the study provides empirical evidence for this mechanism. In many cases, more than one mechanism was mentioned in the discussion, but no empirical evidence was provided.

Since only few studies reported epigenetic (Liebl & Martin, 2014) and maternal effects (Forister et al., 2013), we restricted our analyses to two types of mechanisms that were commonly reported: rapid genetic adaptation and learning. A record of genetic adaptation was noted if it was documented that a behavioural change during the invasion of a species was based on a genetic change. This happened, for example, in the Polynesian field crickets *Teleogryllus oceanicus*, where the flatwing morphology is more common in males in the invaded range (Oceanian islands like Kauai). This mutation disables courtship songs, but renders males less susceptible to the acoustically oriented parasitoid fly *Ormia ochracea*. As males do not perform courtship songs, females have evolved relaxed mating requirements (Tinghitella & Zuk, 2009). We noted a behavioural change through learning if the change occurred after (and not before) the interaction with the stimulus, either directly by the focal individual or through observation of or communication with con-specifics. The soft-shell clam (*Mya arenaria*), for example, changed its burrowing behaviour in the presence of the invaded green crab (*Carcinus maenas*). In this particular case, social cues from attacked con-specifics were enough to increase burrowing depth (Flynn & Smee, 2010).

Additionally to the mechanisms, we noted if there is evidence for a pre-disposition of the focal species to shift to the new behaviour. The native Australian whelk *Haustrum vinosum*, for example, recognizes predator cues from the invasive *Carcinus maenas* independently if the crab was present 0, 20 or 100 years at the site. According to the authors, the "recognition of invasive predators may occur innately through ‘‘exaptation’’ or ‘‘coincidental pre-adaptation’’" (Freeman, Wright, Hewitt, Campbell, & Szeto, 2013). These latent traits – as they are termed in the White Knight Hypothesis (Wagner, 2017) – accelerate behavioural shifts and allow for behavioural flexibility.

2.3 Weighting records in the database

To correct for potential biases that arise with multiple records in one study, we analysed both weighted and unweighted data. Following previous studies (e.g. Heger & Jeschke, 2014; Willer, Li, & Abecasis, 2010; Zaykin, 2011), the relative weight of a record was calculated as 1/sqrt(number of records in the study), so that the combined weight of all records in one study was sqrt(number of records in the study). Since there were no qualitative differences in the results between weighted and unweighted data, we chose to present the results for unweighted data in the main article for higher accessibility, while those for the weighted analyses are provided in the Supplementary Material (Appendix A).

3 Results and Discussion

We present and discuss our results in the same order as the questions were outlined in the Introduction. We conclude with future perspectives based on our main findings. First, however, we look at potential biases in the dataset.

Out of the 360 records of behavioural change in total, birds were most frequently studied (65 records), followed by mammals (58 records) and insects (48 records). A similar bias can be found for the general field of behavioural ecology where most studies are focused on species that are relatively closely related or appealing to humans or show supposedly complex behavioural patterns, i.e. mammals and birds. For example, Rosenthal et al. (2017) reported that about half of the studies published in the journal Animal Behaviour from 1953 to 2015 focused on mammals and birds. Our sample is actually less taxonomically biased towards mammals and birds, as about two thirds of the records of behavioural change we found were documented in reptiles, amphibians, fish and invertebrates. Interestingly, our dataset indicates that invasive species have been mainly investigated for mammals and insects, whereas the relative majority of studies looking at native species focused on birds, with significant numbers also for fishes, mammals and molluscs (see Figure 1.1).

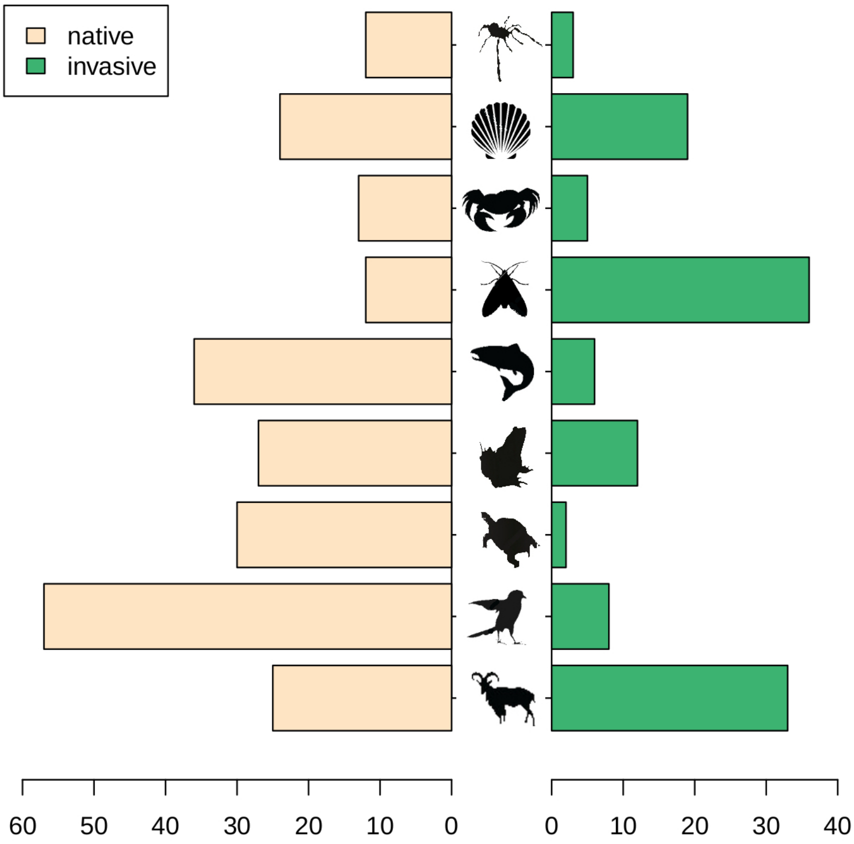

Figure 1.1 - Cases of behavioural change across taxonomic groups in native vs invasive species.

Looking at all 360 records of behavioural change included in our dataset, only 15 species appeared in four or more records; six of these 15 species are included in the "100 of the World's Worst Invasive Alien Species" list of IUCN's Global Invasive Species Database (www.iucngisd.org/gisd/100_worst.php; the black rat *Rattus rattus*, the cane toad *Rhinella marina*, the zebra mussel *Dreissena polymorpha*, the golden apple snail *Pomacea canaliculata*, the feral pig *Sus scrofa* and the Argentine ant *Linepithema humile*). This also means that while the taxonomic bias (see Figure 1.1) should be kept in mind when interpreting the results of our cross-taxonomic analyses, the results reported in the following sections are not primarily driven by a few species.

3.1 Different behavioural changes reported for native and invasive species

We found records of different types of behaviour changing in native and invasive species (Figure 1.2; Chi-square test, 100'000 bootstrap simulations with the numbers of records across natives and invasives across the six categories; $X^2=54.95$, $p<0.001$). More specifically, defence behaviour – avoiding predation and parasitism – was more commonly reported to change in native as compared to invasive species. These included native Australian marsupials dealing with the cane toad (*Rhinella marina*) invasion, the North American fence lizard (*Sceloporus undulatus*) coping with invasive ants, but also records of the avoidance of the Turkish crayfish (*Astacus leptodactylus*) by the common toad (*Bufo bufo*) in France (Langkilde, 2009; Llewelyn et al., 2010; Mandrillon & Saglio, 2007).

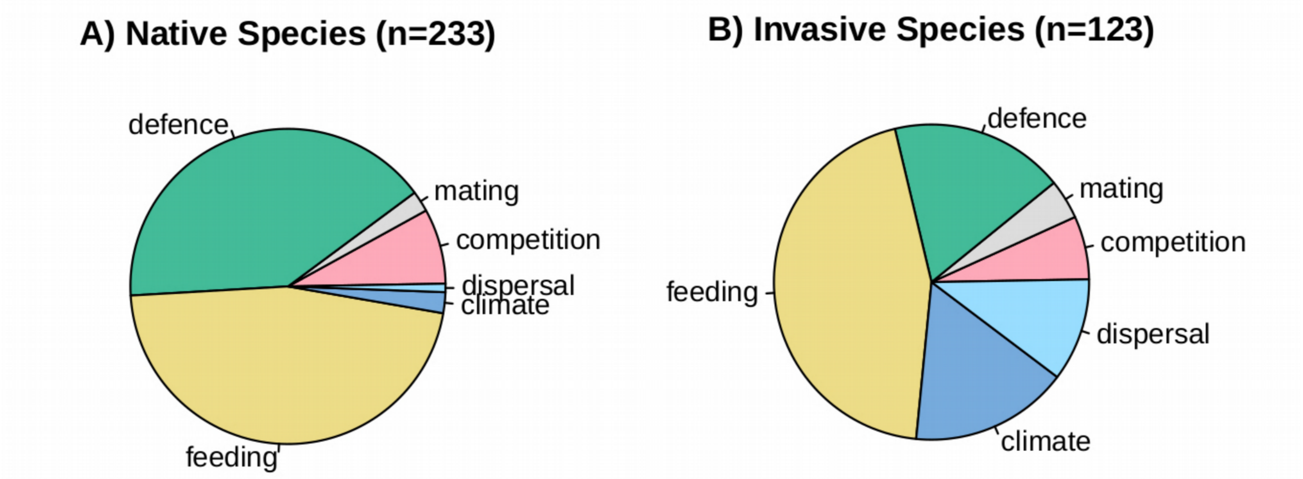

Figure 1.2 - Types of behaviour across native and non-native species.

The observation that behavioural changes to avoid enemies have been more frequently reported for native than invasive species is in line with previous studies based on smaller sample sizes (Berthon, 2015; Strauss et al., 2006). It also provides potential support for the enemy release hypothesis which posits that the absence of enemies in the exotic range of invasive species is a cause of invasion success (Heger & Jeschke, 2014;

2018; Keane & Crawley, 2002). A more specific variant of this hypothesis says that "Invaders are released from enemies", which is empirically better supported than the enemy release hypothesis in general (Heger and Jeschke 2018). We found the behavioural changes that were less frequently observed in invasive species were defence measures against predation. A possible underlying reason is their lower risk of predation by local predators. An alternative explanation may be a research bias: It is more fitting to the classic image that an invader is a dangerous new predator, while native species need to hide and run. But this paradigm is shifting and the role of invasive prey's antipredator behaviour in invasions is increasingly being recognised (Mennen & Laskowski, 2018).

Changes in dispersal behaviour and coping with the abiotic environment were more frequently reported for invasive than native species. Behavioural traits linked to dispersal were expected to have changed more often in invasive species, as dispersal and spread are part of the invasion process. For example, cane toads were found to move faster and follow straighter paths following selection in their new environment, the open Australian landscape (G. P. Brown, Phillips, & Shine, 2014). Environmental conditions in new habitats can be challenging for invasive species, requiring changes in activity, movements or strategies against dehydration. Invasive species commonly have different environmental characteristics in the invaded range to cope with, but also native species can be forced to change their behaviour due to invasions. The native lizard *Liolaemus wiegmannii* changed its basking pattern after the spread of acacia trees (*Acacia longifolia*) in Argentina, which produces significantly more shade than the native vegetation (Block, Stellatelli, García, Vega, & Isacch, 2013).

3.2 Specific types of behaviour change at different speeds

The speed of behavioural change varied substantially between the different categories of behaviour (Figure 1.3). We found that behavioural coping strategies to changed climatic condition, oxygen levels in water and hydration in terrestrial habitats was the behavioural category with most records of instant change (Figure 1.3). While such environmental changes usually manifest over long periods of time, an invasive species entering a new range will have to cope with the changed conditions immediately. The invasive green mussel *Perna viridis*, for example, closes its valves in waters with low salinity in the invaded range rapidly in order to survive osmotic stress (McFarland, Donaghy, & Volety, 2013). Similarly, native species that were pushed out of their abiotic optimal niche through predation or competition had to cope with the new abiotic conditions instantly.

Feeding behaviour changed relatively rapidly, but only in invasive species (Figure 1.3). There is a large and still growing body of research showing how exactly this dietary flexibility explains the success of invasive species (Sol & Lefebvre, 2000; Wright et al., 2010). The field of innovation research quantifies the innovation in a new behaviour of a species. In birds in particular, this literature distinguishes between simple "food type innovations" and more complex "technical innovations" (Ducatez, Clavel, & Lefebvre, 2014; Overington et al., 2009). It is often not the greater innovation propensity of invaders, but simply the choice of a new food source without the accompanying behavioural innovation that facilitate invasion.

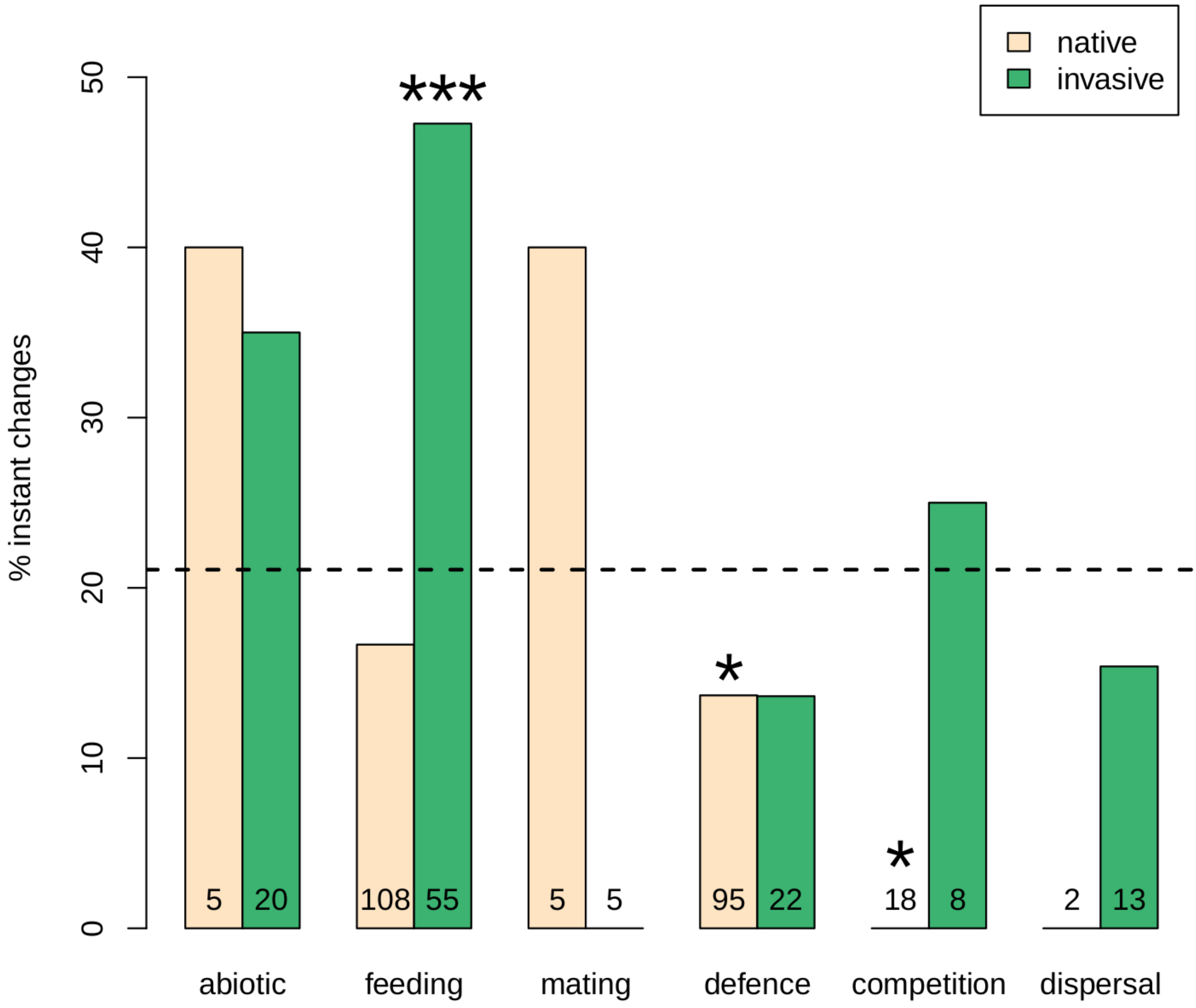

Figure 1.3 - Percentage of records of behavioural change that happened instantly across types of behaviour in native and invasive species. The numbers of records in each category is given at the bottom of each bar. Significant differences from the mean (shown as dashed line) are indicated above bars (*p<0.05, ***p<0.001).

On the other side, defence or escape strategies against new predators or parasites are relatively slow (Figure 1.3). These kinds of behavioural change were more prevalent in native than invasive species. When combined with the finding above, this suggests a dire situation for potentially endangered natives. If the invasive species is a predator readily feeding on the native species and the latter takes a longer time to react with an appropriate defence mechanism, it is under increased pressure from an effective novel predator. Furthermore, while we found that defence behaviour changes less often instantly, even a behavioural change in time is not guaranteed to be effective for the prey species.

Following the proposed definitions of Banks & Dickman (2007), there are three levels of naiveté. First, most harmful to the respective species is level-1 naiveté where the prey does not recognize the predator as a potential threat. In level-2 naiveté, the prey species recognizes the danger, but the reaction is inappropriate as an antipredator response. Finally, if the prey shows level-3 naiveté, it manages to recognize the potential threat and shows an appropriate response, but it is not skilled enough to escape. For example, Australian bilbies (*Macrotis lagotis*) were trained to recognize and avoid introduced predatory feral cats (*Felis catus*) and foxes (*Vulpes vulpes*), but survival rates after release into the wild did not improve significantly (Moseby, Cameron, & Crisp, 2012). The bilbies were trained to show the appropriate response, which is leaving the burrow when smelling the scent of the predator, but it was still ineffective, therefore showing level-3 naiveté. We describe only the speed of behavioural changes in native or invaders and do not have data on their population dynamics outcomes. However, we can say that not changing the behaviour (therefore staying in the most harmful level-1 or level-2 naiveté) is happening more commonly for native than invasive prey species.

3.3 Mechanisms enable change at different speeds

For behavioural changes that did not happen instantly, we found differences between the speed of learning compared to rapid genetic adaptation (Figure 1.4). Rapid genetic adaptation takes longer in both native (Hedge's g=1.9 (large), CI: 1.16, 2.64) and invasive species (Hedge's g=0.87 (large), CI: 0.05, 1.69). There was less difference in speed between native and invasive species (Hedge's g=0.53 (negligible), CI: 0.07, 0.99). The results are qualitatively the same for the absolute time span not corrected for age at sexual maturity (see Appendix A).

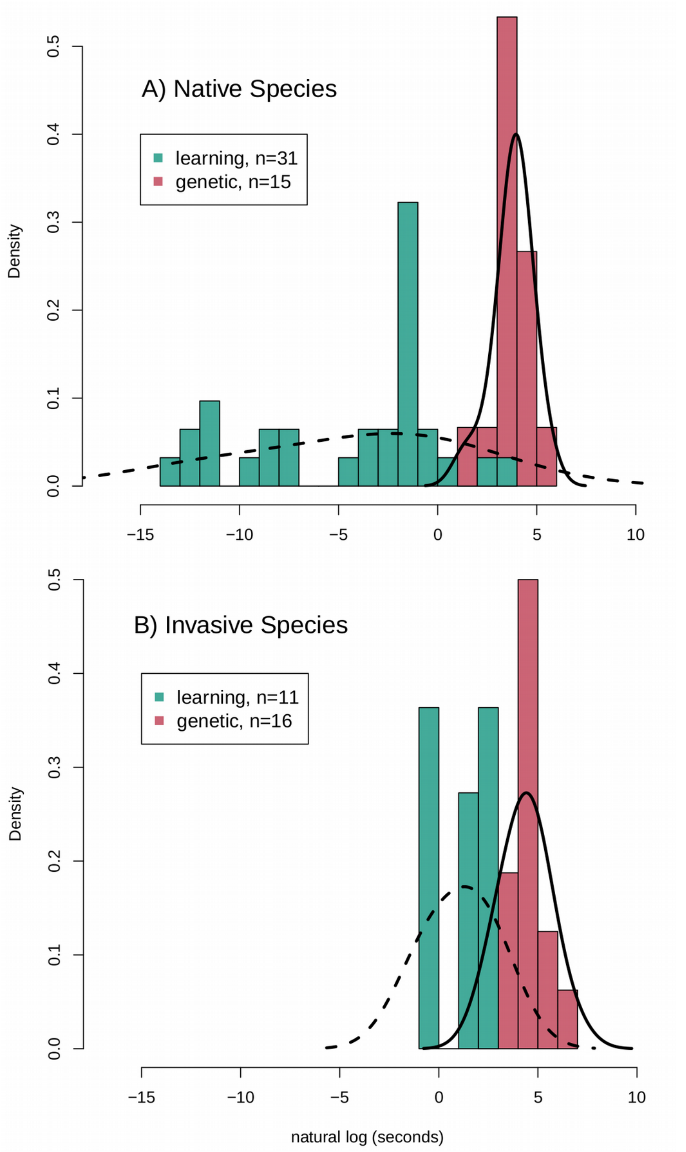

Figure 1.4 - Density plots of the speed of behavioural changes that did not happen instantly, split by the mechanisms learning and rapid genetic adaptation, for (A) native and (B) invasive species. Speed is displayed as the natural logarithm of the time it took for the change to occur divided by the age at sexual maturity of the focal species.

It has been conceptually proposed how learning in this context will act at a faster speed than rapid genetic adaptation (Zuk, Bastiaans, Langkilde, & Swanger, 2014); however, we are not aware of a study showing such empirical data across taxonomic groups. It is possible that the observation of a behavioural change over a certain time span inspires authors to interpret the underlying mechanism a posteriori. For example, if a given behaviour changed quickly, a researcher may assume the underlying mechanism was learning. Such a posteriori author interpretations are obviously not useful for our analysis; using them would result in circular reasoning. Thus, we only used records for which actual empirical evidence for a mechanism was available.

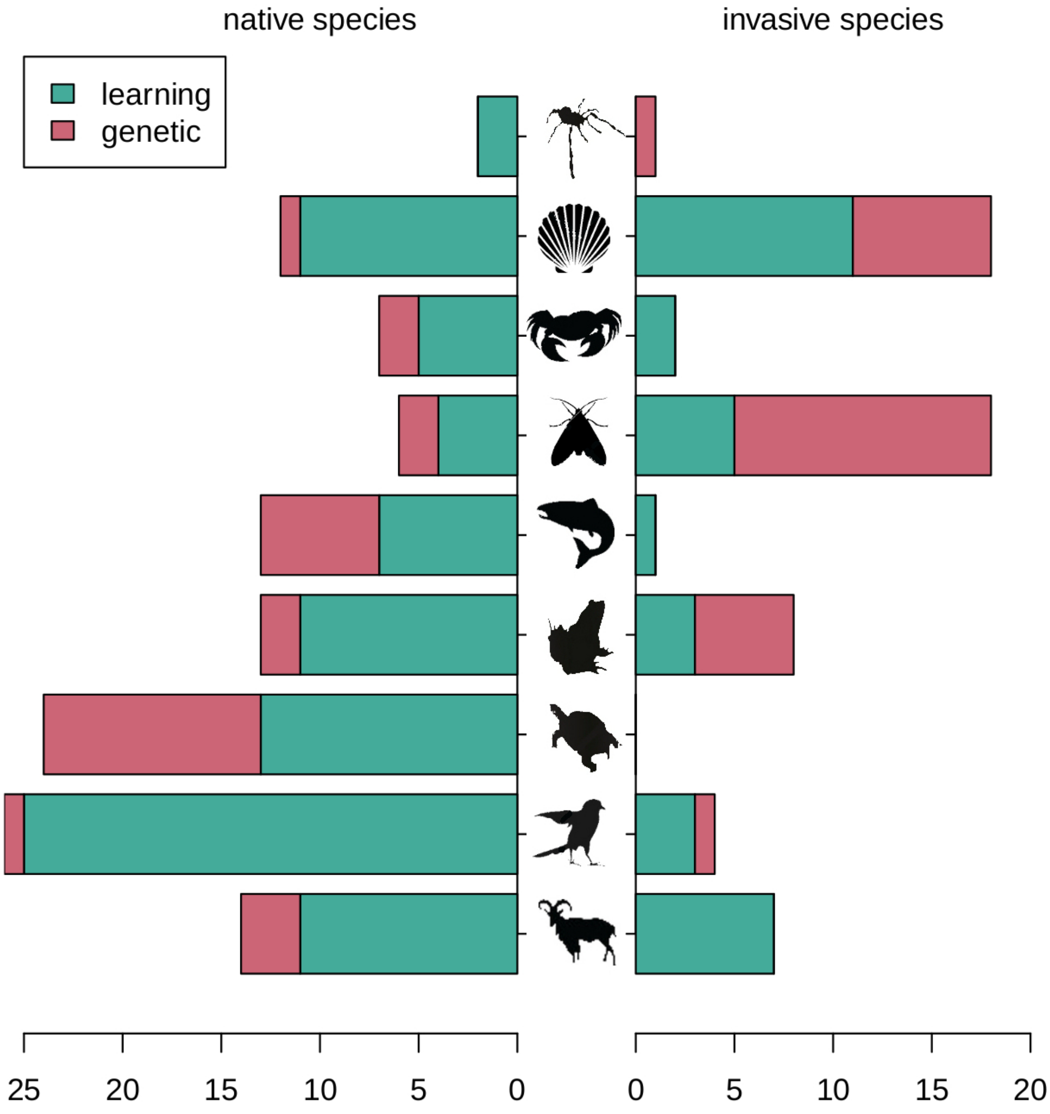

Figure 1.5 - Cases of behavioural change through learning or rapid genetic adaptation across taxonomic groups in native vs invasive species.

We found that all taxa changed their behaviour at least to some degree through both learning and rapid genetic adaptation (Figure 1.5). We expected a taxonomic bias, that learning would be more commonly reported for vertebrate than invertebrate species, as traditionally the focus lies on mammals and birds for studies on learning (Avital & Jablonka, 2000). This was not the case, however (Chi-Square test with 100'000 bootstrap simulations: $X^2 = 3.26$, p-value = 0.09); more experimental setups have recently been developed for learning experiments with invertebrates. Only when specifically comparing the nine taxonomic groups in our dataset (five vertebrate and four invertebrate groups) did we find differences, as insects were frequently reported to show rapid genetic adaptation, and birds to learn (Chi-Square test with 100'000 bootstrap simulations: $X^2 = 26.1$, p-value < 0.001).

Native species more often changed their behaviour through learning compared to invasive species, which was not exclusively explained by the taxonomic bias in the data (Chi-Square test with 100'000 bootstrap simulations: $X^2 = 8.7$, p-value < 0.01). In the most represented taxonomic group of our invasive species sample - insects, molluscs and amphibians - the ratio of rapid genetic adaptation to learning is higher than in its native counterparts.

It may be counter-intuitive to find that invasive species change their behaviour less often through learning than native species. But this is only the learning that happens within an individual's lifetime through behavioural plasticity or across generations. In contrast, the instant changes through behavioural flexibility – where species are pre-disposed to perform a new behaviour – are more common in invasive than native species (Chi-Square test with 100'000 bootstrap simulations: $X^2 = 14.97$, p-value < 0.001, see Table 1.1).

Table 1.1 - Numbers of records of behavioural change in native and invasive species that happened instantly or not.

	Native species	*Invasive species*
Instant changes	35	40
Non-instant changes	201	84

We found significant differences in the speed of behavioural change across taxonomic groups (Figure 1.6, Chi-square test with 100'000 bootstrap simulations, $X^2 = 24.13$, $p < 0.001$). Learning was not evenly distributed across taxa, thus we expected a corresponding difference in the speed of change. There was no difference in the frequency of instant changes between vertebrates and invertebrates (Chi-Square test with 100'000 bootstrap simulations: $X^2 = 3.8$, p-value = 0.06). Results from the analysis with weighted records were similar (see Appendix A).

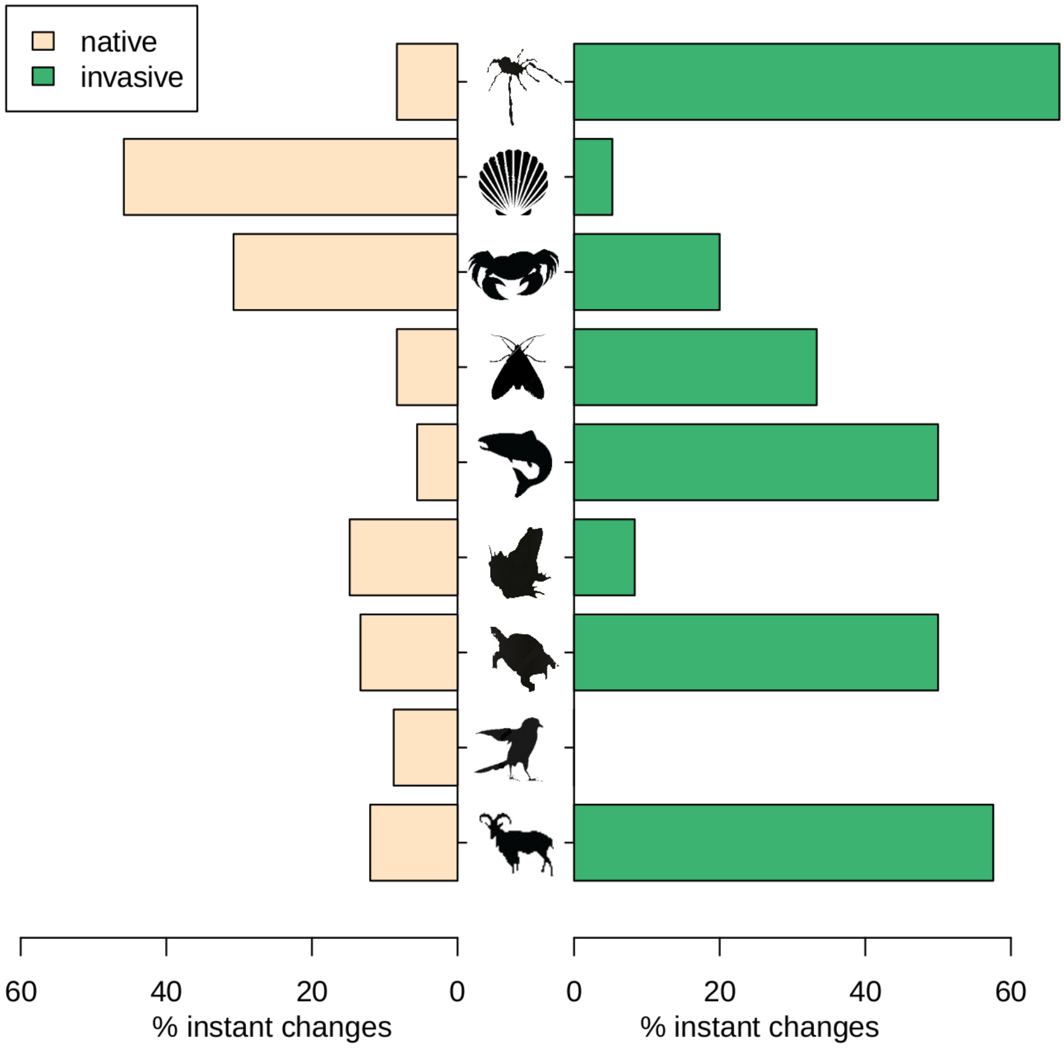

Figure 1.6 - Percentage of behavioural changes that happened instantly across taxa in native vs invasive species.

3.4 Specific types of behavioural change are associated with specific mechanisms

We found evidence for the mechanisms of behavioural change to differ between types of behaviour (Figure 1.7). Among invasive species, dispersal was most strongly associated with genetic adaptation, followed by feeding, coping with abiotic environmental differences and mating. Across categories, learning was more common in native than invasive species, most pronounced in defence behaviour, although not significantly so. It may be more challenging to recognize and behaviourally adapt to a new threat in the form of a predator or parasite than to a change in temperature. Sensory input from changing climatic conditions is immediate and clear, while threat cues from novel predators require interpretation before an appropriate response can be performed. Defence behaviour is more complex and not happening instantly, but still has to develop over a relatively short time period to be effective, and this is better possible through learning than genetic selection (cf. Figure 1.4).

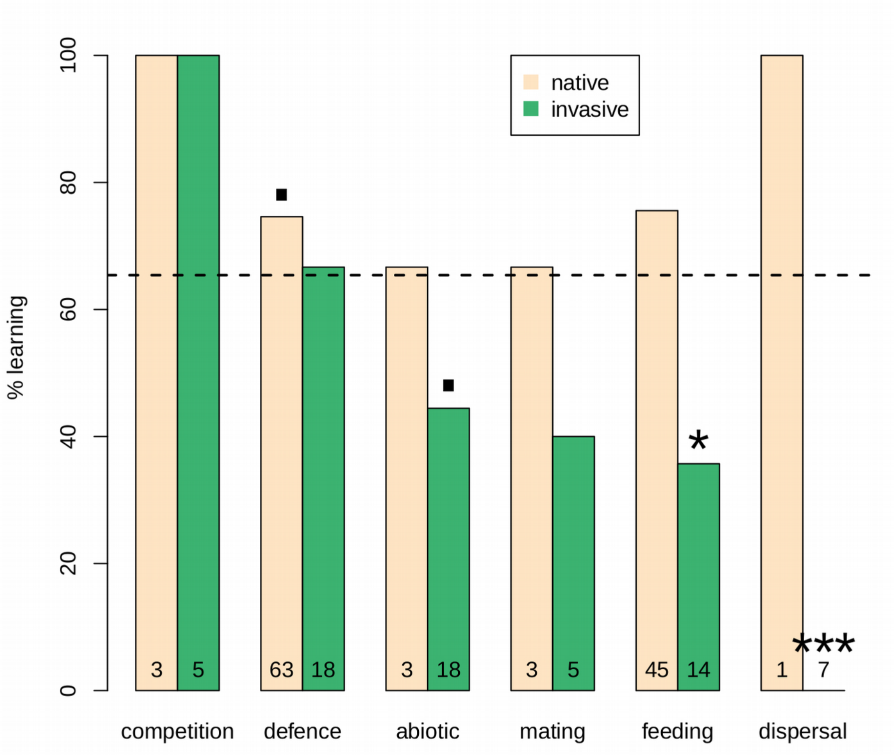

Figure 1.7 - Percentages of behavioural change through learning (as compared to rapid genetic adaptation) across types of behaviour in native vs invasive species. The dashed line indicates the mean percentage across all records. Sample sizes are indicated at the bottom of the bars. Significant differences from the mean are indicated above bars (■$p<0.1$, *$p<0.05$, ***$p<0.001$).

4 Conclusions

This study represents a general, cross-taxonomic overview of behavioural changes caused by biological invasions, considering both native and invasive species and a wide range of different data. We found that some taxonomic groups, particularly mammals and birds, are more frequently investigated than other taxa. We also found support for the enemy release hypothesis, as behavioural adjustments to a novel predator were more commonly described in native than invasive species, although this finding could also be due to a research bias.

Furthermore, we showed that different types of behaviour change at different speeds. For example and worryingly from the perspective of native species, feeding-related behaviour changes faster than avoidance behaviour against predators and parasites. The latter type of behavioural change was more prevalent among natives, thus our findings suggest a disadvantage in the arms race between invasive predators and native prey. This may in part explain cases of boom-bust population dynamics of predator invaders, which swiftly shift to new prey in their exotic range (leading to a "boom"), but decrease in their abundance (the "bust") when their prey either have finally developed avoidance strategies or have become (locally) extinct.

These differences in the speed of behavioural changes are enabled by different mechanisms. For instance, the mechanism underlying a change in defence behaviour of prey against predators was typically learning. It seems that at least for the cases of biological invasions covered by the studies analysed here – either introduced predators interacting with resident prey, or resident predators interacting with introduced prey – predators frequently have an advantage due to a high eco-evolutionary experience (sensu Saul & Jeschke, 2015) in these interactions. This higher experience relates to a higher frequency of pre-dispositions in predators as compared to prey species. Whether this result is robust for cases of biological invasions beyond those covered in our dataset is a question to be addressed in the future.

We publish our dataset of 360 records extracted from 191 studies along with this study to provide a resource for additional analyses and encourage other scientists to expand it. The dataset allows for several analyses that we could not focus on here, for example in-depth analyses for particular taxonomic groups. To foster the investigation of mechanisms underlying behavioural change, we also encourage that future empirical studies include targeted observations or experiments focusing on such mechanisms. Behaviour and, more specifically, behavioural changes have only been recently recognized as shaping outcomes of biological invasions (Weis & Sol, 2016). As pointed out above, these shifts can be of high interest for other research fields such as animal learning, innovation and conservation biology. We hope to inspire more research in that direction to (1) help predicting how changes in invader behaviour affect communities and ecosystems, (2) protect native species by assisting their behavioural change and (3) draw general conclusions on the role of behaviour and its temporal dynamics for biological invasions.

Acknowledgements

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References

Ardura, A., Zaiko, A., Morán, P., Planes, S., & Garcia-Vazquez, E. (2017). Epigenetic signatures of invasive status in populations of marine invertebrates. Scientific Reports, 7, 1–10. doi: 10.1038/srep42193

Avital, E. & Jablonka, E. (2000). Animal traditions: Behavioural inheritance in evolution. Cambridge University Press.

Badyaev, A. V. (2005). Maternal inheritance and rapid evolution of sexual size dimorphism: Passive effects or active strategies? American Naturalist, 166, 17–30. doi: 10.1086/444601

Bae, M. J., Chon, T. S., & Park, Y. S. (2015). Modeling behavior control of golden apple snails at different temperatures. Ecological Modelling, 306, 86–94. doi: 10.1016/j.ecolmodel.2014.10.020

Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. Trends in Ecology & Evolution, 22, 229–230. doi: 10.1016/j.tree.2007.02.006

Bellard, C., Genovesi, P., & Jeschke, J. M. (2016). Global patterns in threats to vertebrates by biological invasions. Proceedings of the Royal Society B: Biological Sciences, 283, 220152454. doi: 10.1098/rspb.2015.2454

Berger-Tal, O., Blumstein, D. T., Carroll, S., Fisher, R. N., Mesnick, S. L., Owen, M. A., … Swaisgood, R. R. (2016). A systematic survey of the integration of animal behavior into conservation. Conservation Biology, 30, 744–753. doi: 10.1111/cobi.12654

Berger-Tal, O., & Saltz, D. (Eds, 2016). Conservation behavior: applying behavioral ecology to wildlife conservation and management. Cambridge University Press.

Berthon, K. (2015). How do native species respond to invaders? Mechanistic and trait-based perspectives. Biological Invasions, 17, 2199–2211. doi: 10.1007/s10530-015-0874-7

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., … Richardson, D. M. (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26, 7, 333–339. 10.1016/j.tree.2011.03.023

Block, C., Stellatelli, O. a., García, G. O., Vega, L. E., & Isacch, J. P. (2013). Factors affecting the thermal behavior of the sand lizard *Liolaemus wiegmannii* in natural and modified grasslands of temperate coastal dunes from Argentina. Journal of Thermal Biology, 38, 560–569. doi: 10.1016/j.jtherbio.2013.09.009

Blumstein, D. T. (2016). Habituation and sensitization: new thoughts about old ideas. Animal Behaviour, 120, 255–262. doi: 10.1016/j.anbehav.2016.05.012

Brodin, T., & Drotz, M. K. (2014). Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. Current Zoology, 60, 410–416. doi: 10.1093/czoolo/60.3.410

Brown, C. (2012). Experience and learning in changing environments. In Candolin U., Wong, B. (Eds), Behavioural Responses to a Changing World: Mechanisms and Consequences (pp. 46–60). Oxford University Press. doi: 10.1093/acprof:osobl/9780199602568.003.0004

Brown, G. P., Phillips, B. L., & Shine, R. (2014). The straight and narrow path: The evolution of straight-line dispersal at a cane toad invasion front. Proceedings of the Royal Society B: Biological Sciences, 281, 20141385. doi: 10.1098/rspb.2014.1385

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. Biological Reviews, 89, 932–949. doi: 10.1111/brv.12087

Chabaane, Y., Laplanche, D., Turlings, T. C. J., & Desurmont, G. a. (2015). Impact of exotic insect herbivores on native tritrophic interactions: A case study of the African cotton leafworm, *Spodoptera littoralis* and insects associated with the field mustard *Brassica rapa*. Journal of Ecology, 103, 109–117. doi: 10.1111/1365-2745.12304

Ducatez, S., Clavel, J., & Lefebvre, L. (2014). Ecological generalism and behavioural innovation in birds: Technical intelligence or the simple incorporation of new foods? Journal of Animal Ecology, 84, 79–89. doi: 10.1111/1365-2656.12255

Dunn, A. M., Torchin, M. E., Hatcher, M. J., Kotanen, P. M., Blumenthal, D. M., Byers, J. E., … Perkins, S. E. (2012). Indirect effects of parasites in invasions. Functional Ecology, 26, 1262–1274. doi: 10.1111/j.1365-2435.2012.02041.x

Epanchin-Niell, R. S., & Liebhold, A. M. (2015). Benefits of invasion prevention: Effect of time lags, spread rates, and damage persistence. Ecological Economics, 116, 146–153. doi: 10.1016/j.ecolecon.2015.04.014

Flynn, A. M., & Smee, D. L. (2010). Behavioral plasticity of the soft-shell clam, *Mya arenaria* (L.), in the presence of predators increases survival in the field. Journal of Experimental Marine Biology and Ecology, 383, 32–38. doi: 10.1016/j.jembe.2009.10.017

Fogarty, S., Cote, J., & Sih, A. (2011). Social personality polymorphism and the spread of invasive species: A model. American Naturalist, 177, 273–287. doi: 10.1086/658174

Forister, M. L., Scholl, C. F., Jahner, J. P., Wilson, J. S., Fordyce, J. a., Gompert, Z., … Nice, C. C. (2013). Specificity, rank preference, and the colonization of a non-native host plant by the Melissa blue butterfly. Oecologia, 172, 177–188. doi: 10.1007/s00442-012-2476-8

Freeman, A. S., Wright, J. T., Hewitt, C. L., Campbell, M. L., & Szeto, K. (2013). A gastropod's induced behavioral and morphological responses to invasive *Carcinus maenas* in Australia indicate a lack of novelty advantage. Biological Invasions, 15, 1795–1805. doi: 10.1007/s10530-013-0409-z

Griffin, A. S. (2016). Innovativeness as an emergent property: A new alignment of comparative and experimental research on animal innovation. Philosophical Transactions of the Royal Society B: Biological Sciences, 371, 20150544. doi: 10.1098/rstb.2015.0544

Heger, T., & Jeschke, J. M. (2014). The enemy release hypothesis as a hierarchy of hypotheses. Oikos, 123, 741–750. doi: 10.1111/j.1600-0706.2013.01263.x

Heger, T. & Jeschke, J. M. (2018). Enemy release hypothesis. In Jeschke J. M. & Heger T. (Eds), Invasion biology: hypotheses and evidence (pp. 92–102). CABI.

Holway, D. a., & Suarez, A. V. (1999). Animal behavior: An essential component of invasion biology. Trends in Ecology & Evolution, 14, 328–330. doi: 10.1016/S0169-5347(99)01636-5

Jaworski, C. C., Bompard, A., Genies, L., Amiens-Desneux, E., & Desneux, N. (2013). Preference and prey switching in a generalist predator attacking local and invasive alien pests. PLoS ONE, 8, e82231. doi: 10.1371/journal.pone.0082231

Jeschke, J. M., Keesing, F., & Ostfeld, R. S. (2013). Novel organisms: Comparing invasive species, GMOs, and emerging pathogens. Ambio, 42, 541–548. doi: 10.1007/s13280-013-0387-5

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution, 17, 164–170. doi: 10.1016/S0169-5347(02)02499-0

Langkilde, T. (2009). Invasive fire ants alter behavior and morphology of native lizards. Ecology, 90, 208–217. doi: 10.1890/08-0355.1

Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. Animal Behaviour, 78, 103–110. doi: 10.1016/j.anbehav.2009.03.018

Liebl, A. L., & Martin, L. B. (2014). Living on the edge: Range edge birds consume novel foods sooner than established ones. Behavioral Ecology, 25, 1089–1096. doi: 10.1093/beheco/aru089

Llewelyn, J., Webb, J. K., Schwarzkopf, L., Alford, R., & Shine, R. (2010). Behavioural responses of carnivorous marsupials (*Planigale maculata*) to toxic invasive cane toads (*Bufo marinus*). Austral Ecology, 35, 560–567. doi: 10.1111/j.1442-9993.2009.02067.x

Mandrillon, A. L., & Saglio, P. (2007). Herbicide exposure affects the chemical recognition of a non native predator in common toad tadpoles (*Bufo bufo*). Chemoecology, 17, 31–36. doi: 10.1007/s00049-006-0354-8

McFarland, K., Donaghy, L., & Volety, A. K. (2013). Effect of acute salinity changes on hemolymph osmolality and clearance rate of the non-native mussel, *Perna viridis*, and the native oyster, *Crassostrea virginica*, in Southwest Florida. Aquatic Invasions, 8, 299–310. doi: 10.3391/ai.2013.8.3.06

Mennen, G. J., & Laskowski, K. L. (2018). Defence is the best offence: invasive prey behaviour is more important than native predator behaviour. Animal Behaviour, 138, 157–164. doi: 10.1016/j.anbehav.2018.02.017

Michelangeli, M., Smith, C. R., Wong, B. B. M., & Chapple, D. G. (2017). Aggression mediates dispersal tendency in an invasive lizard. Animal Behaviour, 133, 29–34. doi: 10.1016/j.anbehav.2017.08.027

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. Journal of Clinical Epidemiology, 62, 1006–1012. doi: 10.1016/j.jclinepi.2009.06.005

Moseby, K. E., Cameron, A., & Crisp, H. A. (2012). Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? Animal Behaviour, 83, 1011–1021. doi: 10.1016/j.anbehav.2012.01.023

Overington, S. E., Morand-Ferron, J., Boogert, N. J., & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. Animal Behaviour, 78, 1001–1010. doi: 10.1016/j.anbehav.2009.06.033

Robert, M., & Sorci, G. (1999). Rapid increase of host defence against brood parasites in a recently parasitized area: The case of village weavers in Hispaniola. Proceedings of the Royal Society B: Biological Sciences, 266, 941–946. doi: 10.1098/rspb.1999.0727

Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. Trends in Ecology & Evolution, 28, 552–560. doi: 10.1016/j.tree.2013.04.004

Rosenthal, M. F., Gertler, M., Hamilton, A. D., Prasad, S., & Andrade, M. C. B. (2017). Taxonomic bias in animal behaviour publications. Animal Behaviour, 127, 83–89. doi: 10.1016/j.anbehav.2017.02.017

Saul, W.-C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. Ecology Letters, 18, 236–245. doi: 10.1111/ele.12408

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Animal Behaviour, 85, 1077–1088. doi: 10.1016/j.anbehav.2013.02.017

Sih, A., Trimmer, P. C., & Ehlman, S. M. (2016). A conceptual framework for understanding behavioral responses to HIREC. Current Opinion in Behavioral Sciences, 12, 109–114. doi: 10.1016/j.cobeha.2016.09.014

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America, 102, 5460–5465. doi: 10.1073/pnas.0408145102

Sol, D., & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos, 90, 599–605. doi: 10.1034/j.1600-0706.2000.900317.x

Strauss, S. Y., Lau, J. a., & Carroll, S. P. (2006). Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters, 9, 357–374. doi: 10.1111/j.1461-0248.2005.00874.x

Strayer, D. L., D’Antonio, C. M., Essl, F., Fowler, M. S., Geist, J., Hilt, S., … Jeschke, J. M. (2017). Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecology Letters, 20, 1337–1350. doi: 10.1111/ele.12822

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. Trends in Ecology & Evolution, 21, 645–651. doi: 10.1016/j.tree.2006.07.007

Tinghitella, R. M., & Zuk, M. (2009). Asymmetric mating preferences accommodated the rapid evolutionary loss of a sexual signal. Evolution, 63, 2087–2098. doi: 10.1111/j.1558-5646.2009.00698.x

Trewavas A. (2014). Plant Behaviour and Intelligence. Oxford University Press.

