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ON LETHAL AND NONLETHAL IMPACTS OF NATIVE, ALIEN AND INTRAGUILD PREDATORS - EVIDENCE OF TOP-DOWN CONTROL

by

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PAKKONEULOOSI

Pakkoneuloosi on pakko-oireisesta neulomisvimmasta käytetty nimitys. Pakkoneuloosin oireita ovat lähes jatkuva ja katkeamaton neulominen eri vuorokauden aikoina, missä hyvänsä (junassa, luennolla, TV:n äärellä, työpaikan kokouksissa) sekä taukoamaton lankoihin ja neuleisiin keskittyvä ajattelu. Usein oirekuvaa täydentää hallitsematon lankojen hamstraus. Henkilö itsekin käsittää vimmaisen villasukkien, pipojen, toppien, huivien, neuleiden ym. kutomisen mielettömäksi lankojen nykyhinnoilla ja odotettavissa olevan eliniän rajoituksilla, mutta ei kykene kuitenkaan lopettamaan neulomista. Neulomisen lopettamisyritykset voivat jopa saada aikaan ahdistusta ja pahentaa neuloosia. Jopa lyhyet, olosuhteiden aiheuttamat tauot (esimerkiksi jännetupin tulehdus) neulomisessa saattavat aiheuttaa hallitsemattoman pakkovirkkuloosin puhkeamisen neuloottisella henkilöllä. Pakkoneuloosin syitä ei tarkkaan tiedetä. Neuloosia esiintyy kuitenkin usein saman suvun naisissa, joten tila saattaa olla jossain määrin perinnöllinen tai tarttuva. Tilaa tavataan hyvin harvoin miessukupuolen edustajilla ainakaan neuloosiin asti edenneenä, joten miehiset sukuelimet suojannevat henkilöä pakkoneuloositartunnalta. Pakkoneuloosia ei voida hoitaa (vrt. tilan paheneminen), joten neuloottisen henkilön ympäristön tulee suhtautua tilaan ymmärryksellä ja tarjota kaikki käytettävissä oleva tukensa pakkoneuloottiselle henkilölle.

- nimim. Maikku, Novitan Neulomo -

CONTENTS

LIST OF ORIGINAL PAPERS

This thesis is based on the following publications and manuscripts which are referred to in the text by their Roman numerals:

I. Salo, P., Banks, P. B., Dickman, C. R. & Korpimäki, E. Predator manipulation experiments: impacts on prey populations and journal citations. Submitted manuscript.

II. Salo, P., Korpimäki, E., Banks, P. B., Nordström, M. & Dickman, C. R. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B*, 274, 1237-1243.

III. Salo, P., Nordström, M., Thomson, R. L. & Korpimäki, E. 2008. Risk induced by a native top predator reduces alien mink movements. *Journal of Animal Ecology*, 77, 1092-1098.

IV. Salo, P., Toivola, M., Nordström, M. & Korpimäki, E. Effects of home range characteristics on the diet composition of female American mink in the Baltic Sea archipelago. Submitted manuscript.

V. Salo, P., Ahola, M. & Korpimäki, E. Habitat-mediated impact of alien mink predation on common frog densities in the outer archipelago of the Baltic Sea. Submitted manuscript.

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1. INTRODUCTION

Predation, defined here as the process of catching, killing and consuming another animal, is a very strong element of natural selection in all ecosystems, as the future fitness of those individuals falling prey will reduce to zero. While the concrete act of predation can be considered very dramatic (especially by modern man, who mainly predates on plastic-packed steaks in a grocery store) and the result (death of prey, meal for predator) very obvious for the individuals concerned, the impacts of predation on population levels of both predators and prey are usually more subtle and complicated. These subtleties arise from a variety of direct and indirect interactions between predators, prey and their environment.

1.1 PREDATOR IMPACTS ON PREY POPULATIONS - DOOMED SURPLUS OR PREDATOR REGULATION?

The intuitive view of pre-historic humans on predation was that predators reduce the availability of prey to humans (Reynolds & Tapper 1996). Many predator species were seen as competitors and pests, and killing them a social duty (Myrberget 1990). Thus predator control, which was first used to protect livestock and later to enhance prey populations for human harvest (Reynolds & Tapper 1996), is one of the oldest forms of wildlife management (Berger 2006). Only much later on, with the rise of ecological research, different views emerged on the role of predators in regulating prey population numbers and the species composition of communities. According to one view predators did not have large detrimental effects on the population sizes of their prey, because these predators had coexisted with their prey for long periods and killed only non-reproductive or surplus individuals that were destined to die in any case (Errington 1956). Mortality caused by predation was therefore considered only compensating for other mortality sources in this “doomed surplus” hypothesis. The ecosystem-wide elaboration of this is the bottom-up view of population limitation where both herbivore and carnivore population abundances are limited from below by the availability of food (Lack 1954, White 1978). Food shortage limits populations of both trophic levels by reducing reproductive success, while both the abundance and quality of food are ultimately determined by weather (White 2008).

An opposing view uses top-down regulation to explain why “the world is so green” (Hairston *et al*. 1960). According to this hypothesis, the top-down regulation launches a trophic cascade (Paine 1980) where predators limit the abundance of herbivores, which releases plants from grazing pressure. While the existence of trophic cascades is well established in many aquatic and terrestrial systems (e.g. Schmitz *et al*. 2000, Shurin *et al*. 2002, Borer *et al*. 2005, 2006), examples on the indirect effects of vertebrate predators on plants via impacts on mammalian herbivores are still quite few (Sinclair *et al*. 2000, Norrdahl *et al*. 2002). However, several studies have offered support for this hypothesis by showing that predators indeed can limit or even regulate the population sizes of their prey (e.g. Korpimäki & Krebs 1996, Côté & Sutherland 1997, Sinclair *et al*. 1998, Gurevitch *et al*. 2000) and, on occasion, locally obliterate them (e.g. Kavanagh 1988).

Closely related to these two opposing views is the long-lasting debate of the importance of density-dependence in the regulation of populations. The density-dependent approach suggests that population growth rates decrease with increasing population densities because of negative feedback mechanisms (such as increased competition or predation), thus returning the population back to its equilibrium (Nicholson 1933, Sinclair 1989, Turchin 1995). Opponents of this paradigm argue e.g. against the idea of a constant equilibrium in nature (Andrewartha & Birch 1954, Turchin 1995) and remind that population sizes of both predators and prey are ultimately determined by food supply (White 2001, 2004, 2007, 2008). Further, the advocates of the mechanistic paradigm note that density-dependence has little practical value because of non-repeatability (Krebs 2003). The mechanistic paradigm is an effort to advance population ecology beyond density-dependence. It suggests that factors decreasing population growth rate, such as predators, parasites or food limitation, should be recognized directly through manipulative experiments and not via density-dependence (Krebs 1995, 2002, 2003).

Well-known examples of predator-prey interactions, where both bottom-up and top-down impacts have been suggested, include the large-scale population cycles of snowshoe hares *Lepus americanus*, lemmings and voles in northern latitudes. These species undergo regular high-amplitude fluctuations in 3-5 (voles and lemmings) or even 9-11 (hares) year-periods (Korpimäki *et al*. 2004). Hypotheses explaining these population cycles range from sunspots, food limitation and predators, to stress, pathogens and weather (Norrdahl 1995). Korpimäki *et al*. (2004) concluded that predator-induced mortality is the most likely cause of the high-amplitude population cycles, and that predators are especially responsible for the decline phase of these cycles while food limitation prevents populations from increasing further. Another famous example is the Isle Royale ecosystem with moose *Alces alces* and wolves *Canis lupus*, effectively a single predator – single prey –system, where 40 years of research has revealed both bottom-up and top-down regulation as well as the importance of abiotic factors on moose population dynamics (Vucetich & Peterson 2004a, 2004b, Wilmers *et al*. 2006). Indeed, Sinclair and Krebs (2002) concluded that population growth rates are primarily determined by food supply, but that occasionally this bottom-up control can be overridden by top-down processes.

