Doctoral thesis

For the degree of Doctor of Philosophy

Predation and Shorebirds: Predation Management, Habitat Effects, and Public Opinions

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Abstract Many shorebird populations are rapidly declining and a high nest predation rate is one of the threats facing these populations. Thus, factors that affect predation and how to manage it in an effective way are receiving increased attention. This thesis deals with nest predation in two ground-nesting shorebirds (waders): the Northern lapwing *Vanellus vanellus,* and the redshank *Tringa totanus* nesting in coastal pastures. I study how habitat structures affect nest predation and distribution. I also test the effectiveness of two non-lethal methods for managing predation, and survey public attitudes towards predator control and animal conservation.

Predators that hunt by sight often search for prey from elevated perches, such as trees, stone walls and fences. Theory suggests that prey visibility depends strongly on predator perch height and distance. I estimated how prey (a mounted bird) visibility depends on predator perch height, distance and vegetation height in coastal pastures. Visibility increases strongly with observer perch height and proximity. For example, from the lowest perch (0.2 m), visibility of the target bird declines to < 5% beyond 20 m distance, but 40% of it remains visible from the highest perch (8 m), even as far as 120 m. The strong increase of prey visibility with predator search height suggests that the removal of predator perches can improve the survival of endangered prey populations in open habitats.

Predators such as the hooded crow *Corvus cornix* use raised structures for perching and to elude lapwing attacks. I find that crows spent more time at or near raised structures than expected and that wader nests were placed farther away from these structures than expected in two out of three years. Waders thus tend to avoid breeding close to raised structures, which therefore reduces the suitable breeding area and probably also the local wader population size.

Habitat management is just one technique for reducing nest predation, and apart from lethal predator control, there are several non-lethal methods. I tested the effect of nest exclosures to protect individual wader nests from predation. Protected nests had a higher hatching success than unprotected nests. Protected redshanks suffered increased predation on incubating adults, which often sit on the nest until a predator is close by. These results emphasize the need for caution in the use of nest exclosures, particularly in redshanks and other species with similar incubation behaviours. Exclosures can, however, be a useful management tool in shorebirds that leave their nests early, when an approaching predator is still far away. I also tested predator avoidance of wader eggs by placing mimic eggs injected with an illness-producing substance in artificial nests. Compared to control areas, the daily survival rate was higher for wader nests during the first three weeks in areas with aversive eggs, but there was no difference for the nesting season as a whole. Egg predation by foxes and other nocturnal mammals may have masked a greater aversion effect in avian predators. I suggest that the dose of the illness-producing substance should be increased and the aversion-learning period prolonged in future tests of this potentially useful technique.

Predation management sometimes includes lethal predator control, which can be controversial, and knowledge of public attitudes is essential for successful conservation measures. Using a mail survey sent to a representative sample of the Swedish public (1 751 replies) I found that there is support for protecting threatened animals. Although the support for a general control of animals was low, a majority supported several specific reasons for control, including control of animals that pose a risk to threatened species or to traffic. The support for control varied depending on species, being the lowest for raptors and the highest for mice and rats. A majority did not support the use of more costly non-lethal control in place of lethal methods, but urban residents and animal rights supporters were more positive than the others.

I conclude that available perches can have significant effects on prey detection and distribution of wader nests. It is possible to reduce nest predation in some shorebird species using non-lethal techniques such as nest exclosures. When using lethal predator control, I suggest that information about the reasons for control as well as the species involved is highly important, especially as in regard lethal control in urban regions.

Keywords: Conservation, waders, predation, coastal pastures, redshank, lapwing, attitudes, human dimensions.

List of papers

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

I. Andersson, M., Wallander, J., Isaksson, D. 2009. Predator perches: a visual search perspective. *Functional Ecology, in press*. doi: 10.1111/j.1365-2435.2008.01512.x

II. Wallander, J., Isaksson, D., Lenberg, T. 2006. Wader nest distribution and predation in relation to man-made structures on coastal pastures. *Biological Conservation*. 132, 343-350.

III. Isaksson, D., Wallander, J., Larsson, M. 2007. Managing predation on ground-nesting birds: The effectiveness of nest exclosures. *Biological Conservation*. 136, 136-142.