Vanderwerf, E. a. (2012). Evolution of nesting height in an endangered Hawaiian forest bird in response to a non-native predator. Conservation Biology, 26, 905–911. doi: 10.1111/j.1523-1739.2012.01877.x

Vilà, M., & Hulme, P. E. (Eds, 2017). Impact of biological invasions on ecosystem services. Springer.

Wagner, A. (2017). The white-knight hypothesis, or does the environment limit innovations? Trends in Ecology & Evolution, 32, 131–140. doi: 10.1016/j.tree.2016.10.017

Weis, J. S., & Sol, D. (Eds, 2016). Biological invasions and animal behaviour. Cambridge University Press.

Willer, C. J., Li, Y., & Abecasis, G. R. (2010). METAL: Fast and efficient meta-analysis of genomewide association scans. Bioinformatics, 26, 2190–2191. doi: 10.1093/bioinformatics/btq340

Wlodarczyk, R., & Janiszewski, T. (2014). Can expansion of zebra mussel, *Dreissena polymorpha* (Bivalvia) influence the numbers and behaviour of traditionally herbivorous mute swan, *Cygnus olor* (Aves)? Acta Zoologica Bulgarica, 66, 235–238.

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. Behavioral Ecology, 26, 665–673. doi: 10.1093/beheco/aru183

Wright, T. F. F., Eberhard, J. R. R., Hobson, E. a. A., Avery, M. L. L., & Russello, M. a. A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethology Ecology & Evolution, 22, 393–404. doi: 10.1080/03949370.2010.505580

Zaykin, D. V. (2011). Optimally weighted Z-test is a powerful method for combining probabilities in meta-analysis. Journal of Evolutionary Biology, 24, 1836–1841. doi: 10.1111/j.1420-9101.2011.02297.x

Zuk, M., Bastiaans, E., Langkilde, T., & Swanger, E. (2014). The role of behaviour in the establishment of novel traits. Animal Behaviour, 92, 333–344. doi: 10.1016/j.anbehav.2014.02.032

Appendix A

2.1 Literature Search

A flow chart showing the number of studies found in our initial search and how many records remained after each of our processes of scanning for eligibility is shown in Figure A.1.

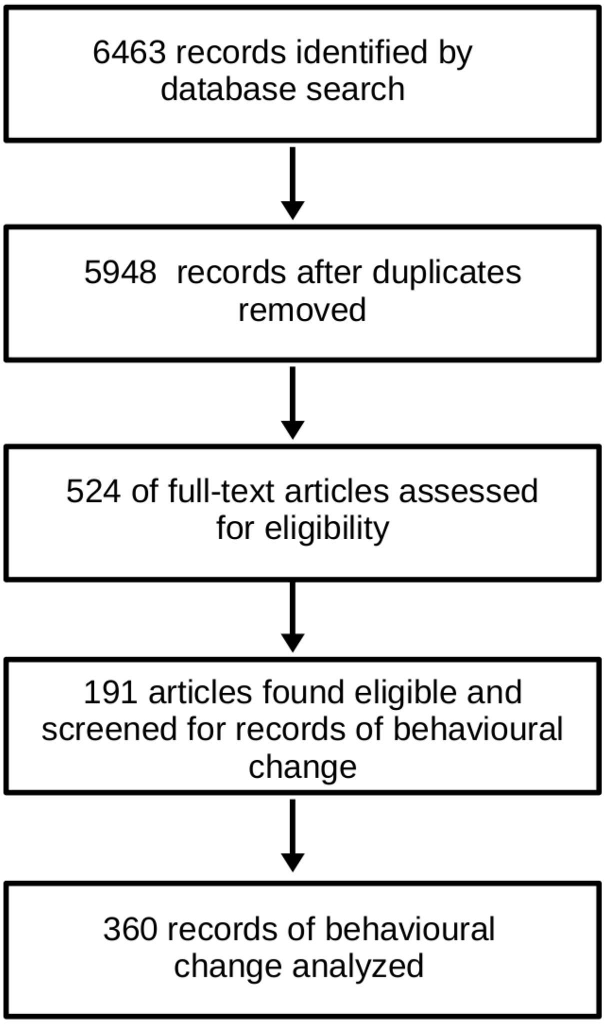

Figure A.1 - Flowchart with numbers of studies collected, scanned for eligibility and analysed in this study (modified after Moher et al. 2014).

3 Bias in Taxonomy and Origin of Species

When records of behavioural change in each study are sqrt-weighted, mammals, birds and insects remain the most studied taxa. Also, mammals and insects remain the taxa with the most invasive species studied. Distribution of non-natives/natives across taxa is non-random (Chi-square test with 100'000 bootstrap simulations, X²=58.86, p<0.001, see Figure A.2).

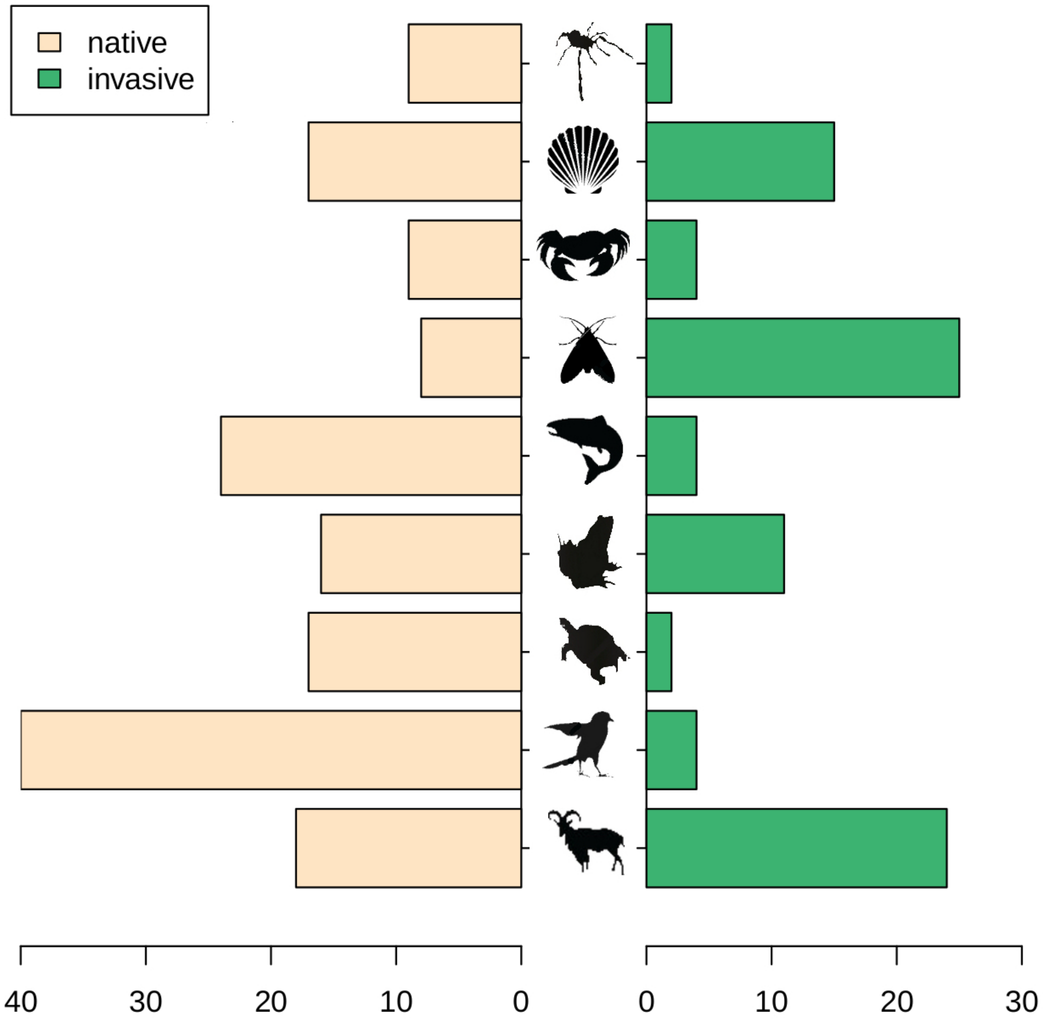

Figure A.2 - Records of behavioural change weighted by /sqrt of n of records per study.

3.1 Different changes in behaviour reported for native and invasive species

Predator- or parasite-avoidance behaviour was more frequently changing in native species, while behavioural changes to cope with climate and dispersal behaviour was more often documented to change in invasive species, also if records of behavioural change were subjected to sqrt-weighting (Chi-square test with 100'000 bootstrap simulations, $X^2=38.74$, $p<0.001$, see Figure A.3).

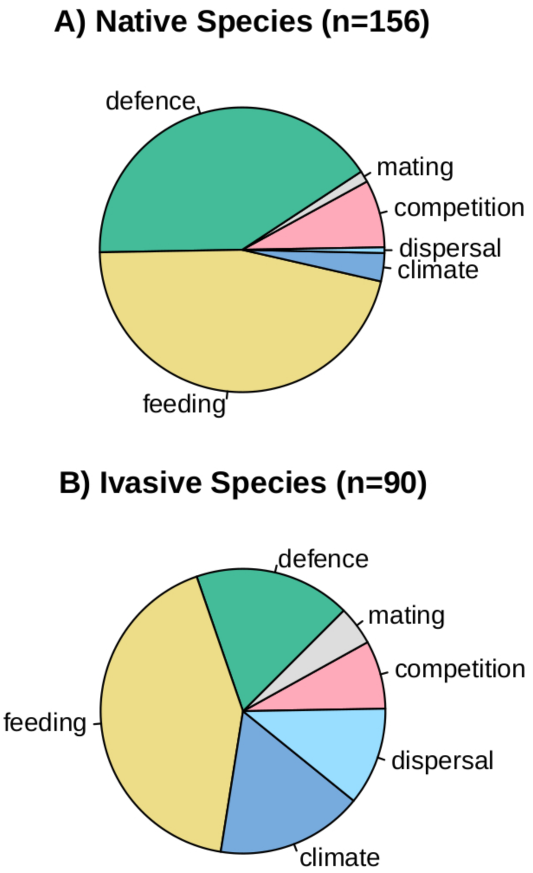

Figure A.3 - Types of behaviour across native and non-native species. Records of behavioural change were sqrt-weighted.

3.2 Specific types of behaviour change at different speeds

Changes in feeding behaviour of invasive species happened faster than other types of behaviour, also if records of behavioural change were subjected to sqrt-weighting (see Figure A.4). Defence behaviour changed more slowly, although not significantly so.

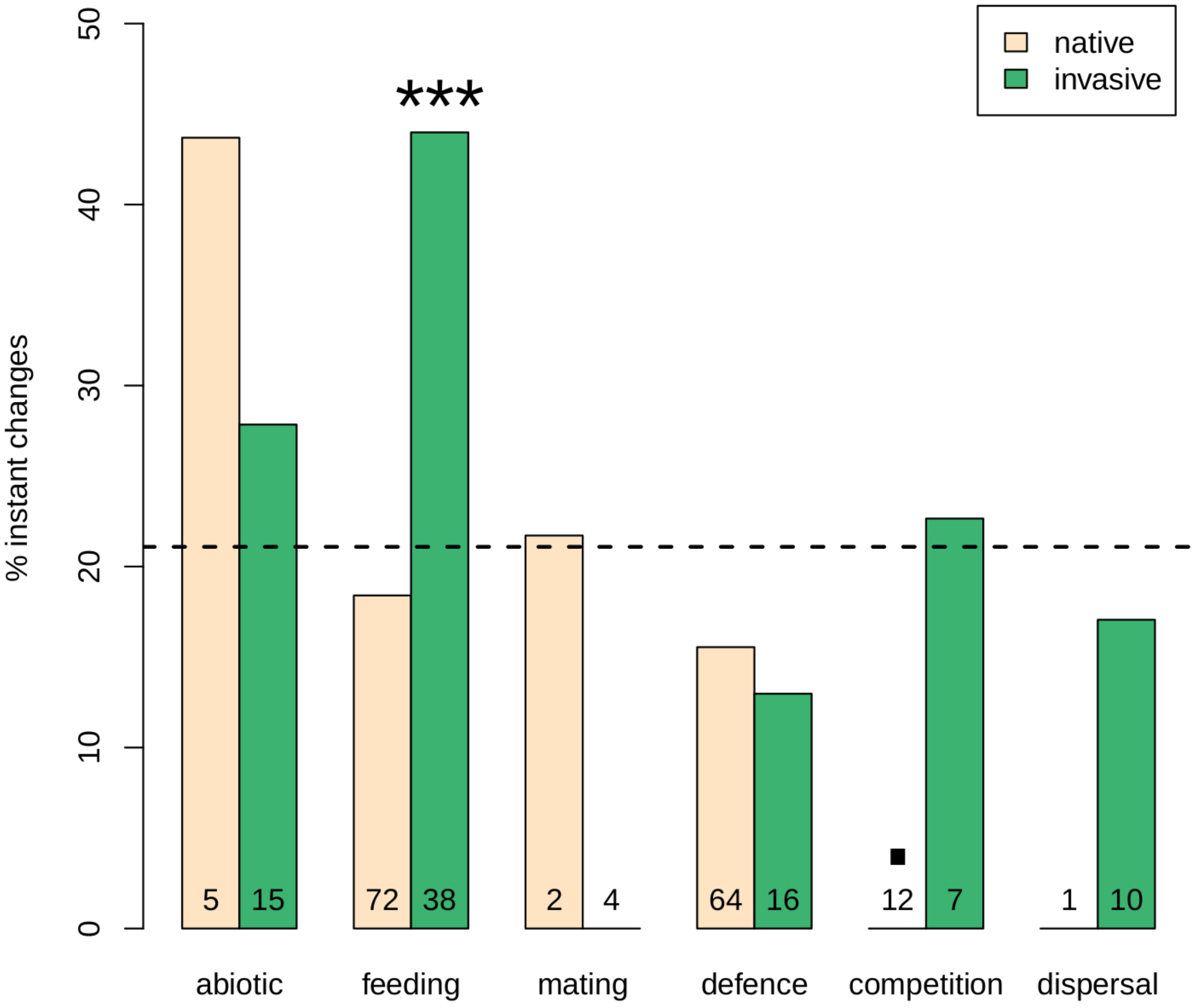

Figure A.4 - Percentage of records of behavioural change that happened instantly across types of behaviour in native and invasive species. Records of behaviour were sqrt-weighted and rounded, and are given at the bottom of each bar. The dashed line indicates the mean percentage. Significance levels of the outcomes of Chi-square tests with 100'000 simulations between the respective subsample and the rest are indicated above bars (■p<0.1, ***p<0.001).

3.3 Mechanisms enable change at different speeds

In absolute time, learning was also faster than rapid genetic adaptation in both native (Hedge's g = 1.72 (large), ci = [1.06; 2.37], Figure A.5) and invasive species (Hedge's g = 1.34 (large), ci = [0.5; 2.18], Figure A.5A). No difference between invasive and native species was observed: Hedge's g = 0.03, ci = [-0.46; 0.41].

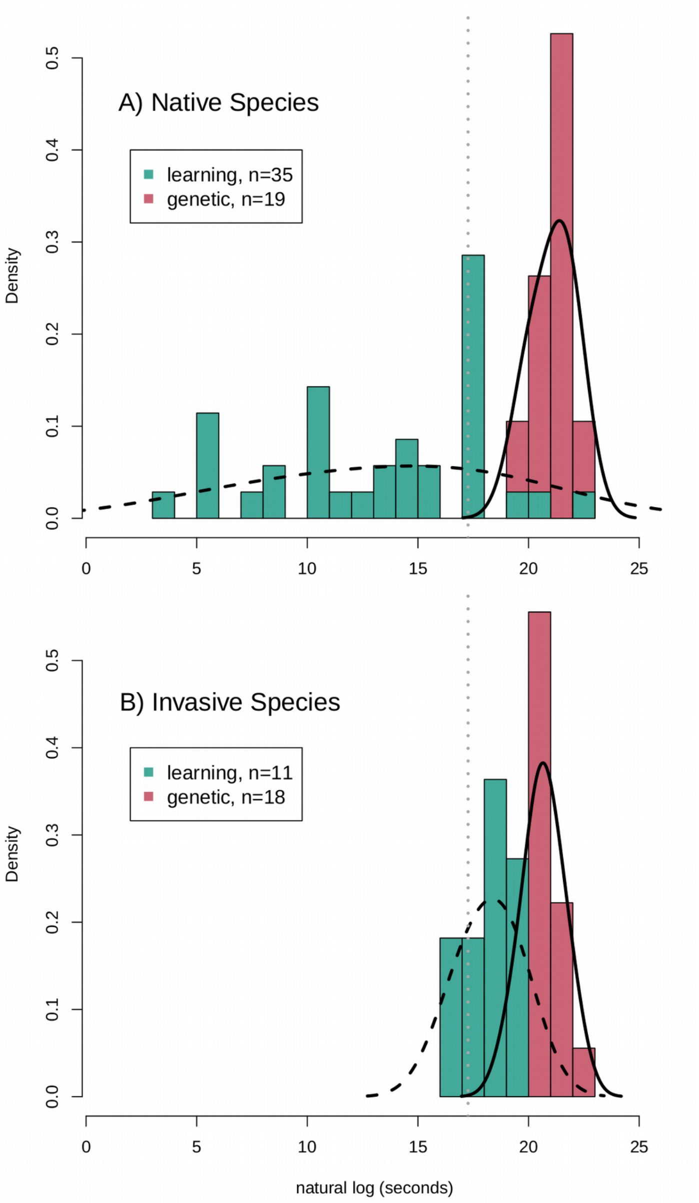

Figure A.5 - Density plots of the speed of behavioural changes that did not happen instantly, split by the mechanisms learning and rapid genetic adaptation, for (A) native and (B) invasive species. A vertical grey dashed line indicates one year.

There were significant differences between the distribution of mechanisms across the taxonomic groups, also when records were subjected to sqrt-weighting (Chi-square test with 100'000 simulations: $X^2=5.03$, $p<0.05$, Figure A.6). Learning was especially rare for insects and reptiles, while it was most common for birds.

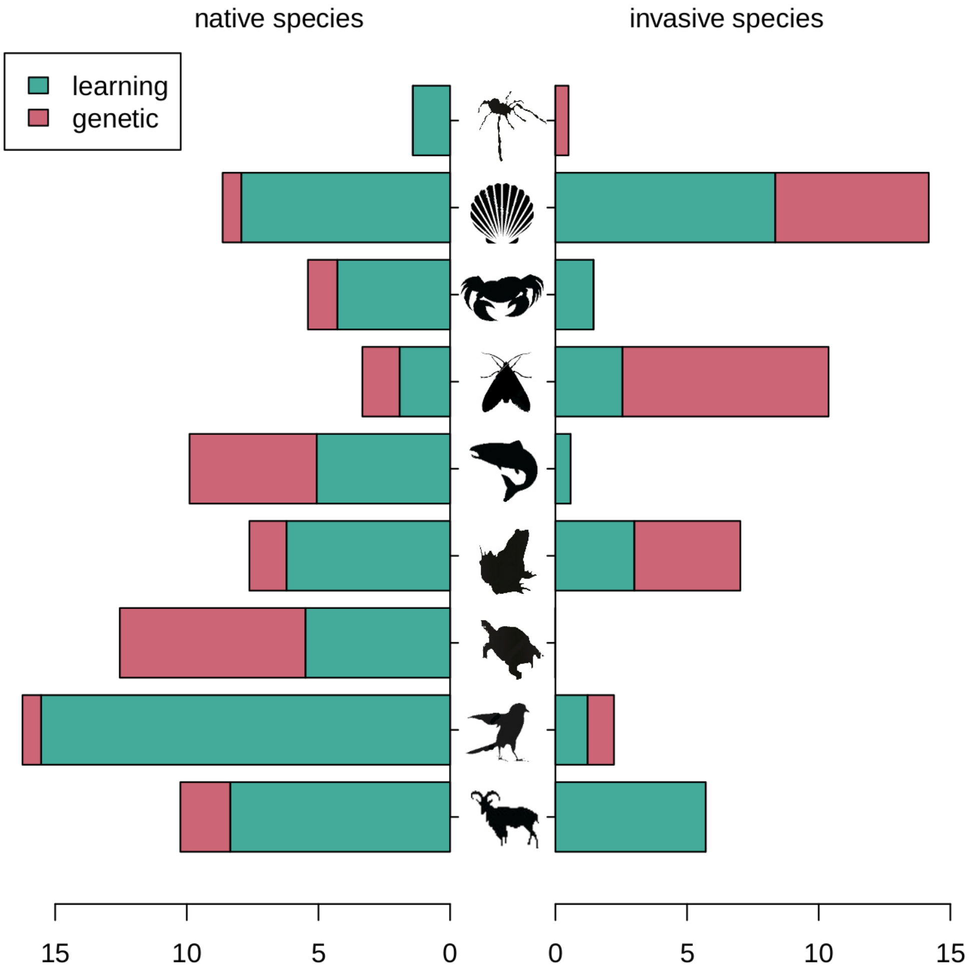

Figure A.6 - Cases of behavioural change through learning or rapid genetic adaptation across taxonomic groups in native vs invasive species. Records of behavioural change were sqrt-weighted.

There were significant differences between the speed of behavioural change across the taxonomic groups, also when records were subjected to sqrt-weighting (Chi-sqare test with 100'000 simulations: $X^2=16.37$, $p<0.05$, Figure A.7). Invasive species changed their behaviour faster than native species ($X^2=5.47$, p-value < 0.05) and there was no difference between vertebrates and invertebrates ($X^2=1.23$, p-value $= 0.33$).

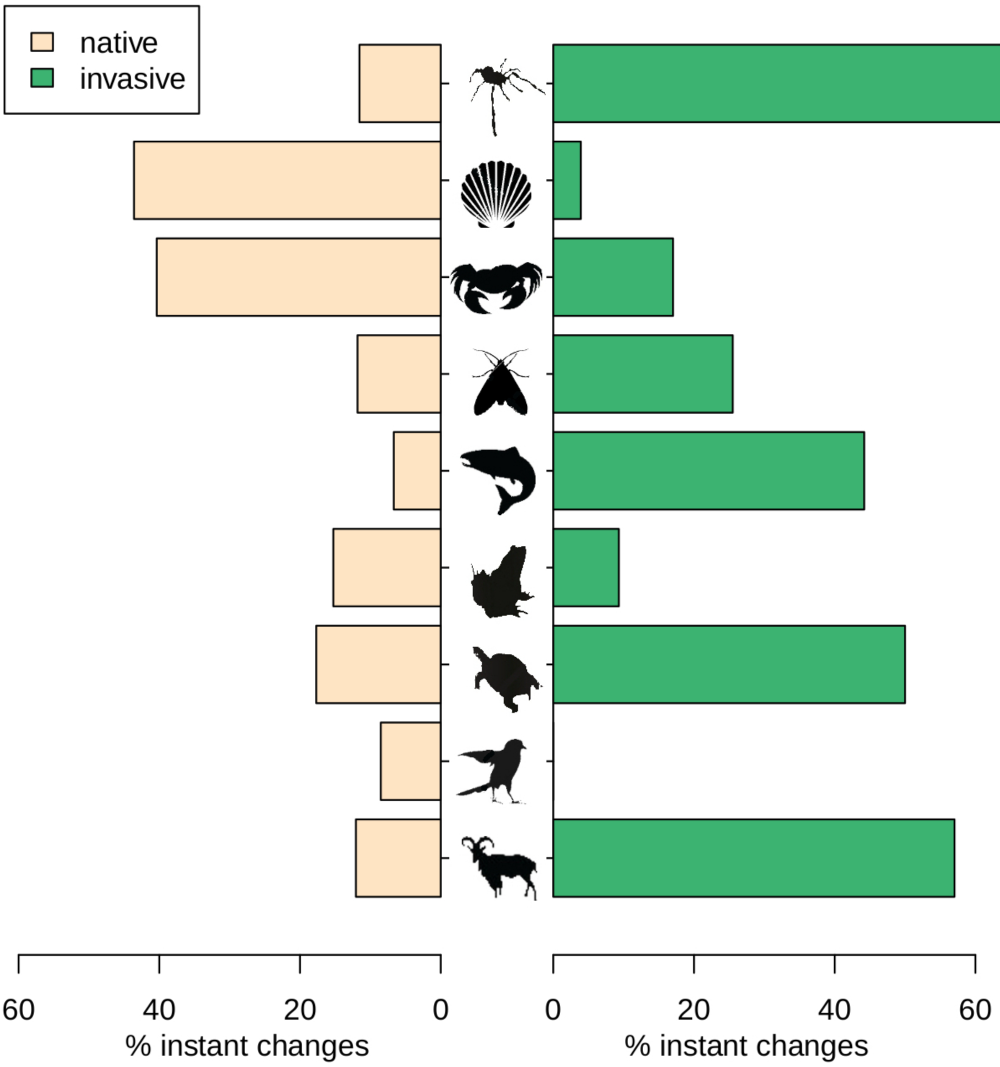

Figure A.7 - Percentage of behavioural changes that happened instantly across taxa in native vs invasive species. Records of behavioural change were sqrt-weighted.

3.4 Specific types of behavioural change are associated with specific mechanisms

As for non-weighted data, dispersal in invasive species was associated with genetic adaptation, while native species' defence behaviour was mostly changing through learning (see Figure A.8).

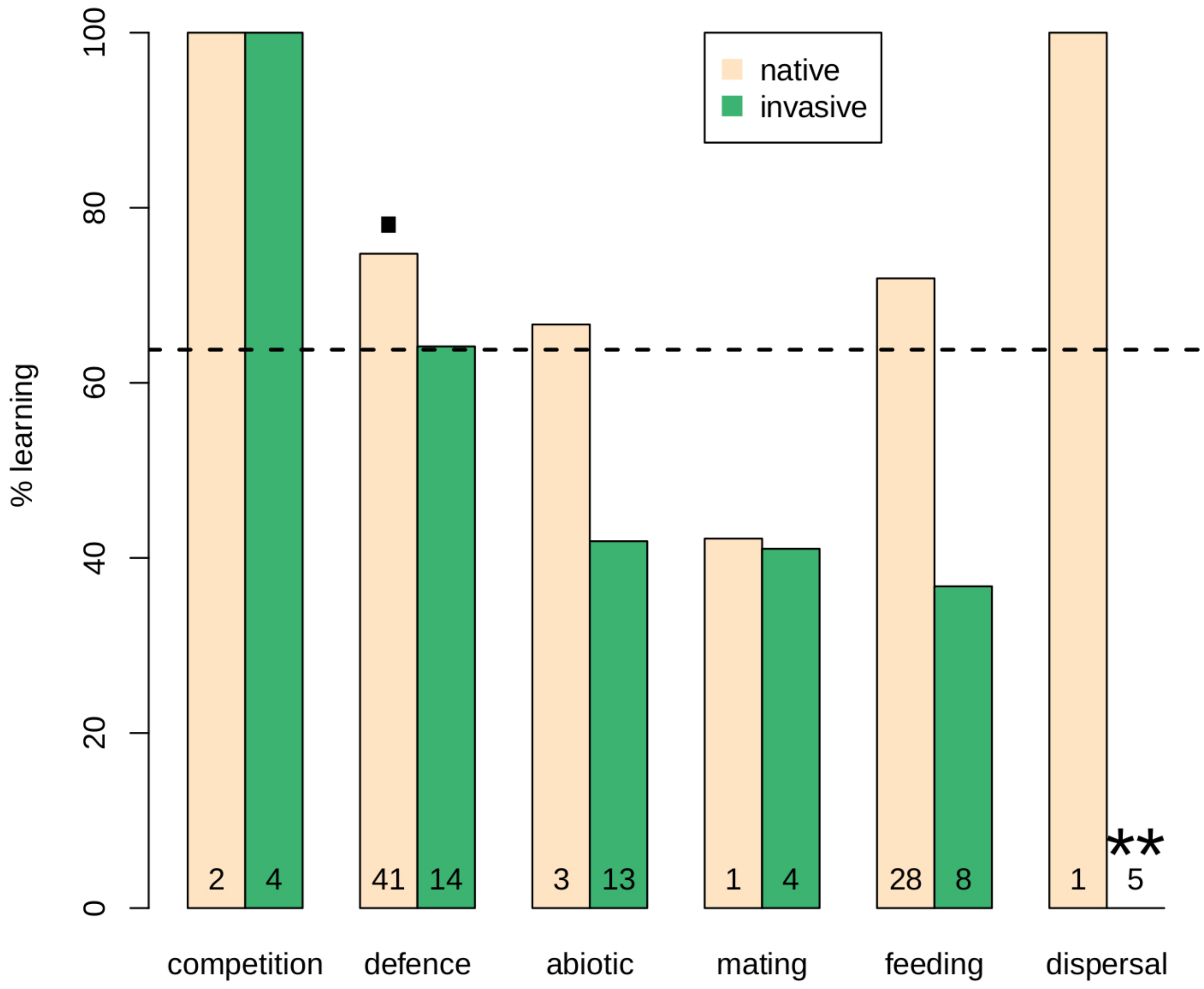

Figure A.8 - Percentages of behavioural change through learning (as compared to rapid genetic adaptation) across types of behaviour in native and invasive species. Records of behavioural change were sqrt-weighted and rounded, and are given at the bottom of each bar. The dashed line indicates the mean percentage. Sample sizes are indicated at the bottom of the bars. Significant differences from the mean are indicated above bars (■$p<0.1$, **$p<0.01$).

Chapter 2: Behavioral differences in an over-invasion scenario: marbled vs. spiny-cheek crayfish

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Abstract

New species often invade ecosystems already dominated by previous invaders. Ornamental freshwater crayfish, particularly parthenogenetic marbled crayfish (*Procambarus virginalis*), increasingly establish in European water bodies where they interact with resident native and non-native species. Behavioral traits and behavioral syndromes can influence the outcome of these species interactions. The behavior of non-native crayfish is often studied in notorious invaders but rarely in new and emerging species, although those provide the best opportunity for management. Activity, aggressiveness, and boldness have repeatedly been associated with invasion success and species displacement. Further, crayfish can adapt their behavior after they have established in the new range. We investigated whether marbled crayfish can displace the widely established spiny-cheek crayfish (*Orconectes limosus*). Specifically, we compared their behavioral traits and evaluated whether these traits differ, using marbled crayfish populations from aquaria and the field and spiny-cheek crayfish from the field. We staged agonistic ecounters, measured activity levels, and recorded the response to a simulated threat of both species and both origins (field and aquarium) in laboratory trials. We found that in agonistic encounters, marbled crayfish were on average more aggressive than spiny-cheek crayfish, even against larger opponents. Aggressiveness and activity were positively correlated, which is indicative for an aggression syndrome. Marbled crayfish from the field were less active than those from aquaria, but there was no difference in aggressiveness. Marbled crayfish often froze in response to a simulated threat, whereas spiny-cheek crayfish reacted either offensively or defensively. These results from the laboratory illustrate potentially important behavioral mechanisms behind crayfish over-invasions and show behavioral plasticity in a species where all known individuals are genetically identical. To better understand the invasion process in nature, the species' reproductive biology and interactions with other members of the community should be considered. We conclude that the recent success of marbled crayfish in establishing new populations could be influenced by their behavioral flexibility and their potential to competitively persist in the presence of established invasive crayfish.

Keywords: aggression; behavioral flexibility; behavioral syndromes; behavioral variability; biological invasions; freshwater crayfish; shelter use; threat response.

Introduction

Species invasions have already massively altered aquatic communities and are still increasing worldwide (Gallardo et al. 2016, Seebens et al. 2017). Consequently, more and more invasive species compete with already established, functionally similar invasive species, a process that has been termed over-invasion (Russell et al. 2014). In novel communities, such over-invasions and species introduction dates are of great relevance and allow for more detailed analyses than a simple, dichotomous distinction between native vs. non-native species that ignores species residence times (Dornelas et al. 2014).

The consequences of multiple species invasions are largely unknown (Hewitt and Huxel 2002), but the invasion outcome and interaction strength between invading and resident species can be assessed by behavioral differences and correlated suites of behavioral traits (i.e., behavioral syndromes; Chapple et al. 2012, Sih et al. 2012, Penk et al. 2017). Some behavioral traits such as activity, aggressiveness, and boldness have repeatedly been associated with invasion success (Weis 2010, Chapple et al. 2012). Furthermore, the ability to behaviorally adapt to a new environment, that is, behavioral flexibility, promotes invasion success (Wright et al. 2010). Naïve non-native species have to adapt to new prey, competitors, or predators by means of evolution or learning (Saul and Jeschke 2015, Wong and Candolin 2015). Comparative studies across invading species can help elucidate what makes some invaders more successful than others (van Kleunen et al. 2010).

Ornamental crayfish invasions

Particularly since the beginning of the 20th century, decapod crayfish invasions have resulted in a decline of native crayfish populations and severe changes to ecosystems, for example, in Europe (Holdich et al. 2009, Lodge et al. 2012). Nowadays, increasing numbers of new non-native crayfish species are imported by the pet trade from North America and Australasia to Europe, and some species have already been released in nature (Chucholl 2013, Chucholl and Wendler 2017). As more of these recently arrived species have started to establish populations, interactions with other invasive species will shape future crayfish distributions and novel species communities (Kouba et al. 2014). However, the propagule pressure of the new invaders and the incumbent advantage of the old invaders will be decisive for potential competitive displacement in these over-invasion scenarios (Lockwood et al. 2005, Russell et al. 2014). Crayfish from the pet trade have the disadvantage that they are naïve to prey, predators, or competitors when they are released from aquaria (Hazlett 1994, Martin 2014). For example, aquaria or other hatchery-reared fish are more vulnerable to predation than those that have experienced predation (Kellison et al. 2000, Yokota et al. 2007). Some studies looked at agonistic behaviors among competing old and new invasive crayfish species (Chucholl et al. 2008, Hudina et al. 2011, James et al. 2016), but broader behavioral comparisons are necessary to investigate the invasive potential of species before or at an early stage of invasion.

Invasive crayfish: behavioral differences and flexibility

Non-native crayfish are model organisms in invasion ecology and are also frequently used in behavioral studies (Gherardi et al. 2012, Lodge et al. 2012). Evidence suggests that highly invasive crayfish typically display stronger interspecific aggression toward resident congeners, in that way limiting access to critical resources for competitors (e.g. Gherardi and Cioni 2004, Klocker and Strayer 2004, Chucholl et al. 2008). Also, larger body and chela size are advantageous in these agonistic interactions (Garvey and Stein 1993, Vorburger and Ribi 1999). Invasive crayfish species are often more active (Bubb et al. 2006), perceive more predation cues (Hazlett et al. 2003), or avoid predation more effectively (Garvey et al. 1994) than native crayfish. Activity, aggressiveness, and boldness in crayfish are often correlated and thought to be part of an aggression syndrome (Pintor et al. 2008, 2009). These behavioral syndromes can be explained by state variables (such as growth) that often covary with sets of behaviors (Biro et al. 2014). Furthermore, invasive crayfish adapt behavioral traits after introduction in response to resident crayfish species and the community of invaded water bodies (Pintor et al. 2008, Hanshew and Garcia 2012). For example, native crayfish that had experience with an invasive competitor were more aggressive toward the opponent than naïve native individuals (Hayes et al. 2009). Also, the presence of predators alters the activity of invasive and native crayfish (Hirvonen et al. 2007, Aquiloni et al. 2010). It has been shown that invasive crayfish and crabs can learn how to respond to newly emerging threats after invading new territories (Hazlett et al. 2002, Roudez et al. 2008). By looking at multiple behavioral traits and integrating behavioral flexibility and new concepts like behavioral syndromes (Gherardi et al. 2012), species displacements and ecological invasions might be better understood and managed.

Model organisms

Spiny-cheek crayfish (*Orconectes limosus*) and marbled crayfish (*Procambarus virginalis*) are examples for invaders with a high functional similarity. They can thus be used as comparator organisms sensu Penk et al. (2017): Comparing marbled crayfish to resident spiny-cheek crayfish allows assessing the invasive capacity of marbled crayfish. Furthermore, both species are included in the List of Invasive Alien Species of Union Concern (EU Regulation 1143/2014). They co-occur in some lakes in Germany, but differ in their invasion history and morphology (Chucholl and Pfeiffer 2010, Chucholl et al. 2012).

Spiny-cheek crayfish have been spread across Central Europe since the late 19th century, now being one of the most common European crayfish species (Kouba et al. 2014). They display sexual dimorphism with males having larger chelae than females (Souty-Grosset et al. 2006). In parts of their native range, spiny-cheek crayfish were outcompeted by other invasive species from the genus Orconectes (Klocker and Strayer 2004). The interactions of spiny-cheek crayfish with other crayfish in their invasive range, however, have rarely been studied (Musil et al. 2010).

The peculiar marbled crayfish are triploid descendants of the sexually reproducing slough crayfish (*Procambarus fallax*; Martin et al. 2010, Lyko 2017, Gutekunst et al. 2018). Marbled crayfish represent the only known decapod crustacean capable of apomictic parthenogenesis (Scholtz et al. 2003, Seitz et al. 2005). What makes marbled crayfish even more unique is the fact that no native population has been recorded so far (summarized in Chucholl et al. 2012 and citations therein). The obscure origin of marbled crayfish lies in the tanks of traders or breeders of crayfish, and neither behavior nor ecology of the species within invaded lakes is yet understood (Chucholl et al. 2012). The first naturalized marbled crayfish population (i.e., in the field) was reported near Freiburg, Germany, in 2003 (Marten et al. 2004). In recent years, sightings from the Netherlands, Italy, Slovakia, Sweden, and other German lakes followed (see Chucholl et al. 2012 for review). Since these populations stem from marbled crayfish previously reared in aquaria, they can be considered to have been naïve to interspecific competition and predators before they were released. The aquarium origin and the beginning establishment of isogenic populations in pre-invaded lakes provide a unique opportunity to study behavioral mechanisms of species displacement and behavioral flexibility in the natural environment.

Goals and hypotheses

We compared the behavior of marbled and spiny-cheek crayfish to assess competitive interaction strength, flexibility in behavior of an invader, and possible species displacement in crayfish (over-)invasions. Specifically, we assessed interspecific aggressiveness, activity, and boldness of the two focal species. In addition, we compared naïve, aquarium, and naturalized populations of marbled crayfish that are sympatric to spiny-cheek crayfish with each other to elucidate changes in behavior that result from naturalization. Finally, we looked for correlations between aggressiveness and activity, associated with aggression syndromes in individuals of both crayfish species. We hypothesized that crayfish species differ in behavioral traits that are important for invasion success, for example, agonistic behavior. Resident spiny-cheek crayfish were expected to dominate marbled crayfish because their males have large chelae in contrast to the all-female marbled crayfish. The latter were thought to be more active than spiny-cheek crayfish and respond less appropriately to a threat since they originate from aquaria without natural selection regimes. Marbled crayfish should generally exhibit less variability in behavior since they are isogenic. We further hypothesized that after marbled crayfish came in contact with spiny-cheek crayfish and predators in a natural environment, they will adapt their behavior. Marbled crayfish from invaded water bodies were expected to be more aggressive than aquarium crayfish to compete and coexist with spiny-cheek crayfish. Finally, marbled crayfish experiencing predation in the field should be less active and more responsive to threats than aquarium marbled crayfish.

Material and Methods

Study sites

Spiny-cheek crayfish were collected in lake Müggelsee in front of the institute (52°26’06″ N, 13°38’06″ E), Germany, with crayfish traps (type PIRAT, 610 × 315 × 250 mm, mesh width 40 × 10 mm, Rapurosvo, Parainen, Finland) between April 2015 and June 2016. The traps were baited with dog food or dead fish and were set overnight and checked on the next day. Aquarium stocks of marbled crayfish were provided by Peer Martin (Comparative Zoology, Humboldt University, Berlin, Germany). Additional marbled crayfish that live in sympatry with spiny-cheek crayfish were mostly hand-collected or, to a minor degree, caught by traps in the littoral zone from lakes (1) Moosweiher (48°01’51″ N, 7°48’17″ E) in Baden-Württemberg, Germany, and (2) Krumme Lanke (52°2700″ N, 13°13’52″ E) in Berlin, Germany. Crayfish were transported in Styrofoam boxes filled with water 30 mm deep and macrophytes in excess.

Maintenance of test animals

All crayfish were sexed and measured manually with a sliding caliper to the nearest millimeter. The length was measured as carapace length (CL) from the tip of the rostrum to the posterior edge of the carapace. Tanks were set up on shelves in a climate chamber with a constant temperature at 17 °C under a photoperiod of 14:10 h light:dark. All crayfish were kept in the laboratory for at least one month before being used in experiments. All aquarium marbled crayfish, naturalized marbled crayfish from lake Krumme Lanke, and all spiny-cheek crayfish used for individual measurements (>3 replicates) in behavioral experiments were kept individually in tanks (300 × 200 × 200 mm) filtered by air-driven sponge filters. Naturalized marbled crayfish from lake Moosweiher and additional spiny-cheek crayfish that have been used only as opponents in agonistic encounters were marked and housed in filtered single-species community tanks separated by sex (800 × 400 × 200 mm). All housing tanks were filled with 30 mm of fine gravel, and PVC pipes (150 mm, diameter 50 mm) were provided for shelter. Communal tanks were provided with a surplus of shelters (>2 per crayfish) to minimize aggression. To differentiate among the crayfish kept in communal tanks, we used the non-invasive, numerical marking system of Abrahamsson (1965) where crayfish were marked with a point code on top of their carapace. The crayfish were marked with a white outdoor marker (Edding 8055, Ahrensburg, Germany). After molts, we waited for the exoskeleton to be hardened completely and measured the new length before remarking the animals. Tanks were cleaned once a week and around 75% of water was exchanged with fresh tap water. Individual crayfish were fed half a ring of commercial crayfish food (Crabs natural, sera, Heinsberg, Germany) daily. Dried and blanched oak leaves were provided ad libitum as additional food and environmental enrichment. After the end of the study, crayfish were used for further experiments on their prey choice and feeding mechanics.

The protocol and procedures employed were ethically reviewed and approved by the Landesamt für Gesundheit und Soziales (LAGeSo), Berlin, Germany. All experiments were performed in accordance with

Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes.

Setup and standard procedure

All experiments were conducted in the climate chamber to reduce handling and guarantee minimal disturbance from outside. Two tanks measuring 400 × 400 × 200 mm were set up in the chamber, each filmed by two cameras (one vertically above the tank and another one at the side of the tank). All experiments were recorded or photographed with network cameras (Dinion HP 1080p, Bosch, Stuttgart, Germany) capable of recording under infrared illumination. Videos and photographs were recorded and saved with VLC player (version 2.2.1.0). Each setup was covered with an opaque, black plastic tarpaulin to further minimize disturbances.

All crayfish used for the experiments were in good condition (no obvious diseases, all appendages present and intact). Each crayfish was used only for one experimental trial per day. Intermolt individuals of both male and female sex (22 – 50 mm CL) were used in experiments. Females carrying eggs or larvae were excluded from experiments up to at least one week after the release of the brood. Test animals were randomly chosen among available crayfish with a pair of ten-sided dice.

In each experiment, the tanks were filled with 20 mm of fine gravel and 150 mm of tap water of 15 °C temperature. Crayfish were released into experimental tanks and allowed to acclimatize for 30 min prior to the experiment. After each trial, the tank was completely drained before setting up another experiment to avoid a potential bias by remaining pheromones in the water (Breithaupt 2011).

Allometry

Since larger chelae can be advantageous in agonistic encounters, we measured chela length of the right cheliped (in mm) for a random set of crayfish from three groups: male spiny-cheek crayfish (N = 52), female spiny-cheek crayfish (N = 28), and marbled crayfish (N = 81) with CLs between 20 and 50 mm. We fitted linear regression models (command lm()) in R version 3.4.0 (R Core Team 2017) to predict chela size depending on CL in each of these groups. To test for differences in intercept and slope in the three regression lines, we fitted three models for each pair of two of the three groups accounting for CL, the group, and their interaction.

Aggressiveness

We tested agonistic behavior against size-matched opponents (± 1 mm CL) in interspecific encounters of individual spiny-cheek crayfish males (N = 12), spiny-cheek crayfish females (N = 7), aquarium-reared marbled crayfish (N = 14), and naturalized marbled crayfish (N = 13). Three encounters were staged for each individual against three different opponents. The availability of matching pairs was reduced by egg-bearing females and molting individuals and resulted in uneven numbers of replicates. To better discriminate species and size effects, we later staged confrontations of the same individuals with smaller (<4 ± 2 mm CL [mean ± standard deviation, SD]; N = 15 for spiny-cheek crayfish, N = 13 for marbled crayfish) and larger opponents (>4 ± 2 mm CL [mean ± SD]; N = 16 for spiny-cheek crayfish, N = 14 for marbled crayfish; modified from Vorburger and Ribi 1999).

Experimental tanks were separated into two sides with a removable opaque divider (PVC). The corners were rounded with plastic glass to avoid that submissive animals become trapped. For each trial, one crayfish was transferred into each compartment. After acclimatization, the divider was lifted and the encounter recorded on video to later assess and score each interaction. The experiments were conducted in the dark when crayfish are most active and illuminated by infrared headlights (Holdich and Black 2007, Luna et al. 2009). Each confrontation was recorded with both cameras. The recording time was set at 35 min. The first 30 min after opening the divider was analyzed for agonistic behavior, and 5 min was added as buffering time. If fewer than five interactions took place within the 30 min, the buffering time was checked for more interactions. If there were still fewer than five interactions including the buffering time, the experiment was repeated with another opponent for each crayfish on another day.

To quantify interaction strength during the confrontations, the observed behavior was scored with the system developed by Atema and Voigt (1995; Table 2.1). For every five-seconds, each member of the pair was assigned an aggression score. The scoring system was modified by giving ignoring, which was not originally included in the system, the score 0. Ignoring was observed when crayfish were within one body length of one another or had physical contact, but did not show any visible response (i.e., taxis) toward the opponent’s presence (e.g., crawling along the aquarium pane, crawling over or under the body of the opponent). The opponent could show another agonistic behavior at the same time and was scored, respectively. The term separate includes all situations where the individuals were apart for more than one body length and no score was applied. When more than one agonistic behavior was shown within five-seconds, higher scores outranked lower (positive) scores 0–5). Score −2 outranked −1 and both flight behaviors (scores −1 and −2) outranked score 0 or positive scores. The interactions ended with one crayfish fleeing or separating itself from the counterpart by more than one body length.

For every individual and confrontation, we counted the total number of each observed score (for all five-second intervals) during the 30 min of confrontation for each crayfish. To see relative frequencies of certain scores among the groups, a standardized count was calculated by adding up the scores for each group and dividing it by the number of tested individuals. For every individual and confrontation, we calculated an aggression score by multiplying each score with the number of observations and adding them up for all behaviors (Karavanich and Atema 1998). We then adjusted the aggression score by dividing it by the number of interactions (5-s intervals) that were observed during 30 min (adj. AS). We did this adjustment to obtain a better measure of average aggression level since the time spent interacting with the other crayfish differed largely between trials. A negative or low aggression score represents a submissive individual or the loser of the encounter, whereas a high value indicates an aggressive individual or the winner of the encounter.

Table 2.1 - Definitions of agonistic behaviors observed in crayfish and their designated score (modified from Atema and Voigt (1995)).