1.2 NONLETHAL IMPACTS OF PREDATION

While the lethal impacts of predation have long been the center of intensive research, only fairly recently has the focus also turned to so-called nonlethal effects that predators have on prey. In addition to the direct lethal effects (“density-mediated interactions”;

Preisser *et al*. 2005), the mere presence of a predator may have profound impacts on prey populations. These effects have been termed intimidation (Preisser *et al*. 2005), nonlethal (Lima 1998), nonconsumptive (Preisser & Bolnick 2008), fear (Norrdahl & Korpimäki 1998, Brown *et al*. 1999, Thomson *et al*. 2006), trait or trait-mediated (Luttbeg & Kerby 2005, Preisser *et al*. 2005) or risk effects (Creel & Christianson 2008). These effects occur as antipredator changes in prey behavior or use of space to reduce the risk of being preyed upon (Lima 1998, Caro 2005). For example, many studies have shown that prey reduce their movement under higher perceived predation risk (Lima & Dill 1990, Caro 2005). Prey also tend to select a safer habitat under predation risk (Norrdahl & Korpimäki 1998, Caro 2005), for example elk *Cervus elaphus* reduce their use of open grassland in the presence of wolves *Canis lupus* (Creel *et al*. 2005).

While antipredator responses decrease the likelihood of a predator attack, they also reduce prey foraging efficiency. This trade-off may cause deterioriation of individual physical condition and thereby reduction in survival and reproductive success, which may ultimately affect prey population density (e.g. Lima 1998, Creel *et al*. 2007). Stress caused by increased predation risk may also directly impair prey reproduction (Boonstra *et al*. 1998). Overall the nonlethal impacts of predation risk on prey populations may even be stronger than the lethal impacts of predation (Werner & Peacor 2003, Preisser *et al*. 2005), and both of these impacts may cascade down the food web and restructure whole ecosystems (Ripple & Beschta 2004). Indeed, if not considered specifically, nonlethal effects could be mistaken as e.g. food limitation especially in observational studies (Creel & Christianson 2008).

1.3 PREDATORS OF PREDATORS

Traditionally the most important interactions affecting ecosystems are thought to occur between different trophic levels, i.e. between predators and herbivores, and herbivores and plants. However, important predatory interactions may also operate within one trophic level, termed intraguild predation (IGP). Intraguild predation takes place when predators competing for the same resource are also killing and eating each other (Polis *et al*. 1989). IGP is usually asymmetrical, with the larger predator (IG predator) preying on all the smaller ones (IG prey). In doing so, the larger predator simultaneously gains food and removes a competitor. IGP is very common in all ecosystems (Palomares & Caro 1999, Arim & Marquet 2004), and in the last decades its various impacts have started to be unravelled (Polis & Holt 1992, Vance-Chalcraft *et al*. 2007).

IGP has been shown to have a negative effect on the populations of the IG prey (Korpimäki & Norrdahl 1989, Roemer *et al*. 2002, Helldin *et al*. 2006, Young *et al*. 2006, Moehrenschlager *et al*. 2007). In other words, the populations of smaller predators may be limited by larger predators, termed "mesopredator suppression" (Berger &

Conner 2008). Such suppression may result in an increase of prey reproductive success, population diversity or density (Polis & Holt 1992, Palomares *et al*. 1995, Sovada *et al*. 1995, Johnson *et al*. 2007, Sergio & Hiraldo 2008, Berger & Conner 2008). Conversely, if larger predators are removed from the system, the smaller predators experience "mesopredator release" in the absence of IGP (Soulé *et al*.1988, Courchamp *et al*. 1999, Crooks & Soulé 1999). For example, the removal of coyotes *Canis latrans* launched a trophic cascade by increasing the densities of bobcats *Lynx rufus*, badgers *Taxidea taxus* and grey foxes *Urocyon cineroargenteous*, which led to a decrease in rodent species diversity but increase in rodent density and biomass, as the community became dominated by one species, Ord's kangaroo rat *Dipodomys ordii* (Henke & Bryant 1999). The strength of mesopredator release may be determined by the overall productivity of the ecosystem in question and may be negligible in areas where mesopredators are mainly limited by food shortage (Elmhagen & Rushton 2007).

While numerical effects of IGP on IG prey are already quite well known, the more subtle nonlethal impacts are not. Similar to two-trophic-level predation systems, the risk of intraguild predation may alter the activity, space use and other behavioral responses of IG prey, which may ultimately lead to a reduction in their population size (Woodroffe & Ginsberg 2005, Sergio & Hiraldo 2008). For example, coyotes tend to avoid the core areas of wolf territories (Arjo & Pletscher 1999). Tengmalm's owls *Aegolius funereus* avoid breeding near ural owl *Strix uralensis* nests as most breeding attempts near the IG predator fail (Hakkarainen & Korpimäki 1996). Tawny owls *Strix aluco* use both distance-sensitive and habitat-sensitive avoidance depending on the density of their IG predator, the eagle owl *Bubo bubo* (Sergio *et al*. 2007). Such interactions between predators should promote the persistence of prey populations, but are not yet well studied.

1.4 ALIEN PREDATORS AND THEIR PREY

Humans have changed natural ecosystems in countless ways, one of which is the introduction of novel species. The transfer of species over natural dispersal barriers has most likely occurred with every new colonization event since prehistoric times. For example, the dingo *Canis lupus dingo* was introduced from Southeast Asia to Australia ca. 5000 years ago (Savolainen *et al*. 2004). The first humans arriving into Polynesia over 3000 years ago carried with them numerous plant species and animals like dogs *Canis lupus familiaris*, pigs *Sus scrofa*, chicken *Gallus gallus* and Pacific rats *Rattus exulans* (Matisoo-Smith *et al*. 1998). Pacific rats were further the first terrestrial mammals to reach New Zealand with the Maori over 700 years ago (Wilmshurst *et al*. 2008), but introductions became ever more frequent with the rise of European colonialism (Crosby 1986). At least 118 mammalian species and 212 bird species have been introduced into new environments around the world (Ebenhard 1988), and introductions of non-native species continue to occur at an accelerating speed, as globalization facilitates rapid movements of humans and goods around the world (Meyerson & Mooney 2007). Global biological diversity is faced with the threat of biotic homogenization, where the spread of non-native species increases the compositional similarity of previously distinct locations (McKinney & Lockwood 1999). This progress leads us into a new era, the Homogocene (Rosenzweig 2001).

Non-native species may affect native fauna and flora through various mechanisms, for example predation and grazing, competition, hybridization and transmission of pathogens (Williamson 1996, Lockwood *et al*. 2005). Of these, predation is often considered the most severe, as alien predators have been implicated in many species extinctions, especially on oceanic islands historically lacking mammalian predators (Courchamp *et al*. 2003, Blackburn *et al*. 2004). An infamous example is the case of Stephens Island wren *Xenicus lyalli*, a flightless bird which was driven to extinction by feral cats in just a few years in the 1890s (Galbreath & Brown 2004, Medway 2004). Another endemic bird, the Macquarie Island parakeet *Cyanoramphus novaezelandiae erythrotis* survived for decades although cats had been introduced to the island soon after its discovery in 1810. However, the introduction of rabbits in 1879 offered both cats and wekas *Gallirallus australis* (a large rail introduced in 1872) an alternative food source, which resulted in the marked increase of their populations. Increased predation pressure from cats and wekas drove the parakeets to extinction by 1890 (Taylor 1979). However, while these historical extinctions are fairly well documented, many others are anecdotal and the impacts of alien predators may have been coupled with other factors such as habitat loss (Gurevitch & Padilla 2004).

As many alien predators have had such profound effects in their new environments, they may well be considered a special case of predation. The apparent reason for these devastating impacts seems to be the naiveté of prey. In communities where predators and prey have co-existed for long periods, prey often respond to predatory pressure by developing behaviors or morphologies that reduce the chance of encounters with predators or enhance the chance of escape once detected (Lima & Dill 1990). Such antipredatory adaptations may remain for many generations after predators have been removed (Dickman 1992, Berger 1999). In communities with novel, alien predators, prey are likely to be predator-naïve and to lack specific avoidance behaviors. They may not recognize the predator as a threat (level I naiveté), they may recognize the threat but respond in an inappropriate antipredatory manner (level II naiveté), or they may respond in a proper way but are still overwhelmed by alien predation (level III naiveté; Banks & Dickman 2007). Behavioral responses against predation may arise even within a single generation when the predators are familiar to prey in evolutionary scale (Berger *et al*. 2001). Prey may also be more capable to adapt to a novel predator if it is even remotely related to those already present, than to an alien predator which represents an evolutionarily novel archetype (Cox & Lima 2006). Sadly, in many cases it appears that prey have gone extinct before developing a functioning strategy against an alien predator (but see Massaro *et al*. 2008).

The reasons why some introductions succeed while others fail are not well known. Features that have been suggested as predictors include e.g. previous invasion success (success in one location increases probability of success in others), propagule pressure (invasion probability increases with the size of the founder population), intrinsic rate of natural increase (*r*-selected species would be better invaders), taxonomic isolation (species unrelated to native species would be better invaders), abundance and range in native habitats (species common in their native areas could be better invaders), human commensalism (most introductions take place in human-modified habitats and species adapted to such habitats could be better invaders) and the ability to utilize a vacant niche (species that can fulfill a missing function in the ecosystem invade more easily; Williamson 1996, Sax & Brown 2000, Lockwood *et al*. 2005, Sol 2007, Davis 2009). Introduced species should also benefit from enemy release, whereby the competitors, predators and parasites of a species are left behind in the original range (Sax & Brown 2000, Torchin & Mitchell 2004, Hufbauer & Torchin 2007). Thus far only two general predictors have emerged in the case of vertebrate introductions: a broad ecological niche (generalist vs. specialist) and a high degree of behavioral flexibility appear to correlate positively with invasion success (Sol 2007). However, large differences in invasion potential appear even between closely related species (Sol 2007) and different features may be more important in the transition and establishment stages than in the spreading stage (Lockwood *et al*. 2005).

1.5 AMERICAN MINK

One of the most widespread non-native mammals in Europe is the American mink *Mustela vison* Schreber (hereafter mink), a North American mustelid, which was introduced to Europe as a fur animal in the 1920s (Dunstone 1993). The mink is a semi-aquatic generalist predator with very versatile habitat requirements and high reproductive potential (Dunstone 1993). In its native range mink are distributed througout North America, excluding the drier southern parts of the US and the Canadian Arctic coast (Larivière 1999). Mink are mainly associated with water systems such as river banks, lake and marine shores and marshes, and their diet consists of a variety of prey from fish and crayfish to birds (also eggs) and mammals (to the size of muskrats *Ondatra zibethicus* and European rabbits *Oryctolagus cuniculus*) (Dunstone 1993, Jędrzejewska *et al*. 2001).

Escapees from fur farms together with animals from deliberate releases have established feral mink populations throughout Europe and the former Soviet Union, and populations also occur in South America and Asia (Medina 1997, Previtali 1998, Bonesi & Palazon 2007). Throughout its introduced range the mink has been accused of causing the decline of many native species (reviewed in Kauhala 1996a, Macdonald & Harrington 2003, Bonesi & Palazon 2007, Banks *et al*. 2008). For example, the population decline of water voles *Arvicola terrestris* in UK has been connected to mink predation (Woodroffe *et al*. 1990, Macdonald *et al*. 2002), and mink have also been implicated in the decline of the European mink *Mustela lutreola* (Maran & Henttonen 1995, Maran *et al*. 1998, Sidorovich *et al*. 1999). However, both of these declining native species are also affected by habitat change at least in some locations, therefore the American mink is likely not solely to blame. In reported cases of mink effects on breeding seabirds it is obvious that mink have had devastating local effects (e.g. Kilpi 1995, Craik 1997, 2000, Craik & Campbell 2000, Clode & Macdonald 2002, Nordström *et al*. 2002, 2003, Nordström & Korpimäki 2004, Schüttler *et al*. 2009). Especially colonial species like the black guillemot *Cepphus grylle* are often heavily affected, as one mink may destroy the entire colony during one visit (Hario 2002). Mink predation impacts on wetland birds appear more variable (e.g. Halliwell & Macdonald 1996, Ferreras & Macdonald 1999, Opermanis *et al*. 2001, Bartoszewicz & Zalewski 2003). In addition, recolonising Eurasian otters *Lutra lutra* appear to compete with mink (Bonesi & Macdonald 2004a, Bonesi *et al*. 2004), possibly to such an extent that it causes mink populations to decline (Bonesi & Macdonald 2004b, Bonesi *et al*. 2006).

Mink were also brought to Finland for fur farming in the late 1920s, and before long escapees were forming free-living populations. By the early 1980s mink had colonized the whole country, from northernmost Lapland to the outermost islands of the southern coast (Kauhala 1996b). Information on mink diet and predation impacts on the Finnish mainland are quite limited (Tolonen 1982, Pulliainen 1984), but mink is often feared to have serious effects on e.g. waterfowl. Much more is known of mink in the south-western archipelago, where it is truly a novel predator. There have been no resident terrestrial mammalian predators on the isolated islands of the outer archipelago except for otters, which have been locally extinct for decades, (Stjernberg & Hagner-Wahlsten 1994, Kauhala 1996b). In the archipelago mink have been shown to negatively affect the populations of voles (Banks *et al*. 2004, Fey 2008), common frogs *Rana temporaria* (Ahola *et al*. 2006) and many breeding bird species (Nordström *et al*. 2002, 2003, Nordström & Korpimäki 2004). Mink have also been accused of negatively impacting the European mink in Finland, but the decline of the native species began prior to mink becoming established (Maran & Henttonen 1995).

1.6 TAXONOMY AND NOMENCLATURE OF MINK

In recent ecological literature the American mink is often referred to as *Neovison vison* (Schreber). Abramov (2000) distinguished American mink from the other members of genus *Mustela* based on morphological characters, such as skull structure, dentition and baculum (os penis) structure. Other differences between mink and other *Mustela* mentioned in the literature include e.g. chromosome number (Graphodatsky *et al*. 1976), immunochemistry of serum proteins (Belyaev *et al*. 1980), antigenic structures of immunoglobulins (Taranin *et al*. 1991), and chemical composition of anal sac secretion (Brinck *et al*. 1983). However, many of these characters are problematic with regards to taxonomic classifications. For example, chromosome numbers vary widely within studied *Mustela*: in 11 species 2n = 30 – 44, while in seven species the chromosome number remains unknown (Kurose *et al*. 2008). Baculum morphology suffers both from high amount of convergence at higher taxon levels and high variability at species level, and therefore should not be used alone to infer taxonomic relationships (Baryshnikov *et al*. 2003).

Several contemporary phylogenetic studies based on molecular data have shown that *Mustela vison* has been among the first species to diverge from the rest of the genus (Sato *et al*. 2003, Marmi *et al*. 2004, Flynn *et al*. 2005, Kurose *et al*. 2008). The most comprehensive molecular systematic analysis thus far, based on ca. 12 000 base pairs and sampling of over 60 % of *Mustela* species, showed that American mink together with *Mustela frenata* form a sister lineage to the rest of genus *Mustela* (Koepfli *et al*. 2008). Based on this molecular phylogenetic evidence, the recognition of a separate genus *Neovison* for the American mink appears taxonomically unjustified and evolutionarily misleading. Hence, the species is here referred to as *Mustela vison* Schreber. However, a taxonomic revision based on both molecular and morphological data and including all *Mustela* species would be highly warranted in the future.

1.7 AIMS OF THE THESIS

The central theme of this thesis lies within predator impacts on prey. These impacts are explored from various angles and scales, using a variety of different methods. The thesis begins with studies on overall predation impacts and proceeds to detailed studies at the species level, by which I wish to introduce some examples of the wide range of behaviors and mechanisms both predators and prey use in their interactions. Hopefully this thesis will show that there is so much more to predation than the mere predation event we may observe.

Despite massive amounts of research and empirical results on individual species, the issue of vertebrate predator impacts on prey populations still appears to lack a proper quantitative synthesis. Such a synthesis could greatly advance our understanding of predator-prey population dynamics by summarizing what is already known and what needs yet to be done. Besides theory, the discussion of predator limitation or regulation on prey has relevance also in the practice of wildlife management and biodiversity conservation. These disciplines regularly apply predator control as a method among others; therefore it would be important to identify both the possibilities and limitations of such an approach. I set out to resolve some of these issues through an extensive review on published experimental studies on terrestrial vertebrate predators and their prey (I).

Alien species and especially alien predators are nowadays an increasingly hot topic in the media, with militaristic metaphors such as “attack”, “eradication strategy”, and “war against invasion” commonly used (Larson 2005). Alien predators can be considered a special case of predation because they often seize prey that is at least to some extent naïve to their predation; in the worst case, alien predators may represent a completely novel predator archetype. Numerous examples especially from oceanic islands have led us to believe that the impacts of alien predators on prey populations are much more devastating than those of native predators. Since this view has never been quantitatively tested, I used meta-analytical methods on published studies to measure the impacts of alien and native predators and to explore whether alien predators indeed have more detrimental effects (II).