Scor	**Behavior**	**Definition**
−2	Fleeing	Walking away (rapidly), walking backwards (rapidly), tail-flipping (rapid contraction of the abdomen)
−1	Avoidance	Walking away (slowly), walking backwards (slowly), turning away
0	Ignoring	Indifference towards each other within less than one body-length, or even in contact
1	No physical contact (initiation)	Facing, approaching, turning towards, following
2	No physical contact (threat display)	High on legs, claw open, meral spread, claw forward, antenna point
3	Physical contact (claws not used to grasp)	Antenna touching, claw touching, claw tapping, claw pushing, antenna whipping, claw boxing, claw scissoring
4	Physical contact (claws used to grasp)	Claw lock
5	Unrestrained use of claws	Claw snapping, claw ripping
n/a	Separate	Opponents one body-length or more apart

We performed analyses using linear mixed-effects models to detect agonistic score differences between the groups or species with individual as random factor (command lmer() from package lme4, (Bates et al. 2014)). As fixed effects, we used species, CL at the time of the fight (molting and therefore growth can occur between days of the experimental period), origin (aquarium or naturalized, only applicable to marbled crayfish), and sex (only applicable to spiny-cheek crayfish). All possible combinations of fixed effects and interactions between fixed effects were calculated—except between species, origin, and sex as these are confounded. Models were ranked by Akaike's information criterion (AIC) and Akaike's model weight. Marginal (fixed factors only) and conditional (fixed factors and random factor) R2 values for the best model were calculated using the MuMIn package (Bartón 2013).

Activity

We tested the activity (time spent outside of the shelter) of individual spiny-cheek crayfish males (N = 11), spiny-cheek crayfish females (N = 5), aquarium-reared marbled crayfish (N = 13), and naturalized marbled crayfish (N = 14). Each individual crayfish was tested in three trials. The experimental tanks were filled with gravel 20 mm deep and completely divided by half with an opaque divider (PVC). A PVC pipe (l = 150 mm, diameter 50 mm) in each compartment was provided as shelter. A crayfish was transferred into each compartment. After acclimatization, photographs were taken in the dark under infrared light every 30 min for 6 h, starting 30 min after artificial nightfall. Photographs were later checked for the position of the crayfish in the tank. Crayfish were considered to be outside the shelter when all of the carapace and the pereopods were visible outside the PVC pipe, as viewed from above. We summed up the number of observations outside the shelter and the number of observations inside the shelter for each trail.

We then applied a generalized linear mixed-effects model (GLMM) for binary responses with R to detect differences in time spent outside and inside the shelter among spiny-cheek crayfish males, spiny-cheek crayfish females, aquarium-reared marbled crayfish, and naturalized marbled crayfish (command glmer; package lme4). The individual was included in the model as random factor. Similar to the aggression scores, we calculated all possible combinations of fixed effects and interactions between fixed effects— except between species, origin, and sex as these are confounded. Models were ranked by AIC and Akaike's model weight and we calculated marginal and conditional R2 values for the best model using the MuMIn package (Bartón 2013).

Threat response

The response to a simulated threat as a measure of boldness was tested for spiny-cheek crayfish males (N = 15), spiny-cheek crayfish females (N = 15), aquarium-reared marbled crayfish (N = 13), and naturalized marbled crayfish (N = 19). Individual crayfish were placed in the experimental tank with 20 mm of sand as substrate and allowed to acclimatize. The crayfish were then approached from the upper front, using an angle of ~45°, by the hand of the experimenter in a steady but brisk movement. Threat responses were recorded under dim light conditions from above the tank. Each individual crayfish was tested three times but only once per day. The experiment followed the approach by Pintor et al. (2008), but with a modification since most crayfish in preliminary trials did not show a response to the hand if its movement was stopped above the surface. Thus, the movement of the hand was extended into the water, aiming for the front of the crayfish until a contact would occur. The hand was put through a hole in the tarpaulin when the crayfish was in a suitable position. Before the crayfish was approached, it needed to be at least one body length away from the aquarium pane, so it would not be constrained when displaying a flight reaction. Hands were washed with warm water after each trial to avoid a potential bias by remaining pheromones (Breithaupt 2011).

The first, initial response of the crayfish to the hand was assessed. Crayfish responded either by tail-flipping, that is, shooting backward (flight; score −1); stop moving and ducking (freezing; score 0); or by showing a threat display, that is, lifting their claws (fight; score 1). The scores of the three trials were summed up, and a general response score was given to each individual crayfish. A negative sum resulted in a general flight response, a positive score resulted in a fight response, and a sum of 0 was classified as freeze. We tested for differences between the groups with a chi-square test in R (command chisq.test) with 100,000 bootstrap simulations. We also compared all combinations of groups of crayfish and corrected for multiple testing using the Bonferroni-Holm method. Additionally, all groups of crayfish were checked for potential effects of CL using Spearman rank correlations.

Results

Allometry

Carapace length was a significant predictor of chela length for crayfish from all groups (Figure B.1). The average chela length was significantly smaller, and the slope was less steep for marbled than for spiny-cheek crayfish males (linear regression, $t = 8.75$, $P < 0.001$ and $t = -13.49$, $P < 0.001$). There were also significant differences in chela length and slope of the regression lines between spiny-cheek crayfish females and males (linear regression, $t = 4.60$, $P < 0.001$ and $t = -7.16$, $P < 0.001$). There was no significant difference in chela size between marbled crayfish and spiny-cheek crayfish females or slope of regression lines (linear regression, $t = 1.55$, $P = 0.12$ and $t = -1.3$, $P = 0.20$).

Aggression

All linear mixed-effects models were sorted according to their delta-AIC value and AIC weights. Models with an AIC weight above 0.05 are presented in Table 2.2 (see Table B.1 for all models). The best model includes species and individual CL (size) as predictors (marginal R2 = 0.16; conditional R2 = 0.31). All other models with a model weight above 0.05 also include species and size plus either origin, sex, or interaction terms. Species and size thus seem to be the most important predictors for aggressiveness, whereas other factors are less important. Carapace length was positively correlated with adj. AS. We considered individual as random factor in the analyses but found no statistical effect on aggression. In initial exploratory analyses, we also looked for an effect of the day of experiment (1st, 2nd, or 3rd) but did not find such an effect.

Table 2.2: Linear mixed-effects models of adjusted aggression score (adj. AS) analysis.

Model (fixed effects)	**delta-AIC**	**AIC weight**
– species(SC) + size	0	0.221
species(SC) + size – species(SC):size	1.3	0.116
– species(SC) + size + origin(aq)	1.7	0.095
– species(SC) + size − sex(m)	2	0.082
– species(SC) + size + sex(m) – size:sex(m)	2.5	0.063
species(SC) + size + origin(aq) – species(SC):size	2.9	0.053

Notes: Listed are the best models according to Akaike's model weight (Akaike's information criterion [AIC] weight). Indicated positive or negative effects of variables relate to the values of these variables given in brackets (m, male; SC, spiny-cheek crayfish; aq, aquarium origin); these are compared to female marbled crayfish from the field as reference. All models include the individual (IND) as random factor (Adj. AS ~ intercept + fixed effects + (1|IND)).

The adj. AS of marbled crayfish was on average 0.67 ± 0.16 standard error (SE) higher than the adj. AS of spiny-cheek crayfish (Figure 2.1). The results of the mixed-effects models that neither (1) sex nor (2) origin is important predictor of aggression are also illustrated in Figure 2.1: adj. AS of (1) male and female spiny-cheek crayfish, and (2) aquarium-reared and naturalized marbled crayfish were similar.

Aggression encounters rarely escalated (scores 4 and 5 were rare; Figure C.2) and were mostly resolved by claw pushing or boxing (score 3). Marbled crayfish rarely initiated fights with a threat display or responded equally to spiny-cheek threat displays (score 2). Furthermore, marbled crayfish often ignored their opponent (score 0). Higher negative scores indicated that spiny-cheek crayfish lost more encounters than marbled crayfish.

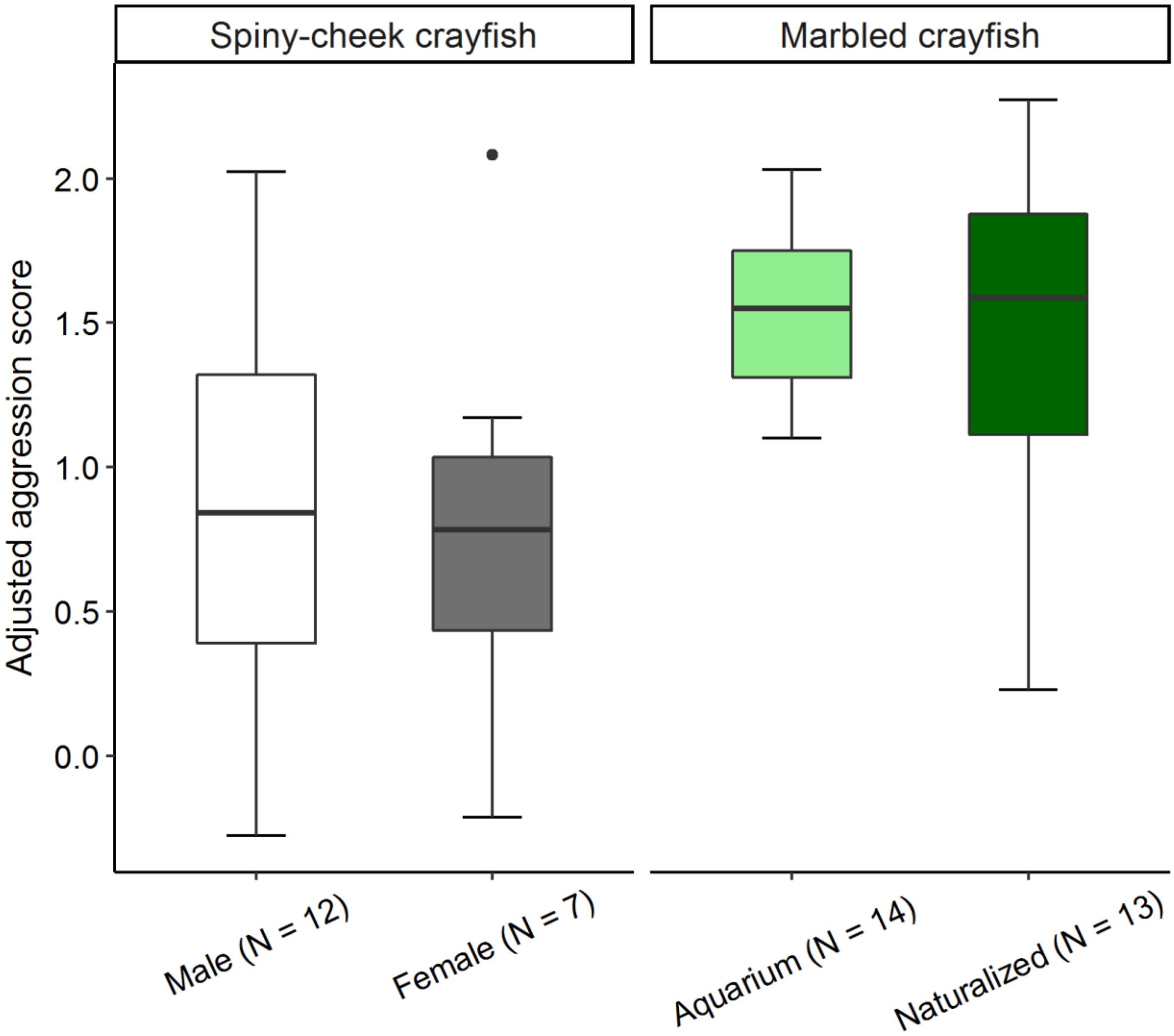

Figure 2.1 - Adjusted aggression scores in pairwise interspecific interactions among spiny-cheek crayfish males (open boxplot), spiny-cheek crayfish females (gray boxplot), and marbled crayfish from aquaria (light green boxplot) and naturalized populations (darkgreen boxplot).

In agonistic encounters against smaller opponents from either sex, marbled crayfish differed significantly from spiny-cheek crayfish and won all interactions, whereas spiny-cheek crayfish lost most interactions (Fisher's exact test, df = 25, $P < 0.001$; Figure 2.2). Against larger opponents, marbled crayfish similarly won 64% of encounters and spiny-cheek only 31%, but this difference was not statistically significant (Fisher's exact test, df = 28, $P = 0.14$).

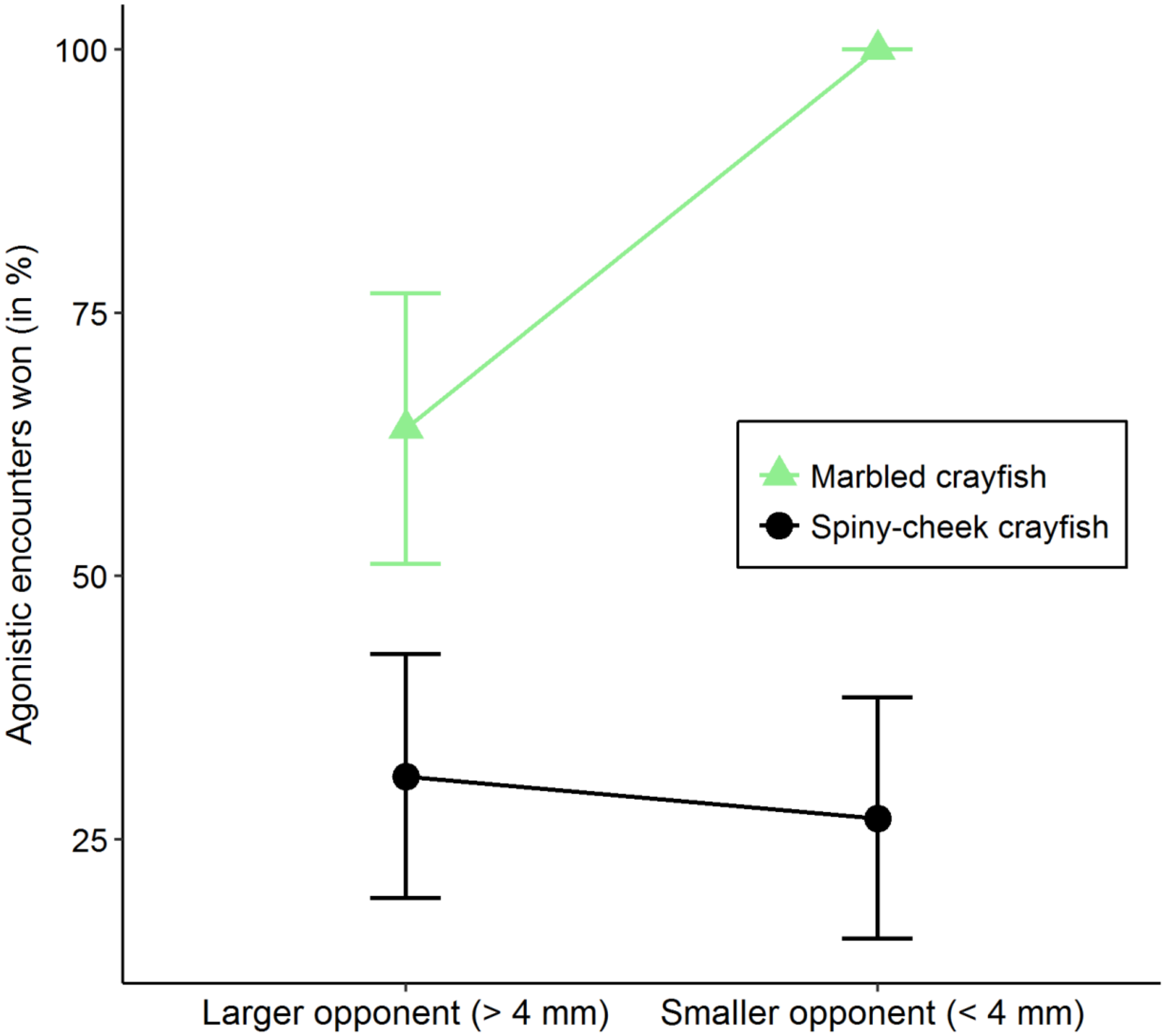

Figure 2.2 – Agonistic encounters won (in percent ± standard error) by marbled crayfish (triangles, light green) and spiny-cheek crayfish (both sexes; circles, black) with opponents of unequal size of the other species. The left side shows the outcomes against larger opponents (spiny-cheek crayfish, N = 16; marbled crayfish, N = 14) and the right side against smaller opponents (spiny-cheek crayfish, N = 15; marbled crayfish, N = 13).

Activity

The best model (marginal R2 = 0.10; conditional R2 = 0.21) uses origin and size as predictors: Aquarium marbled crayfish were more active than all other groups (Table 2.3, Figure 2.3; see Table C.2 for all models). Activity was negatively correlated with size for all crayfish. Spiny-cheek crayfish males, spiny-cheek crayfish females, and naturalized marbled crayfish spent more time inside than outside the shelter. All models using other predictors along origin were weaker than the one with origin and size as the sole predictors, and models not accounting for origin were negligible in explanatory power (AIC weights <0.001; Table 2.3). In conclusion, shelter use did not differ markedly among sex or species, but the rearing environment (origin) and size were meaningful predictors of activity. We considered individuals as random factor, but these had no effect on shelter use. In initial exploratory analyses, we also looked for an effect of the day of experiment but did not find one.

Table 2.3 - Generalized linear mixed-effects model results of activity analysis.

Model (fixed effects)	**delta-AIC**	**AIC weight**
origin(aq) – size	0.0	0.161
origin(aq)	0.4	0.131
origin(aq) – size – origin(aq):size	1.4	0.079
origin(aq) + sex(m) – size – sex(m):size	1.5	0.077
origin(aq) + sex(m) – size − sex(m):size – origin(aq):size	1.8	0.066
origin(aq) + sex(m) – size	1.9	0.062
origin(aq) – size – species(SC)	2.0	0.060
origin(aq) + sex(m)	2.3	0.051

Notes: Listed are the best models with decreasing Akaike's model weight. Indicated positive or negative effects of variables relate to the values of these variables given in brackets (m, male; SC, spiny-cheek crayfish; aq, aquarium origin); these are compared to female marbled crayfish from the field as reference. All models include the individual (IND) as random factor (ratio of time spent outside/inside the shelter ~ intercept + fixed effects + (1|IND)). AIC, Akaike's information criterion.

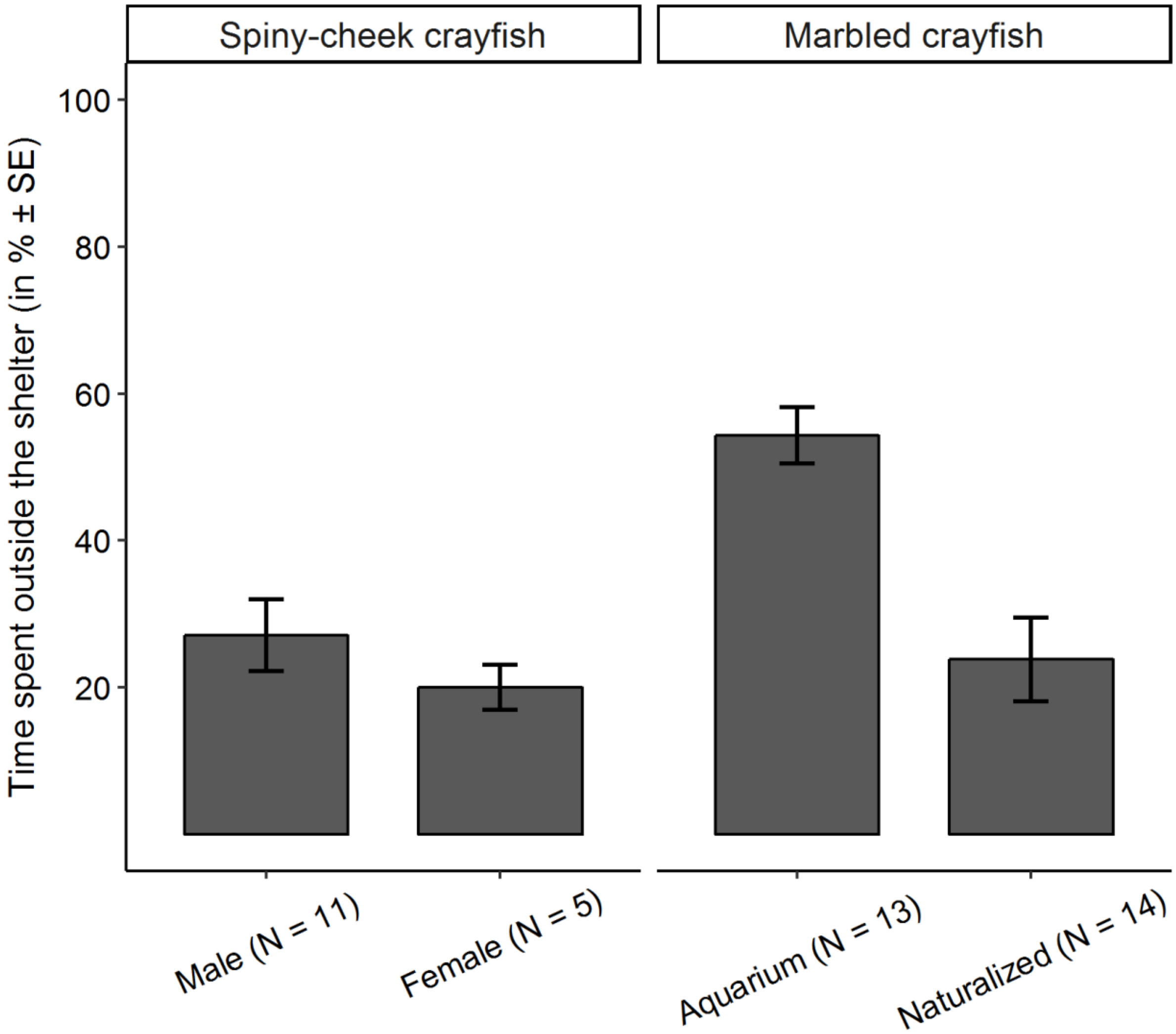

Figure 2.3 - Percentage of time spent outside the shelter (± standard error) over 6 h for spiny-cheek crayfish males, spiny-cheek crayfish females, and marbled crayfish from aquarium and naturalized populations.

Aggression syndrome

We tested for correlations between activity and aggression. Therefore, we used the means of individual aggression scores and ratios of time spent outside or inside the shelter for all individuals where we had at least three observations for aggression and activity. We calculated separate linear regressions for spiny-cheek crayfish, aquarium marbled crayfish, and naturalized marbled crayfish. Individuals of both sexes of spiny-cheek crayfish have been combined in the analysis since we did not find differences in activity and aggression (see above). Naturalized marbled crayfish and marbled crayfish from aquaria have been tested separately; as they differed in activity (see above).

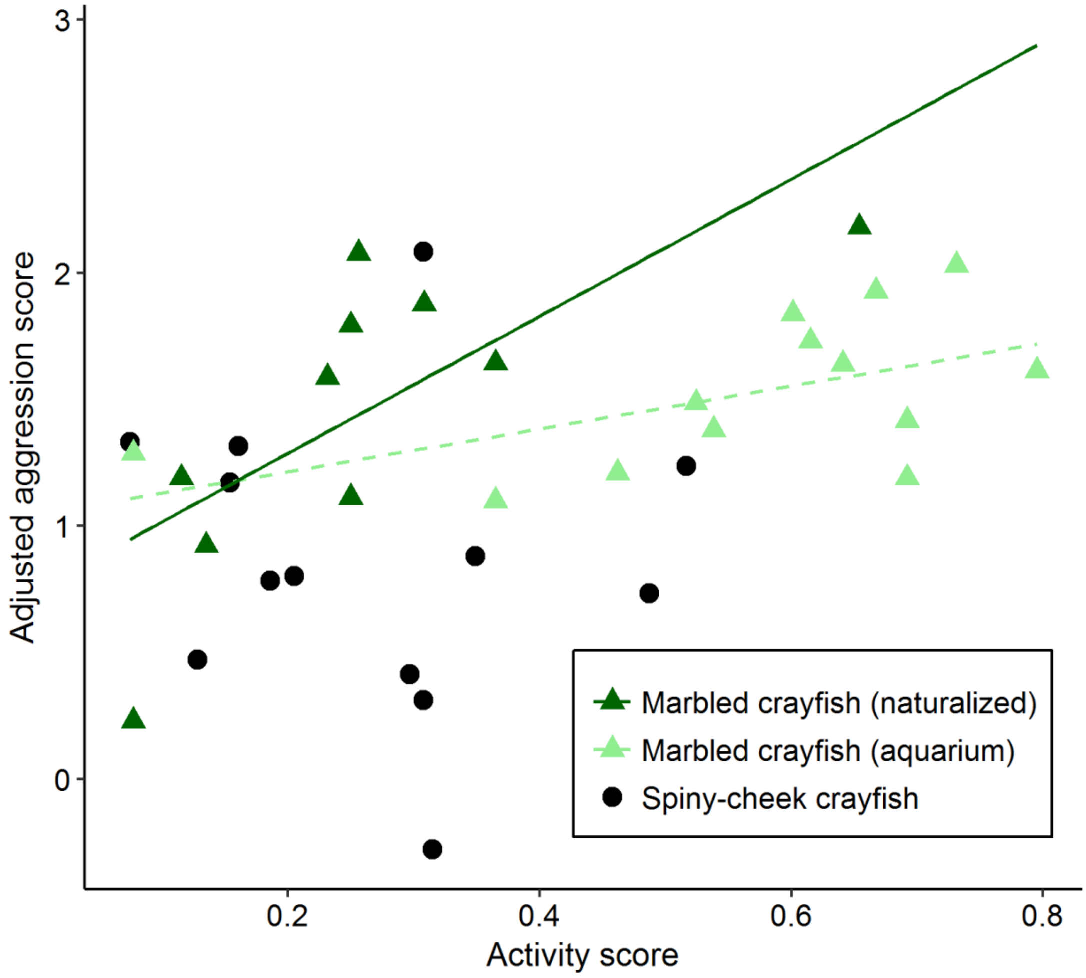

Figure 2.4 - Correlations between mean activity score (ratio of time spent outside/inside the shelter; ACT) and mean adjusted aggression score (adj. AS) of spiny-cheek and marbled crayfish individuals across experiments. Regression lines: naturalized marbled crayfish, Adj. AS ~ 0.75 + 2.7·ACT (linear regression, t = 3.09, P = 0.015, adj. R2 = 0.49); aquarium marbled crayfish, Adj. AS ~ 1.05 + 0.85·ACT (linear regression, t = 2.10, P = 0.06, adj. R2 = 0.22). No line is shown for spiny-cheek crayfish, as no trend was observed, Adj. AS: ~ 0.97 – 0.39·ACT; linear regression: t = −0.295, P = 0.77, adj. R^2 = 0.08).

One aquarium marbled crayfish had only two aggression scores because an interspecific mating took place during the third experiment; thus, the observation was excluded. Also, one naturalized marbled crayfish had only two observations for activity because it was cannibalized during molting before the third experiment could be conducted.

We found that in naturalized marbled crayfish, mean adj. AS (aggression) was positively correlated with the ratio of time spent outside or inside a shelter (activity; Figure 2.4). A similar trend was observed for aquarium-reared marbled crayfish, whereas no such correlation was found for spiny-cheek crayfish.

Threat response

Crayfish groups significantly differed in their threat response (Pearson's Chi-squared test with simulated P-value, based on 100 000 replicates: $\chi2 = 54.91$, $P < 0.001$, Figure 2.5, Table 2.4). The CL was not related to threat response in any of the groups (spiny-cheek crayfish (male): rS = −0.046, P = 0.87; spiny-cheek crayfish (female): rS = 0.149, P = 0.60; marbled crayfish (aquarium): rS = −0.321, P = 0.29; marbled crayfish (naturalized): rS = 0.217, P = 0.40. Remarkably, marbled crayfish frequently stopped and ducked in response to the approaching threat (37% or 47% for aquarium or naturalized marbled crayfish, respectively), whereas spiny-cheek crayfish did not show such behavior. Male spiny-cheek crayfish mainly responded with aggression (93% of all trials), whereas females mostly displayed flight behavior (93%). If not “freezing” in response to a threat, marbled crayfish most often fled from the threat (62% or 37% for aquarium or naturalized marbled crayfish, respectively). Aquarium marbled crayfish did not fight, whereas naturalized marbled crayfish showed fight behavior in about 15% of the trials.

Table 2.4 - Chi-square statistics (χ^2) of all pairwise comparisons between groups of crayfish and among all groups tested for their threat response.

Comparison	χ^2	*P*
spiny-cheek (female) *vs.* spiny-cheek (male)	19.29	<0.001
marbled crayfish (naturalized) *vs.* marbled crayfish (aquarium)	3.20	0.21
spiny-cheek crayfish *vs.* marbled crayfish (species)	21.96	<0.001
marbled crayfish (aquarium) *vs.* all naturalized crayfish (origin)	7.20	0.055
all female crayfish *vs.* male spiny-cheek crayfish (sex)	35.81	<0.001
comparison between all groups	50.44	<0.001

Notes: *P*-values are corrected for multiple testing using the Bonferroni-Holm method.

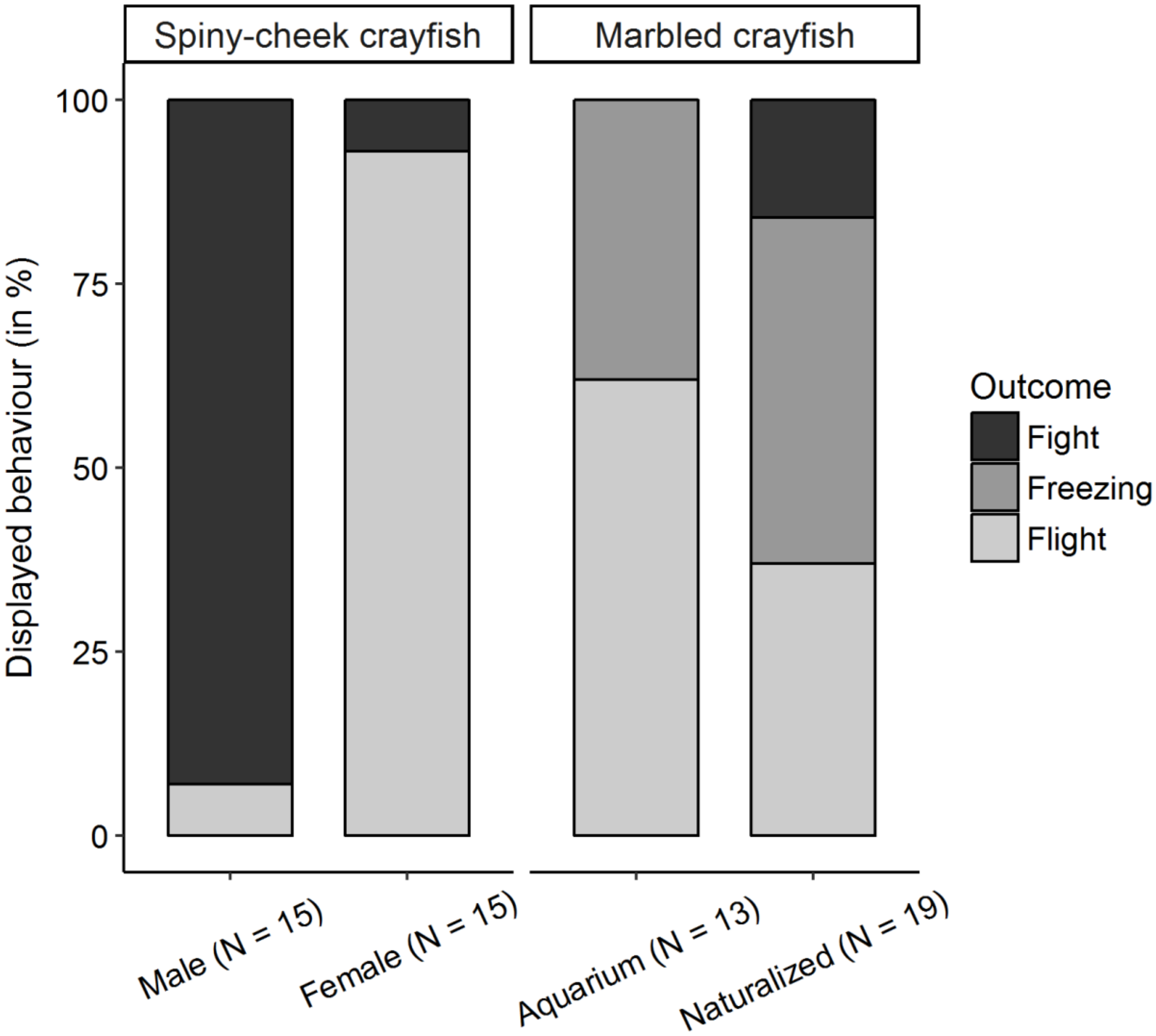

Figure 2.5 - The percentage of displayed behaviors in response to a simulated threat for spiny-cheek crayfish of either sex and marbled crayfish from aquarium and naturalized populations. The behaviors displayed encompass aggressive behavior (dark grey bars), freezing (grey bars) or flight behavior (light grey bars).

Discussion

Differences between species and implications

Our results illustrate some of the key behavioral characteristics in invasion success of crayfish. In the over-invasion scenario we investigated, the recently invading marbled crayfish were able to dominate resident spiny-cheek crayfish of either sex in agonistic encounters even if their opponents were larger and had larger claws.

Aggressiveness has been one of the main behavioral traits associated with species displacement in crayfish (Capelli and Munjal 1982, Usio et al. 2001). So far, interspecific aggression has only been tested for juveniles of marbled crayfish interacting with red swamp crayfish (*Procambarus clarkii*), which were similarly aggressive (Jimenez and Faulkes 2011). As we demonstrated here, the lack of sexual dimorphism does not constrain the ability of marbled crayfish to win agonistic encounters against another species. Aggressive dominance also translates to superiority in competition over shelters, an important resource for crayfish that relieves them from predation pressure (Gherardi and Daniels 2004, Moore 2007). Thus, we assume that preferred resources of spiny-cheek crayfish like shelters would be frequently occupied by invading marbled crayfish where both species co-occur.

In former invasions of North American species across Europe, interspecific competition between crayfish was mostly no relevant determinant of invasion success because the crayfish plague (*Aphanomyces astaci*, Leptolegniaceae) often completely eradicated native competitors before or shortly after introduction of non-native crayfish (Gherardi and Holdich 1999). The die-off of potential competitors and its high tolerance toward poor habitat quality probably had a major effect on the former success of spiny-cheek crayfish. There is surprisingly little work on the competitive ability of spiny-cheek crayfish in contrast to other major invasive crayfish in Europe like the red swamp crayfish or the signal crayfish (*Pacifastacus leniusculus*). In the few available studies on spiny-cheek crayfish aggression, they were usually inferior in agonistic encounters (either in their native range against an invader or against another invader in their introduced range (Klocker and Strayer 2004, Hudina et al. 2011). It should be noted that the average aggression level of the tested spiny-cheek crayfish might be even lower since they were caught with traps, which can select for aggressive individuals (Ogle and Kret 2008).

In the invasion scenarios we are facing today, crayfish plague-resistant species over-invade other plague-resistant species, and the traits and interactions with the community will become paramount for distribution and impacts of crayfish (Russell et al. 2014, James et al. 2016). In general, species distributions and impacts in novel communities and ecosystems can probably be better understood when considering the time of introduction of species rather than simply dividing species into native and non-native ones. The latter, dichotomous classification is often based on a reference year, for example, 1492 which is sometimes rounded to 1500 (DAISIE 2009): Species present before this year are considered native, and species introduced thereafter are considered non-native. A finer approach considering the time of introduction and the eco-evolutionary experience of introduced and resident species (Saul and Jeschke 2015) seems to be a promising way forward.

Behavioral syndromes

We also explored the flexibility and the correlations among behaviors (i.e., behavioral syndromes). We observed two traits in particular that are beneficial during the introduction and spread of species: Higher aggression jointly with higher activity was observed in marbled as compared to spiny-cheek crayfish. Positive correlations of aggressiveness and activity have been referred to as so-called aggression syndromes in invasive species (Sih et al. 2004, Pintor et al. 2009). Our results suggest that marbled crayfish exhibit such an aggression syndrome which can lead to more agonistic encounters, but may also be positively related to attacks on prey, that is, increased foraging rate (Sih et al. 2004, Sih and Bell 2008, Pintor et al. 2009). Both would facilitate species displacement through either interspecific aggression or competition for resources.

Thus far, marbled crayfish have not outcompeted spiny-cheek crayfish in water bodies where both species co-occur (Chucholl and Pfeiffer 2010). Trade-offs associated with the aggression syndrome, for example, higher intraspecific aggression, might limit the success of marbled crayfish. Elevated intraspecific aggression levels might, for example, constrain marbled crayfish densities. We did not include intraspecific aggression in our study design, but from our observations in communal tanks, we suspect intraspecific aggression to be low. High genetic relatedness has been shown to lower intraspecific aggression in insects (Carazo et al. 2014, Jandt et al. 2014), but marbled crayfish also form dominance hierarchies (Luna et al. 2009).

Marbled crayfish might also suffer higher predation rates despite similar activity levels because their antipredator behavior (i.e., threat response) is not appropriate or their morphology makes them easier to attack. After handling both species for years, we have the impression that spiny-cheek crayfish have a thinner carapace and they have, as their name implies, spines in contrast to marbled crayfish. To our knowledge, data on exoskeleton thickness are not available in the literature for either species. We also noted that, if lifted up, spiny-cheek crayfish pull their legs together beneath the carapace and the abdomen to form a spiny ball that is difficult to swallow for gape-limited predators like fish. The importance of the aggression syndrome for population dynamics and invasion success should therefore be examined in relation to predators foraging on marbled crayfish (Pintor et al. 2009).

Species displacement in crayfish can take decades, as a long-term study on a Finnish lake has demonstrated (Westman et al. 2002). Higher reproduction rates, activity, and aggressive behavior were suspected to promote the displacement of noble crayfish (*Astacus astacus*) by plague-free signal crayfish in the Finnish lake, but the mechanisms of displacement have remained unclear.

Individual differences in behavior are often linked to variation in life-history parameters and morphology. Biro et al. (2014) found that individual differences in life-history and behavior of common yabby (*Cherax destructor*) express very early in life, and variation might arise primarily from genetic or permanent environmental effects. The limited genetic diversity of marbled crayfish, however, should not allow for significant effects on variability in behavior. Permanent environmental effects such as maternal effects, epigenetic effects, and other effects that influence development already before hatching can be the cause for this variation (Dochtermann et al. 2015). For example, clonal Amazon mollies (*Poecilia formosa*) consistently showed individual variation in behavior among isogenic individuals reared in isolation, and social experience during ontogeny had no effect on individual behavioral variation (Bierbach et al. 2017). In marbled crayfish, developmental variation probably explains much of the variation in coloration, growth, lifespan, reproduction, number of sense organs, and behavior, even when they are reared under identical conditions (Vogt et al. 2008). The emergence of personality and its genetic basis are yet barely understood, and studies on isogenic marbled crayfish might help deepen our understanding.

Will these behaviors promote marbled crayfish invasions?

We presented evidence that marbled crayfish are more aggressive and active competitors than spiny-cheek crayfish. Risk assessments confirm that marbled crayfish have many traits promoting high invasiveness (Twardochleb et al. 2013, Chucholl and Wendler 2017). For example, marbled crayfish cope well with low water temperatures despite their origin in warm-water aquaria (Veselý et al. 2015). High aggression and activity together with high potential population growth rates make marbled crayfish exemplary for a fast pace-of-life species (Réale et al. 2010). Marbled crayfish have a higher reproductive potential than most other crayfish, as they lay more clutches and are not bound to mating seasons due to parthenogenesis (Scholtz et al. 2003, Souty-Grosset et al. 2006). By parthenogenetic reproduction, marbled crayfish overcome many challenges that invasive species face after introduction. For example, small founder populations of marbled crayfish should not be impaired by failing to recognize conspecifics or mate choice (Chapple et al. 2012). A single marbled crayfish is sufficient to establish a population. However, parthenogenetic reproduction also reduces adaptability to cope with parasites or changes in the environment.

Predation by native predators, for example, might limit the spread of marbled crayfish. The response to threat or boldness that we observed in marbled crayfish differs from many other crayfish species. We expected marbled crayfish to respond inappropriately to a threat because organisms from the pet trade should be naïve to threats. Fight-or-flight behavior is most often observed in crayfish as appropriate responses to predation threats (Stein and Magnuson 1976). However, marbled crayfish ducked or seemed to freeze before the approaching hand. We tried to minimize contacts with the crayfish during cleaning or feeding and never approached them upfront, but their aquarium legacy might have made them more used to handling. A comparable antipredator behavior was found in New Zealand big-handed crabs (*Heterozius rotundifrons*) that remained immobile when an enemy approached them (Hazlett and McLay 2005). Marbled crayfish have the eponymous marbled pattern and might rely more on their camouflage, like it was reported for invasive green crabs (Carcinus maenas; Lohrer and Whitlatch 2002). The camouflage made marbled crayfish less conspicuous than spiny-cheek crayfish when we caught them in the lakes. We also observed freezing when we approached marbled crayfish in the lakes in a brisk and steady movement, but they still tail-flipped when the movement was more sudden.

Also, chemical stimuli might have been more important for marbled crayfish to elicit tail flips. For example, northern-clearwater crayfish (*Orconectes propinquus*) showed a stronger tail-flip behavior when chemical and tactile cues were presented simultaneously (Bouwma and Hazlett 2001). We can only speculate whether natural enemies like birds or fish are faced in an effective way. Active predators that can detect the crayfish might prey more heavily on marbled crayfish than passive predators that rely on movement of their prey. Studying predator–prey interactions with natural enemies would help to shed light on these questions and could explain population dynamics in invaded lakes.

In the direct agonistic interactions, marbled crayfish sometimes did not react to the threat display of spiny-cheek crayfish and simply ignored them. Ignoring behavior of competitors or predators is rarely included in behavioral studies on crayfish (Bergman and Moore 2003). However, ignoring was found to be pronounced in marbled crayfish. It might be related to problems in sensing signals of the opponent. Chemical communication via the urine plays an important role in intraspecific recognition and social dominance in crayfish (Breithaupt 2011); agonistic interactions last longer when chemical cues are absent (Zulandt Schneider et al. 2001). Both species are part of the same family (Cambaridae), but they are relatively distantly related (Martin et al. 2010). We speculate that marbled crayfish cannot recognize signals of the opponent and engage more strongly in agonistic interactions.

Aquarium vs. naturalized populations of marbled crayfish

We compared a naturalized and an aquarium population of marbled crayfish to look for changes in behavior. In contrast to our predictions, no differences were found in aggressiveness, and small differences in boldness toward a threat. As marbled crayfish are generally more aggressive than spiny-cheek crayfish, they do not have to elevate aggressiveness in sympatry to better compete in agonistic encounters. By contrast, resident spiny-cheek crayfish that live in sympatry with marbled crayfish might have adapted their aggressiveness. For example, native populations of virile crayfish (*Orconectes virilis*) have been shown to be more aggressive when they had prior experience with invading rusty crayfish (*Orconectes rusticus*; Hayes et al. 2009). Additional trials with sympatric spiny-cheek crayfish, which we did not test, might show more elevated aggression levels in these populations. Hayes et al. (2009) asked whether behavioral flexibility or evolution of genotypes in naïve and experienced populations underlie this difference. Marbled crayfish are genetically uniform due to parthenogenesis (see Martin et al. 2007), and behavioral differences should therefore be mostly linked to behavioral flexibility or learning, respectively. However, the correlation of activity and aggressiveness was not decoupled by adapting a lower activity in naturalized marbled crayfish, but instead persisted on a different level. Some individuals seem to be generally more aggressive and active than others, but are still flexible enough to adapt their activity to different environments.

Naturalized marbled crayfish had a lower activity level than aquarium animals and mimicked the activity levels of spiny-cheek crayfish. Rearing conditions in early juvenile stages might have had an influence on their activity. However, the marbled crayfish from the aquarium were reared under similar, stable laboratory conditions. In the critical phase after introduction of a new species, flexibility in behavior is crucial for survival and helps to overcome the problem of small propagule size (Sagata and Lester 2009). Invaders often lack experience in ecological interactions with competitors, prey, and predators (Saul and Jeschke 2015). Invasive signal crayfish, for example, reduced shelter use and increased their foraging activity despite the presence of predator cues (Hirvonen et al. 2007). Behavioral flexibility can counteract potentially maladaptive responses (Wright et al. 2010). The lower activity in naturalized marbled crayfish could be a response to predation. For example, European eels (*Anguilla anguilla*) reduced foraging activity in invasive red swamp crayfish (Aquiloni et al. 2010). In a recent study on rusty crayfish, Reisinger et al. (2017) found that prior experience had a strong effect on activity (i.e., time spent walking or feeding) in the presence of predatory smallmouth bass, but not when predators were absent (*Micropterus dolomieu*). However, they also found that crayfish raised with predatory fish exhibited reduced activity levels in general. We found activity to be lower in experienced individuals even in the absence of predators, which can be attributed to a high capacity of flexible behavior and a notable memory capacity. Invasive crayfish and crabs are behaviorally flexible and able to learn and memorize new predation cues quickly (Hazlett et al. 2002, Roudez et al. 2008). Leaving the shelter to forage is very risky in an environment with predators. Naturalized individuals that have experienced predation seem to have adapted their activity and memorized predation threat also under safe laboratory conditions.

Conclusions

Ecological consequences of over-invasions, specifically the interactions of invaders with other invaders in the community, are largely unknown (Russell et al. 2014). The recent success of marbled crayfish in establishing new populations might be influenced by their superiority in agonistic encounters and their behavioral flexibility. Marbled crayfish seem to be very adaptive and have the potential to competitively exclude or coexist with the most common invasive crayfish in Central Europe when competing for limited resources. Furthermore, experience with natural conditions can reduce activity of invasive crayfish. Marbled crayfish that originated in the aquarium trade showed that they adapt their behavior to the new environment. This trade-off between foraging and defense might, however, limit the impact of marbled crayfish. Behavioral syndromes in marbled crayfish can occur despite genetic uniformity and thus should stem from permanent environmental effects. Our results from the laboratory explain important behavioral mechanisms behind crayfish over-invasions and reveal large behavioral variability in an isogenic crayfish. To predict invasion success and assess ecological risks in nature, the species' reproductive biology, feeding behavior, and predator– prey relationships in the community should be considered. Marbled crayfish (and spiny-cheek crayfish) have been listed in the new EU regulation on invasive alien species (No 1143/2014). This regulation lays the foundation for the prevention of further spread and future introductions of non-native crayfish.

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References

Abrahamsson, S. 1965. A method of marking crayfish *Astacus astacus* Linné in population studies. Oikos 17:228–231.

Aquiloni, L., S. Brusconi, E. Cecchinelli, E. Tricarico, G. Mazza, A. Paglianti, and F. Gherardi. 2010. Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of Procambarus clarkii. Biological Invasions 12:3817–3824.

Atema, J., and R. Voigt. 1995. Behavior and sensory biology. Pages 313–348 in J. R. Factor, editor. The Biology of the Lobster. Academic Press, San Diego, USA.

Bartón, K. 2013. MuMIn: Multi-Model Inference (ver. 1.9) [R package]. Retrieved from https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bergman, D. A., and P. A. Moore. 2003. Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. The Biological Bulletin 205:26–35.

Bierbach, D., K. L. Laskowski, and M. Wolf. 2017. Behavioural individuality in clonal fish arises despite near-identical rearing conditions. Nature Communications 8:15361.