The first two parts of this thesis may appear to consider prey as passive objects of predation, “lambs to the slaughter”. Nothing could be further from the truth; prey possess various behaviors aimed to reduce the risk of being caught, but by employing these behaviors prey incur a cost. The resulting nonlethal predation impacts on prey may be just as strong as direct predation impacts. In particular, the nonlethal impacts of intraguild predation have been poorly studied, while they could have important applications in both wildlife management and conservation. Because of the claimed devastating effects of alien predators, it would be a great relief for conservation managers if the natural predator community would be able to resist and mitigate the effects of an invading novel predator. Therefore I studied the nonlethal impacts of one returning top predator, the white-tailed sea eagle *Haliaeetus albicilla*, on alien American mink in the outer archipelago of the Baltic Sea, where mink have been shown to negatively affect birds, mammals and amphibians (III). As mink are most vulnerable to sea eagle predation while swimming, I hypothesized that mink would reduce their inter-island movements in the presence of eagles.

The American mink has been incredibly successful in the harsh conditions of the Baltic outer archipelagos, considering that it is mostly accustomed to inland wetland habitats in its native range. The mink is truly a novel predator in the archipelago ecosystem, which may be the key to its success: it has managed to occupy a vacant niche with enough resources and almost without natural enemies and competitors. As a generalist the mink tends to include different prey items in its diet according to their availability. In order to improve knowledge of mink ecology in the outer archipelago I studied the relationship between mink summer diet composition and home range characteristics (IV). I hypothesized that the patchy structure of archipelago mink home ranges would be reflected in their diet: mink living in home ranges containing large islands would have a more diverse diet, whereas mink inhabiting small and isolated home ranges would mostly prey on fish.

Compared to the animal groups handled in the other parts of this thesis (birds and terrestrial mammals), amphibians are still relatively poorly studied. However, we do know that amphibians are facing population declines all over the world, with alien predators suggested as one possible cause for their demise. While amphibians are not usually a major part of mink diet, alien mink have previously been shown to suppress common frog populations in the outer archipelago. I wanted to study this system in more detail to see how common frog distribution on the islands might be affected by mink predation (V). I hypothesized that under mink predation common frog densities would be highest on large, more vegetated islands with more refuges for frogs.

2. METHODS

2.1 REVIEWS (I AND II)

The first part of this thesis consists of two studies which utilize the work of other scientists in the form of quantitative reviews. Reviews and syntheses are milestones of science: they explore the evidence for and against a specific hypothesis, evaluate the importance and quality of this evidence, form a conclusion and point the way forward. Traditional syntheses are based on narrative reviews, while meta-analyses provide quantified summaries of articles, giving both the magnitude and direction of the impact, instead of staring only at *P*-values of statistical tests (which depend on sample size, among other things). Recently meta-analyses have become more common in ecology: A search in the ISI Web of Knowledge (on 24th April 2009) using a keyword “meta-analysis” and restricting subject area to “ecology” yielded 56 references published in 1990-1999, and 436 references published in 2000-2009!

2.1.1 Data collection and analysis

For both the general review on predator impacts and the special focus on alien predator effects, I conducted a data search for relevant published studies using the on-line databases of the Web of Science, Biosis Previews, and Biological Abstracts. Bibliographies of earlier reviews (Côté & Sutherland 1997, Newton 1998, Sundell 2006) and of papers already retrieved were also used to find new references. For both articles I selected publications that described the effect of reduction or enhancement of terrestrial vertebrate predator populations on vertebrate prey, excluding livestock.

For chapter I the search yielded 113 predator manipulation experiments which met the criteria. These included 61 replicated studies (those with at least two control and two treatment plots or a before-and-after design) and 52 unreplicated experiments (only one treatment or control sample). Most of them were published in international scientific journals on ecology, conservation and wildlife, but I also included book chapters and unpublished Ph.D. and M.Sc. theses. Articles were published between 1939 and 2007, with 60 % originating from the last ten years.

For chapter II a subset of the aforementioned dataset was used, including 45 replicated and 35 unreplicated predator manipulation experiments on either alien or native predators. Prey in this case had to be a native species. Studies that had removed both native and introduced predators were excluded, if the effects of these predator groups could not be separated.

In a meta-analysis the magnitude and direction of impact of each study is summarized in an effect size. In chapter II the effect size was calculated as Hedges' *d* (standardized difference between experiment and control means, divided by pooled standard deviation), using MetaWin 2.1 (Rosenberg *et al.* 2000). Positive values of *d* indicate that the predator manipulation had a positive effect on prey species, zero means that there was no difference between treatment and control, and negative values signify a greater response in controls. Unreplicated studies lack the standard deviations needed for calculating *d*, but such studies comprised about half of my dataset. Therefore I also calculated a more simple effect size as X_e/X_c where X_e and X_c are the treatment and control prey responses. $X_e/X_c > 1$ indicates that prey populations benefitted from predator manipulation. This simpler effect size was used throughout chapter I and also in chapter II. Effect sizes have been calculated to account both for predator removal and predator density enhancement, thus "predator manipulation effect" always refers to the response of prey to smaller predator density

In chapter I, I explored not only the overall predator effect on prey, but also the different variables of experimental design which I hypothesized could possibly affect the results. These included e.g. the spatial and temporal scale of the experiment, the number of predator species manipulated, the efficiency of predator manipulation and whether the experiment was conducted in an exclosure or an open field. Manipulations were deemed "high efficiency" if they provided verbal, tabular or statistical evidence of the success of predator removal or enhancement (e.g. demonstrated a significant difference in predator densities between control and experimental areas); in "low efficiency" experiments the manipulations did not markedly affect predator populations. I attempted to use multiannually cyclic and non-cyclic prey species at their peak and low densities as well as their overall population variability to investigate whether predators may have limiting or regulating effects on their prey. Last, I explored factors that appear to affect the citation rates, and thus impact, of published experimental studies.

In chapter II, I tested for the overall difference in impact of alien as opposed to native predators on prey populations. As the most dramatic examples of alien predator impacts come from insular ecosystems, I also tested whether the effects of alien and native predators were different in mainland vs island conditions. In addition, I examined the influence of different experimental design variables, such as the spatial and temporal scale of the experiment.

2.1.2 Pitfalls of meta-analysis

Meta-analyses can provide powerful summaries of ecological results, but should be used rigorously to avoid publication and other biases (Kotiaho & Tomkins 2002). Publication bias occurs when published studies are not representative of all studies conducted (Csada *et al*. 1996, Møller & Jennions 2001). For example, statistically significant results may get published more often than nonsignificant results, a source of bias termed the “file drawer problem” (Rosenthal 1979). Significant results are also more likely to be published in English, which may lead to more citations through indexing in an electronic database (Egger *et al*. 1997a). In addition, results supporting currently fashionable hypotheses may be easier to publish than contradicting ideas (Simmons *et al*. 1999). Testing publication bias should be a compulsory part of meta-analysis (Kotiaho & Tomkins 2002). In my thesis I followed the recommendations of Gates (2002) to increase confidence in the generality of my results.

Several methods are available for testing publication bias. One method is to calculate a fail-safe number, i.e. the number of unpublished, non-significant studies needed to overturn the conclusions of the analysis (Rosenthal 1979). Funnel plot analysis is a graphical method in which the effect size is plotted against the sample size (Egger *et al*. 1997b). If there is no bias, a typical “funnel” shape will be seen: variation around the effect size decreases as sample size increases. A statistical analogue of the funnel plot is a rank correlation test (Begg & Mazumdar 1994). Another graphical method with some advantages over funnel plot is the normal quantile plot (Wang & Bushman 1998). The normal quantile plot is easier to interpret (especially if the sample size is small) and also tests the assumption of normal distribution of effect sizes. I used this latter method in chapters I and II to check for publication bias from Hedges’ *d* values of replicated studies. This analysis was not possible for unreplicated studies, and therefore the publication of such studies may have been biased towards large, positive effects of predator removal on prey. However, it is rather unlikely that the results, whether being significant or not, of very expensive, long-lasting predator removal experiments remain unpublished, strongly reducing the likelihood for the file-drawer problem in these particular meta-analyses.