Biro, P. A., B. Adriaenssens, and P. Sampson. 2014. Individual and sex specific differences in intrinsic growth rate covary with consistent individual differences in behaviour. Journal of Animal Ecology 83:1186–1195.

Bouwma, P., and B. A. Hazlett. 2001. Integration of multiple predator cues by the crayfish *Orconectes propinquus*. Animal Behaviour 61:771–776.

Breithaupt, T. 2011. Chemical communication in crayfish. Pages 257–276 in T. Breithaupt and M. Thiel, editors. Chemical communication in crustaceans. Springer, New York/Dordrecht/Heidelberg/London.

Bubb, D. H., T. J. Thom, and M. C. Lucas. 2006. Movement, dispersal and refuge use of co occurring introduced and native crayfish. Freshwater Biology 51:1359–1368.

Capelli, G., and B. L. Munjal. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus Orconectes. Journal of Crustacean Biology 2:486–492.

Carazo, P., C. K. Tan, F. Allen, S. Wigby, and T. Pizzari. 2014. Within-group male relatedness reduces harm to females in Drosophila. Nature 505:672–675.

Chapple, D. G., S. M. Simmonds, and B. B. Wong. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? Trends in Ecology & Evolution 27:57–64.

Chucholl, C. 2013. Invaders for sale: trade and determinants of introduction of ornamental freshwater crayfish. Biological Invasions 15:125–141.

Chucholl, C., K. Morawetz, and H. Groß. 2012. The clones are coming–strong increase in Marmorkrebs [*Procambarus fallax* (Hagen, 1870) *f. virginalis*] records from Europe. Aquatic Invasions 7:511–519.

Chucholl, C., and M. Pfeiffer. 2010. First evidence for an established Marmorkrebs (Decapoda, Astacida, Cambaridae) population in Southwestern Germany, in syntopic occurrence with *Orconectes limosus* (Rafinesque, 1817). Aquatic Invasions 5:405–412.

Chucholl, C., H. B. Stich, and G. Maier. 2008. Aggressive interactions and competition for shelter between a recently introduced and an established invasive crayfish: *Orconectes immunis* vs. *O. limosus*. Fundamental and Applied Limnology / Archiv für Hydrobiologie 172:27–36.

Chucholl, C., and F. Wendler. 2017. Positive selection of beautiful invaders: long-term persistence and bio-invasion risk of freshwater crayfish in the pet trade. Biological Invasions 19:197–208.

DAISIE. 2009. Handbook of alien species in Europe. Springer, Dordrecht, The Netherlands.

Dochtermann, N. A., T. Schwab, and A. Sih. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proceedings of the Royal Society B: Biological Sciences 282:20142201.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science 344:296–299.

Gallardo, B., M. Clavero, M. I. Sánchez, and M. Vilà. 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22:151–163.

Garvey, J. E., and R. A. Stein. 1993. Evaluating how chela size influences the invasion potential of an introduced crayfish (*Orconectes rusticus*). American Midland Naturalist 129:172–181.

Garvey, J. E., R. A. Stein, and H. M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. Ecology 75:532–547.

Gherardi, F., L. Aquiloni, and E. Tricarico. 2012. Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: an imperfect map is better than no map. Current Zoology 58:567–579.

Gherardi, F., and A. Cioni. 2004. Agonism and interference competition in freshwater decapods. Behaviour 141:1297–1324.

Gherardi, F., and W. H. Daniels. 2004. Agonism and shelter competition between invasive and indigenous crayfish species. Canadian Journal of Zoology 82:1923–1932.

Gherardi, F., and D. M. Holdich. 1999. Crayfish in Europe as alien species. CRC Press, Boca Raton, USA.

Gutekunst, J., R. Andriantsoa, C. Falckenhayn, K. Hanna, W. Stein, J. Rasamy, and F. Lyko. 2018. Clonal genome evolution and rapid invasive spread of the marbled crayfish. Nature Ecology & Evolution 2:567–573.

Hanshew, B. A., and T. S. Garcia. 2012. Invasion of the shelter snatchers: behavioural plasticity in invasive red swamp crayfish, Procambarus clarkii. Freshwater Biology 57:2285–2296.

Hayes, N. M., K. J. Butkas, J. D. Olden, and M. J. V. Zanden. 2009. Behavioural and growth differences between experienced and naïve populations of a native crayfish in the presence of invasive rusty crayfish. Freshwater Biology 54:1876–1887.

Hazlett, B. A. 1994. Crayfish feeding responses to zebra mussels depend on microorganisms and learning. Journal of Chemical Ecology 20:2623–2630.

Hazlett, B. A., P. Acquistapace, and F. Gherardi. 2002. Differences in memory capabilities in invasive and native crayfish. Journal of Crustacean Biology 22:439–448.

Hazlett, B. A., A. Burba, F. Gherardi, and P. Acquistapace. 2003. Invasive species of crayfish use a broader range of predation-risk cues than native species. Biological Invasions 5:223–228.

Hazlett, B. A., and C. McLay. 2005. Responses to predation risk: alternative strategies in the crab Heterozius rotundifrons. Animal Behaviour 69:967–972.

Hewitt, C. L., and G. R. Huxel. 2002. Invasion success and community resistance in single and multiple species invasion models: Do the models support the conclusions? Biological Invasions 4:263–271.

Hirvonen, H., S. Holopainen, N. Lempiäinen, M. Selin, and J. Tulonen. 2007. Sniffing the trade-off: effects of eel odours on nocturnal foraging activity of native and introduced crayfish juveniles. Marine and Freshwater Behaviour and Physiology 40:213–218.

Holdich, D. M., and J. Black. 2007. The spiny-cheek crayfish, *Orconectes limosus* (Rafinesque, 1817) [Crustacea: Decapoda: Cambaridae], digs into the UK. Aquatic Invasions 2:1–15.

Holdich, D. M., J. D. Reynolds, C. Souty-Grosset, and P. J. Sibley. 2009. A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. Knowledge and Management of Aquatic Ecosystems 394–395:11.

Hudina, S., N. Galić, I. Roessink, and K. Hock. 2011. Competitive interactions between co-occurring invaders: identifying asymmetries between two invasive crayfish species. Biological Invasions 13:1791–1803.

James, J., J. Thomas, A. Ellis, K. Young, J. England, and J. Cable. 2016. Over-invasion in a freshwater ecosystem: newly introduced virile crayfish (*Orconectes virilis*) outcompete established invasive signal crayfish (*Pacifastacus leniusculus*). Marine and Freshwater Behaviour and Physiology 49:9–18.

Jandt, J. M., S. Bengston, N. Pinter Wollman, J. N. Pruitt, N. E. Raine, A. Dornhaus, and A. Sih. 2014. Behavioural syndromes and social insects: personality at multiple levels. Biological Reviews 89:48–67.

Jimenez, S. A., and Z. Faulkes. 2011. Can the parthenogenetic marbled crayfish Marmorkrebs compete with other crayfish species in fights? Journal of Ethology 29:115–120.

Karavanich, C., and J. Atema. 1998. Individual recognition and memory in lobster dominance. Animal Behaviour 56:1553–1560.

Kellison, G., D. Eggleston, and J. Burke. 2000. Comparative behaviour and survival of hatchery-reared versus wild summer flounder (*Paralichthys dentatus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1870–1877.

Klocker, C. A., and D. L. Strayer. 2004. Interactions among an invasive crayfish (*Orconectes rusticus*), a native crayfish (*Orconectes limosus*), and native bivalves (Sphaeriidae and Unionidae). Northeastern Naturalist 11:167–178.

Kouba, A., A. Petrusek, and P. Kozák. 2014. Continental-wide distribution of crayfish species in Europe: update and maps. Knowledge and Management of Aquatic Ecosystems 413:05.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223–228.

Lodge, D. M., A. Deines, F. Gherardi, D. C. Yeo, T. Arcella, A. K. Baldridge, M. A. Barnes, W. L. Chadderton, J. L. Feder, and C. A. Gantz. 2012. Global introductions of crayfishes: evaluating the impact of species invasions on ecosystem services. Annual Review of Ecology, Evolution, and Systematics 43:449–472.

Lohrer, A. M., and R. B. Whitlatch. 2002. Interactions among aliens: apparent replacement of one exotic species by another. Ecology 83:719–732.

Luna, A. J. F., J. I. Hurtado-Zavala, T. Reischig, and R. Heinrich. 2009. Circadian regulation of agonistic behavior in groups of parthenogenetic marbled crayfish, *Procambarus sp*. Journal of Biological Rhythms 24:64–72.

Lyko, F. 2017. The marbled crayfish (Decapoda: Cambaridae) represents an independent new species. Zootaxa 4363:544–552.

Marten, M., C. Werth, and D. Marten. 2004. The Marbled crayfish (Cambaridae, Decapoda) in Germany - another neozoan in the Rhein basin. Lauterbornia 50:17–23.

Martin, C. W. 2014. Naïve prey exhibit reduced antipredator behavior and survivorship. PeerJ 2:e665.

Martin, P., N. J. Dorn, T. Kawai, C. van der Heiden, and G. Scholtz. 2010. The enigmatic Marmorkrebs (marbled crayfish) is the parthenogenetic form of *Procambarus fallax* (Hagen, 1870). Contributions to Zoology 79:107–118.

Martin, P., K. Kohlmann, and G. Scholtz. 2007. The parthenogenetic Marmorkrebs (marbled crayfish) produces genetically uniform offspring. Naturwissenschaften 94:843–846.

Moore, P. A. 2007. Agonistic behavior in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive behavior and dominance. Pages 90–112 in J. E. Duffy and M. Thiel, editors. Evolutionary ecology of social and sexual systems: Crustacea as model organisms. Oxford University Press, New York, USA.

Musil, M., M. Buřič, T. Policar, A. Kouba, and P. Kozák. 2010. Comparison of diurnal and nocturnal activity between noble crayfish (*Astacus astacus*) and spinycheek crayfish (*Orconectes limosus*). Freshwater Crayfish 17:189–193.

Ogle, D. H., and L. Kret. 2008. Experimental evidence that captured rusty crayfish (*Orconectes rusticus*) exclude uncaptured rusty crayfish from entering traps. Journal of Freshwater Ecology 23:123–129.

Penk, M., W.-C. Saul, J. T. A. Dick, I. Donohue, M. E. Alexander, S. Linzmaier, and J. M. Jeschke. 2017. A trophic interaction framework for identifying the invasive capacity of novel organisms. Methods in Ecology and Evolution 8:1786–1794

Pintor, L. M., A. Sih, and M. L. Bauer. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. Oikos 117:1629–1636.

Pintor, L. M., A. Sih, and J. L. Kerby. 2009. Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. Ecology 90:581–587.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org/.

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences 365:4051–4063.

Reisinger, L. S., A. K. Elgin, K. M. Towle, D. J. Chan, and D. M. Lodge. 2017. The influence of evolution and plasticity on the behavior of an invasive crayfish. Biological Invasions 19:815–830.

Roudez, R. J., T. Glover, and J. S. Weis. 2008. Learning in an invasive and a native predatory crab. Biological Invasions 10:1191–1196.

Russell, J. C., N. S. Sataruddin, and A. D. Heard. 2014. Over invasion by functionally equivalent invasive species. Ecology 95:2268–2276.

Sagata, K., and P. J. Lester. 2009. Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant *Linepithema humile*. Journal of Applied Ecology 46:19–27.

Saul, W. C., and J. M. Jeschke. 2015. Eco-evolutionary experience in novel species interactions. Ecology Letters 18:236–245.

Scholtz, G., A. Braband, L. Tolley, A. Reimann, B. Mittmann, C. Lukhaup, F. Steuerwald, and G. Vogt. 2003. Ecology: Parthenogenesis in an outsider crayfish. Nature 421:806–806.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. Winter, and M. Arianoutsou. 2017. No saturation in the accumulation of alien species worldwide. Nature Communications 8:14435.

Seitz, R., K. Vilpoux, U. Hopp, S. Harzsch, and G. Maier. 2005. Ontogeny of the Marmorkrebs (marbled crayfish): a parthenogenetic crayfish with unknown origin and phylogenetic position. Journal of Experimental Zoology Part A: Comparative Experimental Biology 303:393–405.

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19:372–378.

Sih, A., and A. M. Bell. 2008. Insights for behavioral ecology from behavioral syndromes. Advances in the Study of Behavior 38:227–281.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Souty-Grosset, C., D. M. Holdich, P. Y. Noël, J. D. Reynolds, and P. Haffner. 2006. Atlas of crayfish in Europe. Muséum national d'Histoire naturelle, Paris, France.

Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology 57:751–761.

Twardochleb, L. A., J. D. Olden, and E. R. Larson. 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. Freshwater Science 32:1367–1382.

Usio, N., M. Konishi, and S. Nakano. 2001. Species displacement between an introduced and a ‘vulnerable’crayfish: the role of aggressive interactions and shelter competition. Biological Invasions 3:179–185.

van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. Jeschke, and M. Fischer. 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology Letters 13:947–958.

Veselý, L., M. Buřič, and A. Kouba. 2015. Hardy exotics species in temperate zone: can “warm water” crayfish invaders establish regardless of low temperatures? Scientific Reports 5:16340.

Vogt, G., M. Huber, M. Thiemann, G. van den Boogaart, O. J. Schmitz, and C. D. Schubart. 2008. Production of different phenotypes from the same genotype in the same environment by developmental variation. Journal of Experimental Biology 211:510–523.

Vorburger, C., and G. Ribi. 1999. Aggression and competition for shelter between a native and an introduced crayfish in Europe. Freshwater Biology 42:111–119.

Weis, J. S. 2010. The role of behavior in the success of invasive crustaceans. Marine and Freshwater Behaviour and Physiology 43:83–98.

Westman, K., R. Savolainen, and M. Julkunen. 2002. Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a small, enclosed Finnish lake: a 30 year study. Ecography 25:53–73.

Wong, B., and U. Candolin. 2015. Behavioral responses to changing environments. Behavioral Ecology 26:665–673.

Wright, T. F., J. Eberhard, E. Hobson, M. L. Avery, and M. Russello. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethology Ecology & Evolution 22:393–404.

Yokota, T., R. Masuda, N. Arai, H. Mitamura, Y. Mitsunaga, H. Takeuchi, and T. Tsuzaki. 2007. Hatchery-reared fish have less consistent behavioral pattern compared to wild individuals, exemplified by red tilefish studied using video observation and acoustic telemetry tracking. Hydrobiologia 582:109–120.

Zulandt Schneider, R. A., R. Huber, and P. A. Moore. 2001. Individual and status recognition in the crayfish, *Orconectes rusticus*: the effects of urine release on fight dynamics. Behaviour 138:137–153.

Appendix B

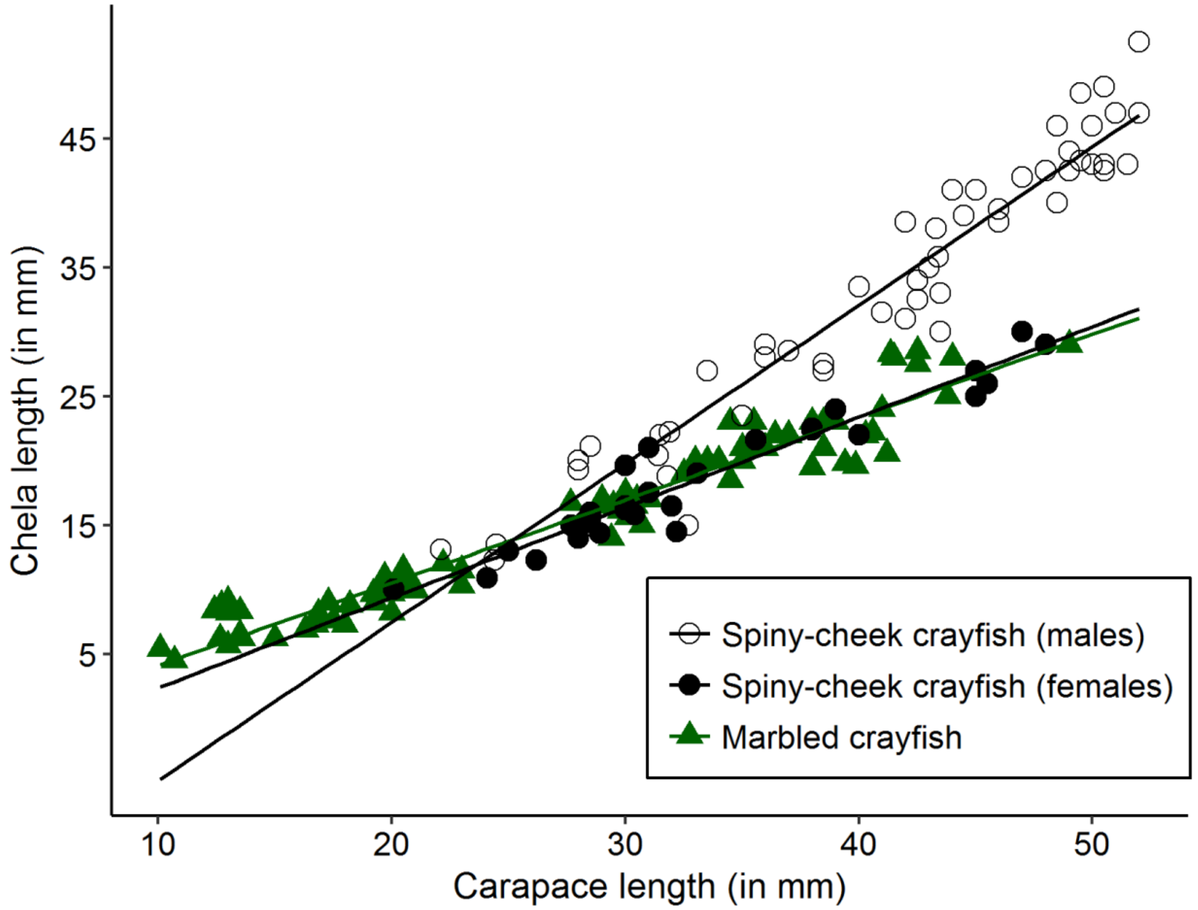

Figure B.1 - Chela length (in mm) plotted against carapace length (in mm) for spiny-cheek crayfish males (open circles; N = 52), spiny-cheek crayfish females (solid circles; N =28) and all-female marbled crayfish (dark green triangles; N = 81). Regression lines: spiny cheek crayfish females: Chela length ~ $-4.66 + 0.7 \cdot CL$ ($t = 18.26$, $P < 0.001$, adj. $R^2 = 0.92$); spiny-cheek crayfish males: Chela length ~ $-17.15 + 1.23 \cdot CL$ ($t = 26.45$, $P < 0.001$, adj. $R^2 = 0.93$); marbled crayfish: Chela length ~ $-2.33 + 0.64 \cdot CL$ ($t = 35.46$, $P < 0.001$, adj. $R^2 = 0.94$).

Table B.1 - Linear mixed-effects models of adjusted aggression score (adj. AS) analysis. All models include the individual as random factor. Indicated positive or negative effects of variables relate to the values of these variables given in brackets (m = male, SC = spiny-cheek crayfish, aq = aquarium origin); these are compared to female marbled crayfish from the field as reference. The table lists all models with decreasing Akaike's model weight (AIC).

Model	delta-AIC	AIC weight
− species(SC) + size	0	0.22057
species(SC) + size − species(SC):size	1.291	0.11567
− species(SC) + size + origin(aq)	1.686	0.09494
− species(SC) + size − sex(m)	1.978	0.08204
− species(SC) + size + sex(m) − sex(m):size	2.497	0.06329
species(SC) + size + origin(aq) − species(SC):size	2.851	0.05302
− species(SC)	3.018	0.04878
species(SC) + size − sex(m) − species(SC):size	3.291	0.04255
− species(SC) + size + origin(aq) − sex(m)	3.662	0.03535
− species(SC) + size − origin(aq) + origin(aq):size	3.672	0.03517
− species(SC) + size + origin(aq) + sex(m) − sex(m):size	4.059	0.02898
− species(SC) + size + sex(m) + species(SC):size − sex(m):size	4.497	0.02328
species(SC) + size + origin(aq) − species(SC):size − origin(aq):size	4.788	0.02013
species(SC) + size + origin(aq) − sex(m) − species(SC):size	4.851	0.01951
− species(SC) + origin(aq)	4.983	0.01826
− species(SC) + sex(m)	5.007	0.01804
− species(SC) + size − origin(aq) − sex(m) + origin(aq):size	5.65	0.01308
− species(SC) + size + origin(aq) + sex(m) − sex(m):size − origin(aq):size	6.007	0.01094
− species(SC) + size + origin(aq) + sex(m) − species(SC):size − sex(m):size	6.056	0.01068
species(SC) + size + origin(aq) − sex(m) − species(SC):size − origin(aq):size	6.787	0.00741
− species(SC) + sex(m) + origin(aq)	6.973	0.00675
size + origin(aq) − sex(m)	7.178	0.00609
size + origin(aq) + sex(m) − sex(m):size	7.231	0.00593
− species(SC) + size + origin(aq) + sex(m) − species(SC):size − sex(m):size − origin(aq):size	7.992	0.00406
size − sex(m)	8.26	0.00355
size + sex(m) − size:sex(m)	8.606	0.00298
sex(m) + size + origin(aq) − sex(m):size − origin(aq):size	9.058	0.00238
− sex(m) + size + origin(aq) − origin(aq):size	9.176	0.00224
size + origin(aq)	9.491	0.00192
size + origin(aq) + size:origin(aq)	11.49	0.00071
origin(aq) − sex(m)	11.772	0.00061
− sex(m)	11.821	0.0006
origin(aq)	13.462	0.00026
size	14.54	0.00015
null model	16.717	0.00005

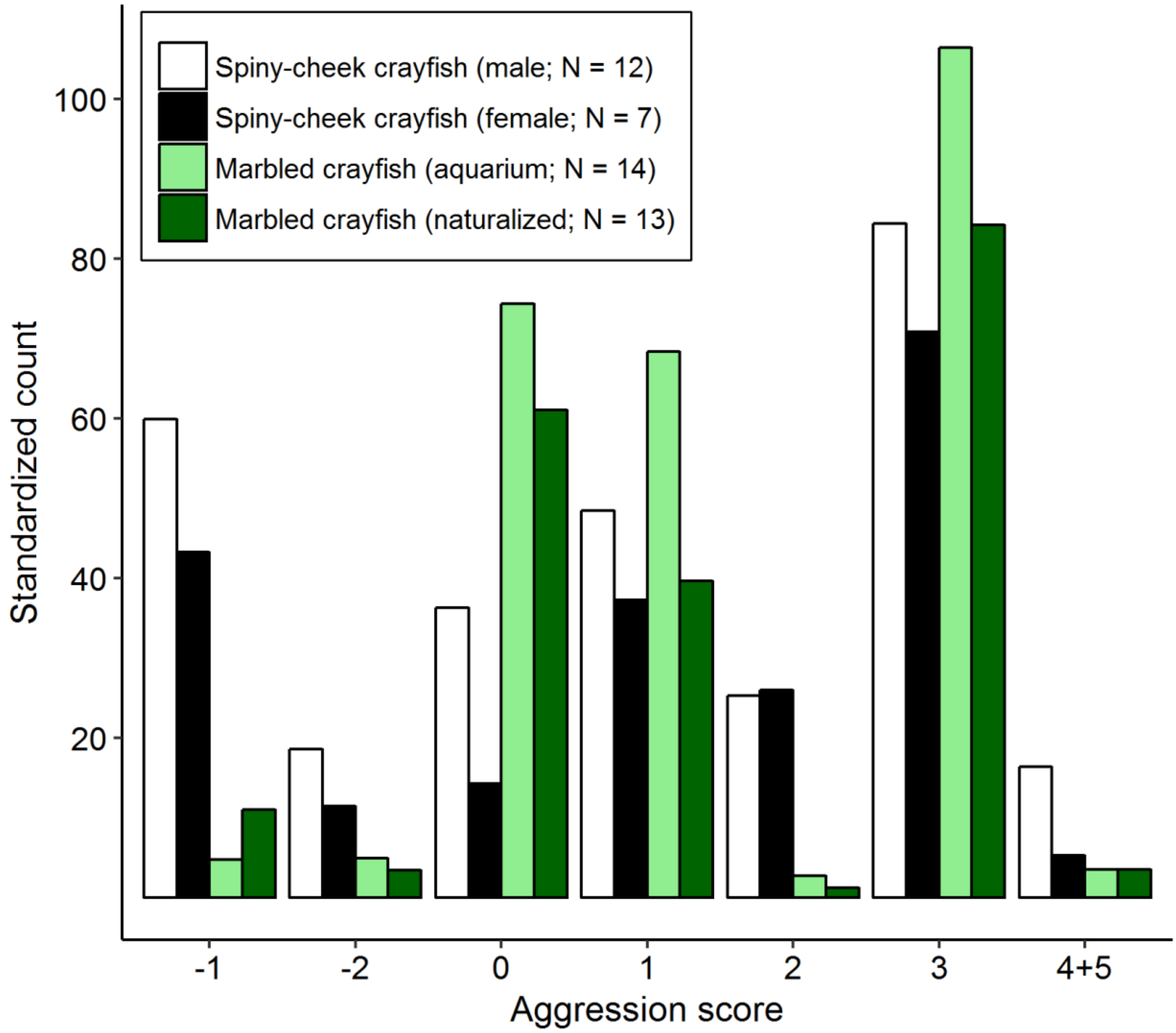

Figure B.2 - Standardized counts (by sample size) of the different scores corresponding to different behaviors in agonistic encounters. The counts are given as the total number of recorded behaviors divided by the number of trials (N) for spiny-cheek crayfish males (open bars), spiny-cheek crayfish females (black bars) and marbled crayfish from aquaria (light green bars) and naturalized populations (dark green bars).

Table B.2 - Generalized linear mixed-effects model results of activity analysis. All models include the individual as random factor. Indicated positive or negative effects of variables relate to the values of these variables given in brackets (m = male, SC = spiny-cheek crayfish, aq = aquarium origin); these are compared to female marbled crayfish from the field as reference. The table lists all models with decreasing Akaike's model weight (AIC).

Model	delta-AIC	AIC weight
origin(aq) – size	0.000	0.16063
origin(aq)	0.403	0.13132
origin(aq) – size – origin(aq):size	1.427	0.07870
sex(m) + origin(aq) – size – sex(m):size	1.465	0.07722
sex(m) + origin(aq) – size – sex(m):size – origin(aq):size	1.779	0.06600
sex(m) + origin(aq) – size	1.890	0.06243
– species(SC) + origin(aq) – size	1.985	0.05954
sex(m) + origin(aq)	2.276	0.05148
– species(SC) + origin(aq)	2.400	0.04838
– species(SC) + sex(m) + origin(aq) – size – sex(m):size	3.218	0.03214
sex(m) + origin(aq) – size – origin(aq):size	3.312	0.03066
– species(SC) + origin(aq) – size – origin(aq):size	3.418	0.02908
– species(SC) + sex(m) + origin(aq) – size – sex(m):size – origin(aq):size	3.588	0.02671
– species(SC) + sex(m) + origin(aq) – size	3.614	0.02637
species(SC) + origin(aq) – size – species(SC):size	3.837	0.02359
– species(SC) + sex(m) + origin(aq)	4.074	0.02095
– species(SC) + sex(m) + origin(aq) – size + species(SC):size – sex(m):size	4.450	0.01736
species(SC) + origin(aq) – size – species(SC):size – origin(aq):size	4.742	0.01500
– species(SC) + sex(m) + origin(aq) – size – origin(aq):size	5.066	0.01276
– species(SC) + sex(m) + origin(aq) – size – species(SC):size – sex(m):size – origin(aq):size	5.382	0.01089
species(SC) + sex(m) + origin(aq) – size – species(SC):size	5.423	0.01067
species(SC) + sex(m) + origin(aq) – size – species(SC):size – origin(aq):size	6.304	0.00687
– species(SC) – size	12.357	0.00033
– species(SC) + sex(m) – size	14.099	0.00014
– size	14.239	0.00013
– species(SC) – size + species(SC):size	14.263	0.00013
– species(SC) + sex(m) – size + species(SC):size – sex(m):size	14.522	0.00011
– species(SC) + sex(m) – size – sex(m):size	14.678	0.00010
– sex – size	14.870	0.00009
sex(m) – size – sex(m):size	15.472	0.00007
– species(SC) + sex(m) – size + species(SC):size	16.025	0.00005
– species(SC)	16.397	0.00004
– species(SC) + sex(m)	18.213	0.00002
null model	19.004	0.00001
sex(m)	19.166	0.00001

Chapter 3: Eco-Evolutionary Experience and Behavioral Innovation in Interactions with Non-Native Species

In revision at *Behavioral Ecology* as:

Ruland F, Meltl AA, Neugebauer MS, Jeschke JM. Eco-Evolutionary Experience and Behavioral Innovation in Interactions with Non-Native Species.

Abstract

Behavioral changes have been recognized to play an important role in human-induced rapid environmental change (HIREC). In the context of biological invasions, both native and non-native species can change their behavior. The level of eco-evolutionary experience (EEE) of native and non-native species is also relevant, as it potentially relates to (a) the impact of non-native species and thus (b) the necessity of native species to be innovative. We developed classification schemes to score both EEE and the degree of innovation in behavioral changes (adjusted innovation gradient, AIG). We applied these schemes to 81 records of native vertebrate species that have changed their behavior when interacting with non-native species (39 records for birds, 21 for mammals, 21 for amphibians). We found that native species with high EEE tend have a positive population trend when interacting with non-native species, whereas the opposite is true for native species with low EEE. Our results also show that species with low EEE show more innovation than species with high EEE. Thus, innovation by native prey species was often insufficient to counter negative effects of non-native species. This study gives insights on the interconnectedness of the eco-evolutionary experience of native with non-native species, the role of animal innovation and the effects of both on population dynamics of native species. Furthermore, it provides two new classification schemes that we hope will be useful for future studies of animal behavior and inform conservation ecology.

Keywords: behavioral flexibility, biological invasions, ecological novelty, global change, eco-evolutionary experience, animal innovation

1 - Introduction

Animal behavior has been recognized to be a crucial mechanism for animal species to cope with all forms of human-induced rapid environmental change (HIREC, Sih 2013) including biological invasions (Holway and Suarez 1999). The number of publications on the role of behavior in invasions has greatly increased over the last 20 years. These studies follow different goals and apply different methods. For example, some aim at explaining the success of invasive species by their behavioral flexibility (e.g. Wright et al. 2010; Sol et al. 2012), whereas others focus on the behavior of native species interacting with non-native species (e.g. Schlaepfer et al. 2005; Berthon 2015).

While innovative behavior and high plasticity are considered beneficial for both native and non-native species (Griffin and Guez 2014), their quantification has remained difficult (Logan and Logan 2016). Methods from other fields are either too detailed to be used for quantitative data collection (Ramsey et al. 2007) or focus on feeding behavior as the most reported type of innovation (Overington et al. 2009; Ducatez et al. 2014). While the latter has been very useful to, for example, predict bird invasion success in New Zealand (Sol and Lefebvre 2000), feeding behavior accounts for less than half of behavioral changes reported in empirical studies (Ruland and Jeschke, submitted). Thus, other types of innovative behavior cannot be quantified with this existing method.

In addition, it has been hypothesized that the eco-evolutionary experience (EEE; Saul et al. 2013; Saul and Jeschke 2015) of interacting native and non-native species can predict invasion success. While evolutionary adaptations after the onset of the interaction are widely documented (Prentis et al. 2008; Moran and Alexander 2014), the EEE concept synthesizes evidence of how a priori experience with similar species can shape the outcome of the interaction, may they be framed as contact experience (Kondoh 2006) or evolutionary legacy (Pianka 2000). The degree of familiarity and the corresponding appropriateness of the behavioral response has been described in the framework of naiveté (Banks and Dickman 2007), which has recently been connected to the shared evolutionary history of the interacting species (Steindler et al. 2018).

The consequences of interactions between native and non-native species vary greatly and are of high conservation concern (Keller, Cadotte and Sandiford 2015): While some native species are not affected by invasion or even benefit from an invader, for example as a novel food source (Wlodarczyk and Janiszewski 2014), populations of other native species collapse (Blackburn et al. 2004). Saul and Jeschke (2015) have worked out how EEE should affect the consequences of interactions between native and non-native species, but have not provided an easy-to-use framework on how to measure EEE. In addition to measuring EEE, we here additionally consider the importance of behavioral innovation, as highly innovative native species should be better able to mitigate negative effects of non-native species than less innovative species.

In this study, we thus measure and analyze both innovation in behavior and eco-evolutionary experience of native species interacting with non-native species, and investigate how these affect population trends of the native species. Our study focuses on mammals, birds and amphibians, and we addressed the following three research questions: (1) Do taxonomic groups differ in the types of behavior they change? (2) Do these types of behavior differ in their degree of innovation? (3) Do taxa differ in the degree of innovation within our dataset?

Furthermore, we addressed the following three hypotheses: (Hypothesis H1) There is a negative correlation between EEE and innovation, as invaders similar to the ecological environment of the native species do not require the native species to drastically change its behavior. (Hypothesis H2) More innovative behavior should lead to a more positive outcome of the interaction for the native species in terms of population trend compared to less innovative behavior. In other words, there should be a positive correlation between the degree of innovation and population trend. (Hypothesis H3) A higher level of eco-evolutionary experience of the native species interacting with the non-native species should lead to a more positive outcome in terms of population trend. Hence, there should be a positive correlation between EEE and population trend.

2 - Material and Methods

2.1 Data collection

All records of behavioral change come from the systematic literature review of Ruland and Jeschke (submitted). For this study, the Web of Science database was searched for studies documenting behavioral change during species invasions using a general search string. A study was selected as eligible when either the native or non-native species was documented to show a behavioral change since or during the invasion. The dataset used in this study was restricted to behavioral changes in native species. We included birds as the most numerous taxon in our dataset as well as mammals and amphibians as taxa with a different expected observed degree of innovation in behavior.

While the original dataset also contains cases of behavioral change associated with other species or the abiotic environment, the present study focuses on changes in interactions with the non-native species. We used the six mutually non-exclusive types of behavior defined in the original publication (Ruland & Jeschke, submitted): "feeding", "predator or parasite avoidance" (henceforth called "defense"), "mating", "competition", "thermoregulation, hydration and oxygenation" (henceforth called "climate") and "locomotion".

For all native species, we checked if the population dynamics were positive, stable or negative after the arrival of the non-native species. Information was - if available - taken directly from the original publication. If not, the authors of the study were contacted which were in many cases the most knowledgeable experts of the system. The population trend had to be directly related to the invasive species. We also checked available information on the IUCN Red List of Threatened Species (IUCN, 2018) and the Encyclopedia of Life (EOL, 2018). Only if the respective population trend of the focal native species was known for the location and directly related to the invasive species did we use it in the analyses.

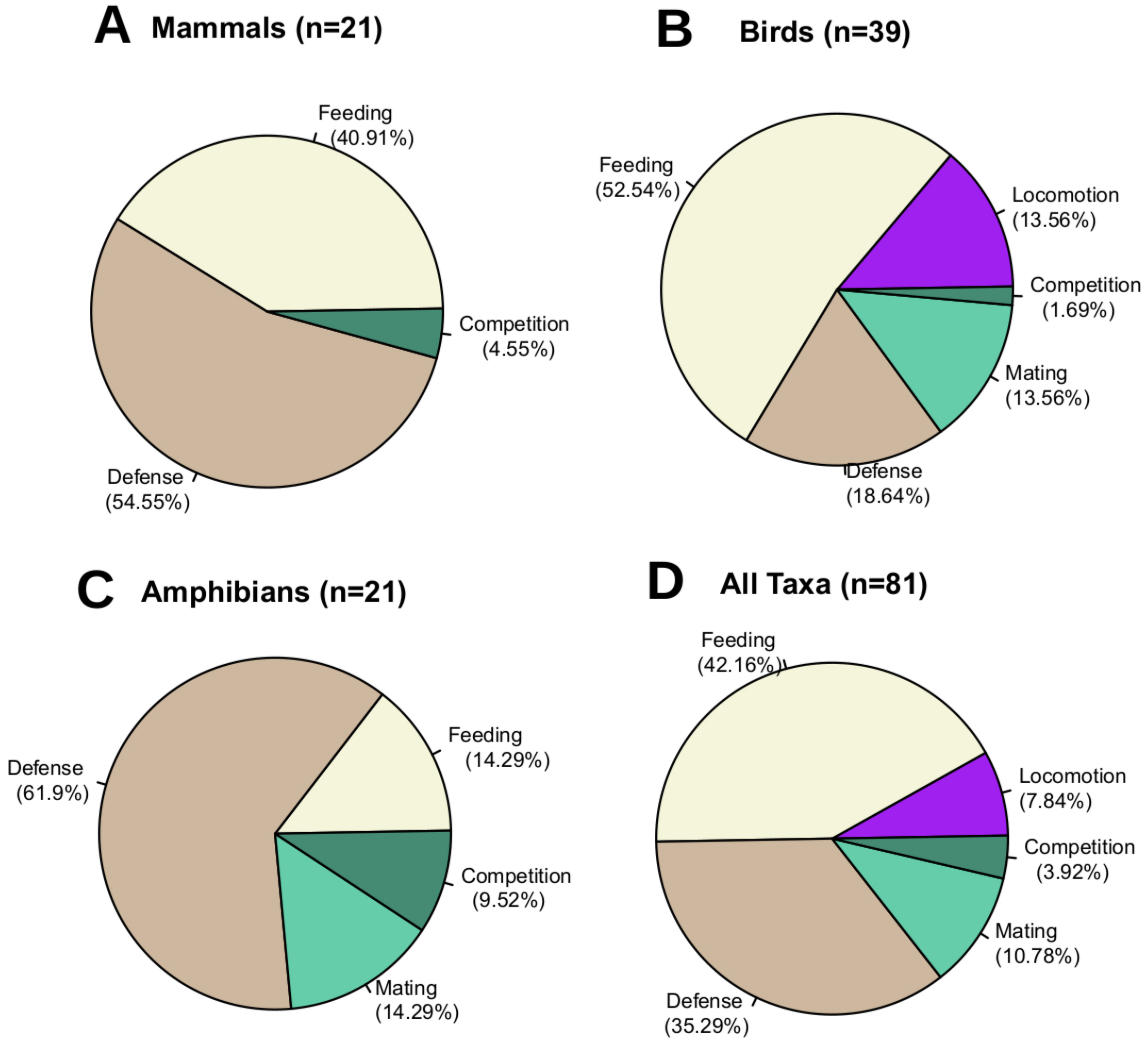

Figure 3.1 - Occurrences of different types of behavioral change in native (A) mammals, (B) birds, (C) amphibians and (D) all three combined when interacting with non-native species.

Of the six types of behavior defined in the original publication (Ruland & Jeschke, submitted), five were present in this subset (Figure 3.1). Most cases of behavioral change documented changes in feeding behavior (42.2%), closely followed by predator and parasite avoidance behavior (35.3%). The remaining types of behavioral change accounted for less than a third of the total mentions of types of behavior with mating behavior (10.8%), locomotion behavior (7.8%) and competition (3.9%). For later analysis of differences between types of behavior, we split the records of behavioral change into "feeding" (43 records), "defense" (36 records) and "other" (10 records of behavioral change not connected to defense or feeding). Types of behavior are mutually non-exclusive, therefore numbers add up to more than 81.

2.2 Classification schemes

Our innovation gradient (IG) scheme consists of four questions, all about the new behavior displayed by the native species (Figure 3.2). The first question asks if the behavior has been observed before. If that is the case, we follow the left branch and ask if the focal species displays the behavior with a different rate than before; if not, we arrive at a score of 0 (no new behavior); if yes, the score is 1 (modification of behavior). If the behavior has not been observed before, we ask if the object of interest is new; if yes, the IG is increased by 2. If this is the only question that is answered positively, the final score is 2 and the new behavior is an object innovation. If the object of interest is new and the behavior is additionally displayed with a different rate than before, the total score is 3 and the new behavior is a modified object innovation. Analogously to Overington et al.'s (2009) classification scheme related to feeding behavior, the next question is if the action pattern of the behavior is new. Such a new action pattern was, for example, observed in the black-capped chickadee (*Poecile atricapillus*) in Western Montana (Ortega et al. 2014). The exotic pest control *Urophora sp.* larvae are commonly found in risky open habitat on the invasive spotted knapweed (*Centaurea stoebe*). The larvae can be accessed by a new hovering technique that black-capped chickadees now show and which minimizes time in the open habitat. Since such a new action pattern is a strong innovation – stronger than the object innovation – an increment of 4 is given. That means when only this question is answered with yes, we arrive at a score of 4 (technical innovation). An innovation can be both on a new object and by a new technique, resulting in a total score of 6 (invention). There is no possibility for a total score of 5, as the action pattern cannot be new and the behavior at the same time not be defined as new.

As our dataset represents a special ecological situation, we adapted the innovation gradient, hereafter called the adjusted innovation gradient (AIG). In all studies used in our analyses, the non-native species is the stimulus for the change in behavior. It is very common that the non-native species is also the new object of interest which overestimates the degree of innovation in the focal species in our study. Therefore, in the AIG the total score is reduced by 2 if the object of interest was the non-native species itself (see dashed box in Figure 3.2). Object innovations are still regarded as such as long they are not directed towards the non-native species. For example, there was a shift towards steeper habitats of the Tibetan argali (*Ovis ammon hodgsoni*) in Ladakh, India, after the arrival of competing sheep and goats (Namgail et al. 2007). The introduced grazers are the stimulus for the behavioral change in the argali, but the new object of interest is the steeper habitat and not the species. While the IG was developed to score the level of innovation in all kinds of species across types of behavior and interactions, in our subset the AIG gives more reliable information without circularity.

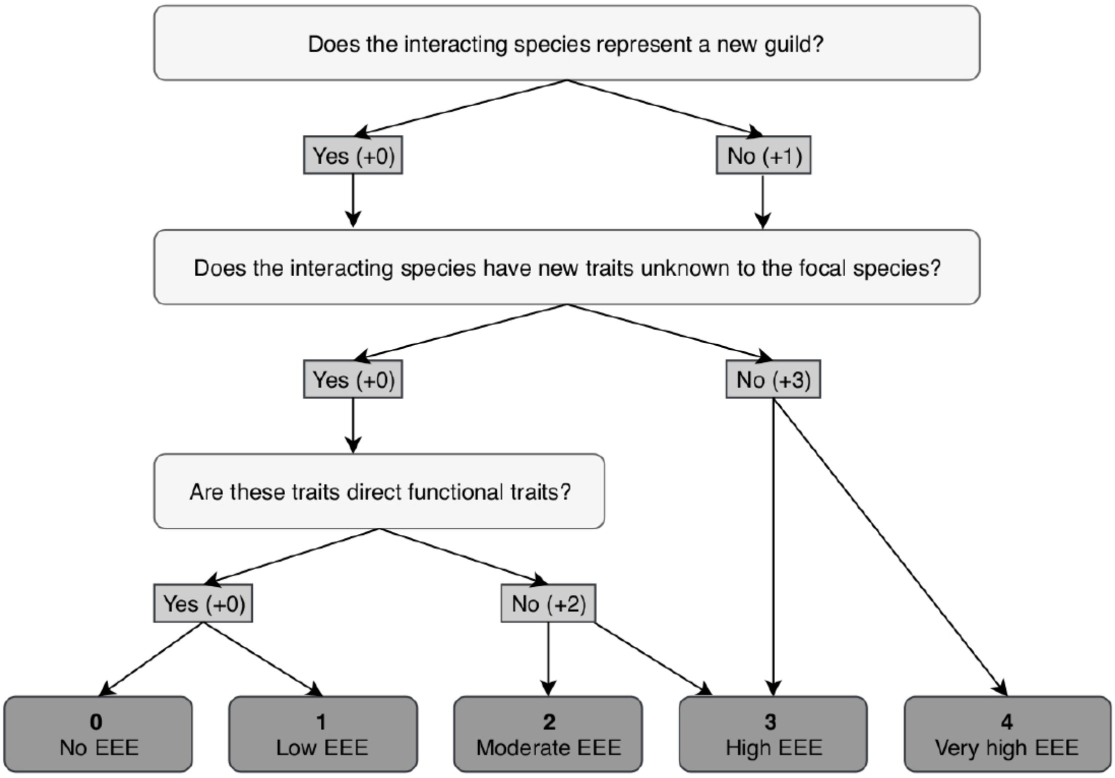

Figure 3.2 - Classification scheme for the eco-evolutionary experience. Questions relate to the non-native species interacting with the focal native species. Scores are added up from the top to the bottom.

The eco-evolutionary experience of the focal native species interacting with the non-native species was scored by applying a framework with three questions about the characteristics of the non-native species in relation to the native species (Figure 3.3). First, does the non-native species represent a new guild in the community? When addressing this question, we followed Root's (1967) guild definition as "a group of species that exploit the same class of environmental resources in a similar way". The second question is if the non-native species shows traits that are new to the native species. And in the third question, we ask if this trait/these traits serve a function in the interaction between the two species, thus defined as "direct functional traits". If the answer to a question is "no", it means the non-native species is closer to the known environment of the focal species, therefore the EEE score is raised by 1 (no new guild or no new trait) or 2 (no new direct functional trait). Positive answers to the questions do not increase the EEE score. The final sum is therefore between 0 (no EEE) and 4 (very high EEE). Scores are unambiguous except for a sum of 3 (high EEE) which can result from either (i) a new guild but no new traits or (ii) no new guild but one or more new, not direct functional, traits.

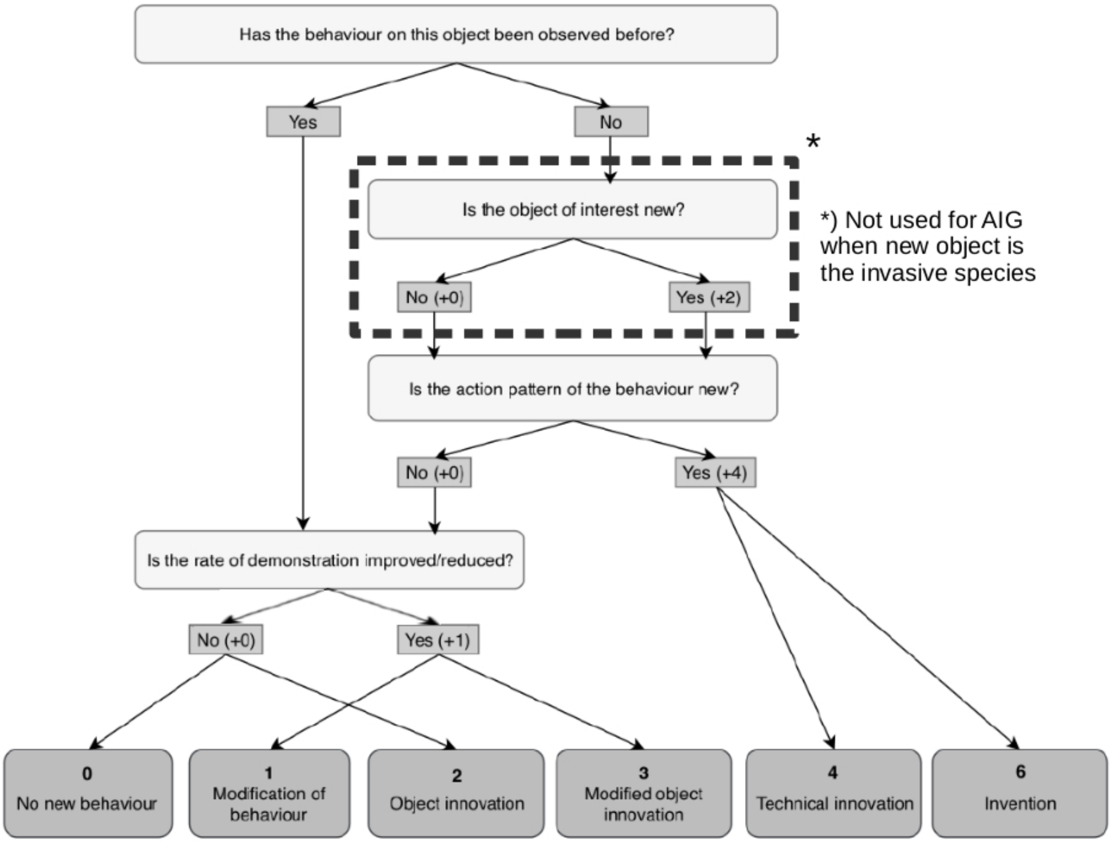

Figure 3.3 - Classification scheme for the innovation gradient (IG) and adjusted innovation gradient (AIG, see box). Questions relate to the behavior of the focal native species interacting with the non-native species. Scores are added up from the top to the bottom.

To minimize subjectivity and arrive at a more robust score for EEE as well as AIG, we used a Delphi consensus method (Linstone & Turoff 1975) for both classification schemes. All records of behavioral change in our dataset were independently scored by two of the authors (AAM and MSN). We calculated intra-class correlation coefficients between both observers for EEE and AIG. Second, the results were exchanged between both researchers, and each of them reassessed and possibly changed the scores for the records in which the rankings differed. Third, the revised rankings were compared to identify records that were still classified differently by the two researchers. Finally, there was a joint discussion between both researchers and a third author, FR, as moderator to arrive at consensus for each of these remaining records. Following this method, we were able to reach consensus about all EEE and AIG scores for all records of behavioral change analyzed in this study. To quantify inter-observer reliability, we calculated the intra-class correlation coefficient for EEE and AIG values.

2.3 Statistical Analyses

To detect taxonomic differences in our dataset, we compared the distribution of types of behavior, EEE, AIG and population trend between the three taxonomic groups. In order to test for differences between types of behavioral change, we split the distributions of EEE, AIG and population trend by the above defined groups "feeding" (43), "defense" (36) and "other" (10). We used Fisher tests between each subset (taxon or type of behavior) and the rest. As there were partly low estimated probabilities and many ties, we performed 100'000 p-value simulations per test.

To test for relationships between the parameters, we performed Kendall's tau correlation analyses, each one for mammals, birds and amphibians separately as well as all combined. The correlations were calculated between EEE and AIG, AIG and population trend as well as EEE and population trend. To decrease leverage of single values and multiple observations per species/study, we performed bootstrap analyses with 10'000 simulations each (Davison & Hinkley 1997). All analyses were performed using the core package of R (version 3.4.4), the "ICC" package (Wolak et al. 2012) and the 'boot' package (Canty & Ripley 2017).

3 - Results

3 -1 Distribution of variables across taxa

Types of behavior

The three taxonomic groups significantly differed in the occurrences of behavioral types (Table 3.1, Figure 3.1). Birds were the only taxon to show changes in all five behavioral types in our study, and the only ones to show changes in locomotion behavior. Amphibians changed their defense behavior most frequently, while feeding behavior changed less commonly than in other taxa. The range of behavioral types in mammals was narrow with only three of five behavioral types covered.

Table 3.1 - P-values resulting from pairwise Fisher tests comparing each taxonomic group with the other groups for occurrences of: (i) types of behavior, (ii) adjusted innovation gradient scores, (iii) eco-evolutionary experience scores and (iv) population trends. All tests with 100'000 simulated p-values, p-values <0.05 are highlighted in **bold.**

	Mammals	Birds	Amphibians
Types of Behavior	0.07	**< 0.001**	**< 0.01**
Adj. Innovation Gradient	0.33	**0.0078**	**0.028**
Eco-Evolutionary Experience	0.074	**0.0081**	**0.0024**
Population Trend	0.8	**0.028**	**0.0068**

Adjusted innovation gradient (AIG)

The majority of AIG scores are either 0 or 1 (Figs. 4, 5). This is mostly because the object of interest was often the non-native species in our subset of studies, and therefore many scores were reduced by 2 when calculating AIG from an original "object innovation" or "modified object innovation". The effect was particularly strong in birds, where 21 records of behavioral change were known action patterns performed on new objects of interest, resulting in an IG score of 2 and an AIG score of 0 because the new object of interest was the non-native species. As a result, the AIG of birds is most commonly 0, and more frequently so than in other taxa. On the other hand, they were the only taxonomic group showing a technical innovation without object innovation (AIG of 4). This was, for example, the case for the O’ahu’elepaio (Chasiempis ibidis) in Hawaii that started to build nests at elevated heights in order to avoid predation by the invasive black rat (Rattus rattus) (Vanderwerf 2012).

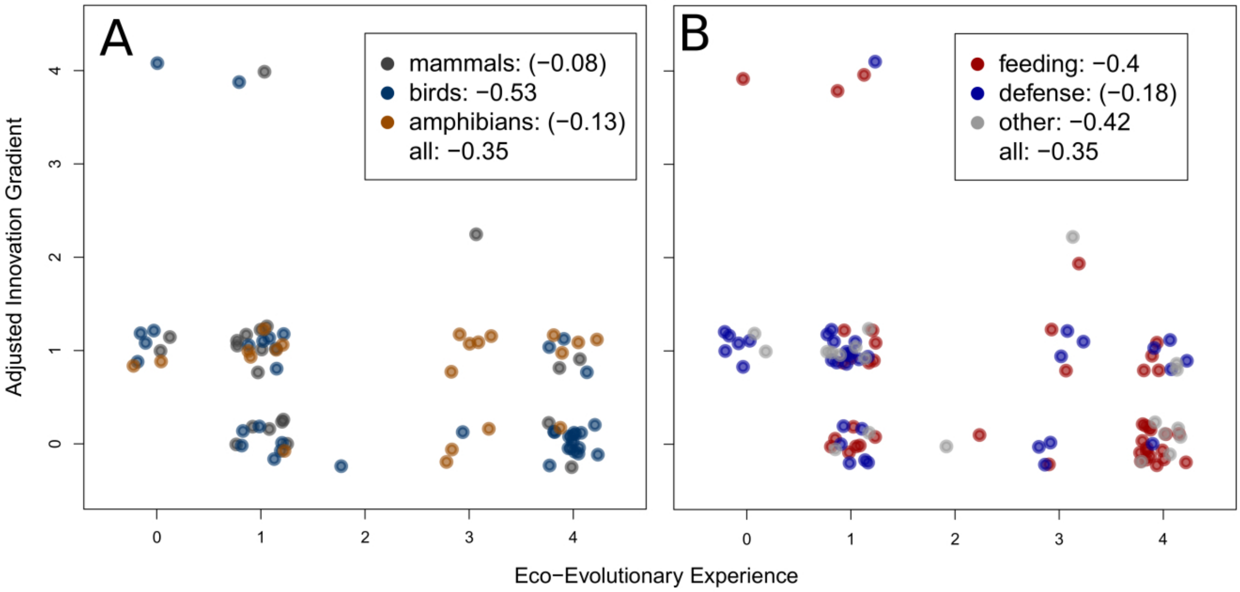

Figure 3.4 - Adjusted innovation gradient (AIG) plotted against eco-evolutionary experience. Records of behavioral change were split by taxonomic group of the native species (A) or type of behavioral change (B). Results of all Kendall correlation analyses with 10'000 bootstrap simulations are given; Kendall's τ is in brackets if 95%-confidence interval overlaps with 0. Sample sizes: mammals=21, birds=39, amphibians=21, feeding=43, defense=36, other=10, all=81

"Modification of behavior" was most common for defense behaviors, for example an increased amount of time spent hiding. Despite three cases of technical innovation directed to the non-native species, the most common innovation in feeding behavior was a shift to the non-native species without changing predation strategy (therefore resulting in an AIG score of 0). There was no case of a new technique involving a new object of interest that was not the non-native species.

Eco-evolutionary experience (EEE)

The distribution of eco-evolutionary experience scores in our data is bimodal, with most species either possessing EEE scores of 1 or 4 (Figures 3.4, 3.6). While mammals had the highest frequency of an EEE score of 1, their distribution of EEE scores did not differ significantly from the other taxa. Birds showed a significantly higher frequency of a score of 4 and the only record where a species had an EEE score of 2 (see Table 3.1). The distribution of amphibian EEE scores also differed significantly from the other taxa, as it was more homogeneous with a higher than average number of species with an EEE score of 3. Feeding behavior changed significantly more frequently in cases of high EEE, while EEE was significantly lower for changes in defense behavior (Table 3.2, Figure 3.4B).

Table 3.2 - P-values resulting from pairwise Fisher tests comparing each type of behavior (feeding, defense, other) with the remaining types for occurrences of: (i) adjusted innovation gradient scores, (ii) eco-evolutionary experience scores and (iv) population trends between each taxon and the respective rest. All tests with 100'000 simulated p-values, p-values <0.05 are highlighted in **bold.**

	Feeding	**Defense**	**Other**
Adj. Innovation Gradient	**< 0.001**	**0.0035**	0.85
Eco-Evolutionary Experience	**0.0045**	**0.0036**	0.35
Population Trend	**< 0.001**	0.087	**0.01**

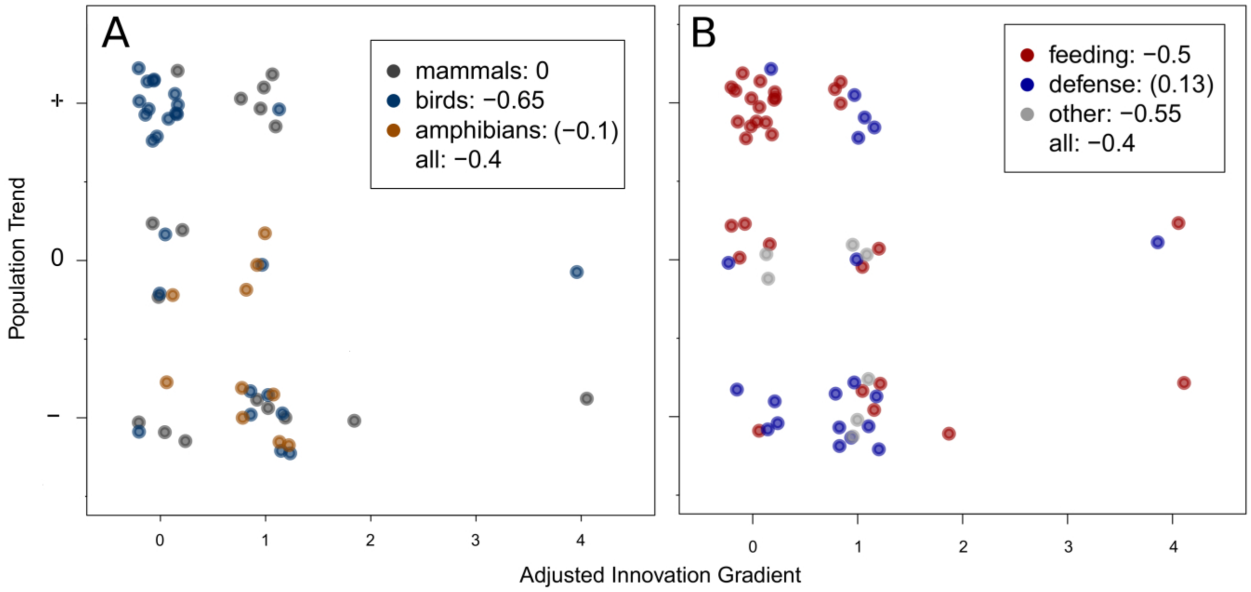

Figure 3.5 - Adjusted innovation gradient (AIG) plotted against the population trend of the native species. Records of behavioral change were split by taxonomic group of the native species (A) or type of behavioral change (B). Results of all Kendall correlation analyses with 10'000 bootstrap simulations are given; Kendall's τ is in brackets if 95%-confidence interval overlaps with 0. Sample sizes: mammals=17, birds=26, amphibians=10, feeding=31, defense=20, other=7, all=53.

Population trends

Population trends were only counted for publications where reliable information was available (Figures 3.5, 3.6). The native species had a decreasing population in most cases, but roughly a third of the species showed a positive population trend. Bird species had significantly different population trends, with most species showing a positive trend (Table 3.1). Population trends of amphibians were significantly different from the rest, with no species showing a positive trend (Table 3.1).

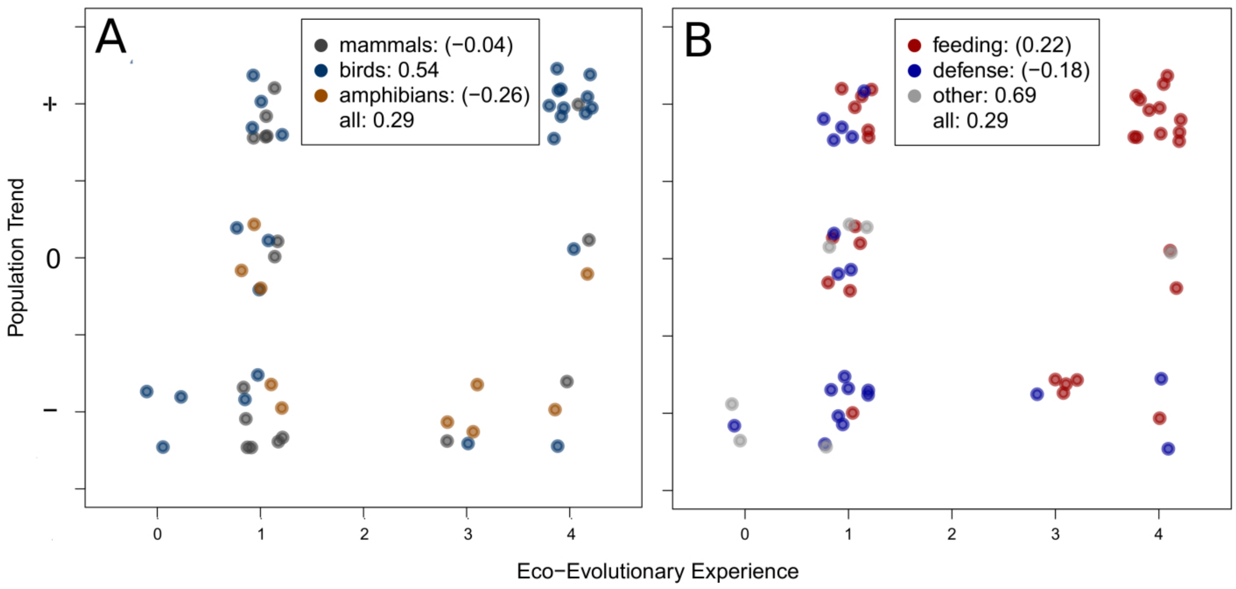

Figure 3.6 - Eco-evolutionary experience (EEE) plotted against the population trend of the native species interacting with the non-native species. Records of behavioral change were split by (A) taxonomic group of the native species or (B) type of behavioral change. Results of Kendall correlation analyses with 10'000 bootstrap simulations are given; Kendall's τ is in brackets if 95%-confidence interval overlaps with 0. Sample sizes: mammals=17, birds=26, amphibians=10, feeding=31, defense=20, other=7, all=53.

While species changing their feeding behavior more commonly showed a positive population trend than species changing their defense behavior, this difference was not significant (Table 1.2, Figure 3.5B). Changes in behavior not connected to feeding or defense, however, led to a significantly more negative population trend.

Inter-observer reliability

We followed the categorization of inter-observer reliability as proposed in Cicchetti (1994) with ranges of intra-class correlation coefficients (ICC) classified as poor (ICC < 0.4), fair (0.4 < ICC < 0.6), good (0.6 < ICC < 0.75) and excellent (0.75 < ICC). Our results indicated fair inter-observer reliability for both EEE (ICC = 0.46, $p < 0.01$) and AIG (ICC = 0.55, $p < 0.001$). To be more careful, we did not use the original values, but values obtained from the consensus finding method for all subsequent analyses.

3.2 – Correlation analyses

AIG and EEE

All correlations - in all taxa and all types of behavior - between the adjusted innovation gradient (AIG) and EEE were negative (Figure 3.4). There was a significant overall negative correlation and 95%-confidence intervals not overlapping with 0 for birds, feeding behavior and other types of behavior. This correlation indicates - in line with our hypothesis H1 - that low eco-evolutionary experience is related to more drastic changes in behavior. In other words, high eco-evolutionary experience is related to small changes in behavior; there were no innovative changes in behavior with high eco-evolutionary experience (Figure 3.4).

AIG and population trend

There was a negative relationship between AIG and population trend (Figure 3.5). Again, birds showed the same correlation, also the subsets of feeding behavior and other types of behavior. This contradicts our hypothesis H2, which expected innovative changes in behavior to be beneficial for the focal species. This was, however, only indicated in defense behavior, which showed a weak positive correlation between AIG and population trend. A big change in behavior does not seem to be beneficial in itself for the native species interacting with the invader.

EEE and population trend

In line with our hypothesis H3, eco-evolutionary experience was a significantly positive predictor for the population trend over all records combined (Figure 3.6). This seems to be driven mostly by bird species in our dataset, as the sign of correlations for the other taxa was negative but insignificant (Figure 3.6A). There was no significant correlation for changes in feeding or defense behavior, but EEE and population trend were strongly positively correlated for changes in other types of behavior.

4 - Discussion

4.1 - Animal innovation is context-dependent

Animal innovation can be observed and documented in a wide range of contexts, either when researchers actively looked for it and highlighted it in a publication, but also when the focus of a study lies elsewhere. We are aware of the benefits of studies that look for keywords in papers to find records of animal innovation as done in comparative studies in birds (Lefebvre et al. 1997) or primates (Reader and Laland 2002). In these studies, papers on innovation were found by a keyword search for innovative behavior and not through individual assessment by the researchers. While inter-observer reliability is higher when making decisions about the degree of innovation in an observed behavior by keywords, it misses papers where innovative behavior might have been described but not named as such. This is why we decided to look for more general terms like "shift" and "change", and individually assessed the degree of innovation. While our inter-observer reliability was only low, we followed the Delphi consensus method to remove error from the data. We encourage researchers who will in the future use the classification schemes proposed here to also apply a consensus method.

The dataset we used is particular in terms of the ecological setting where the observations of animal behavior were made: all studies were conducted with a focus on native species that changed their behavior after the arrival of a non-native species. First, we excluded cases where species changed their behavior towards the abiotic environment. Second, all focal native species changed their behavior after being subjected to an environmental stimulus in the form of a new species. Our distinction between environmental induction and innovation is therefore gradual (Ramsey et al. 2007). The definition of (Kummer and Goodall (1985) of innovation being a "solution to a novel problem or a novel solution for a known problem" is split by our classification scheme into a "solution to a novel problem" (object innovation) and a "novel solution for a known problem" (technical innovation). We do not distinguish between innovation and invention according to Slater & Lachlan (2003, page 117), where innovations are the creation of new means in contrast to inventions as the creation of new ends. In contrast, we defined inventions within the range of innovations, which is in line with Ramsey et al.’s (2007, page 396) notion that inventions are "a subset of innovations".

The application of the innovation gradient scheme in our specific subset of observations of behavioral changes in new species interactions was possible by accounting for the non-native species as the stimulus (adjusted innovation gradient, AIG). We believe this step is important to remove circularity and inherent bias towards more innovative behavior, and recommend everyone using our classification scheme in very specific areas (e.g. urbanization) to do the same. This adjustment and the fact that innovation was not the focus of the studies we used rendered the innovation score expectedly low. On the other hand, it increases the contrast between observations in our study to better compare correlations with EEE and population trend in different subsets (taxa or types of behavior) in our data. This helps to identify the innovators among natives interacting with non-native species more clearly. Let us look at two examples. First, black-capped chickadees (Poecile atricapillus) feeding on introduced Urophora larvae in western Montana showed innovative behavior by way of a novel hovering technique to pick the larvae from the seedheads of invasive spotted knapweed (*Centaurea stoeb*e) (Ortega et al. 2014). Second, the long-fingered bat (*Myotis capaccinii*) has been documented to feed on invasive mosquitofish (*Gambusia affinis*) in North-Western Israel (Levin et al. 2006). This is not only a novel food item, but the first species of bats in the middle East where piscivory has been shown. So in both cases, the change in behavior was more than a simple interaction with the stimulus species.

When scoring innovations of species more generally or when pooling observations from more diverse ecological contexts, however, it is not necessary to adjust the innovation gradient, thus unadjusted IG scores should then be used.

4.2 - Causes and population-level consequences of innovation

The consistent negative relationship between AIG and EEE across all taxonomic groups and types of behavior is supporting our hypothesis H1, according to which low EEE requires more innovative behavior. This indicates high and sometimes unprecedented flexibility in for example feeding mode (see the two examples above) triggered by a novel species. While this is a positive sign of species matching the degree of innovation in their behavioral change to the degree of novelty in the invader, it is not clear if this behavioral plasticity suffices to buffer adverse effects (Wong and Candolin 2015).

In fact, we found evidence that in the cases of native species dealing with non-natives, it often does not. Contradictory to our hypothesis H2, the relationship between innovation and population trend was negative. One possible underlying factor is the cost of innovation (Hendry 2016). Furthermore, it seems that innovative behavior of native species with low eco-evolutionary experiences was insufficient to effectively respond to the non-native species. This was true for feeding and other types of behavior, whereas for defense the relationship was positive (although not significant).

Thus, while innovation seems to be generally beneficial to invasive species (Sol and Lefebvre 2000; Wright et al. 2010), the ecological situation for native species is quite different. Incorporating a new prey species into the diet is - even though often beneficial – a rather optional choice, reacting to a new predator with behavioral defense mechanisms is critical to survive. This logic can explain why innovation in a feeding technique in response to a non-native species is less beneficial than innovation in a defense response against predation.

4.3 - Naïveté and beneficial experience

The positive relationship between EEE and population trend is in line with hypothesis H3 outlined in the Introduction. It means that native species failed to sufficiently adapt to those non-native species that are very different from the types of species they interacted with in their evolutionary past (i.e. for which they have a low EEE). Theory predicts this effect to be driven by native prey species failing to defend against a non-native predator they are naïve to (Carthey and Banks 2014). In our data, however, we found this relationship to be mainly driven by feeding and other types of behavior. This makes sense, as the selection of a new prey item for a native species is a choice they can make (see above). If the native species recognizes the non-native prey species and has the necessary predation technique in its behavioral repertoire, it may start incorporating the new species into its diet; this is optional, though, and not normally critical to survival. In contrast and in order to survive, the native prey species will have to change its behavior under predation pressure of the non-native predator independently of its EEE. In such cases in which species had to change defense behavior, we observed a negative relationship between EEE and population trend. Indeed, all three cases of high EEE in our dataset showed a negative population trend (Figure 3.6); these were the Australian common bushtail (*Trichosurus vulpecula*) and in two cases the common parsley frog in Europe (*Pelodytes punctatus*).

Conclusions and outlook

This first application of our EEE and AIG classification schemes provided results for three groups of vertebrates. For bird species, for which we had a higher number of records than for mammals and amphibians, we have demonstrated clear relationships between EEE and AIG, population trend and EEE, and population trend and AIG. Birds were in many ways the most convenient subset to work with, as they (i) showed the most diverse changes in types of behavior, (ii) had most species diversity and (iii) their EEE scores were most balanced. The sample size of birds with 39 records of behavioral change was roughly the number of records in mammals and amphibians combined. Further analyses will have to be performed with different datasets to see if the results of birds can be reproduced in other taxa and under which circumstances. The distinction between food-type and technical innovations, which inspired our AIG classification, was also designed for and applied to birds.

While our EEE classification scheme, including its integrated questions (Figure 3.2), is based on various discussions and pre-analyses, additional questions can, of course, be added to make it more detailed and adapt it for specific purposes. We do not believe, however, that a distinctly more complicated catalogue of questions would generally be a good way forward, as it would require very detailed knowledge of both species that will often be impossible to obtain, e.g. for rare or understudied species. Our approach was to design a ready-to-use simple framework that still has predictive power in terms of how a non-native species will affect a native species. Its application can lead to swifter action in order to protect species threatened by invasion, and to a more diverse and quantifiable analysis of animal innovation.

The (A)IG innovation scheme can also be applied in other studies of animal behavior. Compared to previous studies (e.g. Overington et al. 2009), we extended the range of types of behavior that are now easy to score. The (A)IG scheme can be used for future comparative or correlational analyses of innovation. In Ruland and Jeschke (submitted), we showed that less than half of the types of behavioral changes observed during species invasions fit the feeding category. Studying only cases of this category leaves an estimated 60% of changes of behavior untapped, a source of data we hope will be exploited using the (A)IG classification scheme. The search for big innovations will be easier if a larger set of data can be tapped using the (A)IG scheme, and high scoring records can be studied more intensely thereafter. Applying the (A)IG classification to invertebrates and species that are usually missed when looking for innovative behavior would be a particularly promising next step.

References

Banks PB, Dickman CR. 2007. Alien predation and the effects of multiple levels of prey naiveté. Trends Ecol Evol. 22(5):229–230. doi:10.1016/j.tree.2007.02.006.

Berthon K. 2015. How do native species respond to invaders? Mechanistic and trait-based perspectives. Biol Invasions. 17(8):2199–2211. doi:10.1007/s10530-015-0874-7.

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ. 2004. Avian extinction and mammalian introductions on oceanic islands. Science. 305(5692):1955–1958. doi:10.1126/science.1107333.

Canty, A. and Ripley, B (2017). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-20.

Carthey AJR, Banks PB. 2014. Naiveté in novel ecological interactions: Lessons from theory and experimental evidence. Biol Rev. 89:932–949. doi:10.1111/brv.12087.

Cicchetti D V. 1994. Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments in psychology. Psychol Assess.(4):284–290. doi:10.1037/1040-3590.6.4.284

Davison, A. C. & Hinkley, D. V. (1997) Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2

Ducatez S, Audet JN, Lefebvre L. 2014. Problem-solving and learning in Carib grackles: individuals show a consistent speed-accuracy trade-off. Anim Cogn. 18(2):485–496. doi:10.1007/s10071-014-0817-1.

Encyclopedia of Life. URL: https://eol.org/ (last accessed: 2018-08-30).

Griffin AS, Guez D. 2014. Innovation and problem solving: A review of common mechanisms. Behav Processes. 109(PB):121–134. doi:10.1016/j.beproc.2014.08.027.

Hendry AP. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. J Hered. 107(1):25–41. doi:10.1093/jhered/esv060.

Holway D a., Suarez A V. 1999. Animal behavior: An essential component of invasion biology. Trends Ecol Evol. 14(99):328–330. doi:10.1016/S0169-5347(99)01636-5.

IUCN Global Species Programme – Red List Unit. Version 3, Cambridge, United Kingdom. URL: https://www.iucnredlist.org/ (last accessed: 2018-08-30).

Keller, R. P., M. W. Cadotte, G. Sandiford. 2015. Invasive species in a globalized world. University of Chicago Press

Kondoh, M. 2006. Contact experience, alien-native interactions, and their community consequences: a theoretical consideration on the role of adaptation in biological invasions. In: Cadotte, M. W., S. M. McMahon, T. Fukami (Eds.) Conceptual ecology and invasion biology. Springer, Dordrecht, 225-242.

Kummer H, Goodall J. 1985. Conditions of Innovative Behaviour in Primates. R Soc London. 308(1135):203–214. doi:10.1098/rstb.1985.0020

Lefebvre L, Whittle P, Lascaris E. 1997. Feeding innovations and forebrain size in birds. Anim Behav. (1983):549–560. doi:10.1006/anbe.1996.0330

Levin E, Barnea A., Yovel Y, Yom-Tov Y. 2006. Have introduced fish initiated piscivory among the long-fingered bat? Mamm Biol. 71(3):139–143. doi:10.1016/j.mambio.2006.01.002.

Linstone HA, Turoff M (eds.), The Delphi Method: Techniques and Applications; vol. 29. Reading, MA: Addison-Wesley, 1975.

Logan CJ. 2016. How far will a behaviourally flexible invasive bird go to innovate? R Soc open sci. doi:http://dx.doi.org/10.1098/rsos.160247.

Mella VS a, Cooper CE, Davies SJJF. 2010. Predator odour does not influence trappability of southern brown bandicoots (*Isoodon obesulus*) and common brushtail possums (*Trichosurus vulpecula*). Aust J Zool. 58(5):267–272. doi:10.1071/ZO10049.

Moran E V., Alexander JM. 2014. Evolutionary responses to global change: Lessons from invasive species. Ecol Lett. 17(5):637–649. doi:10.1111/ele.12262.

Namgail T, Fox JL, Bhatnagar YV. 2007. Habitat shift and time budget of the Tibetan argali: The influence of livestock grazing. Ecol Res. 22(1):25–31. doi:10.1007/s11284-006-0015-y.

Ortega YK, Greenwood LF, Callaway RM, Pearson DE. 2014. Different responses of congeneric consumers to an exotic food resource: Who gets the novel resource prize? Biol Invasions. 16(8):1757–1767. doi:10.1007/s10530-013-0625-6.

Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav. 78(4):1001–1010. doi:10.1016/j.anbehav.2009.06.033.

Pianka, E. R. 2000. Evolutionary ecology. Benjamin Cummings, Addison-Wesley-Longman, San Francisco, 528pp.

Polo-Cavia N, Gomez-Mestre I. 2014. Learned recognition of introduced predators determines survival of tadpole prey. Funct Ecol. 28(2):432–439. doi:10.1111/1365-2435.12175.

Prentis PJ, Wilson JRU, Dormontt EE, Richardson DM, Lowe AJ. 2008. Adaptive evolution in invasive species. Trends Plant Sci. 13(6):288–94. doi:10.1016/j.tplants.2008.03.004.

Pujol-Buxó E, San Sebastián O, Garriga N, Llorente G a. 2013. How does the invasive/native nature of species influence tadpoles' plastic responses to predators? Oikos. 122(1):19–29. doi:10.1111/j.1600-0706.2012.20617.x.

Ramsey G, Bastian ML, van Schaik C. 2007. Animal innovation defined and operationalized. Behav Brain Sci. 30(4):393–407; discussion 407-32. doi:10.1017/S0140525X07002373.

Reader SM, Laland KN. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci. 99(7):4436–4441. doi:10.1073/pnas.062041299.

Root RB. 1967. The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. Ecol Monogr. 37(4):317–350. doi:doi.org/10.2307/1942327.

Saul W-C, Jeschke JM, Heger T. 2013. The role of eco-evolutionary experience in invasion success. NeoBiota. 17:57–74. doi:10.3897/neobiota.17.5208.

Saul W-C, Jeschke JM. 2015. Eco-evolutionary experience in novel species interactions. Ecol Lett. 18(3):236–245. doi:10.1111/ele.12408.

Schlaepfer MA, Sherman PW, Blossey B, Runge MC. 2005. Introduced species as evolutionary traps. Ecol Lett. 8(3):241–246. doi:10.1111/j.1461-0248.2005.00730.x.

Sih A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Anim Behav. 85(5):1077–1088. doi:10.1016/j.anbehav.2013.02.017.

Slater, P. J. B., & Lachlan, R. F. (2003). Is innovation in bird song adaptive? In S. M. Reader & K. N. Laland (Eds.), Animal innovation (pp. 117-135). New York, NY, US: Oxford University Press.

Sol D, Lefebvre L. 2000. Behavioural Flexibility Predicts Invasion Success in Birds Introduced to New Zealand. Oikos. 90(3):599–605.doi.org/10.1034/j.1600-0706.2000.900317.x

Sol D, Maspons J, Vall-Llosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP. 2012. Unraveling the life history of successful invaders (Supplementary Material). Science. 337(6094):580–3. doi:10.1126/science.1221523.

Steindler LA, Blumstein DT, West R, Moseby KE, Letnic M. 2018. Discrimination of introduced predators by ontogenetically naïve prey scales with duration of shared evolutionary history. Anim Behav. 137:133–139. doi:10.1016/j.anbehav.2018.01.013.

Vanderwerf E a. 2012. Evolution of Nesting Height in an Endangered Hawaiian Forest Bird in Response to a Non-Native Predator. Conserv Biol. 26(5):905–911. doi:10.1111/j.1523-1739.2012.01877.x.

Wlodarczyk R, Janiszewski T. 2014. Can expansion of Zebra Mussel, *Dreissena polymorpha* (Bivalvia) influence the numbers and behaviour of traditionally herbivorous mute swan, *Cygnus olor* (Aves)? Acta Zool Bulg. 66(2):235–238.

Wolak, M.E., Fairbairn,D.J., Paulsen, Y.R. (2012). Guidelines for Estimating Repeatability. Methods in Ecology and Evolution 3(1):129-137. https://doi.org/10.1111/j.2041-210X.2011.00125.x

Wong BBM, Candolin U. 2015. Behavioral responses to changing environments. Behav Ecol. 26(3):665–673. doi:10.1093/beheco/aru183.

Wright TF, Eberhard JR, Hobson E a., Avery ML, Russello M a. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethol Ecol Evol. 22(4):393–404. doi:10.1080/03949370.2010.505580.

Chapter 4: Climate and predator presence drive nest site and number of the common eider (*Somateria mollissima*) in West Iceland

In preparation as:

Jónsson JE, Ásgeirsson A, Ruland F. Climate and predator presence drive nest site and number of the common eider (*Somateria mollissima*) in West Iceland.

Abstract

The Northern Atlantic avifauna is highly dependent on resources from the sea due to low terrestrial productivity and therefore breeding success is dependent on climatic processes. At the same time, high breeding densities make colonies attractive targets for nest predation by terrestrial predators. The common eider (*Somateria mollissima*) commonly breeds on islands in Breiðafjörður in West Iceland the moste remote of which offer safety from predation by the native Arctic fox (*Vulpes lagopus*). In the 1930s, the American mink (*Neovison vison*) was introduced and spread in the area in the late 1940s. We used data from two archipelagos, Brokey (95 islands with data from 1892-2014) and Purkey (39 islands from 1986-2012) to quantify the effect of climate fluctuations and predator presence on nest numbers. Our results show, how eider breeding corresponded to resource availability approximated by the Atlantic-multidecadal oscillation index (AMO) until numbers were suppressed by the mink invasion. Furthermore, we show that nest relocation to isolated islands is an effective strategy against the native arctic fox but does not buffer adverse effects of mink predation. When predators colonize a given archipelago, condensing nesting into safe islands (inaccessible to predators) may be the only option to maintain a colony.Our study shows how eco-evolutionary experience can shape the outcome of native species responses to invasion.

Introduction

The ways in which humans shape ecosystems worldwide are diverse, fast and drastic with species introductions being among the most important factors threatening local biodiversity. It is often difficult to disentangle these processes, as chlimate change happens simultaneously with species introductions and for the latter often data of the ecosystem from before the introduction are lacking. The North Atlantic, a large and threatened ecosystem, is undergoing a period of climatic change while simultaneously species are moving northward. Within lies the relatively young volcanic island Iceland is a distinct ecosystem more than 300 km from the next landmass. Its terrestrial productivity is low but it is an important breeding ground for a large number of bird species due to highly productive waters around. That makes it 1) very sensitive to climatic changes, especially changes that affect marine biota and 2) vulnerable to introduction of terrestrial species by humans.

Effects of climate on Icelandic biota

Oceanic conditions can change dramatically within a short period with prolonged future impacts on ecosystems (Collie et al. 2004). Many studies on how climate change affects birds at high latitudes are related to distribution of sea ice in spring or how sea ice affects predator access (Chaulk et al. 2006, Lehikoinen et al. 2006, Dey et al. 2017) but in relatively ice-free regions climate change affects populations via food webs (for example via mussel growth, see Waldeck and Larsson 2013), frequencies of storms or inclement weather (Jónsson et al. 2009, 2013) or multi-stressor effects by combinations of these or other unknown mechanisms (Bårdsen et al. 2018). Some species respond to such stochastic regime shifts in oceanic conditions, seemingly without correlations to climate parameters (Agler et al. 1999, Flint 2013). A regime shift is reflected in population data as a “turning point”, i.e. a major shift in trends which happens before or after the climatic regime shift. Collie et al. (2004) defined regime shifts as “low-frequency, high-amplitude changes in oceanic conditions that may be especially pronounced in biological variables and propagate through several trophic levels.” Regime shifts have been implicated in to changes in nutrient flows within ecosystems and subsequent changes in species abundances in the North Atlantic, North Sea and the Pacific (Alvarez-Fernandez et al. 2012, Beaugrand et al. 2014, Hátún et al. 2016).

The common eider (*Somateria mollissima*, hereafter eider) underwent several regime shifts due to climate shifts and predation over the last century. With about 16% of the world population and 32% of the European population of eiders nesting in Iceland, the fluctuations in these colonies are quite important (Birdlife International 2018). Their nest initiation dates respond to warmer climate (D’Alba et al. 2010, Jónsson 2017) and there are mass deaths occured in the especially cool summer of 1918 following a harsh winter (Anonymous 1918, Guðmundsson 1918, Helgason 1919, Guðmundsson 1940, Jónsson et al. 2013). There are two climate indices, the Atlantic Multidecadal Oscillation index (hereafter AMO) and the North Atlantic

Oscillation index (hereafter NAO), both of which influence temperature, nutrient availability and therefore the presence of fish around Iceland (Alheit et al. 2014). The presence of nutrients in the water and its implications for a trophic cascade through plankton to crustaceans and mollusks, especially during the breeding season of the eider, is an important "bottom-up" factor determining nest numbers and densities of eiders (Fauchald et al. 2015). But also predator presence affects nesting of eiders and other seabirds.

Native and introduced predators

Predator presence can affect nesting of eiders and other seabirds (Gerell 1985, Nordström et al. 2002, Barros et al. 2016). Only two mammalian predators live in Iceland (after all, there are 300 km to the next mainland mass): 1) arctic fox (*Vulpes lagopus* hereafter fox) is the most significant predator on ground-nesting birds in the Arctic (Petersen et al. 2015, Waltho & Coulson 2015) and has lived in Iceland since before human settlement (Hersteinsson 2004, Dalerum et al. 2012), and 2) American mink (*Neovison vison* hereafter mink) was introduced in Iceland in 1932 and has been problematic to bird populations, like elsewhere in Europe (Jónsson 2001, Desholm et al. 2002, Nordström and Korpimäki 2004, Chen 2016, Stefansson et al. 2016).

Nesting on offshore islands is considered an adaptation against arctic fox predation (Schamel 1977, Petersen et al. 2015) but such a strategy potentially is less effective against the semi-aquatic mink, unless the islands are somewhat isolated, are farther from shores or offer some sort of safety (Nordström and Korpimäki 2004). Arctic fox is less able to reach island colonies some distances from shore (1 km or greater) than the mink, which can reach the closest offshore islands, i.e. those 5-9 km from the shoreline (Björnsson & Hersteinsson 1991, Jónsson 2001). Mink and arctic fox do not just predate on nests and females, they also elicit nest relocation (Dall 1875, Petersen et al. 2015, Barros et al. 2016), delayed nest initation, nest relocation or even abandonment (Jónsson 2001, Chen 2016).

Most eiders nest therefore off-shore islands (5-9 km from shore or greater) or specific near-shore islands (≤5 km from the shore) which land predators cannot reach (i.e. due to strong tidal currents between adjacent islands or islands and mainland; Björnsson & Hersteinsson 1991). On the islands of Breiðafjörður, West Iceland, eider generally is only affected by avian predators (Common Raven (*Corvus corax*), Gulls (*Larus spp.*), White-tailed sea eagles (*Haliaeetus albicilla*). Most islands were completely safe from land predation by the fox, but things changed with mink introduction in Breiðafjörður in 1948. It played an important role in reductions in local bird populations of near-shore islands, including those of eiders, black guillemot (*Cepphus Grylle*), and Atlantic puffin (*Fratercula arctica*) (Stefansson et al. 2016 and citations therein). Mink dens are found annually on most near-shore Breiðafjörður islands until this day whereas arctic fox dens were rarely found in the 20th century (Hallgrímsson and Petersen 2005). This means, while the eiders evolved a nesting strategy that was effective against arctic fox predation (Petersen et al. 2015), they had significantly lower eco-evolutionary experience with the aptly swimming mink (Saul and Jeschke 2015).

Species nesting in archipelagoes allow study of relationships between patch size, proximity, geographical features and local population stability and also behavioral responses to predators (Nordström and Korpimäki 2004, Petersen et al. 2015). Eider down is harvested in Breiðafjörður for centuries and numbers of nests per island are meticuosly documented per year by some families (Chen 2016). We were able to use a uniquely long time-series of 95 islands in the Brokey archipelago (1892-2014) and a shorter time series of 39 islands in the Purkey archipelago (1986-2012) to answer questions about the relationship of climate and predator presence with eider nest density and location.

Goals and hypotheses

We analysed changes in nest numbers and nest distributions in the Brokey and the Purkey archipelagos. First, we used the total nest numbers of the Brokey archipelago to calculate change points in populations from 1892 to 2014. We were especially interested in potential correlation with the climate indices AMO and NAO, as well as the effect of the arrival of the American mink in Breiðafjörður in 1948. We also took the interaction between mink arrival and climate into account, as we were interested if the population was more climate- or predator driven after 1948. We used the shorter time series combining Purkey and Brokey (1986-2012), as well as of Purkey separately to test for similar climate correlations and a potential effect of the return of the fox into the islands in 1998. While some islands are more or less attractive breeding grounds in the presence of the two predators, we tested if the number of islands changed according to the climate and predation factors in Brokey or Purkey over the respecite time series. Finally, we tested to nest densities on all individual islands of both archipelagos and its correlation with the above parameters plus their area and predator accessibility.

Material and methods

Data sources

Eider nest data

Eider colonies are defined by ownership (Jónsson et al. 2013, Chen 2016), which in our study correspond to the two archipelagos Brokey and Purkey in the south-east of Breiðafjörður (Figure 4.1, Björnsson et al. 1989, Jónsson et al. 2013). We used nest counts done annually in a consistent manner by the respective local eider down collectors (see Jónsson et al. 2013), which maintain their ancestral homes, i.e. the Brokey and Purkey properties, for summer farming, such as small-scale sheep husbandry, eider-down collection and traditional egg collection (Björnsson et al. 1989).

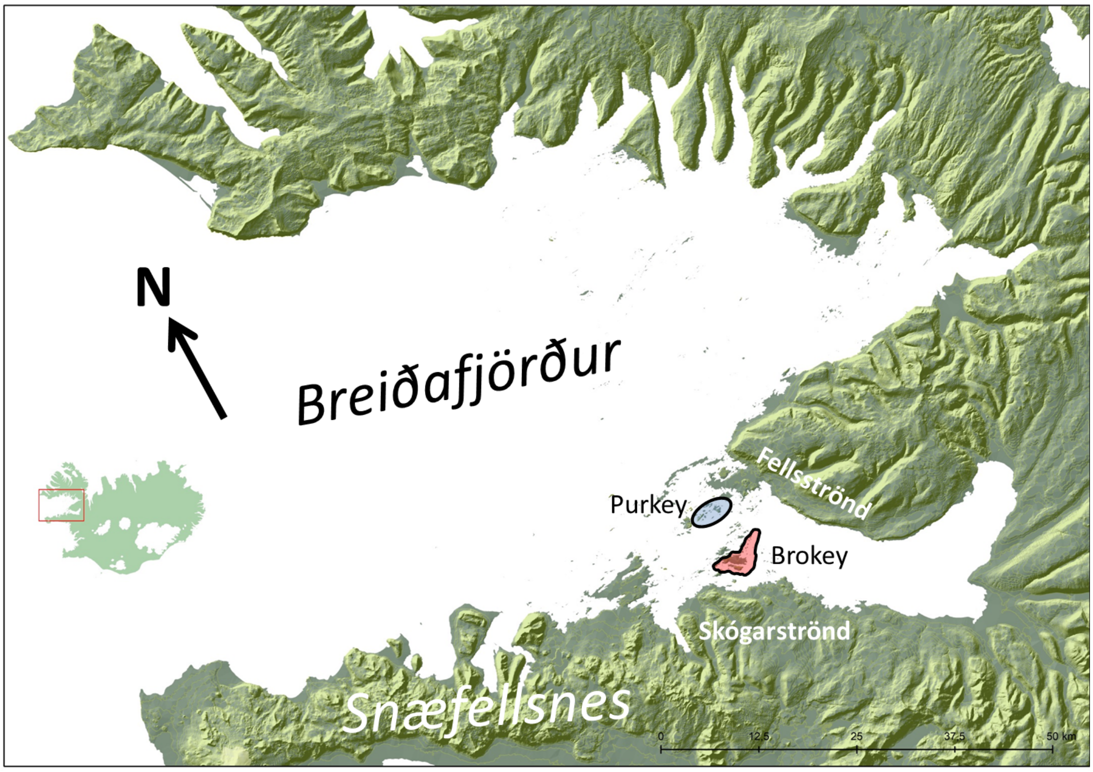

Figure 4.1 - Map of the study area in Breiðafjörður, West Iceland, showing locations of Brokey (Red shape), Purkey (blue oval), mainland municipalities (Fellsströnd and Skógarströnd). Brokey and Purkey are 4 km from each other.

Climate data

In the northern hemisphere, two main indices have been implicated as indicators of climate change affecting biological systems: 1) ambient and oceanic temperatures, often indexed by regional indices such as the Atlantic Multi-decadal Oscillation index (AMO; Trenberth et al. 2017) and 2) changes in frequencies and occurrences of prevailing wind conditions or storminess; in Europe, the North Atlantic Oscillation index (NAO; Hurrell et al. 2016) often is used to explain changes in species abundances. We used both, the AMO and the NAO as these are not co-linear with one another.

Predator indices

Icelandic eider farmers commonly possess ecological knowledge about predators near their properties (Chen 2016). We based our predator indices on interviews (our own and interviews with local eider farmers, found in the Icelandic newspaper database timarit.is), personal accounts and journals of land-owners in Brokey and Purkey from 1900-2014. Consequently, we were able to have precise presence/absence temporal data for the mink and the fox, specific to each archipelago. For Brokey, we marked all years prior to the well-documented mink introduction in 1948 as "mink absent" (0) and all subsequent years as "mink present" (1). The first fox den was recorded in Brokey in 1998, after more than a century of absence. Therefore, in Brokey the fox variable was "fox absent" (0) before 1998 and "fox present" (1) from 1998-2014. The fox can access all islands in Brokey, they were therefore marked as "fox accessible".

For Purkey, the local farmers reported that mink were ever-present 1986-2012, and thus, no mink index was employed for Purkey. The fox index was the same as for Brokey, the years from 1986-1997 were marked as "fox absent" (0) while the years from 1998-2012 were marked as "fox present" (1). There are 14 islands in Purkey that are not fox accessible and were therefore marked as "fox inaccessible" (0), while the other 25 islands were marked as "fox accessible" (1). All these islands were located in the south east of Purkey and are protected by strong tidal currents (Jón Helgi Jónsson of Purkey pers. obs.).

Statistical analyses

We used four different methods of analysis, which we present in the logical order of the research questions we tackled. i) We first used the total number of nests on all islands to look for change points. ii) Then we fitted linear models to predict this total number of nests using the predator and climate variables described above, performed explorative model selection and discuss the best models. iii) The same analysis was performed on the total number of inhabited islands (i.e. islands hosting at least one eider nest in the given year). iv) Finally, we calculated the log(density) of nests on each individual island and performed mixed model analyses using the predator and climate variables and the area of each island as potential predictors. All analyses were performed for the two archipelagos individually as well as both archipelagos combined with the archipelago as an additional potential predictor. The structure of the next sections follows the research questions around the mink arrival in the region in1948 and the return of the fox in 1998. The analyses are described for the two archipelagos separately but joint analyses of the years from 1986-2012 are presented in the supplementary material.