2.2 FIELD STUDIES (III – V)

2.2.1 Study areas

Fieldwork for chapters III-V was conducted on both state and private lands in three areas in the Archipelago National Park joint working area of the Baltic Sea, SW Finland: Trunsö and Brunskär in Korppoo and Vänö in Dragsfjärd (Fig. 1). Brunskär covers 117 km^2, with 3.4 km^2 land area and a mean island size of 1.9 ha (range 0.16 - 24 ha). Trunsö covers 47 km^2, with 1.4 km^2 land area and a mean island size of 2.0 ha (range 0.18 – 12.9 ha). Vänö covers 60 km^2, with 2 km^2 land area and a mean island size of 1.1 ha (range 0.15 - 21 ha).

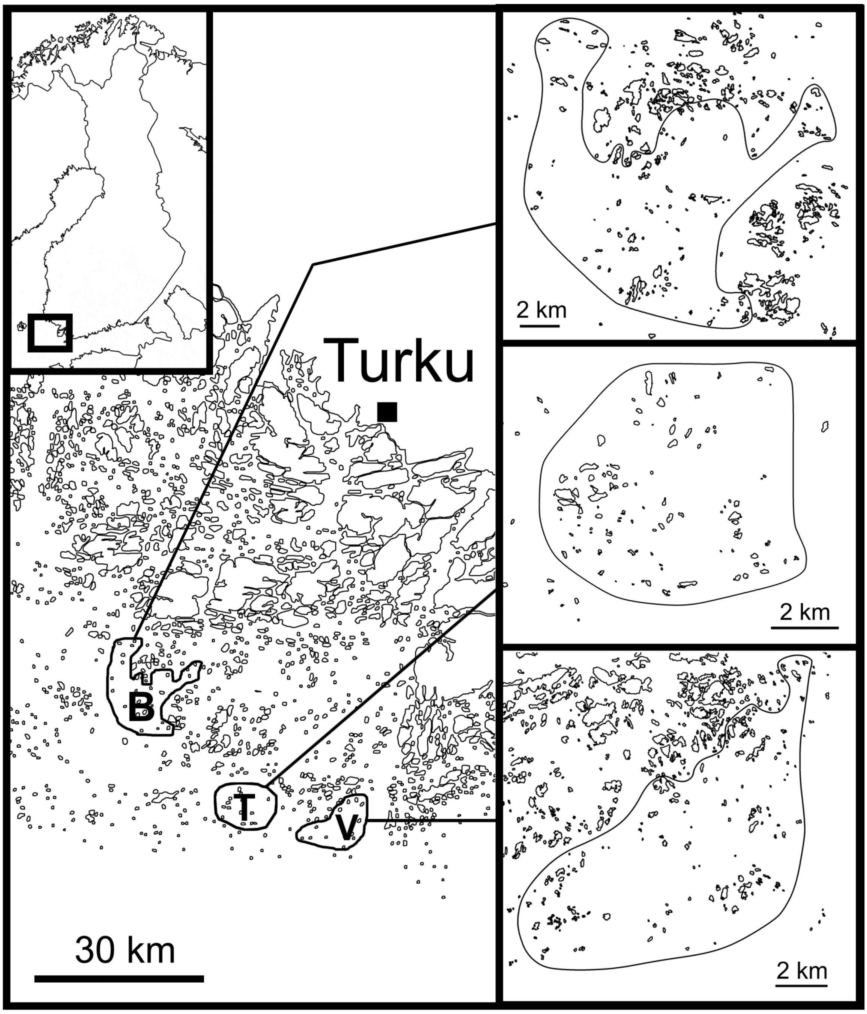

Figure 1. The location of the three field study areas in the Archipelago National Park in Archipelago Sea, SW Finland. B = Brunskär, control area where mink were not removed. T = Trunsö, mink removal since autumn 1992. V = Vänö, mink removal since autumn 2006.

Islands in these study areas are mostly small and rocky, and their sparse vegetation is characterized by grasses (Poaceae, Cyperaceae) and a shrub layer consisting of bog bilberry *Vaccinium uliginosum,* heather *Calluna vulgaris*, crowberry *Empetrum nigrum*, and juniper *Juniperus communis*. A few of the largest islands have solitary trees, mainly pine *Pinus sylvestris*, rowan *Sorbus aucuparia*, or alder *Alnus glutinosa*.

The islands host quite diverse fauna during the summer. For example, many species of migratory birds breed in the areas from May to July. The most common species are common eider *Somateria mollissima*, common gull *Larus canus*, herring gull *Larus argentatus*, and arctic tern *Sterna paradisaea*. A few species of passerines are also common: wagtail *Motacilla alba*, rock pipit *Anthus petrosus* and meadow pipit *Anthus* *pratensis* nest under rocks and in the shrub layer of the islands. Birds in the study areas have been surveyed yearly by Metsähallitus Forest and Park Service.

Voles are the only herbivorous mammals common in the outer archipelago, with field vole *Microtus agrestis* being the dominant species (Pokki 1981). Bank voles *Myodes glareolus* and shrews *Sorex* spp. are scarce, and mountain hares *Lepus timidus* occasionally occur on larger (≥ 4 ha) forested islands. Three species of amphibians include common frog, common toad *Bufo bufo* and common newt *Triturus vulgaris*. Two species of snakes are also resident: adders *Vibera berus* and grass snakes *Natrix natrix*. The most common fish species in the areas are perch *Perca fluviatilis*, Baltic herring *Clupea harengus membras*, roach *Rutilus rutilus*, flounder *Platichthys flesus* and whitefish *Coregonus lavaretus* (Ådjers *et al*. 2006).

Feral American mink are the only resident terrestrial mammalian carnivores in outer archipelago; European mink has apparently never occurred in the archipelago (Westman 1968) and otters have been extinct for decades (Stjernberg & Hagner-Wahlsten 1994, Kauhala 1996b). Red foxes *Vulpes vulpes* and raccoon dogs *Nyctereutes procyonoides* occasionally occur and breed on larger islands. White-tailed sea eagles and eagle owls are the only resident raptors in the area, while other raptors may visit the islands during migration.

Mink have been removed in the area of Trunsö every year in spring and autumn since autumn 1992 (see Nordström *et al*. 2002, 2003 for details). The number of mink caught in the area fell rapidly to only a few individuals per year after the beginning of removal (Nordström *et al*. 2002), and no mink signs (sightings, scats, prey remains) were observed in Trunsö in spring 2007. Vänö and Brunskär serve as control areas where mink have not been trapped. In autumn 2006, the mink removal area was extended into Vänö. However, the initiation of mink removal had not markedly affected the local mink population by spring 2007, as several observations of mink on the islands were then made.

2.2.2 Mink radio-tracking and home ranges (III – IV)

Mink were trapped and radio-tracked in June-August 2004 in Vänö and in May-July 2005 both in Vänö and Brunskär (III-IV). Altogether 20 mink were caught: in 2004, 5 females and 2 males in Vänö, and in 2005, 3 females and 1 male in Vänö and 5 females and 2 males in Brunskär. Mink were caught either in box traps baited with dried fish and mink scent or by flushing them out of their dens with a leaf-blower into a net (a nonlethal modification of the method described by Nummelin & Högmander 1998). Trained dogs were used to locate mink on the islands. Mink were anaesthetized immediately after capture, after which they were sexed, weighed, and fitted with a waterproof radiotransmitter attached to a collar (Teflon Collar, model TW-4, Biotrack Ltd., Poole, UK).

Positions of radiocollared mink were found at least twice per day, preferably at dawn and dusk. Mink were initially located on an island from a boat and then on land by approaching from the downwind side to a denning animal and taking GPS coordinates from a distance of about 5-10 m. Occasionally we were also able to directly observe active mink for minutes without being noticed, either on land (downwind side) or from the boat. Locations obtained within 24 h of the collaring procedure were ignored in the analyses to account for the impact of catching, handling and collaring on the movements of the animal (Gerell 1969).