Long-term population dynamics in Brokey

We performed change point analyses in the total nest numbers in Brokey for the years 1892-2014 (Zeileis et al. 2003), using the "strucchange"-package of R (Zeileis et al. 2015). Then we fitted linear models to both the nest numbers and the number of inhabited islands using our climate and predator indices. The full model for the Brokey archipelago was:

[I] total nest number [Brokey] ~ AMO + NAO + mink + foxPresence + AMO:mink + NAO:mink

We performed model selection with the dredge() command of the MuMIn package (Bartón 2013), sorted models by AIC value and calculated their relative AIC weights. To discuss the relative importance of predictors we considered all models with an accumulated relative AIC weight of >0.95.

Both analyses - the change point analysis and the linear model comparison - were performed using the total number of inhabited islands in the in Brokey instead of the total nest number as the dependent variable (see supplement S1).

Behavioural shifts in the Brokey

We used mixed-effects models from the "lme4"-package (Bates et al. 2015) to estimate the effect of climate variables, island characteristics and predator presence on eider nest density of individual islands in. We analyzed the eider nest density in Brokey depending on mink and fox arrival into the area, as well as the interaction of mink and climate variables as well as island area. Therefore, we can estimate which islands with which size were preferred with the arrival of the mink. The full model therefore was:

[II] log(density)[Brokey] ~ area + AMO + NAO + mink + foxPresence + mink:area + mink:AMO + mink:NAO

We used the same model selection method as for the analysis of model [I].

Short-term population dynamics in Purkey

We performed the same change point and model selection analyses with the total nest numbers in the Purkey archipelago from 1986-2012. The full models were:

[III] total nest numbers [Purkey] ~ AMO + NAO + foxPresence

We used the same model selection method as for the analysis of models above. The same analyses were performed using the number of inhabited islands in Purkey as a response variable, as well as using all nest numbers of both archipelagos combined and the number of inhabited islands of both archipelagos (see supplement S1).

Behavioural shifts in the Purkey population

Finally, we estimated the effect of the return of the fox on eider nest density on islands in Purkey, while including the differences in accessibility of individual islands by the fox. Therefore we used the years from 1986 to 2012 and fitted the full model:

[IV] log(density) [Purkey] ~ area + AMO + NAO + foxPresence + foxAccessibility +
foxPresence:foxAccessibility

We used the same model selection method as of the analyses above and fitted models using both datasets combined for the same years (see supplement S1).

Results

Long-term population dynamics and nest relocation in Brokey

We detected 12 change points in the total nest numbers from the Brokey archipelago (see Figure 4.2). Numbers went up in 1896 and 1909 to reach the maximum at just above 2400 nests until 1917 when they dropped to ~1900. Numbers increased again in 1923 but further decreased to ~ 1500 in 1933. The downward trend continued with further decreases in 1939, 1953 and 1971 to the minimum of the study period of below 400 nests from 1971 to 1983. Nest numbers increased fast after 1983 and again in 1986 to ~1700 nests from 1986 to 2002 but then decreased to ~1200 and again in 2010 to values below 900 nests.

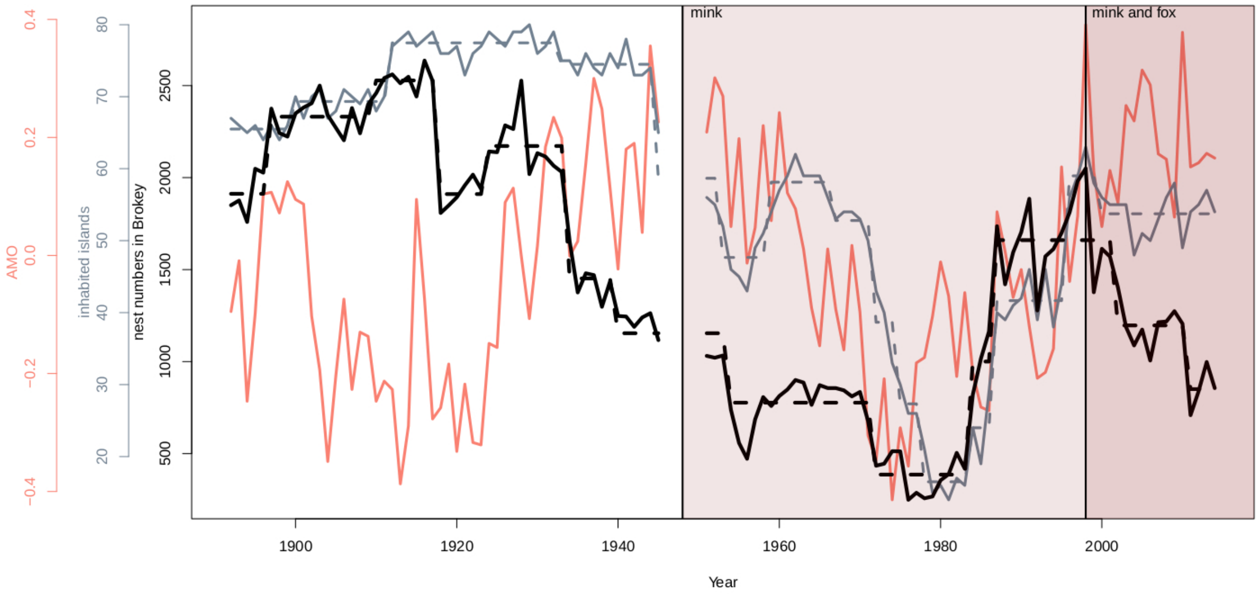

Figure 4.2 - Nest number dynamics of eider nests in Brokey from 1892 to 2014 (black line) as well as its regimes and regime shifts (black dashed line). The grey line shows the numbe rof inhabited islands in the Brokey archipelago, the dashed grey line the respective regimes and regime shifts. The AMO is shown by the salmon coloured line. Mink arrival into Brokey is indicated by a vertical line in 1947 and subsequent background colour change. Fox arrival in 1998 is indicated by a vertical line and further background colour change.

The model comparison for the total nest numbers in Brokey yielded a plateau of six models with similar predictive power and a combined AIC weight of >0.95 (see table 4.1). AMO and mink presence decreased nest numbers in all these models, while their interaction is always positive (Figure 4.2). Our results do not provide evidence for the return of the fox 1998 or changes in NAO to have an effect on total nest numbers in the Brokey archipelago.

Table 4.1 - Results of pairwise model comparison of total nest numbers in Brokey from 1892 to 2014.

Model	ΔAIC	AIC weight
- AMO +NAO - mink + AMO:mink	0	0.308
- AMO + NAO - mink + AMO:mink + NAO:mink	0.66	0.222
- AMO - mink + AMO:mink	1.32	0.16
- AMO + NAO - mink + fox + AMO:mink	1.66	0.134
- AMO - mink + fox + AMO:mink	2.51	0.088
- AMO + NAO - mink + fox + AMO:mink + NAO:mink	2.53	0.087

The number of inhabited islands was highly correlated with the total nest numbers in Brokey over the study period (Pearson's r = 0.73, $p < 0.001$, Figure 4.2, see Appendix D). Total nest numbers and number of inhabited islands have largely overlapping change points and the results of the pairwise model comparison of models predicting the number of inhabited islands in Brokey yielded qualitatively the same results as for nest numbers (see Appendix D).

We did find evidence that eiders changed their nest site in response to the arrival of the mink in Brokey in 1948. As in the total nest number dynamics, AMO and mink arrival were negative predictors for individual island nest density; their interaction being positive (see table 4.2). Additionally, island area appeared as a negative predictor of density with a positive interaction with the mink. The best six models with accumulated relative AIC weight of >0.95 were all possible combinations using these parameters. Our analysis found no evidence that that NAO or the return of the fox affected density or island choice of the eiders in Brokey.

Table 4.2 - Results of pairwise model comparison of the log(density) of nests on individual islands in Brokey from 1892 to 2014.

Model	ΔAIC	AIC weight
- area - AMO + NAO - mink + area:mink + AMO:mink	0	0.356
- area - AMO + NAO - mink + area:mink + AMO:mink + NAO:mink	0.64	0.259
- area - AMO + NAO - mink + fox + area:mink + AMO:mink	1.46	0.172
- area - AMO + NAO - mink + fox + area:mink + AMO:mink + NAO:mink	2.3	0.113
- area - AMO - mink + area:mink + AMO:mink	3.54	0.061

In conclusion, Brokey nest numbers underwent dynamic changes in the years from 1892 to 2014, driven chiefly by long-term climatic dynamics through the AMO and the arrival of the introduced mink. While there were periodical oscillations of eider nest numbers and numbers of inhabited islands with the AMO until 1948, these were broken with the arrival of the mink, indicating its importance as driver of ecosystem processes. Our results further demonstrate, that while the eider generally breed more densely on smaller islands than larger islands in Brokey, this relationship became weaker after the arrival of the American mink. Figure 4.3 illustrates this finding, by showing how the ratio of eider nests found on the 20% largest islands fluctuated between 50- and 60% before the arrival of the mink in 1948 and lies between 60% and 90% after.

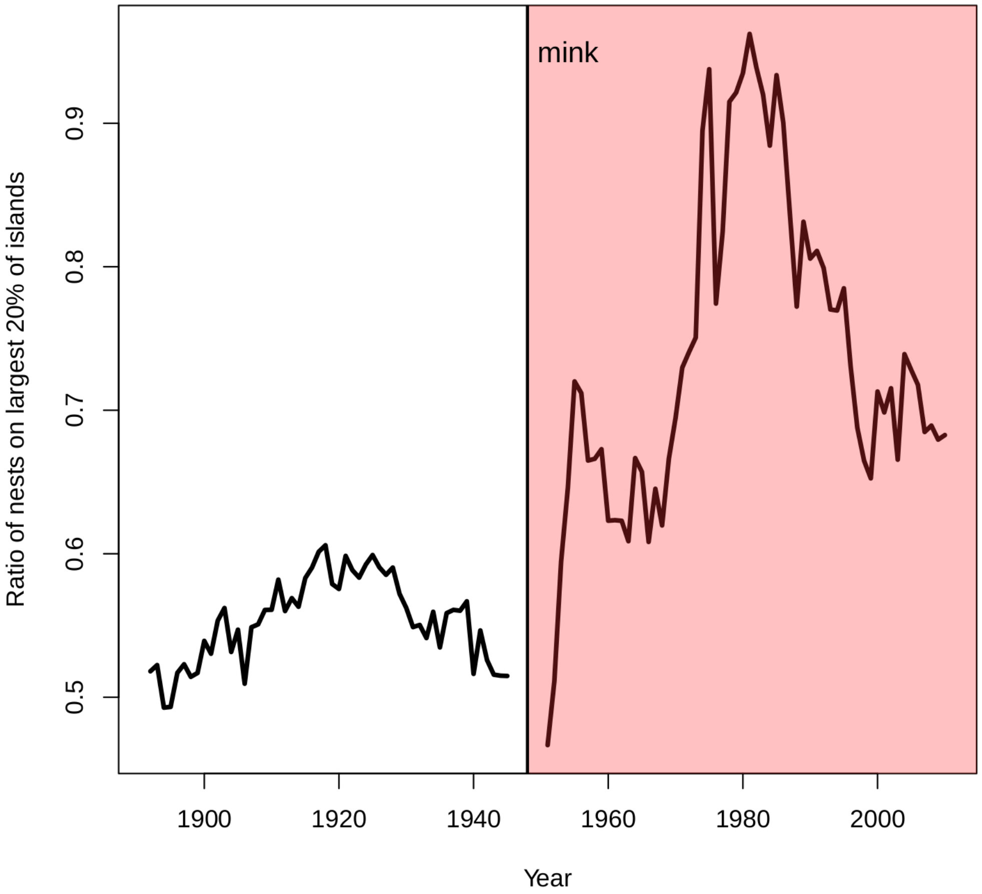

Figure 4.3 - The ratio of nest found on the largest 20% of the islands in Brokey. A vertical line indicates the arrival of the mink in the archipelago with subsequent change in background colour.

Short-term population dynamics and nest relocation in Purkey

There were no change points in nest numbers in the Purkey archipelago from 1986 to 2012 (Figure 4.4). The number of inhabited islands in Purkey decreased drastically, though, with change points in 1998 and 2004 (see Appendix D). half of the islands 1986-2012, with almost 40 inhabited islands before 1998 to just above 20 after 2004 (Figure 4.4). Total nest numbers and number of inhabited islands were not correlated in Purkey (Pearson's r = -0.26, p = 0.19), contrary to their relationship in Brokey. There was no evidence for either the return of the fox, AMO or NAO to predict total nest numbers or the number of inhabited islands in Purkey; the same goes for both archipelagos combined (see Appendix D). In conclusion, numbers of inhabited islands in the Purkey archipelago dropped while nest numbers remained stable.

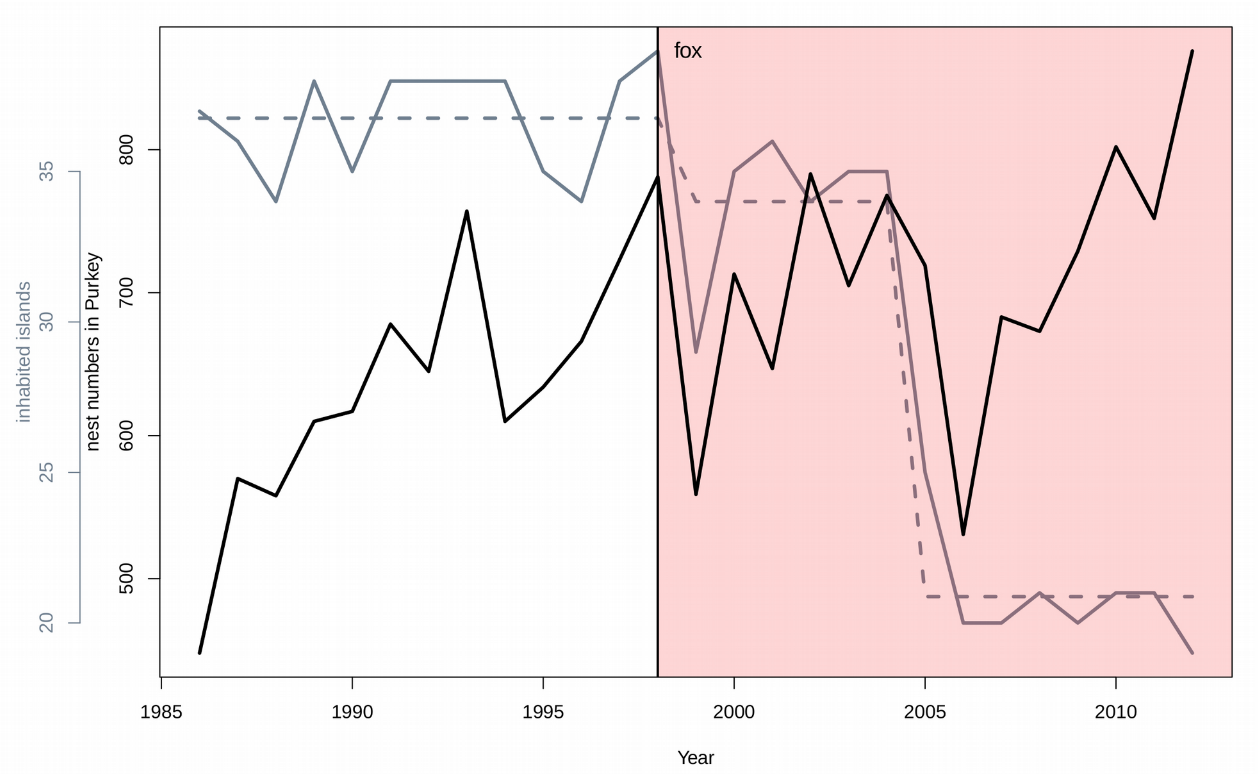

Figure 4.4 - Total nest numbers in Purkey and the number of inhabited islands from 1986 to 2012. There were no regime shifts in the total nest numbers, regimes and regime shifts in the number of inhabited islands are given illustrated by the dashed grey line.

We did find evidence of eider nest relocation in response to the fox arrival in 1998 in Purkey and Brokey. The arrival of the fox and fox accessibility were positive predictors of density, while their interaction was negative, both for the Purkey archipelago as well as both archipelagoes combined (table 4.3 and Appendix D). While there was no evidence for the climatic factors AMO and NAO to have an effect nest density within individual islands, area was always negatively correlated with eider density. In conclusion, the fox drove eiders to nest on more remote islands to avoid nest predation, an apparently effective strategy to buffer declines in the Purkey archipelago.

Table 4.3 - Results of pairwise model comparison of the log(density) of nests on individual islands in Purkey from 1986 to 2012.

Model	ΔAIC	AIC weight
- area + fox + foxAccessible - fox:foxAccessible	0	0.466
- area + NAO + fox + foxAccessible - fox:foxAccessible	1.12	0.266
- area - AMO + fox + foxAccessible - fox:foxAccessible	1.99	0.172
- area - AMO + NAO + fox + foxAccessible - fox:foxAccessible	3.17	0.096

Discussion

Climate fluctuations in Breiðafjörður

We found that before the mink introduction into the Breiðafjörður area in 1948, the Atlantic-multidecadal oscillation index (AMO) was a driver of eider nest numbers in Brokey. The first change point in nest numbers was at the end of the 19th century, when a warm AMO ended and a 25-year long cool AMO began (1901-1925). Nest numbers remained high during this favorable period with high resource abundance, except for a drop around the episodic year of 1918, which was uniquely stochastic and widely reported to have caused mass deaths of live-stock and wildlife, including eiders, oystercatchers, whooper swans etc. (Anonymous 1918, Guðmundsson 1918, Arnþórsson 1979, Ásgeirsson & Jónsson 2017). The year 1918 holds two national records for Iceland: the coldest January on record to date and also the lowest June temperature.

The first of a few change points showing declining nest numbers coincides with a rising AMO but also with the beginning of human de-population, i.e. reduced number of farms in the islands and subsequent urbanization on the mainland in relation to increased fisheries (Anonymous 1960, Björnsson et al. 1989, Kjartansdóttir 2009). Furthermore, new practices and machinery were established in some island farms around 1940 in an attempt to stabilize farming the islands (Skúlason 1970). Nevertheless, humans abandoned most Breiðafjörður island farms; in 1942, 1960 and 1975 there were 26, 8 and 3 island farms inhabited in Breiðafjörður, respectively (Anonymous 1960, 1975; Björnsson et al. 1989).

Nest numbers began long-standing declines after both AMO shifts from cool to warm in 1925 and 1995. There are anecdotal reports that the 1920s were similar to the late 1990s and 2000s in that local people noticed breeding failures among seabirds and an associated “ lack of “healthy sandeel”, such as arctic tern (*Sterna paridisea*), puffin, and kittiwake (*Rissa tridactyla*) (Skúlason 1970, Katz 2014). Thus, during 1926-1962 and 1995-2010 seabirds in Iceland experienced similar, unfavorable oceanic conditions in Iceland or perhaps even the entire Northern Atlantic, during a period of warm AMO.

Environmental changes also affect natural enemies of eiders, i.e. gulls (Larus spp.) benefit from a higher proportion of fish in diets, which correlated with a higher reproductive success (van Donk et al. 2017). But in years the gulls find less of their preferred marine prey, they supposedly rely more on alternative prey such as eggs and young of other birds to feed their young (Guðmundsson 1940). Unfortunately, there are limited population data available on gulls in Iceland and even in the presence of such data, any gull predation effects would also be dependent on context, region or vary by scale (Votier et al. 2008).

The years when eider nest numbers increased 1980-1990 (Jónsson et al. 2013, 2015) were years of recovery in Brokey, after an all-time low in nest numbers in the 1970s, during which period we have no data for Purkey. Causes of the 1980-1990 increase in eider numbers in Iceland are unknown but this decade was a period of cool climate (Hanna et al. 2004), coupled with changed oceanic effects, such as spikes of positive values of the sub-polar Gyre Index, which later turned negative (from 1995 onwards: Hátún et al. 2016) and the migration of cold-water species such capelin (Mallotus villosus) into Icelandic waters (Jónsson 2017). During 1980-1990, capelin fisheries were at record-high in Iceland, and in late winter capelin roe would spill into harbors during off-loading of the fishing boats, allowing large flocks of eiders to forage on the spilled roe; however such practices were abandoned in the 1990s (Jónsson 2017). It is also noteworthy that blue mussel (*Mytilus edulis*), the eider's preferred prey item throughout the range (Waltho and Coulson 2015) attain a greater soft body mass in cooler years, relative to that in warmer years which cause reduced soft body mass (Waldeck and Larsson 2013). Thus, we would expect better nutrient content of mussel and other molluscs in cooler AMO periods compared to warmer AMO periods. Mink introduction in 1948 occurred during an already unfavorable period (warm AMO) when eiders nest numbers declined, either because of climate or possibly lessened emphasis on eider farming (Guðmundsson 1940).

Predation by mink in Brokey

The decline in eider nest numbers after 1950 probably occurred due to combined effects of mink and unfavorable climatic and human conditions, whereas the furthered low in 1972-1983 should only be attributed to mink as this was a cool (favorable) climatic period and there were abundant mink problems reported by Brokey farmer Jón Hjaltalín for this decade (Arnþórsson 1979). We found that mink wiped out eider nesting in many smaller islands and increased the chances of island abandonment after its introduction. Before mink introduction in Brokey, number of islands without nests ranged between 9 and 14 through the first 59 years (1892-1950) but this number more than doubled during the mink-induced low in nest numbers during 1971-1980. Mink generally limit their home-ranges to coastlines (Zabala et al. 2007, Carlsson et al. 2010, Wolff et al. 2015, Palomares et al. 2017) so in the larger islands, eiders will move their nests onto hilltops and central areas which are rarely visited by mink (Anonymous 1949, 1952). Brokey was in decline 2000-2014, which the farmers attributed to the return of the arctic fox in 1998 (Chen 2016). When mink is absent, small islands are preferred by eiders over larger islands because larger islands can support resident arctic foxes, whereas the foxes can only use smaller islands on a temporary basis (Björnsson & Hersteinsson 1991, Petersen et al. 2015, Waltho & Coulson 2015).

Behavior or territoriality of predator (rather than predator numbers) may affect the eiders response to predators (Gerell 1985). Territorial mink have smaller home ranges than non-territorial mink and may thus not visit colonies nearby (Chen 2016). Lastly, eider female experience (possibly via habituation or "learning" with mink or fox may counteract the disturbance effect of the predators (Arnþórsson 1979, Nordström and Korpimäki 2004, Van Den Brink et al. 2012). Newly introduced mink (1948) and subsequent releases of farm mink (1970s) may have caused greatest disturbances thereafter, as nesting eider females were surprised by new predators behaving aberrantly in new surroundings.

During nest initiation, ducks perceive predator presence, possibly by detecting urinal markings from mammals (Eichholz et al. 2012) and eider farmers claim that eiders will hesitate to initiate nesting in particular islands if a mink is present (Chen 2016). Thus, predator effects can be independent of predator numbers but behavioral responses of eider nesting an all-or-nothing response, perhaps to 1-2 animals, leading to island or nest area desertion upon detecting visits of single animals. Eider females avoid mink by nesting away from the shoreline, which explains why there has been more safety in the larger islands or offshore islands (the farmers noted this already in the first mink years; Anonymous 1952). This is shown in our study, the proportion of eiders nesting on large islands where they can nest further away from the shore ("inland") rises significantly after the mink arrives in the archipelago. In Brokey, there are no known islands where they are completely safe from either mink or arctic fox, i.e. islands that offer isolation, which is often the only protection for ground-nesting bird nests against mink (Nordström and Korpimäki 2004, Barros et al. 2016). We would expect such safe islands to fill up with very high nest densities (Jónsson and Lúovíksson 2013) which would not go undetected by eider-down collectors. Such an example was found in Breiðafjörður in 2015-2018, where a small cliff named Helgasker was colonized by 20-30 females within a few years (the authors unpublished data). Eiders can breed in exceptionally high densities when needed or rapidly form new colonies (Waltho & Coulson 2015, Kristjansson and Jónsson 2015); and thus, eiders were quick to settle in safe places in Purkey to successfully cope with the return of the arctic fox into the region.

Predation by arctic foxes in Purkey

The south-east of Purkey is 4 km from the north-east of Brokey (Figure 1), and thus we considered analyzing them as one entity 1986-2012, although our findings show that the two sets of nest numbers behave independently. The shortest distance from Brokey to nearby mainland is 2.5 km. Both colonies have a history of arctic fox and mink problems, especially during colder periods with winter ice (Björnsson et al. 1989, Björnsson & Hersteinsson 1991). Like most islands nearby, Brokey and Purkey employ mink traps year-round and use dogs or additional traps whenever mink are detected. Mink can easily swim to both colonies and if they are eradicated from islands during spring or summer, immigrants re-colonize the archipelagoes in winter (Arnþórsson 1979, Bergur and Páll Hjaltalín, pers. obs). Based on information from the land-owners, we know that for our index of local fox presence: 1) Brokey: when present, arctic fox and mink can access most islands; and 2) Purkey: when present, arctic fox can access all islands except eleven islands in the southeastern part of the archipelago, which are separated by the rest of the archipelago by 200-400 m wide, relatively deep channels with tidal currents (Stangarstraumur and Knarrarbrjótur) that have thus far generally proven impassable to the arctic foxes. Thus, some Purkey islands benefit from a natural barrier to arctic fox and mink traffic whereas there are no such barriers within Brokey.

Nest relocation to safer islands allowed Purkey to maintain increasing nest numbers after 2000. In Purkey, this safe area (14 of 39 islands) highlights how fox presence clump eider numbers (cf. 2005-2012) within safe nesting grounds but eider absence in the remaining 25 islands can be explained by the neighbor island Skáley, which semi-connects Purkey to the mainland and likely provides the arctic foxes with a “land-bridge”. Skáley can be reached on foot from the mainland and Purkey from there by horse at spring low tides (Björnsson et al. 1989); there have been no nesting eiders in Skáley since early 2000s because of arctic fox and mink presence (Authors unpubl. data). In Denmark and United Kingdom red fox (*Vulpes vulpes*) may suppress formation of new colonies or shift eiders into forming new colonies in safer areas (Waltho & Coulson 2015) but Iceland is the only place where this has been documented for arctic fox (Hersteinsson 2004).

Control efforts against the American mink

The relationship between humans and animal species of Breiðafjörður is particular, historically and to this day (Björnsson et al. 1989, Jakobsson 2016). From the first settlements on, people on the islands and the mainland were dependent on using the available animal species for food, clothing and other materials (Björnsson et al. 1989, Garðarsson & Jónsson 2019). Some species highly benefitted from this interaction, as we found that the human presence on the islands actually stabilised eider nest populations. However, the introduction of the mink for pelt farming had strong detrimental effects on the avifauna in the region (Jónsson 2001). These predation effects can only partially be ameliorated by behavioural adaptations in bird species like the eider. This study adds to the evidence that mink control efforts are necessary to keep threatened species like the eider in Iceland.

Studies indicate mixed results from predator control efforts, which began in the 1950s in Iceland. In Finland, eider nest densities did not respond to mink removal in a 9-year long mink removal study (1993-2001; Nordström et al. 2002), which may be explained by a concurrent decline of the Finnish eider population at the time. Conversely, eider populations in Svalbard benefitted from predator control (including that of arctic fox but mink is not found in Svalbard), where predator control increased within-island population growth and also carrying capacity and probability of immigration (Hanssen et al. 2013). Similarly, the Aleutian Islands have been slowly re-colonized by eiders following eradication of imported arctic fox populations (Petersen et al. 2015). Based on our interviews in this study, the timing of the mink control, i.e. ideally timed just before nest initiation, is crucial for the control effort‘s success (Þorvaldur Björnsson pers. com).

Conclusions

The eiders' world is not the same with the presence of mink, the introduced predator; small islands (the historical refuge from arctic fox, the only land mammal) became dangerous places and large islands more attractive. Simultaneously, arctic fox limits eider nest site choices. While the effects of climate change still may play a role for eiders in Iceland, some of it is masked by the dominant role of the American mink in the overall ecosystem. These findings show that local predator presences vs. absences are just as likely to dramatically change nest numbers as are large-scale climatic variables, and can even off-set relationships with climate change. Our results further indicate, that a plastic change in behavior - here: nest site choice - can buffer detrimental effects of predation but are less effective with novel than with known predators.

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References

Agler, B. A. et al. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. - Waterbirds 22: 98–103.

Alheit, J. et al. 2014. Reprint of ‘Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic’. - J. Mar. Syst. 133: 88–102.

Alvarez-Fernandez, S. et al. 2012. Temporal changes in plankton of the North Sea: Community shifts and environmental drivers. - Mar. Ecol. Prog. Ser. 462: 21–38.

Anonymous (1918, September 1918). Óáran við Breiðafjörð [A bad year for Breiðafjörður] Morgunblaðið. Retrieved from http://timarit.is/view_page_init.jsp?issId=98451&pageId=1203195&lang=is&q=Kafb%E1tsminnismerki%20%ED%20Kiel

Anonymous (1949, May 5). Villiminkurinn er að eyða öllu fuglalífi Breiðafjarðareyja. [Feral mink is destroying all birdlife in Breiðafjörður] Tíminn. Retrieved from http://timarit.is/view_page_init.jsp?issId=58027&pageId=1008420&lang=is&q=Villiminkarnir

Anonymous (1952, July 8). Vargur í varpi Eyjabænda við sunnanverðan Breiðafjörð. [Predators in island farm bird colonies in south Breiðafjörður] Retrieved from http://timarit.is/view_page_init.jsp?issId=58954&pageId=1016046&lang=is&q=%ED%20vargur%20%ED%20Eyjab%E6nda%20vi%F0%20sunnanver%F0an

Anonymous (1960, May 20). Eggjatekja góð á Breiðafjarðareyjum. [Good egg harvest in Breiðafjörður islands] Morgunblaðið. Retrieved from http://timarit.is/view_page_init.jsp?issId=111253&pageId=1328710&lang=is&q=%E1%20Brei%F0afjar%F0areyjum%20g%F3%F0

Anonymous (1975, August 29) Hvallátur í eyði – aðeins þrjár Breiðafjarðareyjar eftir í byggð. [Farm in Hvallátur abandoned – only three Breiðafjörður Islands remain inhabited] Tíminn. Retrieved from http://timarit.is/view_page_init.jsp?issId=270896&pageId=3864840&lang=is&q=%ED%20Hvall%E1tur%20%ED%20ey%F0i%20%ED

Arnþórsson, G. (1979, January 12). 40-100 minkar drepnir á ári í Brokey á Breiðafirði [Interview with eider farmer Jón Hjaltalín of Brokey]. Alþýðublaðið. Retrieved from http://timarit.is/view_page_init.jsp?issId=236380&pageId=3223150&lang=is&q=40-100%20minkar%20drepnir

Ásgeirsson Á., & Jónsson, J. E. (2017) Heyskapur, dúntekja og kofnafar í Rifgirðingum í byrjun 20. aldar [Haying, down collection and puffin harvest in Rifgirðingar in the early 20th Century] Breiðfirðingur 65, 60–64 (In Icelandic).

Bårdsen, B. J. et al. 2018. Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird. - Ecosphere in press.

Barros, Á. et al. 2016. Behavioural plasticity in nest-site selection of a colonial seabird in response to an invasive carnivore. - Biol. Invasions 18: 3149–3161.

Bartón, K. 2013. MuMIn: multi-Model Inference, R package version 1.9. https://CRAN.R-project.org/package=MuMIn

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - J. Stat. Softw. in press.

Beaugrand, G. et al. 2014. Detecting plankton shifts in the North Sea: A new abrupt ecosystem shift between 1996 and 2003. - Mar. Ecol. Prog. Ser. 502: 85–104.

BirdLife International (2019) Species factsheet: Somateria mollissima. Downloaded from http://www.birdlife.org on 12/12/2019.

Björnsson, Á., Gíslason, E. G., & Petersen, Æ. (1989) Breiðafjarðareyjar. [Islands of Breiðafjörður]. Árbók Ferðafélags Íslands [Yearbook of the Iceland Touring Association]. Reykjavík: Ferðafélag Íslands. (In Icelandic)

Björnsson, Þ., & Hersteinsson, P. (1991). Mink in southern Breiðafjörður Bay. Wildlife Management News 9: 3-11. (In Icelandic with an English summary) https://issuu.com/skotvis/docs/fv9

Carlsson, N. O. L. et al. 2010. Long-term data on invaders: When the fox is away, the mink will play. - Biol. Invasions 12: 633–641.

Chaulk, K. G. et al. 2006. Extinction, colonization, and distribution patterns of common eider populations nesting in a naturally fragmented landscape. - Can. J. Zool. 84: 1402–1408.

Chen, G. (2016) Ethnoecology of Eider Farmers in Iceland: Typology of a Multiform Experience. Master’s thesis, Joint program with the French National Museum of Natural History and the Paris-Sorbonne University (In French with an English summary). An English version retrieved from: http://rannsoknasetur.hi.is/sites/rannsoknasetur.hi.is/files/pdfs_snaefellsnes/report_english_gilles_25_april.pdf

Collie, J. S. et al. 2004. Regime shifts: Can ecological theory illuminate the mechanisms? - Prog. Oceanogr. 60: 281–302.

D’Alba, L. et al. 2010. Advances in laying date and increasing population size suggest positive responses to climate change in Common Eiders *Somateria mollissima* in Iceland. - Ibis (Lond. 1859). 152: 19–28.

Dalerum, F. et al. 2012. The influence of coastal access on isotope variation in icelandic arctic foxes. - PLoS One 7: 1–8.

Dall, W. H. 1875. Notes on the avifauna of the Aleutian Islands, especially those west of Unalaska. Proceedings of the California Academy of Sciences 5: 270–281.

Desholm, M. et al. 2002. Status of the Baltic/Wadden Sea population of the Common Eider *Somateria mollissima*. - Wildfowl 53: 167–203.

Dey, C. J. et al. 2017. Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. - Glob. Chang. Biol. 23: 1821–1831.

Eichholz, M. W. et al. 2012. Experimental evidence that nesting ducks use mammalian urine to assess predator abundance. - Auk 129: 638–644.

Fauchald, P. et al. 2015. The status and trends of seabirds breeding in Norway and Svalbard - NINA Report 1151.

Flint, P. L. 2013. Changes in size and trends of North American sea duck populations associated with North Pacific oceanic regime shifts. - Mar. Biol. 160: 59–65.

Garðarsson, A., & Jónsson, J.E. (2019) Numbers and distribution of the Great Cormorant in Iceland: Limitation at the regional and metapopulation level. Ecology & Evolution 9: 3984–4000. https://doi.org/10.1002/ece3.5028

Gerell, R. 1985. Habitat selection and nest predation in a common eider population in southern Sweden. - Ornis Scand. 16: 129–139.

Guðmundsson, G. (1918, July 2) Af Barðaströnd. Fréttir (In Icelandic). Retrieved from: http://timarit.is/view_page_init.jsp?pubId=179&lang=is

Guðmundsson, F. (1940) Æðarvarp og dúntekja á Íslandi. [Eider husbandry and eiderdown yield in Iceland] Annex to motions to the Icelandic Parliament regarding I. Protection of common eider and ii. Destruction of greater black-backed gull. 18 pages. (In Icelandic)

Hallgrímsson, G. Þ., & Petersen, Æ. (2005). Stöðuskýrsla um náttúrufarsrannsóknir á Breiðafirði. [Status report on nature research in Breiðafjörður]. Reykjavík: Breiðafjarðarnefnd. (In Icelandic). Retrieved from: https://rafhladan.is/bitstream/handle/10802/4145/NI-05014.pdf?sequence=1

Hanna, E. et al. 2004. An analysis of Icelandic climate since the nineteenth century. - Int. J. Climatol. 24: 1193–1210.

Hanssen, S. A. et al. 2013. A natural antipredation experiment: Predator control and reduced sea ice increases colony size in a long-lived duck. - Ecol. Evol. 3: 3554–3564.

Hátún, H. et al. 2016. An inflated subpolar gyre blows life toward the northeastern Atlantic. - Prog. Oceanogr. 147: 49–66.

Helgason, E (1919, January 1). Árið 1918. [The year 1918] (In Icelandic). Búnaðarrit (pp. 89-95) Retrieved from: http://timarit.is/view_page_init.jsp?issId=314507&pageId=4939550&lang=is&q=%E1ri%F0%201918%20%C1ri%F0%201918%20%E1ri%F0%201918

Hersteinsson, P (ed). 2004. Spendýr [Mammals of Iceland] Reykjavík: Vaka-Helgafell. (In Icelandic).

Hurrell, James & National Center for Atmospheric Research Staff (Eds). Last modified 07 Nov 2017. "The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (station-based)." Retrieved from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based.

Jakobsson, S. (2016) Saga Breiðafjarðar [History of Breiðafjörður]. Háskólaútgáfan, Reykjavík. (In Icelandic).

Jónsson, J. (2001) Æðarfugl og æðarrækt. [Eider and eider husbandry in Iceland]. Reykjavík: Skrudda. (In Icelandic)

Jónsson, J. E. and Lúovíksson, S. J. 2013. A choice between two adjacent islands: Is switching nest sites related to weather or nest density in the Common Eider (*Somateria mollissima*)? - Ornis Fenn. 90: 73–85.

Jónsson, J. et al. 2009. Seasonal weather effects on the common eider, a subarctic capital breeder, in Iceland over 55 years. - Clim. Res. 38: 237–248.

Jónsson, J. E. et al. 2013. Relationships between Long-Term Demography and Weather in a Sub-Arctic Population of Common Eider. - PLoS One in press.

Jónsson, J. E. (2017) Eru tengsl milli æðarvarps og loðnugengdar? [Are capelin stocks correlated to eider nest numbers?] Náttúrufræðingurinn 87, 45–51. (In Icelandic with an English summary).

Katz, C. 2014. Iceland's Seabird Colonies Are Vanishing, With "Massive" Chick Deaths. National Geographic online. Retrieved from https://news.nationalgeographic.com/news/2014/08/140827-seabird-puffin-tern-iceland-ocean-climate-change-science-winged-warning/

Kjartansdóttir Þ. (2009) „Hver einn bær á sína sögu, sigurljóð og raunabögu.“ Lífið í Skáleyjum á Breiðafirði á 19. og 20. öld [Life in Skáleyjar archipelago, Breiðafjörður, in 19th and 20th centuries] (In Icelandic). BA thesis, University of Iceland http://hdl.handle.net/1946/3023

Kristjansson, T. O. and Jónsson, J. E. 2015. Cooperative incubation behaviour in a super dense Common Eider Somateria mollissima colony. - Bird Study 62: 146–149.

Lehikoinen, A. et al. 2006. Winter climate affects subsequent breeding success of common eiders. - Glob. Chang. Biol. 12: 1355–1365.

Nordström, M. and Korpimäki, E. 2004. Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. - J. Anim. Ecol. 73: 424–433.

Nordström, M. et al. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. - Ecography (Cop.). 25: 385–394.

Palomares, F. et al. 2017. Activity and home range in a recently widespread European mink population in Western Europe. - Eur. J. Wildl. Res. in press.

Petersen, M. R. et al. 2015. Re-colonization by common eiders Somateria mollissima in the Aleutian Archipelago following removal of introduced arctic foxes Vulpes lagopus. - J. Avian Biol. 46: 538–549.

Saul, W.-C. C. and Jeschke, J. M. 2015. Eco-evolutionary experience in novel species interactions. - Ecol. Lett. 18: 236–245.

Schamel, D. 1977. Breeding of the Common Eider (*Somateria mollissima*) on the Beaufort Sea Coast of Alaska. - Condor 79: 478–485.

Skúlason, B. (1970). Áratog, þættir úr atvinnusögu Breiðfirðinga. Reykjavík: Leiftur.(In Icelandic)

Stefansson, R. A. et al. 2016. A tale of conquest and crisis: invasion history and status of the American mink (*Neovison vison*) in Iceland. - Acta Biol. 23: 87–100.

Trenberth, Kevin, Zhang, Rong & National Center for Atmospheric Research Staff (Eds). Last modified 03 Mar 2017. "The Climate Data Guide: Atlantic Multi-decadal Oscillation (AMO)." Retrieved from https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo.

Van Den Brink, V. et al. 2012. Melanic color-dependent antipredator behavior strategies in barn owl nestlings. - Behav. Ecol. 23: 473–480.

van Donk, S. et al. 2017. The most common diet results in low reproduction in a generalist seabird. - Ecol. Evol. 7: 4620–4629.

Votier, S. C. et al. 2008. Using inter-colony variation in demographic parameters to assess the impact of skua predation on seabird populations. - Ibis (Lond. 1859). 150: 45–53.

Waldeck, P. and Larsson, K. 2013. Effects of winter water temperature on mass loss in Baltic blue mussels: Implications for foraging sea ducks. - J. Exp. Mar. Bio. Ecol. 444: 24–30.

Waltho, C., & Coulson, J. (2015) The Common Eider. London: T & AD Poyser.

Wolff, P. J. et al. 2015. Habitat selection by American mink during Summer is related to hotspots of crayfish prey. - Wildlife Biol. 21: 9–17.

Zabala, J. et al. 2007. Winter habitat preferences of feral American mink *Mustela vison* in Biscay, Northern Iberian Peninsula. - Acta Theriol. (Warsz). 52: 27–36.

Zeileis, A. et al. 2003. Testing and dating of structural changes in practice. - Comput. Stat. Data Anal. 44: 109–123.

Zeileis, A. et al. 2015. Package ‘strucchange’ in R. - R CRAN Repos. Rep.: 1–69.

Appendix D

Long-term population dynamics in Brokey

Change point analyses of number of inhabited islands in Brokey

The 14 breakpoints in the number of inhabited islands are in up in 1899 and 1911, where it stays at the absolute maximum until 1932 and further decreases in 1944 and 1952, and after an increase 1958 goes down at 1965, 1971, 1974 and to the absolute minimum between 1977 and 1983. After further increases in 1986 and 1995 it goes down in 2000 again.

Linear models - Number of inhabited islands

We fitted linear models using the same predictor variables as for the total nest numbers in Brokey, but using the number of inhabited islands (islands with at least one nest in the given year) as a response variable. The full model therefore was:

[SI] number of inhabited islands[Brokey] ~ AMO + NAO + mink + fox + AMO:mink + NAO:mink

The results of the pairwise model comparison of models predicting the number of inhabited islands in Brokey yielded strikingly similar results, there was a plateau of six similarly strong models (see table D.1), all possible combinations using the interaction of AMO and mink arrival. Again, the numbers of inhabited islands decreases with high AMO and with the arrival of the mink, their interaction is positive.

Table D.1 - Results of pairwise model comparison of the number of inhabited islands in Brokey from 1892 to 2014.

Model	ΔAIC	AIC weight
- AMO - NAO - mink + AMO:mink	0	0.281
- AMO - NAO - mink + foxPresence + AMO:mink	0.29	0.243
- AMO - mink + AMO:mink	1.48	0.134
- AMO - NAO - mink + AMO:mink -NAO:mink	1.52	0.132
- AMO - NAO - mink + foxPresence + AMO:mink - NAO:mink	1.56	0.129
- AMO - mink + foxPresence + AMO:mink	2.49	0.081

Short-term population dynamics in Purkey

Linear models - total nest numbers and number of inhabited islands

The results of the linear model comparisons for the total number of nests on all islands in Purkey were inconclusive (table D.2). There is no clear predictor of total nest numbers in Purkey and the null model is among the six best models with accumulated AIC weight > 0.95.

Table D.2 - Results of pairwise model comparison of total nest numbers in Purkey from 1986 to 2012.

Model	delta-AIC	AIC weight
foxPresence	0	0.424
AMO	1.54	0.198
AMO + foxPresence	2.46	0.124
NAO + foxPresence	2.77	0.106
1	4.21	0.052
AMO + NAO	4.23	0.051

The number of islands, however, dropped with the arrival of the fox, it is a negative predictor in all four best models (table D.3).

Table D.3 - Results of pairwise model comparison of the number of inhabited islands in Purkey from 1986 to 2012.

Model	delta-AIC	AIC weight
- foxPresence	0	0.601
+ NAO - foxPresence	2.56	0.167
- AMO - foxPresence	2.71	0.155
- AMO + NAO - foxPresence	5.58	0.037

Both archipelagos combined

Change point analyses

We found one change point in the total nest numbers of both archipelagos combined in the year 2002 (Figure D.1). It constitutes a decrease, which matches the change point in the Brokey nest dynamics. There were two change points in the dynamics of numbers of inhabited islands in both islands combined, one upwards shift in 1995 and a decrease in 2004.

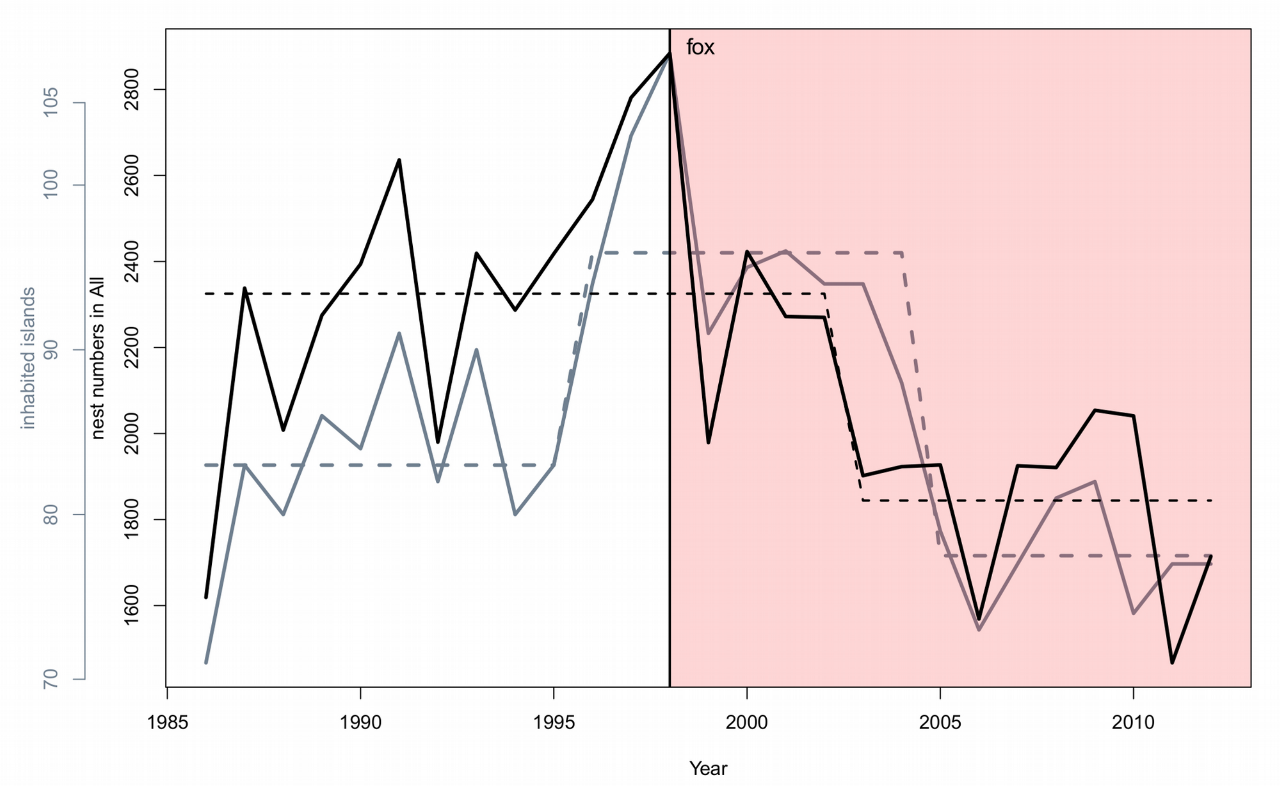

Figure D.1 - Nest number dynamics of eider nests in Brokey and Purkey combined from 1986 to 2012 (black line) as well as its regimes and regime shifts (black dashed line). The grey line shows the number of inhabited islands in both archipelagos, the dashed grey line the respective regimes and regime shifts. Fox arrival in 1998 is indicated by a vertical line and background colour change.