Home range boundaries for each mink were calculated from all locations as minimum convex polygons (MCP) with Ranges 6 (Anatrack Ltd., Poole, UK) and plotted on a map in MapInfo (MapInfo Professional 7.5, MapInfo Corporation, Troy, New York, USA) (Fig. 2). All islands with confirmed radiolocations and within or crossing the MCP were included in the home range, which was calculated as the sum of land area (ha) of all

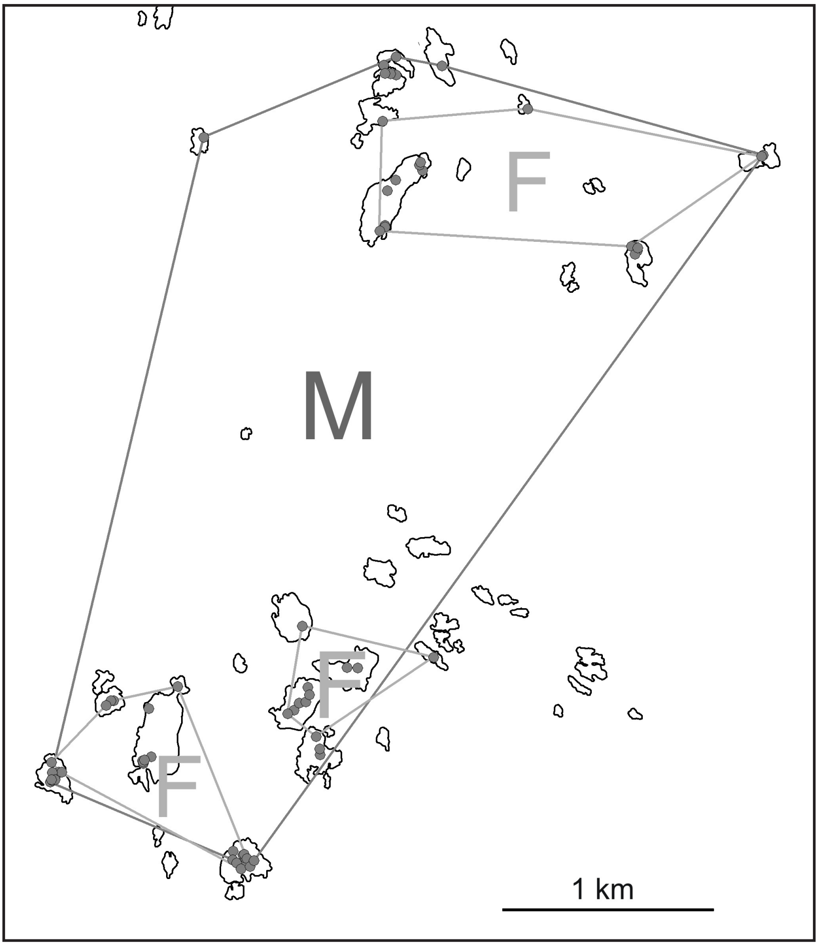

Figure 2. An example of American mink *Mustela vison* home ranges in the outer archipelago of the Baltic Sea, SW Finland in summer 2004. The map shows maximum convex polygons (MCPs) drawn for locations of four radiocollared mink. The home range of one male (M) encompasses those of three females (F).

islands in the home range. Number of islands and the mean distance (m) between islands were used to describe home range structure. Home range isolation from the surrounding archipelago was defined using the number and land area of islands within 1 km radius of the MCP boundaries.

2.2.3 Mink movements and eagle predation risk (III)

To explore the impact of sea eagle predation risk on mink behavior, I calculated observed mink swimming distances based on locations taken at dusk and dawn; as mink are mainly nocturnal (Gerell 1969, Dunstone 1993), most of the shifts between islands occurred during nighttime. Observed mink swimming distances (obs) were calculated from these locations as the minimum swimming distance between two consecutive locations (i.e. mink was assumed to use land bridges whenever possible).

Mean expected swimming distance (exp) for each mink was calculated through a stepwise resampling procedure using all combinations of possible movements within the home range. The effect of eagle predation risk and other factors on explaining variation in observed mink swimming distances was tested using an index (obs-exp)/exp as a response variable. This index describes the proportional deviation from randomly expected swimming distances. Increasingly negative values indicate the degree to which a mink was swimming less than was randomly expected.

Sea eagles were regularly observed while traveling and radio-tracking mink in the two study areas. All sea eagle sightings were recorded as date, time, place and eagle age (juvenile / subadult / adult). The number of eagle observations in each area was related to the distance (km) traveled by boat each day. Occupancy and productivity of all sea eagle territories were checked annually by the members of the WWF's Finnish sea eagle conservation team (see Stjernberg *et al*. 2006 for a nationwide report). During both study years there were four occupied sea eagle nests in or near Brunskär study area and one occupied nest in Vänö. For each mink the sea eagle predation risk was estimated using two variables: (i) the mean distance (m) of the mink from the nearest occupied eagle nest, and (ii) the mean number of eagle observations within 1 km radius.

2.2.4 Mink diet (IV)

Fresh mink scats that could be linked to known mink individuals were collected from den sites found during radio-tracking. From a total of 20 radio-tracked mink, 11 individuals (nine females and two males) yielded enough data from both radio-tracking and scats to be included in the analysis (IV). In addition to radio-tracked individuals, scats from one female with kits in the area of Brunskär were included in the diet analysis. For prey identification the scats were soaked in a detergent solution overnight and then sieved. The remaining material was dried at 50 °C for 24 hours and then weighed.

The three main prey groups identified in the scats were mammals, birds and fish. Mammalian prey was identified to the species level using hair (Teerink 1991) and teeth, while birds were identified by feathers either as waterfowl (Anseriformes), passerines (Passeriformes), or waders, larids and allies (Charadriiformes) using downy barbules (Day 1966). Fish were identified by scales and bones to either order or species with the key of Steinmetz & Müller (1991) and a reference collection. Mink diet was then presented in four ways: (i) % occurrence is the percentage of a prey item of all observed prey items; (ii) % scats is the percentage of scats containing a particular prey item of all scats; (iii) % dry weight is the percentage dry weight of a prey item of the total dry weight of all scats; and (iv) % biomass is the percentage fresh weight of a prey item of the total fresh weight of consumed prey. Log-ratio transformed percent occurrences were then used in a compositional analysis where the proportions of the three prey groups (mammals, fish and birds) were related to mink home range characteristics, such as home range size (land area) and isolation.

2.2.5 Common frog densities under mink predation (V)

Common frogs lay one egg batch per female each spring (Savage 1961), and the number of egg batches can therefore be used to describe the number of breeding females in the population (Laurila 1998). For this study egg batches were counted during surveys in April-May in 1999 and 2007 in two areas, Trunsö mink removal area (47 islands) and Vänö control area (42 islands). The number of egg batches varied from 0 to 36 per pool, and from 0 to 131 per island.

I used island characteristics such as size, % vegetation cover, proportion of shrubs of the vegetation cover, % water cover (proportion of summed pool areas of island area) and pool density (number of pools per island area) combined with variables describing island isolation (minimum distance to the nearest neighbouring island and land area of islands within 1 km range) to explain breeding female frog densities on islands in 2007. Vegetation cover of shrubs and grasses was calculated from digitized aerial images that were verified with field observations during spring 2007 frog census. Altogether over 2 000 pools were counted and measured during the spring 2007 census. I also explored the temporal trend of breeding female frog numbers between surveys in mink removal and control areas in 1999 and 2007, to see whether the mink removal continued to have a positive impact on frog populations.

3. RESULTS AND DISCUSSION

3.1 PREDATION IMPACTS, EXPERIMENTAL DESIGN AND JOURNAL CITATIONS

The worldwide meta-analysis on predator density manipulation experiments (I) showed that vertebrate predators can indeed suppress the population sizes and reproductive success of their prey: on average predator manipulations yielded a 1.7-fold increase in prey populations. This is comparable to the 1.6-fold increase in prey populations found in a recent meta-analysis of veterbrate populations in the UK (Holt *et al*. 2008). One of the factors influencing the magnitude of the manipulation experiment results was manipulation efficiency: high-efficiency experiments showed 1.6-fold higher impacts on prey compared to low-efficiency experiments. Some studies could not confirm that their predator manipulation actually affected predator densities in the study areas; a necessary precondition for drawing reliable conclusions from such experiments. There is also a good reason to monitor densities of other predator species besides the manipulated one, as mortality avoided by removing one predator may be compensated by mortality caused by other predators still present or even attracted to the area (Ford & Pitelka 1984, Norrdahl & Korpimäki 1995). My results for native predators support this view: they showed that manipulating only one predator species may have no positive effects on prey, whereas manipulating multiple predator species benefits prey populations. However, the relationship was reversed in the case of introduced predators, where manipulating only one predator had a large positive impact on prey. The division between alien and native predators was included already in this study, but the detailed impacts of predator origin on prey will be discussed in part 3.2.

The temporal scale of the experiments spanned from 2 months to 15 years (median 36 months), while the spatial scale ranged from 0.13 ha to over 3100 km^2 (median = 2.5 km^2). The magnitude of predator manipulation effects was not related to spatial scale, but showed increasingly positive effects with time for non-cyclic prey, while the opposite was true for cyclic prey. As the experimental prey populations increase after predator manipulation, other factors such as intraspecific competition may come into play; thus experiments, conducted especially on rapidly reproducing small cyclic mammals, could actually show a decreasing trend in effect sizes with time.

A significant interaction between predator/prey weight ratio and the number of predators manipulated revealed a decreasing effect size with increasing predator/prey weight ratio in experiments with only one predator; experiments with multiple predators revealed no relationship. This supports the notion that predators have a diminishing impact on prey outside their optimum prey size, i.e. on alternative prey (Wilson 1975, Fisher & Dickman

1993). The choice of the prey response type measured in experiments may be related to the magnitude of results. Previously it has been shown that predator manipulations have a larger positive impact on prey reproductive success than prey population size (Newton 1993, Côté & Sutherland 1995, Holt *et al*. 2008), but I found no significant support for this view. Usually it is not known how well short-term increases in prey reproductive succes convert to increases in population size.

In support of the hypothesis that predators regulate both cyclic and non-cyclic prey populations, the impacts of predators were larger in the decline and low phases than in the peak phases of the cyclic prey species. In contrast, for non-cyclic species the impacts of predators were larger in the peak phase than in the low phase. While the density dependent view of population regulation (where populations are regulated by a negative feedback mechanism which slows down population growth when population density increases) has increased our understanding of population dynamics, it also suffers from severe practical difficulties, which prohibit feasible applications in wildlife management and conservation. Indeed, Krebs (2003) has claimed that density-dependent –related questions are an unnecessary loop in the search of population-regulating factors. Thus it makes sense to advocate the mechanistic paradigm (Krebs 1995, 2002, 2003), which through manipulation experiments focuses directly on the individual factors that affect population growth rates. After all, the results of this meta-analytical study appear to give strong support for both the popularity and effectiveness of such a manipulative approach.

That being said, it is also obvious that not all populations are limited or regulated by predators all of the time: 25 out of 113 experiments showed no positive effect of predator manipulation on prey. This may be related to the nature of the experiments or some specific circumstances. Predator manipulation efficiency has already surfaced as one important factor, as well as the possibility of other predators compensating for the mortality caused by the manipulated predator. Prey may escape predator limitation during an outbreak, caused for example by a sudden increase of resources; predator manipulation will show no effect because prey population growth is regulated by food (e.g. Pech *et al*. 1992, Letnic & Dickman 2009). Predators may also have positive effects on prey (Abrams 1992), thereby predator removal may result in no increase in the prey population if the predator preys on a major competitor of the targeted prey species, or if predator removal allows the release of mesopredators that in turn suppress the prey species (Glen & Dickman 2005). Especially these detailed predator-prey relationships warrant further attention.

No scientist wishes his or her work to end up in the "file drawer"; science is all about sharing knowledge and results, and thus the influence of published studies is often measured by the rate they are cited in the literature. I explored the citation rates of experimental papers on predator manipulations and found, unsurprisingly, that citation rates increased with the impact factor of the journal and also if the results of the study were positive (i.e. confirming hypothesis). Replication of the experiment did not affect citation rates, although replicated studies may intuitively be considered more reliable than unreplicated ones. There are divergent opinions on the need of replication. Unreplicated experiments are more vulnerable to stochastic variation, but in certain systems replicating may be unfeasible e.g. in the cases of rare and endangered prey species. My results suggest that reasonable conclusions can also be made based on unreplicated manipulations.

Overall, this review showed that predators do have substantial quantitative impacts on their prey, but many questions still remain unanswered. Most experimental predator manipulation designs stand critical observation, but manipulation efficiency is often addressed inadequately, and more detailed information is needed of the most important predators and mortality factors of targeted prey species in the studied systems. Recent knowledge on the importance of both nonlethal predation effects and interactions between predator species (mesopredator release and suppression) should also be taken into account. My results suggest that control of introduced vertebrate predators can be a warranted tool in wildlife management, whereas action to control native predators should be taken cautiously.

3.2 ALIEN VS. NATIVE PREDATORS

The results of the analysis on alien vs. native predator effects on prey (II) showed that overall the effects of introduced predators were double those of native predators. However, further partitioning revealed that this result was largely driven by the consistently high effect sizes of alien predator studies in Australia compared to studies elsewhere. Unexpectedly, alien predator impacts were strongest on mainland and not in insular ecosystems; a result again driven by the large effects of alien predators on the Australian continent.

There are a number of reasons why Australia stands out in this analysis. First, there were comparatively few experiments on alien predators available from other areas and none from mainland situations outside Australia. Australia shares a long history of invasions (Rolls 1969, Dickman 1996, Kinnear *et al.* 2002, Long 2003) which has also prompted numerous studies on the impacts of aliens on native species. In addition, experiments there benefit from the possibility to use poison baiting as an easy and cheap passive method of alien predator removal: a poison called 1080 (sodium monofluoroacetate) occurs naturally in many plant species in Western Australia, which reduces the effects on non-target species (Glen *et al.* 2007) as many native herbivores have a high tolerance to 1080 (McIlroy 1986). Comparable studies on other mainland areas face practical and financial difficulties of building large-scale experiments where alien species should be separated from a diverse native predator community using exclosures or other removal methods.

Second, despite its status as a continent, Australia has many island-like characteristics. These include geographical isolation and diversity of endemic species, which may also have contributed to the profound impacts of alien predators there. The frequent historical biotic interchanges between the contiguous continents of Eurasia, Africa and the Americas have caused them to share similar terrestrial predator archetypes, which may render prey less naïve towards novel predators introduced from the same continents (Cox & Lima 2006). In contrast, Australian marsupials never faced placental carnivores until they were introduced by humans, and if these novel predators use tracking and hunting tactics that differ from those of their extinct marsupial counterparts (Wroe *et al*. 2004), they may well overcome the defences of native prey (Croft & Eisenberg 2006). In addition, due to habitat fragmentation many native prey populations are currently restricted to small, island-like refugia, which makes them especially vulnerable to alien predators (Morton 1990, Letnic & Dickman 2006).

Despite the skew in availability of research on alien predators, there was evidence that the greater impact of alien predators is not simply restricted to Australia. As the accounts of alien predators causing historical extinctions of native prey are mostly correlative and anecdotal (Gurevitch & Padilla 2004, Clavero & Garcia-Berthou 2005), this review was the first to quantitatively reveal an ongoing crisis whereby alien predators can suppress prey populations more than native predators. Together with habitat loss, alien predators pose an increasing risk of extinction for many species.

3.3 PREDATION RISK IMPACTS ON MINK BEHAVIOR

The results on the nonlethal impacts of sea eagles on feral mink movements in the outer archipelago (III) suggested that at least female mink adjusted their behavior according to sea eagle predation risk: female mink significantly reduced their swimming when the number of eagle observations increased and when they were situated closer to a sea eagle nest. For male mink the results were inconclusive because of small sample size and small variation in relation to predation risk indices.

These observed changes in mink movements might alleviate their detrimental effects on bird, small mammal and frog populations in the archipelago by creating high quality (low risk) refuge sites for mink prey, as increasing eagle predation risk could make the potential cost of swimming to some more isolated islands too high for mink. Also, the restriction of female mink movements under eagle predation risk could lead to their impaired nutrition, which could lead to reduced reproductive output and thereby slower mink population growth. Overall there is accumulating evidence that ecosystems where top predators are present sustain more biodiversity than comparable areas without apex predators (Sergio *et al*. 2005, 2006), possibly because intraguild predation may launch trophic cascades. If the increasing sea eagle population could launch such a cascade in the outer archipelago, it would mitigate the adverse effects of alien mink and possibly increase the biodiversity of the archipelagos of the Baltic Sea.