Linear models

The model comparison of linear models to predict total nest numbers in both archipelagos and the sum of inhabited islands of both archipelagos gave no evidence for AMO, NAO or fox arrival to be a significant predictor. In both cases, the null model was the best model (tables D.4 and D.5).

Table D.4 - Results of pairwise model comparison of total nest numbers in both archipelagos combined from 1986 to 2012.

Model	delta-AIC	AIC weight
1	0	0.431
- AMO	2	0.158
- foxPresence	2.19	0.144
NAO	2.26	0.139
- AMO + NAO	4.7	0.041
- AMO - foxPresence	4.76	0.040

Table D.5 - Results of pairwise model comparison of the number of inhabited islands in Purkey from 1986 to 2012.

Model	delta-AIC	AIC weight
1	0	0.305
foxPresence	0.12	0.288
AMO	1.86	0.121
- NAO	2.44	0.09
foxPresence + NAO	2.8	0.075
- AMO + foxPresence	2.85	0.073

Inter-island migration

The results of the model comparison to predict log(density) of all islands of both archipelagos combined are qualitatively the same as for the Purkey archipelago alone (see table D.6): fox presence incresed density, but only on fox-inaccessible islands (negative interaction between fox accessibility and fox presence). There is no evidence for AMO or NAO to be predictors of nest density. The overall densitity of eider nests was lower in Purkey than in Brokey.

Table D.6 - Results of pairwise model comparison of the log(density) of nests on individual islands in both archipelagos from 1986 to 2012.

Model	delta-AIC	AIC weight
- Purkey - area + fox - foxAccessible - fox:foxAccessible	0	0.458
- Purkey - area + NAO + fox - foxAccessible - fox:foxAccessible	1.36	0.232
- Purkey - area + AMO + fox - foxAccessible - fox:foxAccessible	1.68	0.198
- Purkey - area + AMO + NAO + fox - foxAccessible - fox:foxAccessible	2.82	0.112

Chapter 5: Of mink and men: socio-economic factors influence the hunting bag of American mink in Europe and North America

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Stille D, Ruland F, Stefánsson RA, Jeschke JM. Of mink and men: socio-economic factors influence the hunting bag of American mink in Europe and North America.

Abstract

Hunting bag series are widely used and often the only long-term data available for assessing population dynamics of game species. However, such data are prone to influences by extrinsic factors. Although a correction for hunting effort is often recommended when dealing with harvest data, reliable data on hunting effort are rarelyavailable, and the influence of other socio-economic factors on harvest data has not been addressed sufficiently. We present a new approach to the use of harvest data, using the American mink as a case example. We hypothesized that although population dynamics of this successful invader are encapsulated in the hunting bag series, they are masked by extrinsic effects. We thus analysed the influence of socio-economic factors on hunting bag data, then corrected the data for these factors and finally investigated whether the corrected data show so-called boom-bust dynamics. The boom-bust concept posits that strong population declines and fluctuations are typical phenomena in invasive populations. Recent declines in mink hunting bag series of several countries apparently support this concept. Our study focuses on three European countries where the mink is invasive (Denmark, Germany, Iceland) and the USA where it is native, with data covering 19 to 46 years per country. We found strong influences of socio-economic factors on mink hunting bag data, particularly fur price and mink production on farms. After correcting the data for these factors, boom-bust dynamics were not found to be a general phenomenon in invasive mink populations. Our findings suggest that hunting bag data should be controlled for socio-economic factors, particularly for animals with a socio-economic value such as the American mink.

Keywords: Boom-bust dynamics, Fur farming, Hunting bag, Invasive species, Regime shifts

Introduction

The American mink (*Neovison vison*, Schreber 1777), a mammal of the family Mustelidae, is known for its valuable fur. In its native range from Canada and Alaska down to New Mexico, the mink has been among the most hunted furbearer species for centuries (Obbard et al. 1987), and fur trade has been of significant economic importance in North America (Spraakman and Wilkie 2000). In the late 19th century, when the populations of wild mink began to suffer from excessive hunting, first experiments for breeding mink on farms were conducted (Nituch et al. 2011). Starting in the 1920s, American mink have been imported to several European countries for fur farming, and first mink farms were founded in France, Scandinavia and the United Kingdom (Macdonald and Harrington 2003). Within decades, escaped or released farm animals established populations in the wild and by 1960 the American mink had been naturalised in at least 16 European countries (Bonesi and Palazon 2007), making it one of the most successful invasive species in Europe (Nentwig et al. 2010).

The invasion history of the American mink is distinct from other biological invasions. Unlike other invasive species that spread uncontrollably after one or several releases of few individuals, the invasive populations of the American mink in Europe have been characterised by a continuous supplementation with farm mink over a long time period. Despite being one of the most destructive invasive species in Europe (Genovesi et al. 2012; Nentwig et al. 2018), the American mink is still kept on farms for fur production in many European countries and in 2016 mink farms in Europe accounted for 70% of the global mink production (International Fur Trade Federation 2003; Kopenhagen Fur 2016a). Escapees from these farms influence the dynamics of established feral populations to this day (Hammershøj et al. 2005). This constant restocking of feral populations by escaped or released farm animals might have helped to overcome genetic drift and genetic bottlenecks that often occur in populations with a small founder population (Allendorf and Lundquist 2003). In Norway at least 6 subspecies of mink originating from different climate zones have been used for fur farming, possibly leading to a high degree of genetic variability in the feral mink population (Bevanger and Henriksen 1995). In contrast to other invasive species with genetically less diverse founder populations (Simberloff 2009), its multi-subspecies background might have enabled the American mink to rapidly and permanently colonise the greater part of Europe covering several climate zones, from northern Norway to southern Spain (Bonesi and Palazon 2007).

Invasive species have significant impact on native ecosystems, and terrestrial vertebrates have been identified as the most destructive invaders (Robertson et al. 2017). Many publications emphasise the destructive effect of invasive mink on native species (e.g. Manchester and Bullock 2000; Banks et al. 2008). Invasive American mink have been documented to cause damage to a wide range of local wildlife, from crustaceans (Reynolds 1988; Fischer et al. 2009), fish (Zschille et al. 2014) and amphibians (Ahola et al.

2006) to birds (Ferreras and Macdonald 1999; Nordström and Korpimäki 2004) and mammals (Rushton et al. 2000; Brzeziński et al. 2010; Põdra et al. 2013).

Due to its impact on native species, rapid colonisation and well documented invasion history, the American mink is among the best studied invasive species. As furbearers are notoriously hard to census, harvest data have been widely used to assess the population status of the American mink (Bowman et al. 2007). For several countries, severe declines in the annual harvest numbers and mink abundance have been reported, among others in Iceland since 2003 (Magnusdottir et al. 2014; Stefansson et al. 2016), Sweden since 1988 (Carlsson et al. 2010), United Kingdom since the late 1980s (Bonesi et al. 2006) and Canada since the 1950s, with a sharp decline since 1987 (Bowman et al. 2007; Nituch et al. 2011). There exists a variety of hypotheses covering local and global explanations for this decline, but overall there is no definite conclusion about the reasons for this widespread phenomenon.

One possible interpretation of this pattern of rapid growth and spontaneous decline found in the mink hunting bag series is seeing it as an example of boom-bust dynamics. According to the boom-bust concept, an invasive species' population increases during a “boom” phase to an unsustainable peak and then undergoes an apparently spontaneous severe decline (the “bust” phase), sometimes all the way to local extinction of invasive populations that had been well established for decades (Simberloff and Gibbons 2004; Strayer et al. 2017). These dramatic population declines are often considered typical for abundance data of invasive species (Lester and Gruber 2016). However, there is conflicting information in the literature about how common and frequent these dynamics are for invaders (Strayer et al. 2017). In most studies in ecology, boom-bust dynamics are characterised merely based on the observed decline from a peak value (Simberloff and Gibbons 2004), but simulations showed that this method is prone to severe bias towards the detection of boom bust dynamics, especially in noisy data sets (Strayer et al. 2017).

For the detection of boom-bust dynamics, as for many other important questions in ecology and evolutionary biology, long-term data are needed (Clutton-Brock and Sheldon 2010). However, long time series of reliable data are scarce for most invasive species (Strayer et al. 2006) and often hunting bag series are the only long-term data available (Imperio et al. 2010). Hunting bag data, on the other hand, are prone to influences by extrinsic factors, e.g. changing hunting effort, and may not always be a reliable proxy for population size (Ranta et al. 2008). If harvest data are used for analysis of population dynamics, a correction for hunting effort is recommended to reveal the underlying patterns of population change (Sandström et al. 2014). Yet data on hunting effort are not collected in most countries (Astrid Sutor, German Hunting Association (DJV), 14 December 2017, pers. comm.). For game species that are hunted for sport or food by a majority of hunters, data on hunting licences or game firearms might be used as a proxy for hunting effort (Blanco-Aguiar et al. 2012; Herruzo and Martinez-Jauregui 2013). The mink, however, is not commonly hunted for recreational purposes or personal use, but mostly to mitigate negative effects on native wildlife and only a minority of (specialized) hunters in each country commit to the laborious trapping of this species (Stien and Hausner 2018). Additionally, hunting laws (e.g. the ban of certain spring traps in the EU), traditions and hunting methods undergo changes, and the hunting efficiency is dependent on these factors (Little and Crowe 1993). Thus, in order to correct for hunting effort even accurate data on time spent per kill might be insufficient. In consequence, hunting bag raw data have been mostly used without effectual control for extrinsic influences, although the limitations of harvest data are known and a correction for hunting effort is recommended (Hammershøj et al. 2006; Imperio et al. 2010).

Still, harvest data are often the best data available and despite all disadvantages of great interest for ecological studies. In this study, we present a new approach to the use of hunting bag data where data on hunting effort are not available. We identified extrinsic factors that potentially influence the hunting bag of feral mink populations in Europe and native populations in North America, and addressed the question whether invasive American mink populations show boom-bust dynamics. Our specific hypotheses were as follows:

Hypothesis H1: Extrinsic factors affect the mink hunting bag. (H1.1) Fur price influences hunting effort, as hunters are believed to be more motivated to trap mink when furs sell for a higher price. Hence, a higher price is supposed to lead to a higher hunting bag. An exception is Iceland where pelts of feral mink are not sold, but there is a bounty on mink. (H1.2) Mink production (in furs produced or breeding stock on farms) is positively correlated with the hunting bag, as more mink on farms are assumed to lead to more escapees and consequently to a higher number of feral mink. A law in Denmark aiming to restrict mink escapes was expected to mitigate the dependency of the hunting bag on the mink production. The lower demand for mink furs after the German reunification was expected to have a negative impact on the hunting effort. (H1.3) Hunting bag raw data show more fluctuations and consequently a higher number of change points than the residuals of the best fitting models.

Hypothesis H2: Following the boom-bust concept (Simberloff and Gibbons 2004; Strayer et al. 2017), invasive populations more frequently show a pattern of rapid growth followed by a fast decline than native populations. Consequently, we expected more detected change points in the residuals of invasive than native populations.

Material and Methods

Data

We used hunting bag data to analyse population dynamics of the alien, invasive American mink in Denmark, Germany and Iceland, and of the native mink population in the USA. These countries were chosen for the following reasons: First, long-term data on hunting bag and socio-economic factors, such as fur price and mink production were readily available. Second, invasion history and population dynamics of the American mink in Denmark and Iceland are relatively well documented in the literature, providing a solid theoretical background for model fitting. Third, the German time series was particular due to the German reunification in 1990 and its potential consequences on hunting bag, making it an interesting candidate to analyse the dependence on socio-economic factors. Similarly, the mink population in Denmark seems to consist mainly of escaped mink born on farms (Hammershøj et al. 2005). In contrast, the American mink seems to have established a true feral population in Iceland (Stefansson et al. 2016), making these countries good candidates for comparative analyses. Finally, US-American hunting bag data were included in this study to have a comparison with the mink’s native range.

Data were obtained from the German Hunting Association (Datenspeicher Jagd Eberswalde, Thünen-Institut 2017), the University of Aarhus, Denmark, the Environment Agency of Iceland and the U.S. Association of Fish & Wildlife Agencies. In addition, we collected data on (i) extrinsic factors that might influence hunting effort on the American mink and (ii) the supplementation of feral mink populations with farm mink. The length of the time period analysed for each country was determined by the parameter with the shortest time series available, resulting in data series between 19 and 46 years per country. The majority of mink furs in Europe are traded through Kopenhagen Fur, the world’s largest fur auction house owned by the Danish mink breeders (Hansen 2017). Historic fur prices obtained from Kopenhagen Fur were used for analysis of European hunting bag data; these were used in Danish Krone DKK for Denmark Iceland and Germany, which is the currency at Kopenhagen Fur. For the analysis of the US-American hunting bag, data on mink production and fur price (in USD) in the USA were used. These data include the number of mink furs produced on mink farms during the marketing year and the average marketing price per fur in the USA. For Iceland, where a bounty system exists, we calculated the costs for mink eradication (bounty, compensation per working hour and driven km) as (i), costs per mink killed (ii), costs per working hour. Consumer price indices (CPI) and currency rates were used to adjust the fur prices for purchasing power in order to make historic prices comparable.

Analysis

The analysis of mink hunting bag data was conducted in a three-step process. First, the hunting bag raw data were analysed for change points using the Bayesian Information Criterion (BIC). For the detection of regime shifts and unknown change points in time series, it is possible to compute the optimal segmentations for a sequence of break points and order the outcome by a likelihood-based criterion such as BIC (Zeileis et al. 2010). Akaike's Information Criterion (AIC) is in this case thought to overestimate the number of breaks, whereas BIC seems to give more accurate estimates (Bai and Perron 2003). Further, change-point detection methods were found to perform much better than the commonly used decline-from-peak approach (Strayer et al. 2017). We used the R-package strucchange (Zeileis et al. 2002) to conduct change-point detection analysis for multiple change points.

Second, the hunting bag of each country was described as a linear model using socio-economic factors that potentially influence hunting effort or the number of farm mink released into the wild. These factors included mink production data, fur price, and legislation affecting the escape rate or the hunting effort. Model selection was based on AIC corrected for small sample size (AICc; Burnham et al. 2011, Symonds and Moussalli 2011).

Finally, residuals of the best fitting linear models were analysed using change-point detection, and the detected change points were compared with those detected in the hunting bag raw data.

All analyses were conducted with the software R 3.2.1 (R Core Team 2015), using the package strucchange (Zeileis et al. 2002). Several methods used in population dynamics analyses take the auto-correlative nature of reproductive populations into account (Royama 1981; Hagen et al. 2014). Some of the populations of the American mink analysed in this study, however, were thought to be heavily influenced by supplementation through escaped farm mink and changing hunting effort, thus dynamics were not primarily based on reproduction. Hence, we refrained from introducing an auto-correlation term to the models.

Results

Regime shifts and change points in raw hunting bag data

For Denmark, change points were detected in the years 1977, 1988, 1995, 2001 and 2007 (Figure 5.1a). After a period of slow growth with stepwise increases and regimes between 6 and 11 years, the hunting bag showed a strong upward trend starting in 1995 and doubled in the course of just three years, coming to hold on the peak of the hunting bag series for a plateau of 6 years between 1996 and 2001. From 2002 onwards, dynamics changed and the hunting bag declined stepwise back to similar numbers as of the last plateau before the peak.

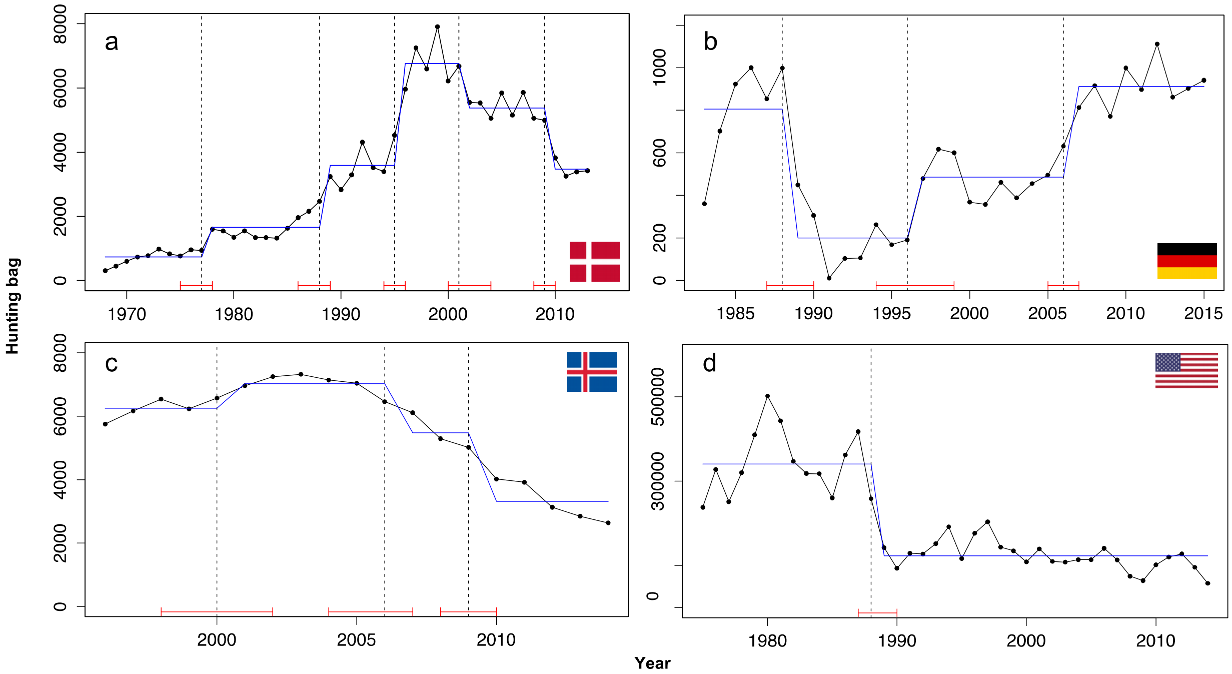

Figure 5.1 - Change points identified with the Bayesian Information Criterion (BIC) (dotted lines, confidence intervals in red, regimes in blue) in mink hunting bag series for (a) Denmark, (b) Germany, (c) Iceland and (d) USA.

For Germany, change points were detected in the years 1988, 1996 and 2006 (Figure 5.1b. After an increase from 1983 to 1988, there was a sharp decline to a plateau and then a stepwise increase back to the pre-bust level.

For Iceland, change points were detected in the years 2000, 2006 and 2009 (Figure 5.1c). After a period of slow growth from 1996 to 2003, the hunting bag reduced by half starting in 2006.

Finally for the USA, one change point was detected in the year 1988 (Figure 5.1d). The first regime in the period 1975 to 1988 was followed by a strong decrease to the second regime from 1989 onwards.

Socio-economic factors affecting hunting bag data

For Denmark, the best model according to AICc includes fur price (negatively related to hunting bag) and production of mink furs in Denmark (positively related; table 5.1). This model explains 67% of the variation in the mink hunting bag series (adj. $R^2 = 0.67$). The second and third best models also include the change in legislation for mink farms in the year 2002. The fur price is included in all of the four best models; all other models have a relative AIC weight of <0.01. Therefore, the price seems to be a crucial predictor for the hunting bag, closely followed by the production of mink furs which is included in the two best models, possessing a combined relative AIC weight of 0.91.

Table 5.1 - Linear regression model results of the analysis of the mink hunting bag in Denmark. The table lists all models with relative AIC weight ≥ 0.01 with decreasing AIC weight. Parameters are: Production of mink furs in Denmark (Production), fur price at Kopenhagen Fur in DKK corrected for purchasing power using the Danish CPI (Price) and a government order (no. 610, July 2002) to restrict mink from escaping from fur farms (Law).

Model	df	AICc	delta AICc	weight
Price + Production	4	773.85	0.00	0.70
Price + Production + Law	5	776.28	2.42	0.21
Price + Law	4	778.20	4.35	0.08
Price	3	781.76	7.90	0.01

For Germany, the best model (adj. $R^2 = 0.35$) only includes fur price, which is positively related to hunting bag (table 5.2). The second best model, which has a relative AIC model weight of 0.23, additionally includes reunification.

Table 5.2 - Linear regression model results of the analysis of the mink hunting bag in Germany. The table lists all models with relative AIC weight ≥ 0.01 with decreasing AIC weight. Parameters are: fur price at Kopenhagen Fur in DKK corrected for purchasing power using the Danish CPI (Price) and legislation change following the German reunification in 1990 (Reunification).

Model	df	AICc	delta AICc	weight
Price	3	463.72	0.00	0.77
Price + Reunification	4	466.10	2.38	0.23

For Iceland, the best model (adj. $R^2 = 0.65$) includes fur price and production (negatively related to hunting bag; Table 3) and the hunting compensation per hour (positively correlated to hunting bag). The fur price is included in all of the eight best-fitting models.

Table 5.3 - Linear regression model results of the analysis of the mink hunting bag in Iceland. The table lists all models with relative AIC weight ≥ 0.01 with decreasing AIC weight. Parameters are: Number of mink on fur farms in Iceland (Production), fur price at Kopenhagen Fur in ISK corrected for purchasing power using the Icelandic CPI (Price), the eradication costs per mink in ISK (Costs Per Mink) and the eradication costs per hunting hour in ISK (Costs Per Hour), each corrected for purchasing power using the Icelandic CPI.

Model	df	AICc	delta AICc	weight
Price + Production + Costs Per Hour	5	262.90	0.00	0.46
Price + Production + Costs Per Mink + Costs Per Hour	4	264.88	1.98	0.17
Price + Production	6	265.10	2.20	0.15
Price + Costs Per Hour	6	266.27	3.37	0.08
Price + Production + Costs Per Mink	5	267.08	4.18	0.06
Price + Costs Per Mink + Costs Per Hour	5	268.14	5.24	0.03
Price	7	268.87	5.97	0.02
Price + Costs Per Mink	6	270.72	7.82	0.01

Finally, for the USA, the best model (adj. $R^2 = 0.57$) includes fur price in US$ and production of mink furs in the USA (both positively related to hunting bag; Table 4).

Table 5.4 - Linear regression model results of the analysis of the mink hunting bag in the USA. The table lists all models with relative AIC weight ≥ 0.01 with decreasing AIC weight. Parameters are: Production of mink furs in the USA (Production) and fur price in the USA in $ corrected for purchasing power using the US-American CPI (Price).

Model	df	AICc	delta AICc	weight
Price + Production	4	965.12	0.00	1.00

Regime shifts and change points in hunting bag residuals

For hunting bag residuals, which can be considered to be corrected for socio-economic factors, change points were detected in the years 1982, 1995, 2001 and 2007 for Denmark (Figure 5.2a). The last three of those were also detected in the hunting bag raw data. There is a steady period between 1969 and 1982 in the residuals, followed by a small decline to another long regime between 1983 and 1995. Starting in 1995, there is a sharp increase in the residuals to a plateau of 6 years between 1996 and 2001. From 2002 onwards, the residuals decline stepwise back to the mean of the values before 1996.

For Germany, one change point was detected in the year 2006 (Figure 5.2b). The first regime in the period between 1983 and 2006 is followed by an increase in the residuals to the second regime between 2007 and 2015.

For Iceland, only one change point in the year 2007 was detected (Figure 5.2c). It marks a regime until 2007 and a substantial decline thereafter.

For the USA, one change point was detected in the year 2005 (Figure 5.2d). The first regime in the period between 1975 and 2005 is followed by a decrease to lower levels thereafter.

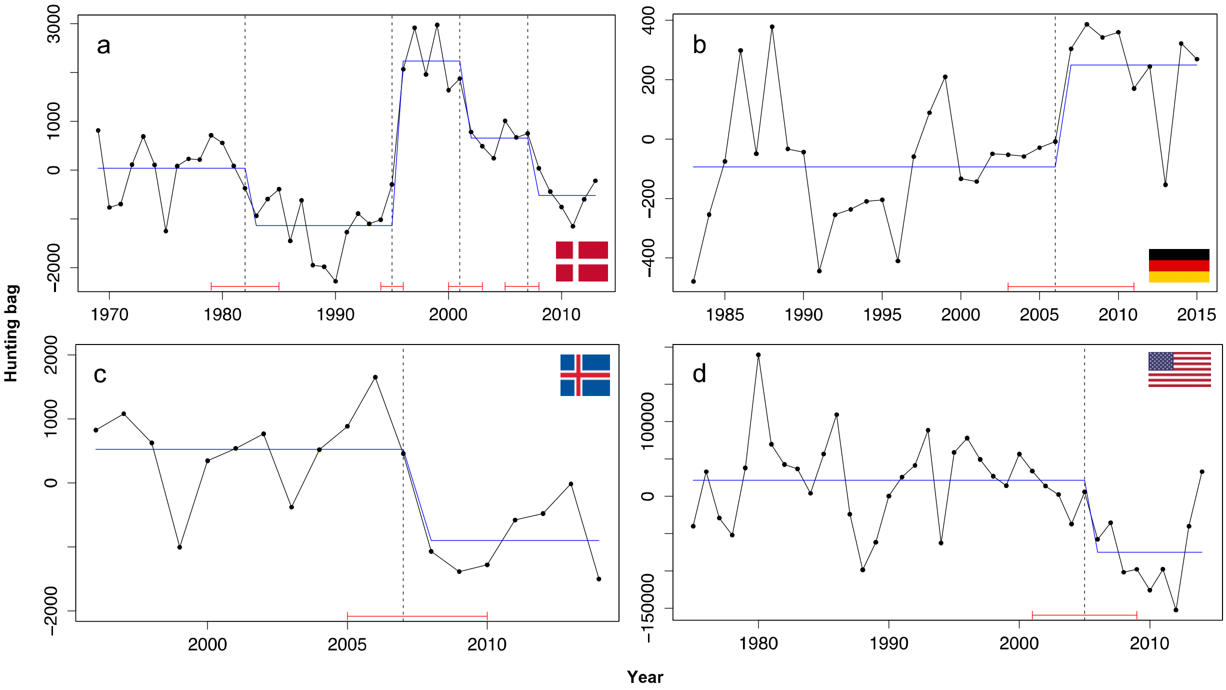

Figure 5.2 - Change points identified with the Bayesian Information Criterion (BIC) (dotted lines, confidence intervals in red, regimes in blue) in the residuals of the best fitting model, i.e. the corrected data, for (a) Denmark, (b) Germany, (c) Iceland and (d) USA.

Discussion

We found support for a strong influence of socio-economic factors on American mink hunting bag data (hypothesis H1 in the Introduction). Linear models including such factors were able to explain high proportions of the variation in the hunting bag data although the dynamics of the correlations were not always as expected.

Specifically, our results suggest that fur price has a strong influence on hunting effort (H1.1). It was included in the best regression models for all countries. In Germany and the USA, fur price was positively related to the hunting bag. In the USA, mink are primarily hunted for their fur. In Germany, our results suggest that the motivation for mink hunting might not be exclusively to eradicate the invasive mink but is also driven by the sale value of mink furs. In Iceland and Denmark, however, fur price was negatively related to the hunting bag. Underlying reasons are discussed in the respective sections of the countries below.

We found that mink production on farms seems to have a strong impact on the number of mink in the wild (H1.2). Mink farming is an important economic factor in several European countries, with over 15 million furs per year produced in Denmark alone (Kopenhagen Fur 2016b). Mink production ended up in the best model for all three countries where this parameter was included in model selection (Denmark, Iceland, USA). For Germany, data on mink production were not available. In Denmark and the USA, mink production was positively related to the hunting bag. It can be assumed that the number of mink escaping from farms increases with the number of mink kept on farms, leading to a higher supplementation of the mink population in the wild with farm mink. This assumption rests on evidence that escaped farm animals play a crucial role in the dynamics of feral mink populations: Denmark has the highest density of mink farms in any country. There, the feral mink population seems to consist of up to 79% escaped farm animals (Hammershøj et al. 2005). In Poland, 17% of American mink caught in the wild were identified as farm mink, and the number of caught farm mink correlated with the size of the farm breeding stocks in the districts where sampling sites were located (Zalewski et al. 2010). Our results of the positive relationship between mink farming and hunting bag in the USA suggest that native American mink populations are similarly supplemented by escaped/released farm mink. This conclusion is confirmed for the Canadian mink population, for which a positive relationship between the change in mink harvest and ranch density was found (Bowman et al. 2007), and nearly two-thirds of mink sampled were either farm escapees or descendants of escapees (Kidd et al. 2009). To our knowledge, the positive relationship between mink production and hunting bag in the USA found here has not been described in the literature before.

Also as expected (H1.3), more change points were found in the raw hunting bag data than in the residuals of the best socio-economic model for each country. This finding also highlights the importance of considering socio-economic factors when analysing hunting bags, particularly in case of species with a clear economic value such as the American mink. One needs to be cautious not to falsely interpret ecological mechanisms into fluctuations of raw hunting bag data, as these might be caused by socio-economic factors.

Boom-bust dynamics do not seem to be dominant in invasive mink populations, thus hypothesis H2 was not supported. No such pattern was found in Germany. In Denmark, the feral mink population consists mainly of escaped farm mink, and the observed change point in 2001 and the subsequent decline may be caused by a government order in 2002 that aimed to restrict the number of escapees from mink farms (Hammershøj et al. 2005). In contrast, a probably genuine decline was observed in Iceland, and also in the USA where the mink is native. In both countries, a severe decline in the corrected hunting bag data was evident after a change point in 2007. For this decrease, no possible socio-economic explanations are known and thus it seems to reflect a real downward trend in mink populations – in Iceland possibly because of climate related changes cascading through the food chain (Magnusdottir et al. 2014), and in the USA possibly due to environmental pollution (Bursian et al. 2013).

Denmark

Against our expectations, harvest number and fur price were negatively correlated in Denmark. This finding might be explained by an indirect relationship of fur price and released mink. When the price is low, enclosures at mink farms may be less maintained and escapes more frequent, resulting in an increasing hunting bag. The decline in fur price in 1988 is followed by a reduction of the mink production approximately 5 years later, and in 1995 a change point detected in both residuals and hunting bag raw data indicates the begin of a sharp increase in harvest numbers. There are signs of a pork-cycle, a lagged interdependence of price and production, in the hunting bag-fur price relationship, as price trends are mirrored by the production numbers with a lag time. It might be speculated that, after a time lag, severe drops of the fur prices result in the bankruptcy of small mink farmers, who in consequence close down their farms and release their animals into the wild, but the exact reason for the negative correlation of harvest numbers and price remains unclear.

Germany

Due to the German reunification and the fact that the American mink occurs in Germany mainly in the area of the former GDR (German Democratic Republic), German hunting bag data show certain characteristics mirroring the change in legislation and hunting effort after 1990. These characteristics are still visible in the residuals of the best model (Figure 5.2b).

Fur crafting has a long tradition in the eastern counties of Germany, and furs were important export products in the GDR that could be traded to Western countries for foreign currencies. Hence, all types of furbearer species were hunted and their furs used (Jürgen Förster, Obermeister der Kürschnerinnung Mitteldeutschland, 26 October 2017, pers. comm.). In the GDR, mink were hunted using efficient leg-hold traps, a trap type that has been considered inhumane and banned in Germany since 1990. Due to these circumstances, it can be assumed that hunting effort on the American mink was higher in the GDR than in Germany after reunification (Astrid Sutor, German Hunting Association (DJV), 14 December 2017, pers. comm.).

The reunification dummy did not end up in the final model. In the residuals of the best model, however, where the hunting bag is corrected for the fur price, the effect of the so-called “Wendejahre”, the years after the German reunification, on the hunting bag is unmasked. A period of 5 years after reunification, from 1991 to 1996, shows a decline in the harvest numbers that is not explained by the fur price. During this period, the fur market collapsed as furs were no longer sought after for export, and fur agencies and fur crafting workshops were closed down (Jürgen Förster, Obermeister der Kürschnerinnung Mitteldeutschland, 26 October 2017, pers. comm.). This period is the regime with the lowest mean of the corrected hunting bag data, an indicator for a low hunting effort during this period of political and economic distortions.

The only change point detected both in the residuals of the best model and in the hunting bag raw data was in the year 2006. This finding may indicate a true increase in the mink population in Germany after 2006. As the high hunting effort in the GDR and the subsequent political changes are not covered by this model, the mink population size is likely to have been increasing at least since the 1980s.

Iceland

The American mink was first brought to Iceland in 1931 for fur farming. A law on security and hunting of feral mink was passed already in 1937. This unusually rapid response can be explained with the risk the mink caused for Iceland's economy: down feathers of the common eider duck (Somateria mollissima), which are still collected today, were exported as an important source of revenue, especially up until the mid-20th century (Skarphedinsson 1996), and mink predation posed a threat to eider colonies. Eiders in Iceland often nest on coastal islands, which the only native mammalian predator, the Arctic fox (Vulpes lagopus), cannot reach (Stefansson et al. 2016). The American mink is often able to swim to the nesting colonies and preys on eiders and their offspring, leading to changes in breeding distribution and lower eider down harvests (Skarphedinsson 1996).

Mink hunting is mostly carried out by specialized hunters, but also eider down harvesters and farmers. The compensation for mink hunting for contract hunters consists of a bounty per mink killed, low salary per working hour and a payment for driving expenses (per km). In Norway, where a similar program exists, bounty payments influenced hunting efficiency positively (Stien and Hausner 2018), although in general, this salary seems too low to be an important income on a yearly basis.

In years with low mink population density, the effort necessary to catch and kill a mink is higher than in high-density years. In these years, the wages resulting from the working hours make up for a higher share of the total compensation per mink than the bounty itself. Hence, the bounty alone is not a good proxy for the hunting effort. In order to adjust for mink density and hunting success rate, we calculated the total compensation per working hour for each year. This parameter ended up in the best model and was positively correlated with the hunting bag. In contrast, the Icelandic mink hunting bag was negatively correlated with fur price. Thus, fur price does not seem to act as a hunting incentive here, which is not surprising as mink in Iceland are not hunted for their fur.

The negative association between mink farm production and hunting bag may have a rational explanation. American mink escaped soon after introduction and reproduced in the wild less than a decade later. During this time, the mink kept on farms were still very similar to the wild mink in North America (Stefansson et al. 2016). In consequence, the feral population that developed from escaped farm mink shared most characteristics with their wild ancestors. Mink farming was banned in Iceland from 1953 to 1969, but a self-sustaining mink population had already developed and the mink had continuously colonized the rest of

Iceland by 1975 (Magnusdottir et al. 2014). Mink kept on farms today have been domesticated to a high degree and are distinct from their wild ancestors (Bowman et al. 2017). Domesticated farm mink have significantly smaller brains, hearts and spleens than wild mink (Kruska and Schreiber 1999), and several colour strains have been developed. Thus, interbreeding of evidently well adapted feral mink with these highly domesticated farm mink might have introduced genes favoured under artificial selection that are maladaptive in a natural environment (Kidd et al. 2009; Beauclerc et al. 2013) and thus lead to a lower survival rate of hybridised mink (Bowman et al. 2007). Another possible explanation might be competition between farm escapees and other feral mink, resulting in higher mortality of feral mink when mink farm production was high and escapes more frequent.

The negative correlation of fur price and hunting bag may be the result of this relationship as well. Fur price and mink production are positively correlated, as more breeding stock is kept on farms when fur price is high. Combining this interdependence of mink production and fur price with the observations that (i) mink in Iceland are not hunted for the value of their fur and (ii) there is a negative correlation of hunting bag and mink production, a negative correlation between fur price and hunting bag is not surprising.

Changes in mink management may partly explain the decrease in the Icelandic hunting bag after 2008. Following the financial crisis of 2008, which had great impact on Iceland’s economy (Goddard et al. 2009; Raza et al. 2018), some of the municipalities cut the budget of mink management by restricting the number of bounties paid. Anecdotal evidence from interviews with mink hunters suggests that this arrangement might have led to a lower hunting effort in the following years in a few areas, although the effect is hard to quantify as bounty quota are not available (Stefansson et al. 2016). The hunters also agree that they have experienced a severe reduction in mink density after the first few years of the 21st century. Therefore, circumstantial evidence suggests that the reduction in the management budget can only explain a minor part of the decrease found in the corrected data after the change point in 2007, but the decline of the mink hunting bag in Iceland is more likely to mainly reflect actual changes in mink population size (Magnusdottir et al. 2014; Stefansson et al. 2016).

USA

In the USA, a positive relationship between fur price and hunting bag was found. This was expected, as mink are hunted in the USA primarily for their fur. A severe decline in the corrected hunting bag data was evident after a change point in 2007. For this decrease, no socio-economic explanations are known, thus it seems to reflect a real downward trend of the American mink population. The American mink is sensitive to environmental contaminants like mercury (Bursian et al. 2013), polychlorinated biphenyls (PCBs) and other dioxin-like compounds (Zwiernik et al. 2008). Due to this sensitivity, the use of mink as “sentinel species” has been proposed, a model organism for the measure of environmental pollution (Basu et al. 2007). It is not really clear, however, if this sensitivity is the reason for the mink’s decline in the USA. Several other explanations have been proposed for this decline, from hybridisation with domesticated mink (Bowman et al. 2007, 2017), to habitat loss and the Aleutian disease (Nituch et al. 2011), but although some may apply locally, it is unlikely that one of these factors has caused the nationwide decline observed in the mink hunting bag.

Conclusions

Although limitations of hunting bag data are known and approaches to correct for biases resulting from inconsistent reporting and changing hunting effort are discussed in the literature (Cattadori et al. 2003; Schmidt et al. 2015), the influence of socio-economic factors on harvest data has not been addressed sufficiently. The American mink is one of the most destructive alien invasive species in Europe and affects at least 47 native species negatively (Genovesi et al. 2012). In order to monitor the development, impact and spreading of invasive populations, reliable data are essential. We found that socio-economic factors massively influence hunting bag data of the American mink. In Denmark, where mink farms produce more than 15 million furs per year, 67% of the variation in the hunting bag data was explained by mink production on farms and the fur price. This finding supports the assumption that the feral mink in Denmark is constantly supplemented with escaped farm mink (Pertoldi et al. 2014). The same is assumed for most other countries with mink farms, although the density of mink farms is unusual in Denmark. It has been shown that the large-scale removal of feral mink is possible where geographical circumstances are suitable, albeit with the concentrated effort of a large number of volunteers (Moore et al. 2003; Bryce et al. 2011; Robertson et al. 2016). Our findings show that monetary rewards might be a useful tool to increase the number of hunters engaging in mink trapping, especially when intrinsic motivation is low (Stien and Hausner 2018). However, all eradication programs are in vain without restricting escapees from mink farms.

Long-term data on invasive species are scarce (Strayer et al. 2006) and furbearer species are hard to census (Bowman et al. 2007). Due to their secret life style, counting mink by sight is hardly ever suitable. Count data based on field signs, however, were shown to be entirely unreliable (Harrington et al. 2010). The best method for mink surveys, the operation of floating rafts with a tracking medium to record footprints (Reynolds et al. 2004; Harrington et al. 2008), is very laborious and probably difficult to operate in coastal areas. Hence, hunting bag series are often the best data available. However, as for most mammals (Imperio et al. 2010), there are no comparative studies to assess the validity of hunting bag data of the American mink and biases caused by external factors are likely. Our findings suggest that hunting bag data should be thoroughly controlled for socio-economic factors, particularly for animals with a socio-economic value such as the American mink.

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References

Ahola M, Nordstrom M, Banks PB, et al (2006) Alien mink predation induces prolonged declines in archipelago amphibians. Proc R Soc B Biol Sci 273:1261–1265. https://doi.org/10.1098/rspb.2005.3455

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr 19:716–723. https://doi.org/10.1109/TAC.1974.1100705

Allendorf FW, Lundquist LL (2003) Introduction: Population Biology, Evolution, and Control of Invasive Species. Conserv Biol 17:24–30. https://doi.org/10.1046/j.1523-1739.2003.02365.x

Andersen T, Carstensen J, Hernández-García E, Duarte CM (2009) Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24:49–57. https://doi.org/10.1016/j.tree.2008.07.014

Bai J, Perron P (2003) Computation and analysis of multiple structural change models. J Appl Econom 18:1–22. https://doi.org/10.1002/jae.659

Banks PB, Nordström M, Ahola M, et al (2008) Impacts of alien mink predation on island vertebrate communities of the Baltic sea archipelago: Review of a long-term experimental study. Boreal Environ Res 13:3–16

Basu N, Scheuerhammer AM, Bursian SJ, et al (2007) Mink as a sentinel species in environmental health. Environ Res 103:130–144. https://doi.org/https://doi.org/10.1016/j.envres.2006.04.005

Beauclerc KB, Bowman J, Schulte-Hostedde AI (2013) Assessing the cryptic invasion of a domestic conspecific: American mink in their native range. Ecol Evol 3:2296–2309. https://doi.org/10.1002/ece3.630

Bevanger K, Henriksen G (1995) The distributional history and present status of the American mink (*Mustela vison* Schreber, 1777) in Norway. Ann. Zool. Fennici 32:11–14

Blanco-Aguiar JA, Delibes-Mateos M, Arroyo B, et al (2012) Is the interaction between rabbit hemorrhagic disease and hyperpredation by raptors a major cause of the red-legged partridge decline in Spain? Eur J Wildl Res 58:433–439. https://doi.org/10.1007/s10344-011-0593-z

Bonesi L, Palazon S (2007) The American mink in Europe: Status, impacts, and control. Biol Conserv 134:470–483. https://doi.org/10.1016/j.biocon.2006.09.006

Bonesi L, Strachan R, Macdonald DW (2006) Why are there fewer signs of mink in England? Considering multiple hypotheses. Biol Conserv 130:268–277. https://doi.org/10.1016/j.biocon.2005.12.021

Bowman J, Beauclerc K, Farid AH, et al (2017) Hybridization of domestic mink with wild American mink (*Neovison vison*) in eastern Canada. Can J Zool 95:443–451. https://doi.org/10.1139/cjz-2016-0171

Bowman J, Kidd AG, Gorman RM, Schulte-hostedde AI (2007) Assessing the potential for impacts by feral mink on wild mink in Canada. Biol Conserv 139:12–18. https://doi.org/10.1016/j.biocon.2007.05.020

Bryce R, Oliver MK, Davies L, et al (2011) Turning back the tide of American mink invasion at an unprecedented scale through community participation and adaptive management. Biol Conserv 144:575–583. https://doi.org/10.1016/j.biocon.2010.10.013

Brzeziński M, Romanowski J, Zmihorski M, Karpowicz K (2010) Muskrat (*Ondatra zibethicus*) decline after the expansion of American mink (*Neovison vison*) in Poland. Eur J Wildl Res 56:341–348. https://doi.org/10.1007/s10344-009-0325-9

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65:23–35

Bursian SJ, Kern J, Remington RE, et al (2013) Dietary exposure of mink (*Mustela vison*) to fish from the upper Hudson river, New York, USA: Effects on reproduction and offspring growth and mortality. Environ Toxicol Chem 32:780–793. https://doi.org/10.1002/etc.2110

Carlsson NOL, Jeschke JM, Holmqvist N, Kindberg J (2010) Long-term data on invaders: When the fox is away, the mink will play. Biol Invasions 12:633–641. https://doi.org/10.1007/s10530-009-9470-z

Cattadori IM, Haydon DT, Thirgood SJ, Hudson PJ (2003) Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. Oikos 100:439–446. https://doi.org/10.1034/j.1600-0706.2003.12072.x

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term , individual-based studies of animals in ecology and evolutionary biology. Trends Ecol Evol 25:562–573. https://doi.org/10.1016/j.tree.2010.08.002

Ferreras P, Macdonald DW (1999) The impact of American mink *Mustela vison* on water birds in the upper Thames. J Appl Ecol 36:701–708. https://doi.org/10.1046/j.1365-2664.1999.00431.x

Fischer D, Pavlučík P, Sedláček F, Šálek M (2009) Predation of the alien American mink, *Mustela vison* on native crayfish in middle-sized streams in central and western Bohemia. Folia Zool 58:45–56

Genovesi P, Carnevali L, Alonzi A, Scalera R (2012) Alien mammals in Europe: Updated numbers and trends, and assessment of the effects on biodiversity. Integr Zool 7:247–253. https://doi.org/10.1111/j.1749-4877.2012.00309.x

Goddard J, Molyneux P, Wilson JOS (2009) The financial crisis in Europe: Evolution, policy responses and lessons for the future. J Financ Regul Compliance 17:362–380. https://doi.org/10.1108/13581980911004352

Hagen R, Heurich M, Kröschel M, Herdtfelder M (2014) Synchrony in hunting bags: Reaction on climatic and human induced changes? Sci Total Environ 468–469:140–146. https://doi.org/10.1016/j.scitotenv.2013.08.022

Hammershøj M, Pertoldi C, Asferg T, et al (2005) Danish free-ranging mink populations consist mainly of farm animals: Evidence from microsatellite and stable isotope analyses. J Nat Conserv 13:267–274. https://doi.org/10.1016/j.jnc.2005.03.001

Hammershøj M, Travis JMJ, Stephenson CM, Incorporating CM (2006) Incorporating evolutionary processes into a spatially-explicit model: Exploring the consequences of mink-farm closures in Denmark. Ecography (Cop) 29:465–476. https://doi.org/10.1111/j.2006.0906-7590.04492.x

Hansen HO (2017) European Mink Industry - Socio-economic Impact Assessment

Harrington LA, Harrington AL, Hughes J, et al (2010) The accuracy of scat identification in distribution surveys: American mink, *Neovison vison*, in the northern highlands of Scotland. Eur J Wildl Res 56:377–384. https://doi.org/10.1007/s10344-009-0328-6

Harrington LA, Harrington AL, Macdonald DW (2008) Estimating the relative abundance of American mink *Mustela vison* on lowland rivers: Evaluation and comparison of two techniques. Eur J Wildl Res 54:79–87. https://doi.org/10.1007/s10344-007-0114-2

Herruzo C, Martinez-Jauregui M (2013) Trends in hunters, hunting grounds and big game harvest in Spain. For Syst 22:114–122. https://doi.org/10.5424/fs/2013221-03371

Imperio S, Ferrante M, Grignetti A, et al (2010) Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? Wildlife Biol 16:205–214. https://doi.org/10.2981/08-051

International Fur Trade Federation (2003) The Socio-Economic Impact of International Fur Farming. www.iftf.com. Accessed 2 May 2017

Kidd AG, Bowman J, Lesbarrères D, Schulte-Hostedde AI (2009) Hybridization between escaped domestic and wild American mink (*Neovison vison*). Mol Ecol 18:1175–1186. https://doi.org/10.1111/j.1365-294X.2009.04100.x

Kopenhagen Fur (2016a) World production of mink drops

Kopenhagen Fur (2016b) Historic data. http://www.kopenhagenfur.com/da/minkavl/historisk-data/verdensproduktion-i-minkskind. Accessed 15 Nov 2016

Kruska D, Schreiber A (1999) Comparative morphometrical and biochemical-genetic investigations in wild and ranch mink (*Mustela vison*: Carnivora: Mammalia). Acta Theriol (Warsz) 44:377–392

Lester PJ, Gruber MAM (2016) Booms, busts and population collapses in invasive ants. Biol Invasions 18:3091–3101. https://doi.org/10.1007/s10530-016-1214-2

Little RM, Crowe TM (1993) Hunting efficiency and the impact of hunting on greywing francolin populations. South African J Wildl Res 23:31–35

Macdonald DW, Harrington LA (2003) The american mink: The triumph and tragedy of adaptation out of context. New Zeal J Zool 30:421–441. https://doi.org/10.1080/03014223.2003.9518350