3.4 MINK DIET IN THE ARCHIPELAGO

The scat-based diet analysis on outer archipelago mink in summers 2004-2005 (IV) revealed that mink diet consisted mainly of fish (33 % occurrence in scats), birds (28 % occurrence) and mammals (15 % occurrence). This coincides well with other studies of coastal and archipelago mink (Niemimaa & Pokki 1990, Jędrzejewska *et al*. 2001), whereas the diets of mainland mink tend to include more mammals and less birds (Tolonen 1982, Jędrzejewska *et al*. 2001). The occurrence of mammals (mainly field voles) in female mink diet was associated with increasing home range land area. This is probably explained by the increasing persistence of vole metapopulations on larger islands (Pokki 1981, Crone *et al*. 2001), while larger mink home ranges also include larger islands. The proportions of fish and birds were not obviously correlated to any of the home range characteristics. Data on male mink was too scarce to run a similar analysis.

The successful invasion of mink in the outer archipelago is probably explained by its opportunistic predation both on land and in water, but also by the lack of competitors and predators compared to mainland. Mink diet composition in the archipelago highlights the importance of fish in ensuring year-round survival in the harsh conditions, and suggests that fish might actually subsidise mink impacts on other prey (mammals, birds and amphibians) in the area. Possible competitors of mink in the area include the great cormorant *Phalacrocorax carbo sinensis* and the white-tailed sea eagle; the latter also preys on mink and may therefore have stronger effects (see III). On the mainland mink face competition and predation from various mammalian and avian predators, and there the impact of mink on prey may be more modest.

3.5 HABITAT-RELATED DISTRIBUTION OF FROGS UNDER ALIEN PREDATION RISK

The analysis on common frog spatial distribution in the outer archipelago of the Baltic Sea (V) revealed a habitat-mediated effect of an alien predator, the American mink, on breeding female common frog densities. As predicted, female frog densities increased in the mink area with an increasing proportion of vegetation. This result apparently arises from the impact of mink on frog mortality, as the high occurrence of philopatry (i.e. tendency to return to the same breeding site; Loman 1994, Semlitsch 2008) mostly excludes the possibility of frogs making an active habitat choice. While there is evidence of some species of anurans avoiding breeding in pools with insect or fish predators

(Resetarits & Wilbur 1989, Murphy 2003, Rieger *et al*. 2004), other studies have found no support for breeding habitat selection (e.g. Laurila *et al*. 1997). To my knowledge there is no data showing habitat selection responses of adult amphibians facing mammalian predation, therefore I conclude that the result stems from differences in female frog survival, and that shrubs and grasses on the islands presumably provide frogs with shelter against mink predation. In the mink removal area an opposite, unexpected trend of decreasing frog densities with increasing vegetation cover was observed. This result may stem from impacts of other predators on the islands; for example adders and grass snakes may have benefitted from mink removal, and vegetation may not give frogs much shelter from snake predation. Unfortunately snake populations as well as their effect on common frogs in the archipelago are largely unknown.

I also compared population census data from spring 2007 to census data from earlier years to test whether common frogs were still increasing in the mink removal area. In 1999, continuous mink removal yielded a 14-fold difference in frog numbers compared to the control area while this difference had reduced to 2.7-fold in 2007 (see Ahola *et al*. 2006 for the situation in 1992-2001). Compared to 1999, breeding frog numbers in 2007 had decreased in the removal area while those in the control area had increased. Frog populations in both study areas are probably similarly limited by drought effects on juvenile recruitment and adult winter mortality (Elmberg 1990, Pechmann *et al*. 1991). Therefore the reason for decline in frog numbers in the mink removal area may be intensified intraspecific competition (Loman 2001, 2004 and references therein) or increased predation by other species (e.g. gulls and snakes), while frogs in the mink area are most likely limited by mink predation. Overall, Ahola *et al*. (2006) and this study are one of the few examples of mammalian predation effects on adult anuran populations. Especially in the face of global amphibian decline these studies raise further questions on the relative roles of different predators and other factors in shaping anuran populations in various environments. Further studies should concentrate on recording frog survival and causes of mortality in different areas, habitats, and developmental stages, and also to disentangle the impacts of mink and snakes on frog populations in the archipelago.

4. CONCLUSIONS

In my thesis I have explored various aspects of predation, both from a more theoretical perspective through reviews of already published papers, and from a practical perspective of both the predator and prey. This mixture of different methods and scales can be considered both a strength and a weakness, but above all, it shows how small pieces of information can be combined into general conclusions that lead us as scientists in search for new pieces to make the puzzle a bit more complete.

The main conclusion arising from all the parts of this thesis is that predators have a regulating or at least a limiting impact on their prey populations in most, but not all cases (I). As such this is not a very novel finding, but lends support to the top-down control hypothesis of ecosystem function. The real value of the predation synthesis (I) lies in its ability to summarize the magnitude of predator impact on prey populations into a single number (an effect size) which can be used as a benchmark for future studies. Further, it allows one to explore various factors of experimental design that may affect that value, such as manipulation efficiency and temporal scale of the experiment.

Based on mostly historical and anecdotal evidence it has long been believed that alien predators are highly detrimental to prey. With my analysis I was able to show that alien predators pose a larger risk to prey compared to native predators, and that their effects on prey may be double those of the native counterparts (II). This should offer conservationists more power in their battle against the worldwide “homogenization” process affecting all ecosystems. Since the complete removal of an established alien predator species is principally impossible, most conservation efforts should concentrate on preventing new invasions and alleviating the detrimental effects on prey. Predator control may be a beneficial method in improving the odds of survival of any threatened prey species facing an extinction risk because of alien predators, but the outcome of such control depends on the dynamics of the whole system. In systems where alien predators consume both native and introduced prey species, their impacts may be enhanced through a process called hyperpredation: introduced prey sustain larger alien predator populations which then deprive native prey populations (Smith & Quin 1996). This is the case with e.g. red foxes, European rabbits and marsupials in Australia (Pech *et al*. 1995) and cats *Felis catus*, rabbits and native birds on many islands (Courchamp *et al*. 1999).

While the review on alien predator impacts suggests strong effects on native prey species (II), having more mainland studies outside Australia might give a more hopeful picture of the situation. Compared to many islands and the special conditions in Australia, alien predators introduced to mainland sites face a far more complex trophic structure with plenty of competitors and predators. As top predators can have both lethal and nonlethal impacts on the smaller predators, like sea eagles have on mink (III), these impacts may ultimately lead to mesopredator suppression. This should alleviate alien predator effects and increase prey density and biodiversity. Top predators like wolves, bears, lynx and large raptors were once persecuted to near extinction, but now they have been acknowledged as conservation tools for native species (Valkama *et al*. 2004, Sergio *et al*. 2008). Perhaps restoring ecosystems by bringing back the top predators could also help fight alien invasions. For example, in Australia dingoes appear to protect medium-sized marsupials from fox and cat predation, although dingoes have thus far been considered introduced pests themselves (Johnson *et al*. 2007).

The importance of nonlethal effects on prey has only recently dawned to ecologists through studies where it has been shown that their impact can be at least as powerful as that of direct consumption (Werner & Peacor 2003, Preisser *et al*. 2005). While I found evidence of sea eagle risk effects on mink movements (III), the consequences of this behavioral change remain to be explored. The reviews on alien and native predation effects (I, II) also ignored the relative impact of fear, as the predator manipulations were effectively reducing both lethal and nonlethal impacts, without the possibility of separating these impacts from each other. Future studies will reveal the multitude of aspects related to predation risk. For example, recently it has been shown that even the most classical examples of direct predator-prey interactions involve strong components of fear and risk reduction (Peckarsky *et al*. 2008).

The American mink is an ideal, albeit also a frightening example of a successful alien species, which has managed to become established and spread practically everywhere that it has been introduced to. Although it seems probable that mink have managed to find a vacant niche in the outer archipelago (IV), this is an unlikely situation in most other mink-invaded ecosystems, where it probably has faced competition and predation from many native species. As a true opportunist the mink is able to survive in the most varying conditions, and in the outer archipelago it has had a detrimental effect on all of the terrestrial prey groups, including both a population decline and a habitat-mediated density shift in an alternative prey, the common frog (V). More attention should be directed to mink ecology on mainland, in order to understand its niche and role in the predator community that it has managed to squeeze itself into. Also, basic ecological knowledge of many amphibians is surprisingly scarce, including survival and dispersal of juveniles and adults, and warrants urgent attention in the face of global amphibian decline.

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