Magnusdottir R, von Schmalensee M, Stefansson RA, et al (2014) A foe in woe: American mink (*Neovison vison*) diet changes during a population decrease. Mamm Biol 79:58–63. https://doi.org/10.1016/j.mambio.2013.08.002

Manchester SJ, Bullock JM (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. J Appl Ecol 37:845–864. https://doi.org/10.1046/j.1365-2664.2000.00538.x

Moore NP, Roy SS, Helyar A (2003) Mink (*mustela vison*) eradication to protect ground-nesting birds in the western isles, scotland, united kingdom. New Zeal J Zool 30:443–452. https://doi.org/10.1080/03014223.2003.9518351

Nentwig W, Bacher S, Kumschick S, et al (2018) More than “100 worst” alien species in Europe. Biol Invasions 20:1611–1621. https://doi.org/10.1007/s10530-017-1651-6

Nentwig W, Kühnel E, Bacher S (2010) A generic impact-scoring system applied to alien mammals in Europe. Conserv Biol 24:302–311. https://doi.org/10.1111/j.1523-1739.2009.01289.x

Nituch LA, Bowman J, Beauclerc KB, Schulte-Hostedde AI (2011) Mink farms predict aleutian disease exposure in wild american mink. PLoS One 6:. https://doi.org/10.1371/journal.pone.0021693

Nordström M, Korpimäki E (2004) Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. J Anim Ecol 73:424–433. https://doi.org/10.1111/j.0021-8790.2004.00816.x

Obbard ME, Jones JG, Newman R (1987) Furbearer harvests in North America. Wild Furbear Manag Conserv North Am 1007–1033

Pertoldi C, Rødjajn S, Zalewski A, et al (2014) Population viability analysis of American mink (*Neovison vison*) escaped from Danish mink farms. 2530–2541. https://doi.org/10.2527/jas2012-6039

Põdra M, Gómez A, Palazón S (2013) Do American mink kill European mink? Cautionary message for future recovery efforts. Eur J Wildl Res 59:431–440. https://doi.org/10.1007/s10344-013-0689-8

R Core Team (2015) R: A Language and Environment for Statistical Computing

Ranta E, Lindström J, Lindén H, Helle P (2008) How reliable are harvesting data for analyses of spatio temporal population dynamics? Oikos 1461–1468. https://doi.org/10.1111/j.2008.0030-1299.16879.x

Raza H, Zoega G, Kinsella S (2018) Capital inflows, crisis and recovery in small open economies. Financ Res Lett. https://doi.org/10.1016/j.frl.2018.03.011

Reynolds JC, Short MJ, Leigh RJ (2004) Development of population control strategies for mink *Mustela vison*, using floating rafts as monitors and trap sites. Biol Conserv 120:533–543. https://doi.org/10.1016/j.biocon.2004.03.026

Reynolds JD (1988) Crayfish extinctions and crayfish plague in central Ireland. Biol Conserv 45:279–285. https://doi.org/10.1016/0006-3207(88)90059-6

Robertson PA, Adriaens T, Lambin X, et al (2016) The Large-Scale Removal of Mammalian Invasive Alien Species in Northern Europe. Pest Manag Sci. https://doi.org/DOI: 10.1002/ps.4224

Royama T (1981) Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. Ecol Monogr 51:473–493. https://doi.org/10.2307/2937325

Rushton SP, Barreto GW, Cormack RM, et al (2000) Modelling the effects of mink and habitat fragmentation on the water vole. J Appl Ecol 37:475–490. https://doi.org/10.1046/j.1365-2664.2000.00504.x

Sandström A, Andersson M, Asp A, et al (2014) Population collapses in introduced non-indigenous crayfish. Biol Invasions 16:1961–1977. https://doi.org/10.1007/s10530-014-0641-1

Schmidt JI, Kellie KA, Chapin FS (2015) Detecting, estimating, and correcting for biases in harvest data. J Wildl Manage 79:1152–1162. https://doi.org/10.1002/jwmg.928

Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions. Annu Rev Ecol Evol Syst 40:81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Simberloff D, Gibbons L (2004) Now you see them, now you don't! - Population crashes of established introduced species. Biol Invasions 6:161–172. https://doi.org/10.1023/B:BINV.0000022133.49752.46

Skarphedinsson KH (1996) The common eider: Ecological and economical aspects. Bull Scand Soc Parasitol 6:90–98

Spraakman G, Wilkie A (2000) The development of management accounting at the Hudson ' s Bay Company , 1670-1820. Account Hist

Stefansson RA, Schmalensee M von, Skorupski J (2016) A tale of conquest and crisis : invasion history and status of the American mink (*Neovison vison*) in Iceland. Acta Biol 23:87–100. https://doi.org/10.18276/ab.2016.23-08

Stien J, Hausner VH (2018) Motivating and engaging volunteer hunters to control the invasive alien American mink *Neovison vison* in Norway. Oryx 52:186–194. https://doi.org/10.1017/S0030605316000879

Strayer DL, D'Antonio CM, Essl F, et al (2017) Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecol Lett 20:1337–1350. https://doi.org/10.1111/ele.12822

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651. https://doi.org/10.1016/j.tree.2006.07.007

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21. https://doi.org/10.1007/s00265-010-1037-6

Zalewski A, Michalska-Parda A, Bartoszewicz M, et al (2010) Multiple introductions determine the genetic structure of an invasive species population: American mink *Neovison vison* in Poland. Biol Conserv 143:1355–1363. https://doi.org/10.1016/j.biocon.2010.03.009

Zeileis A, Leisch F, Hornik K, Kleiber C (2002) strucchange : An R Package for Testing for Structural Change in Linear Regression Models. J Stat Softw 7:1–17. https://doi.org/10.18637/jss.v007.i02

Zeileis A, Shah A, Patnaik I (2010) Testing, monitoring, and dating structural changes in exchange rate regimes. Comput Stat Data Anal 54:1696–1706. https://doi.org/10.1016/j.csda.2009.12.005

Zschille J, Stier N, Roth M, Mayer R (2014) Feeding habits of invasive American mink (*Neovison vison*) in northern Germany – potential implications for fishery and waterfowl. Acta Theriol (Warsz) 59:25–34. https://doi.org/10.1007/s13364-012-0126-5

Zwiernik MJ, Kay DP, Moore J, et al (2008) Exposure and effects assessment of the resident mink (*Mustela vison*) exposed to polychlorinated dibenzofurans and other dioxin-like compounds in the Tittabawassee River basin, Midland, Michigan, USA. Environ Toxicol Chem 27:2076. https://doi.org/10.1897/07-489.1

Appendix E

Supplement to: Of mink and men: socio-economic factors influence the hunting bag of American mink in Europe and North America, Stille et al.: Hunting bag, fur price and fur production of the American mink (Neovison vison), and legislation changes regarding this species in Denmark, Germany, Iceland and the USA

Denmark

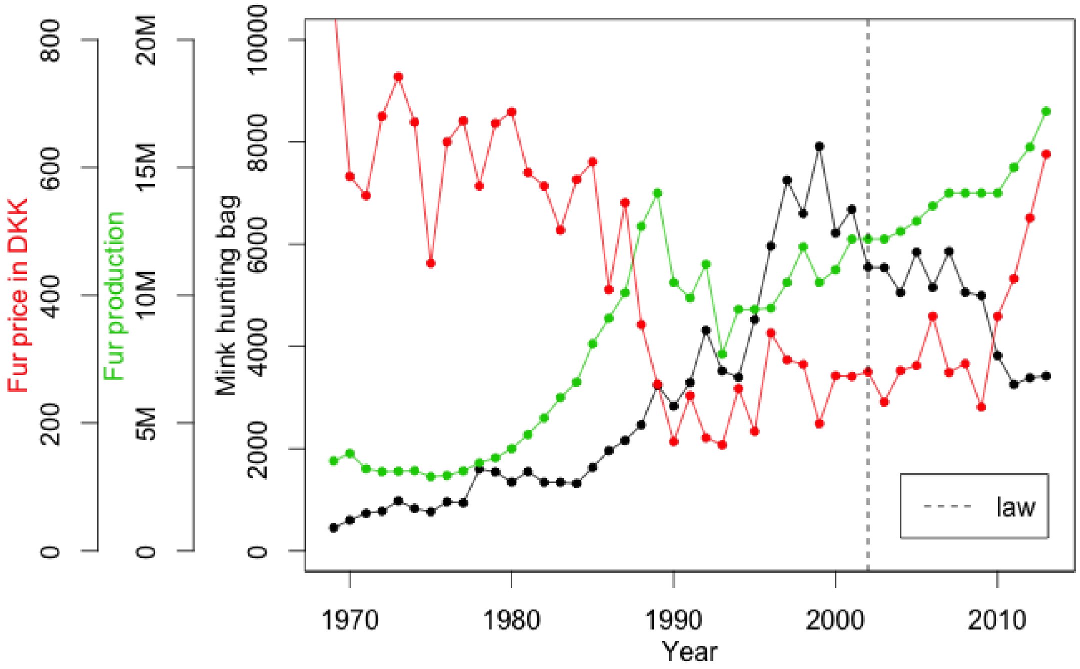

Figure E.1 - Mink hunting bag series in Denmark from 1968 to 2013 (black). Parameters used for model fitting: annual production of mink furs in Denmark (green), fur price at Kopenhagen Fur in DKK corrected for purchasing power using the Danish CPI (red), and a government order (no. 610, July 2002) to restrict mink from escaping from fur farms (dotted line)

Germany

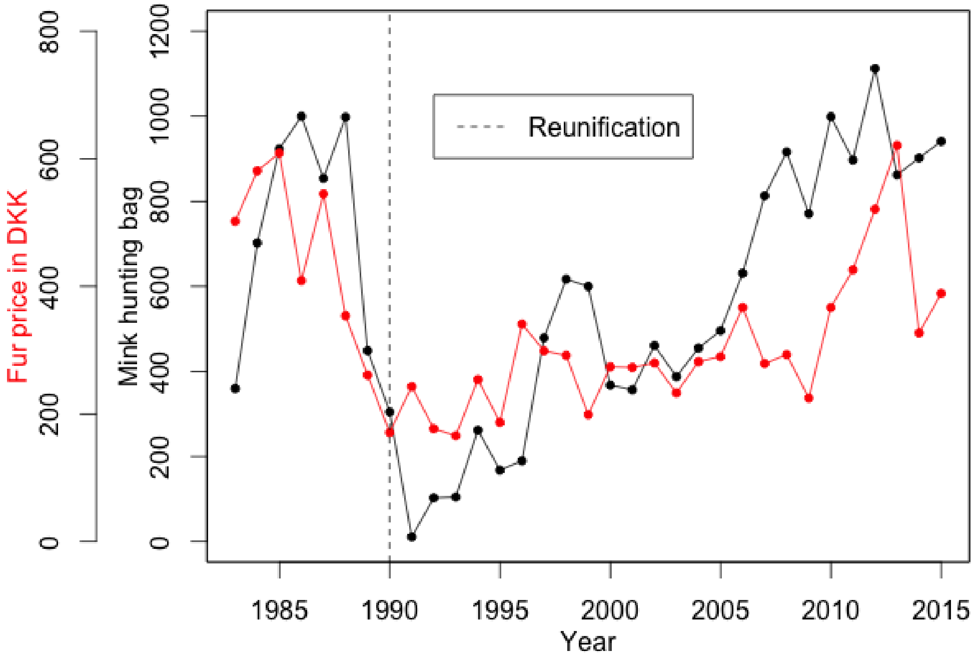

Figure E.2 - Mink hunting bag series in Germany from 1983 to 2015 (black). Parameters used for model fitting: fur price at Kopenhagen Fur in DKK corrected for purchasing power using the Danish CPI (red) and legislation change following the German reunification in 1990 (dotted line).

Iceland

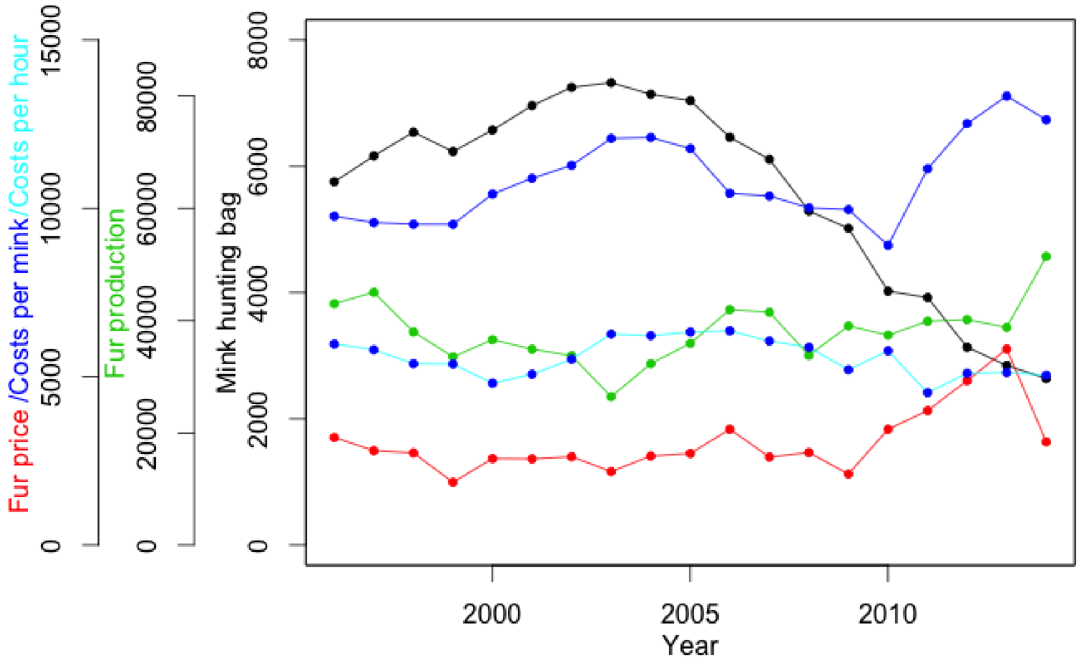

Figure E.3 - Mink hunting bag series in Iceland from 1996 to 2014 (black). Parameters used for model fitting: Production of mink furs in Iceland (green), fur price at Kopenhagen Fur in DKK corrected for purchasing power using the Icelandic CPI (red), the eradication costs per mink in ISK (blue) and the eradication costs per hunting hour in ISK (torquoise).

USA

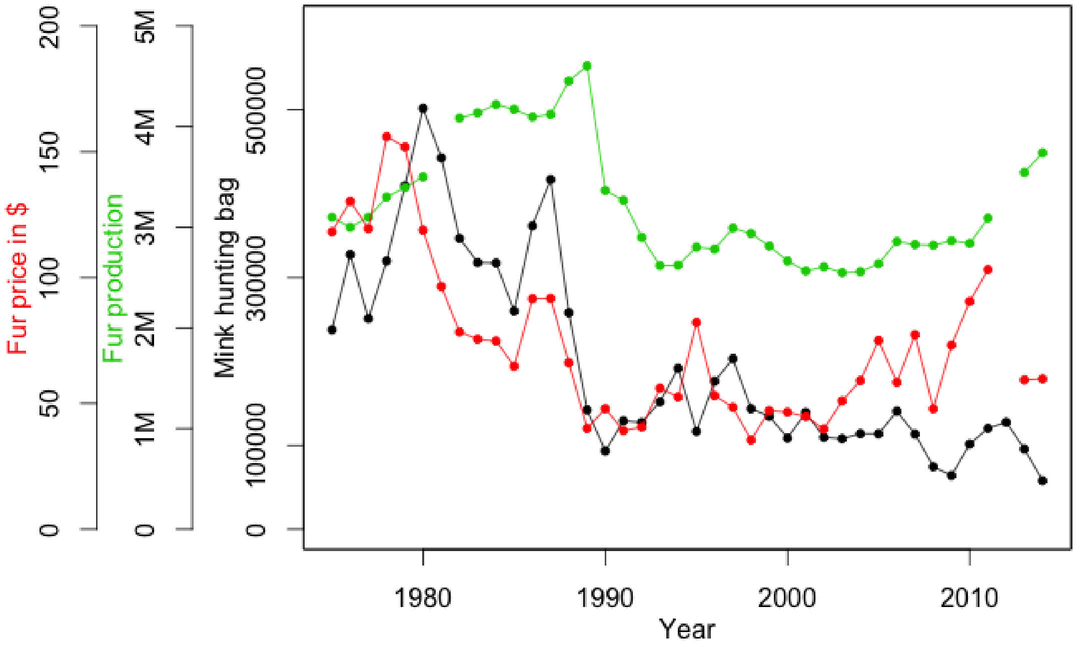

Figure E.4 - Mink hunting bag series in the USA from 1975 to 2014 (black). Parameters used for model fitting: Production of mink furs in the USA (green) and fur price in the USA in $ corrected for purchasing power using the US-American CPI (red)

General Discussion

Behavioural change has been recognized to be a principal component of animals coping with HIREC (Sih 2013). Research on these changes has been mostly focused on particular systems or ecological situations, though: species' behaviour in urban environments (Sol et al. 2013), non-native species' behaviour aiding its invasion (Harms and Turingan 2012; Brodin and Drotz 2014) or native species' behavioural responses to invasion (Berthon 2015). The types of behaviour analysed were also not representative, as most studies focused on either feeding innovation (Ducatez et al. 2014) or problem-solving (Griffin and Guez 2014) as proxies for intelligence. Finally, there is strong taxonomical bias in comparative analyses of behavioural changes in biological invasions or innovation studies, mostly focusing on birds (Lefebvre et al. 2016) or primates (Vale et al. 2017), other mammals (Benson-Amram et al. 2016). Only when using all available information across taxa and types of interaction between species can we make informed statements about which behaviours will change in non-native or native species and with which consequences.

In this thesis, I framed cases of behavioural change in invasions conceptually, made predictions on new meta-parameters and studied three systems in detail. I started with compiling cases of behavioural change in invasions and used these broad data to test hypotheses in invasion ecology. This interaction-focused framework was extended in Chapter 3 and has implications for the case studies of the aquatic over-invasion by a clonal crayfish in Germany (Chapter 3) and the American mink in Europe (Chapter 5) with special emphasis on Iceland (Chapter 4). This thesis is - to the best of my knowledge - the broadest approach to study behavioural innovation in non-human animals and the significance of behavioural changes in invasions. The results can be summarized as follows:

Chapter 1 showed that two advantages of non-native species over natives come from the type of behaviour under change and the underlying mechanism. First, anti-predator behaviour, which was more commonly observed to change in native species, changed more slowly than feeding behaviour. Second, non-native species were more often pre-disposed to the new behaviour, which allowed for faster change than through learning or genetic adaptation.

Chapter 2 showed how the clonal marbled crayfish were more active in a laboratory setting when they came from lab populations (this species originated in captivitiy, hence does not have a native wild population). Also, the threat response was more commonly neither fight nor flight, but a "freezing" behaviour in reaction to the human hand. Both can be interpreted as coping strategies with human presence. Additionally, marbled crayfish were more aggressive and more often victorious in agonistic interactions with the older non-native species, the spiny-cheek crayfish.

In Chapter 3 we found how the degree of innovation in native species' behavioural changes (innovation gradient - IG) is related to the degree of novelty of the non-native species in the action - described by eco-evolutionary experience of the native species with the non-native species (EEE). The more novel the invader is, the bigger the behavioural change has to be and the worse the consequences for the native species on a population level. This is true for the birds in our data, but it has to be further explored how these parameters relate in other taxa.

Chapter 4 shows how the behavioural response of native common eider in Iceland suffice to buffer adverse population effects from the return of the native arctic fox. The arrival of the American mink into the system, however, did have negative population effects on the eider in the region, despite an appropriate nest site relocation. This is an example of how eco-evolutionary experiences shape the outcome of species interactions and gives guidance for conservation efforts towards the American mink in West Iceland.

In Chapter 5 the population dynamics of this non-native predator are studied in detail, showing how they differ between European countries and the USA as its native range. Hunting bag data was shown to be mostly dependent on economic factors like fur price and production in the respective country and legislation. We propose a new method to account for these drivers and get a more precise estimate of the underlying population dynamics.

Studying behavioural change with an interaction-focused approach

The study of behavioural changes in biological invasions faces complex challenges. There are observations that are in conflict, a non-native species - naive to the invaded ecosystem - can still outperform natives in its invaded range, something that may be explained through community assembly theory (Pearson et al. 2018). The work in this thesis therefore generally focuses on the interaction between species. It has been shown that the interactions with native species can limit species spread more than climatic suitability (Sax 2001), and these interactions change the functioning of the whole ecosystem through trophic cascades (Schmitz et al. 2004). If the interactions can be predicted by proxies (Morales-Castilla et al. 2015), it would be most useful to develop a framework where population dynamics outcomes of interactions can be predicted.

I agree with the statement in Tebbich et al. (2016), that there is a need for "a framework for animal innovation that describes the interactions between mechanism, fitness benefit and evolutionary significance". Their framework provides excellent guidance for behavioural assays in experimental studies. However, I found their concept of innovation too detailed to apply in comparative literature studies, especially when using studies from settings where innovation was not the main focus (i.e. studies on biological invasion). Therefore, in Chapter 3 we defined the observation of an innovation on the population level along the lines of the technical/object distinction of earlier comparative analyses (Overington et al. 2009). I will elaborate on this and contrast my approach to other existing studies.

Towards an inclusive concept of animal innovation

While animal innovation studies have recently received more attention and often have an interdisciplinary approach (Reader et al. 2016), the diversity of behaviour they study is generally limited. In non-human animals the focus is mostly on resource-acquisition tasks in experiments (Sterelny 2016) or generally feeding innovations in correlational studies (Ducatez et al. 2014). In this thesis, however, I was able to show that - at least in an invasion context - changes in feeding behaviour only made up ~40% of the behavioural changes (Chapter 1). These studies are also restricted taxonomically, mostly focusing on mammals (Benson-Amram et al. 2016, Vale et al. 2017) or birds (Ten Cate et al. 2017). I argue here that several general questions about the relationships between innovation, intelligence, dispersal and diversification cannot be answered with the data currently available.

The relationship between intelligence and innovation seems to be context-specific. While there is clear evidence for a positive relationship in primates (Reader and Laland 2002), using innovation data from a broad range of behavioural contexts as foraging, mating or aggression (Reader and Laland 2001), this pattern was not observed in an experimental study on meerkats where perseverance was a better predictor of success than cognitive faculties in a novel food-extraction task (Thornton and Samson 2012). In a comparative foraging innovation study on seven bird species, motor diversity was shown to be the best predictor for innovation, but the evolutionary link to cognitive flexibility remains untested (Diquelou et al. 2016).

With the data and models at hand, it remains hard to describe the relationship between innovation and group size. Evidence in humans points at a positive relationship between group size and the number of innovations, both in models (Muthukrishna and Henrich 2016) and experiments (Derex et al. 2013, but see Vaesen 2012 and Henrich et al. 2016 for the controversy). There were difficulties, however, to put these assumptions into decision making models of individuals in populations and see if social learning would be the evolutionary stable strategy (ESS). The assumptions about facilitating and inhibiting effects of group members drive the optimal group size for innovation (Griffin and Guez 2015). The initial modelling solutions showed Roger's paradox, by which social learning does not have a benefit over individual learning at the equilibrium state (Rogers 1988). Critical social learning - in contrast to the random model choice assumed in Rogers (1988) - can solve the paradox (Enquist et al. 2007), as do mixed learning strategies (Aoki and Feldman 2014).

These assumptions about the interplay between individual and social learning across animal groups inspired the Cultural Intelligence Hypothesis (van Schaik and Burkart 2011). The underlying idea is that animals should learn vital cultural skills exclusively, and routine skills faster, through social learning, provided they actually use social learning preferentially (van Schaik and Burkart 2011). This is supported from correlational analyses on primates (Navarrete et al. 2016), again using a broad range of behavioural contexts for innovation. In a cross-taxonomic study on problem-solving and brain size in 39 mammal species, however, such a correlation was not found (Benson-Amram et al. 2016). The reason for this may in fact not be the taxonomic differences, but the differences in data gathered, as innovation is dependent on behavioural context (Perry et al. 2017). Reversal learning, technical innovation or innovative problem solving are psychologically distinct processes and controlled by different neural mechanisms (Audet and Lefebvre 2017). To be able to study this wide range of processes, research has to happen on different types of innovation across diverse taxa (Griffin 2016).

Behavioural changes and evolution

Species invasions offer a perfect setting to look at these mechanism of behavioural change and explore their evolutionary implications: We have information about the mechanism behind the behavioural changes in many non-native species. In a next step, the environmental variability in the home range should be quantified using different indicators (seasonal climatic variability, stochastic climatic variability, biotic variability, …). Quantitatively comparing the distribution of variability indices between mechanisms of behavioural change can answer the question if these different mechanisms evolve in the respective species shaped by their environment. Theory predicts that environments with low variability will foster genetic adaptation, while individual learning particularly evolves in very variable environments. In environments with intermediate variability, social learning is most favourable (Brown 2012). We conducted such a study with data from the study in Chapter 1 and found preliminary evidence for this pattern with stochastic temporal temperature variability as a predictor (Ruland, Wiedenroth et al., in prep.).

This dataset can be expanded for a clearer picture by gathering more instances of behavioural change for a subset of species. That means ideally more than one instance of behavioural change in one species in its native and its invaded range, with evidence for the mechanisms involved. Then the environmental variability of the invaded range – better: ranges – will be quantified in the same way. Now all cross-comparisons are possible: the species might, for example, have evolved through genetic adaptation to a variable home range and use learning as a mechanism of behavioural change in its invaded ranges – evidence for the innovation-precedes-invasion hypothesis. Or it originates from a less variable home range where it shows no clear pattern in mechanisms of behavioural change while it then genetically adapts to very variable invaded ranges – evidence for the selection-for-innovation hypothesis.

The types of behaviour under change are valuable information about potential speciation in the native or non-native species. Drawing from the framework of Duckworth (2009), there are explicit predictions about what kind of evolutionary change is expected for which change in behaviour, covering some, but not all types of behaviour classified in Chapter 1: what we defined as locomotion is called "migratory patterns or habitat selection that causes an organism to move to a novel environment" in Duckworth’s framework and predicted to affect diversification rates (Phillimore et al. 2006). Mating as well as resource use ("feeding") are predicted to result in sympatric speciation (Dieckmann and Doebeli 1999). The behavioural change to cope with abiotic stress like different temperature and salinity in the environment, defined as "climate-related" in Chapter 1, is predicted to inhibit evolutionary change (Huey et al. 2003). What is missing in these predictions are changes in competitive or anti-predator behaviour, which are common behavioural changes and not included in the framework by Duckworth (2009). I predict behavioural changes to cope with competition to inhibit speciation in a similar way as behavioural adaptation to thermoregulation limits selection. The same will be true for successful behavioural change to cope with predation which will directly reduce selective pressure. Chapter 2 on behavioural change in marbled crayfish showed that these crayfish can be successful in competitive interactions with invasive spiny-cheek crayfish without any genetic variation. However, most schemes on invasion success do not consider evolutionary change in the invader and the recipient community (Whitney and Gabler 2008). The growing database that I created for the studies compiled in this thesis will aid to answer these questions in the future.

The behavioural changes observed in the studies compiled in this thesis support the hypothesis that species thriving in association with humans in their native range are more likely successful invaders (Strubbe et al. 2015), as supported by the evidence that urban ecosystems serve as hotspots and hubs for non-native species (Von Der Lippe and Kowarik 2008). Marbled crayfish that came from laboratories showed a different behavioural response to the human hand as a threat. While life in captivity is more monotonous (Mason et al. 2013), it is also safer and possibly the marbled crayfish show the appropriate "freezing" response to human approach, which corresponds to ignoring. This could reduce stress level in crayfish and decrease non-lethal predation effects - missed opportunity costs in foraging - similar to the decreased flushing distance in birds populations in touristic places (Jiménez et al. 2013). If the human hand is seen as a novel predation threat, the observation is inverse to the prediction by Sih et al. (2010), whereby the non-consumptive effects of predation are smaller the more novel the predator is. In this case, marbled crayfish may have learned to ignore the hand in contrast to the spiny-cheek crayfish, which show a generalized fight or flight response towards it. In the end, it is not clear, however, if the freezing response will be adaptive or maladaptive in frequently visited lakes like Krumme Lanke. While few humans will intentionally seek to predate on marbled crayfish there, freezing may increase the chance of getting accidentally stepped on.

We found evidence for a behavioural syndrome in marbled crayfish between aggression and activity (Chapter 2). This could limit the potential for behavioural change, as the change in one trait will always be associated with a - potentially maladaptive - change. The aggression that is rendering individuals more successful at obtaining resources from hetero- and conspecific competitors is predicted to be a positive trait at low densities, but not at high densities (Hudina et al. 2014). Behavioural syndromes may be less pronounced in the wild, though, with increased predation pressure (Niemelä et al. 2012). However, the high observed rate of cannibalism of own offspring in marbled crayfish in the lab (Stefan Linzmaier, pers. comm.) may limit densities in invaded lakes.

Human association of non-native species and sustained disturbance

The relationship with humans is paramount for the success of an invasion and direct predation by humans is not necessarily a disadvantage. While the marbled crayfish is mostly used as an ornamental aquarium species in Europe, it is intentionally spread across rice fields in Madagascar to be harvested for human consumption (Andriantsoa et al. 2019). This is in many cases the most important factor determining spread rate and establishment success: the intentional transport by humans. The marbled crayfish possesses perfect invader traits (Jones et al. 2009; Havel et al. 2015), but its spread across Europe is considerably slower than across Madagascar due to the difference in vectors. This is due to its intentional spread by humans (propagule pressure in uninvaded regions) and its ability to thrive in human affiliation (the deliberate stocking of crayfish in rice fields). These two factors were found to be most important for freshwater fish, mammal and bird species invasion success in Europe and North America (Jeschke and Strayer 2006). The breeding for fur was also the vector how the American mink arrived in Europe, and releases and escapees still restock the feral mink populations in several countries (Hammershøj et al. 2005).

The excellent dataset on breeding eider in Breiðafjörður only exists due to the harvesting of down by the island owners (Jónsson et al. 2013). This commercial interest also makes island owners take action to facilitate breeding by building shelters and controlling nest predators (Jónsson et al. 2013). There is reason to assume that these methods vary among islands, depending on owners' activity and over time. Therefore, the data on eider nest numbers had to be treated as a careful proxy of total eider individual numbers in the area. A study to correct the nest numbers for human activity - gathered through qualitative data from interviews with island owners - will allow for a better estimation of actual eider numbers (Ruland et al., in prep., interviews started in 2017). Also, eiders can - depending on resource availability - decide when to breed or if to breed at all. An agent-based model to predict individual eiders' choice according to environmental condition will give a better estimate of the number of non-breeders in the area (a corresponding Master thesis project started 2019).

Conservation implications

We have seen that behavioural shifts do happen, but are often insufficient to buffer adverse effects of non-native species (Carthey and Banks 2014, Chapter 4). Anti-predator behaviour is subjected to slower change than feeding (Chapter 1). The incorporation of novel food was shown to be less cognitively challenging (Ducatez et al. 2014) which is also reflected in relative brain size of predator-prey species pairs across fish species (Kondoh 2010). Theory predicts that species which do not develop behavioural mechanisms to cope with the new interaction go extinct when selective pressure is high (Strauss et al. 2006). While some observations of rapid genetic evolutionary responses to invasions have been met with great optimism (Carroll 2007), especially fast life-history trait invertebrates, adaptation commonly is too slow to save natives or curb invader effects (Hudgens and Garcelon 2011; Tuomainen and Candolin 2011). Examples of appropriate acquired behavioural response to predators after the invasion are rare and often generalized with high sub-lethal predation effects (e.g. missed opportunity cost, see for example Saxon-Mills et al. 2018). Conservation efforts, therefore, have to be directed towards decreasing non-native species' negative impacts by decreasing propagule pressure and population numbers, as well as training native species for appropriate behavioural responses (Moseby et al. 2012) or even eradication (Robertson et al. 2014) where possible.

It has been observed that non-native species adjust their behaviour to control measures (Diquelou and Griffin 2019), which is one of the problems in fighting invasion after the introduction (Leung et al. 2002). Our analyses of population dynamics show, however, how legislation could effectively decrease the number of feral mink in Denmark without costly control, a trend that can be continued by decreased production and increased security measures (Chapter 5). The EU-regulation No 1143/2014 is a good example for a transnational agreement to curb the spread of non-native species. Internationally, free trade agreements like the North American Free Trade Agreement (NAFTA) are criticized to increase trafficking of non-native species across borders (Margolis et al. 2005, Ricciardi et al. 2017). International action against climate change is also necessary, as there is evidence for a positive relationship between invasion and climate change (Engel et al. 2011; Côté and Green 2012).

Conclusions

With this interdisciplinary thesis, I illustrated how biological invasions are good sources to study biological changes and evolutionary dynamics. They pose large natural experiments and the information I presented has in turn implications for management decisions. The datasets gathered in chapters 1 and 3 were submitted along with the manuscripts and are meant to be extended and applied in the future. The population dynamics of the common eider in West Iceland are as predicted and show that control efforts should be concentrated on the mink (Chapter 4). The numbers of feral mink in Europe can best be controlled by banning mink farms or curbing the release and escape of mink by legislation (Chapter 5). Chapter 1 also demonstrated the importance of the mechanisms behind behavioural changes to define the speed of the change. Chapter 2 demonstrated that the marbled crayfish changed its behaviour after being released into central European lakes within a few generations despite having no genetic variation. I expect to find more innovation in non-human animals and across a broader range of behaviours when using the IG scheme presented in Chapter 3, thereby broadening our understanding of what innovative behaviour is and how it appears across contexts (Griffin 2016). It has to be stressed, however, that despite being in some cases a functional "first line of defence", behavioural shifts do not allow effective responses against all anthropogenic rapid changes in the environment. The work compiled in this thesis supports the claim that the complex issue of novel ecosystems demands a transdisciplinary science of engagement for societal change (Collier 2015). Political and economical action has to be undertaken to limit climate change, habitat destruction and species transport.

References

Andriantsoa R, Tönges S, Panteleit J, Theissinger K, Carneiro VC, Rasamy J, Lyko F. 2019. Ecological plasticity and commercial impact of invasive marbled crayfish populations in Madagascar. BMC Ecol. 19(1):1–10. doi:10.1186/s12898-019-0224-1.

Aoki K, Feldman MW. 2014. Evolution of learning strategies in temporally and spatially variable environments: A review of theory. Theor Popul Biol. 91:3–19. doi:10.1016/j.tpb.2013.10.004.

Audet J-N, Lefebvre L. 2017. What's flexible in behavioral flexibility? Behav Ecol. 28(4):943–947. doi:10.1093/beheco/arx007.

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE. 2016. Brain size predicts problem-solving ability in mammalian carnivores. Proc Natl Acad Sci USA. 113(9):2532–2537. doi:10.1073/pnas.1505913113.

Berthon K. 2015. How do native species respond to invaders? Mechanistic and trait-based perspectives. Biol Invasions. 17(8):2199–2211. doi:10.1007/s10530-015-0874-7.

Brodin T, Drotz MK. 2014. Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. Curr Zool. 60(3):410–416. doi:10.1093/czoolo/60.3.410.

Brown C. 2012. Experience and learning in changing environments. In: Behavioural Responses to a Changing World: Mechanisms and Consequences.

Carroll SP. 2007. Brave New World: The epistatic foundations of natives adapting to invaders. Genetica. 129(2):193–204. doi:10.1007/s10709-006-9014-8.

Carthey AJR, Banks PB. 2014. Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. Biol Rev. 89(4):932–949. doi:10.1111/brv.12087.

Collier MJ. 2015. Novel ecosystems and social-ecological resilience. Landsc Ecol. 30(8):1363–1369. doi:10.1007/s10980-015-0243-z.

Côté IM, Green SJ. 2012. Potential effects of climate change on a marine invasion : The importance of current context. Curr Zool. 58(1):1–8. doi:10.1093/czoolo/58.1.1.

Derex M, Beugin MP, Godelle B, Raymond M. 2013. Experimental evidence for the influence of group size on cultural complexity. Nature. 503(7476):389–391. doi:10.1038/nature12774.

Dieckmann U, Doebeli M. 1999. On the origin of species by sympatric speciation. 400(July):4. papers2://publication/uuid/A1D99DB8-4B7C-4294-BC64-7969FB9CBE00.

Diquelou MC, Griffin AS. 2019. It's a trap! Invasive common mynas learn socially about control-related cues. Behav Ecol.:1–10. doi:10.1093/beheco/arz079.

Diquelou MC, Griffin AS, Sol D. 2016. The role of motor diversity in foraging innovations: A cross-species comparison in urban birds. Behav Ecol. 27(2):584–591. doi:10.1093/beheco/arv190.

Ducatez S, Clavel J, Lefebvre L. 2014. Ecological generalism and behavioural innovation in birds: Technical intelligence or the simple incorporation of new foods? J Anim Ecol.:79–89. doi:10.1111/1365-2656.12255.

Duckworth RA. 2009. The role of behavior in evolution: A search for mechanism. Evol Ecol. 23(4):513–531. doi:10.1007/s10682-008-9252-6.

Engel K, Tollrian R, Jeschke JM. 2011. Integrating biological invasions, climate change, and phenotypic plasticity. Commun Integr Biol. 4(3):247–250. doi:10.4161/cib.4.3.14885.

Enquist M, Eriksson K, Ghirlanda S. 2007. Critical Social Learning: A Solution to Rogers's Paradox of Nonadaptive Culture. Am Anthropol. 109(4):727–734. doi:10.1525/aa.2007.109.4.727.

Griffin AS. 2016. Innovativeness as an emergent property: A new alignment of comparative and experimental research on animal innovation. Philos Trans R Soc B Biol Sci. 371(1690). doi:10.1098/rstb.2015.0544.

Griffin AS, Guez D. 2014. Innovation and problem solving: A review of common mechanisms. Behav Processes. 109(PB):121–134. doi:10.1016/j.beproc.2014.08.027.

Griffin AS, Guez D. 2015. Innovative problem solving in nonhuman animals: The effects of group size revisited. Behav Ecol. 26(3):722–734. doi:10.1093/beheco/aru238.

Hammershøj M, Pertoldi C, Asferg T, Møller TB, Kristensen NB. 2005. Danish free-ranging mink populations consist mainly of farm animals: Evidence from microsatellite and stable isotope analyses. J Nat Conserv. 13(4):267–274. doi:10.1016/j.jnc.2005.03.001.

Harms C a., Turingan RG. 2012. Dietary flexibility despite behavioral stereotypy contributes to successful invasion of the pike killifish, *Belonesox belizanus*, in Florida, USA. Aquat Invasions. 7(4):547–553. doi:10.3391/ai.2012.7.4.011.

Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB. 2015. Aquatic invasive species: challenges for the future. Hydrobiologia. 750(1):147–170. doi:10.1007/s10750-014-2166-0.

Henrich J, Boyd R, Derex M, Kline MA, Mesoudi A, Muthukrishna M, Powell AT, Shennan SJ, Thomas MG. 2016. Understanding cumulative cultural evolution. Proc Natl Acad Sci U S A. 113(44):E6724–E6725. doi:10.1073/pnas.1610005113.

Hudgens BR, Garcelon DK. 2011. Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator. Oecologia. 165(3):699–705. doi:10.1007/s00442-010-1761-7.

Hudina S, Hock K, Žganec K. 2014. The role of aggression in range expansion and biological invasions. Curr Zool. 60(3):401–409.

Huey RB, Hertz PE, Sinervo B. 2003. Behavioral drive versus behavioral inertia in evolution: A null model approach. Am Nat. 161(3):357–366. doi:10.1086/346135.

Jeschke JM, Strayer DL. 2006. Determinants of vertebrate invasion success in Europe and North America. Glob Chang Biol. 12(9):1608–1619. doi:10.1111/j.1365-2486.2006.01213.x.

Jiménez G, Meléndez L, Blanco G, Laiolo P. 2013. Dampened behavioral responses mediate birds' association with humans. Biol Conserv. 159:477–483. doi:10.1016/j.biocon.2012.10.030.

Jones JPG, Rasamy JR, Harvey A, Toon A, Oidtmann B, Randrianarison MH, Raminosoa N, Ravoahangimalala OR. 2009. The perfect invader: A parthenogenic crayfish poses a new threat to Madagascar's freshwater biodiversity. Biol Invasions. 11(6):1475–1482. doi:10.1007/s10530-008-9334-y.

Jónsson JE, Gardarsson A, Gill JA, Pétursdóttir UK, Petersen A, Gunnarsson TG. 2013. Relationships between Long-Term Demography and Weather in a Sub-Arctic Population of Common Eider. PLoS One. 8(6). doi:10.1371/journal.pone.0067093.

Kondoh M. 2010. Linking learning adaptation to trophic interactions: A brain size-based approach. Funct Ecol. 24(1):35–43. doi:10.1111/j.1365-2435.2009.01631.x.

Lefebvre L, Ducatez S, Audet JN. 2016. Feeding innovations in a nested phylogeny of Neotropical passerines. Philos Trans R Soc B Biol Sci. 371(1690):20150188. doi:10.1098/rstb.2015.0188.

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G. 2002. An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. Proc R Soc B Biol Sci. 269(1508):2407–2413. doi:10.1098/rspb.2002.2179.

Von Der Lippe M, Kowarik I. 2008. Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. Divers Distrib. 14(1):18–25. doi:10.1111/j.1472-4642.2007.00401.x.

Margolis M, Shogren JF, Fischer C. 2005. How trade politics affect invasive species control. Ecol Econ. 52(3 SPEC. ISS.):305–313. doi:10.1016/j.ecolecon.2004.07.017.

Mason G, Burn CC, Dallaire JA, Kroshko J, McDonald Kinkaid H, Jeschke JM. 2013. Plastic animals in cages: Behavioural flexibility and responses to captivity. Anim Behav. 85(5):1113–1126. doi:10.1016/j.anbehav.2013.02.002.

Morales-Castilla I, Matias MG, Gravel D, Araújo MB. 2015. Inferring biotic interactions from proxies. Trends Ecol Evol. 30(6):347–356. doi:10.1016/j.tree.2015.03.014.

Moseby KE, Cameron A, Crisp HA. 2012. Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? Anim Behav. 83(4):1011–1021. doi:10.1016/j.anbehav.2012.01.023.

Muthukrishna M, Henrich J. 2016. Innovation in the collective brain. Philos Trans R Soc B Biol Sci. 371(1690):20150192. doi:10.1098/rstb.2015.0192.

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN. 2016. The coevolution of innovation and technical intelligence in primates. Philos Trans R Soc B Biol Sci. 371(1690). doi:10.1098/rstb.2015.0186.

Niemelä PT, DiRienzo N, Hedrick AV. 2012. Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. Anim Behav. 84(1):129–135. doi:10.1016/j.anbehav.2012.04.019.

Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav. 78(4):1001–1010. doi:10.1016/j.anbehav.2009.06.033.

Pearson DE, Ortega YK, Eren Ö, Hierro JL. 2018. Community Assembly Theory as a Framework for Biological Invasions. Trends Ecol Evol. 33(5):313–325. doi:10.1016/j.tree.2018.03.002.

Perry SE, Barrett BJ, Godoy I. 2017. Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. Proc Natl Acad Sci USA. 114(30):7806–7813. doi:10.1073/pnas.1620739114.

Phillimore AB, Freckleton RP, Orme CDL, Owens IPF. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. Am Nat. 168(2):220–229. doi:10.1086/505763.

Reader SM, Laland KN. 2001. Primate innovation: Sex, age and social rank differences. Int J Primatol. 22(5):787–805. doi:10.1023/A:1012069500899.

Reader SM, Laland KN. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci USA. 99(7):4436–4441. doi:10.1073/pnas.062041299.

Reader SM, Morand-Ferron J, Flynn E. 2016. Animal and human innovation: Novel problems and novel solutions. Philos Trans R Soc B Biol Sci. 371(1690):20150182. doi:10.1098/rstb.2015.0182.

Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, et al. 2017. Invasion Science: A Horizon Scan of Emerging Challenges and Opportunities. Trends Ecol Evol. 32(6):464–474. doi:10.1016/j.tree.2017.03.007.

Robertson P a., Adriaens T, Caizergues A, Cranswick PA, Devos K, Gutiérrez-Expósito C, Henderson I, Hughes B, Mill AC, Smith GC. 2014. Towards the European eradication of the North American ruddy duck. Biol Invasions. 17(1):9–12. doi:10.1007/s10530-014-0704-3.

Rogers AR. 1988. Does Biology Constrain Culture. Am Anthropol. 90(4):819–831. doi:10.1525/aa.1988.90.4.02a00030.

Sax DF. 2001. Latitudinal gradients and geographic ranges of exotic species: Implications for biogeography. J Biogeogr. 28(1):139–150. doi:10.1046/j.1365-2699.2001.00536.x.

Saxon-Mills EC, Moseby K, Blumstein DT, Letnic M. 2018. Prey naïveté and the anti-predator responses of a vulnerable marsupial prey to known and novel predators. Behav Ecol Sociobiol. 72(9). doi:10.1007/s00265-018-2568-5.

van Schaik CP, Burkart JM. 2011. Social learning and evolution: The cultural intelligence hypothesis. Philos Trans R Soc B Biol Sci. 366(1567):1008–1016. doi:10.1098/rstb.2010.0304.

Schmitz OJ, Krivan V, Ovadia O. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. Ecol Lett. 7(2):153–163. doi:10.1111/j.1461-0248.2003.00560.x.

Sih A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Anim Behav. 85(5):1077–1088. doi:10.1016/j.anbehav.2013.02.017.

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR. 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos. 119(4):610–621. doi:10.1111/j.1600-0706.2009.18039.x.

Sol D, Lapiedra O, González-Lagos C. 2013. Behavioural adjustments for a life in the city. Anim Behav. 85(5):1101–1112. doi:10.1016/j.anbehav.2013.01.023.

Sterelny K. 2016. Adaptable individuals and innovative lineages. Philos Trans R Soc B Biol Sci. 371(1690):20150196. doi:10.1098/rstb.2015.0196.

Strauss SY, Lau JA, Carroll SP. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol Lett. 9(3):357–374. doi:10.1111/j.1461-0248.2005.00874.x.

Strubbe D, Jackson H, Groombridge J, Matthysen E. 2015. Invasion success of a global avian invader is explained by within-taxon niche structure and association with humans in the native range. Divers Distrib. 21(6):675–685. doi:10.1111/ddi.12325.

Tebbich S, Griffin AS, Peschl MF, Sterelny K. 2016. From mechanisms to function: An integrated framework of animal innovation. Philos Trans R Soc B Biol Sci. 371(1690). doi:10.1098/rstb.2015.0195.

Ten Cate, C, Healy, S, and Healy, SD (Eds.). 2017. Avian cognition. Cambridge University Press.

Thornton A, Samson J. 2012. Innovative problem solving in wild meerkats. Anim Behav. 83(6):1459–1468. doi:10.1016/j.anbehav.2012.03.018.

Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced environmental change. Biol Rev. 86(3):640–657. doi:10.1111/j.1469-185X.2010.00164.x.

Vaesen K. 2012. Cumulative cultural evolution and demography. PLoS One. 7(7). doi:10.1371/journal.pone.0040989.

Vale GL, Carr K, Dean LG, Kendal RL. 2017. The Cultural Capacity of Human and Nonhuman Primates: Social Learning, Innovation, and Cumulative Cultural Evolution. Second Edi. Elsevier.

Whitney KD, Gabler CA. 2008. Rapid evolution in introduced species, “invasive traits” and recipient communities: Challenges for predicting invasive potential. Divers Distrib. 14(4):569–580. doi:10.1111/j.1472-4642.2008.00473.x.