IV. Isaksson, D., and Wallander, J. Does conditioned taste aversion reduce nest predation on ground-nesting birds? A field experiment. *Manuscript*

V. Isaksson, D., Wallander, J., Andersson, M. Lundqvist, L.J. Wildlife conservation and control: public opinions in a western European society. *Manuscript*

Contents

Sammanfattning

Många populationer av vadarfåglar minskar snabbt, och ett av hoten mot dessa arter är en hög bopredation. Därför finns det ett växande intresse för faktorer som påverkar predation och hur man kan minska den på ett effektivt sätt. Den här avhandlingen behandlar bopredation hos markhäckande vadarfåglar, närmare bestämt tofsvipa *Vanellus vanellus* och rödbena *Tringa totanus*, som häckar på strandängar. Jag studerar hur habitatstrukturer påverkar bopredation och fördelningen av bon på strandängar. Jag testar även effektiviteten för två icke-letala metoder för predationskontroll och granskar allmänhetens attityder till predatorkontroll och skydd av hotade djur.

Predatorer som jagar med hjälp av synen söker ofta efter sina byten från högre belägna platser, till exempel träd, gärdsgårdar och staket. Teorier gör gällande att bytets synlighet till stor del beror på höjden på och avståndet till predatorns utkiksplats. Jag uppskattade hur ett bytes synlighet beror på höjden på predatorns utkiksplats, avstånd och vegetationens höjd på strandängarna. Synligheten ökar markant med en högre belägen utkiksplats och närhet till bytet. Från den lägsta sittplatsen (0,2 m) minskar bytets synlighet till exempel till < 5 % på avstånd större än 20 m, medan 40 % av den syns från den högsta sittplatsen (8 m) på avstånd upp till så mycket som 120 m. Den kraftiga ökningen av bytets synlighet vid högre sökhöjd för predatorn innebär att borttagande av lämpliga utkiksplatser skulle kunna förbättra överlevnaden för hotade arter i öppna miljöer.

Predatorer som kråkor *Corvus cornix* använder sig av gärdsgårdar och staket för att hålla utkik samt för att undkomma anfall från tofsvipor. Jag upptäckte att kråkorna tillbringade mer tid än väntat på eller i närheten av upphöjda platser och att vadarbon under två av tre år placerades längre bort från sådana platser än väntat. Det innebär att vadare undviker att häcka i närheten av upphöjda platser, vilket minskar det lämpliga häckningsområdet och sannolikt även den lokala vadarpopulationen.

Habitatskydd är bara en teknik för att minska bopredationen. Bortsett från letal predatorkontroll finns det även flera icke-letala metoder. Jag har testat hur effektivt det är med skyddsburar som skyddar individuella bon till tofsvipor och rödbena från predation. Hos båda arterna hade de skyddade bona en högre kläckningsgrad än oskyddade bon. Skyddade rödbenor drabbades dock av ökad predation av ruvande individer, som ofta stannar kvar i boet tills predatorn är i närheten. Dessa resultat betonar vikten av försiktighet vid användning av skyddsburar, framför allt för rödbenor och andra arter med liknande ruvningsbeteenden. Skyddsburar kan däremot vara en användbar metod för arter som lämnar sina bon tidigt, medan predatorn fortfarande befinner sig på avstånd. Jag har även testat om man kan få predatorer att undvika vadarägg genom att lägga ut liknande ägg som har injicerats med kräkmedel i konstgjorda bon. Jämfört med kontrollområdena var den dagliga överlevnaden för vadarbon högre under de tre första veckorna på områden med utplanterade ägg, men det blev ingen skillnad för hela häckningssäsongen. Äggpredation av rävar och andra nattaktiva djur kan ha dolt en större aversionseffekt hos kråkor. Vi föreslår inför framtida studier av denna potentiellt effektiva metod att dosen med kräkmedel höjs och att inlärningsperioden för aversion ska förlängas.

Skötsel av predation kan inkludera letal predatorkontroll, som kan vara kontroversiell, och kunskaper om allmänhetens attityder är nödvändiga för lyckade naturvårdsåtgärder. Genom en enkät som skickades ut med brev till ett representativt urval av Sveriges befolkning (1751 svar) fann jag att det finns stöd för att skydda hotade arter. Även om stödet för en allmän kontroll av vilda djur är lågt, stöder en majoritet flera specifika skäl till kontroll, bland annat kontroll av djur som kan utgöra en risk för hotade arter eller en trafikfara. Stödet varierade beroende på art, med lägst stöd för rovfåglar och högst för möss och råttor. En majoritet stödde inte användningen av mer kostsamma icke-letala metoder i stället för letala metoder, men stadsbefolkning och djurrättsvänner var mer positiva än andra. Dessa resultat antyder att det är mycket viktigt med information om orsakerna till kontroll, liksom om vilka arter det berör, framför allt när det gäller letal kontroll i urbana regioner.

INTRODUCTION

During the last decades, changing agricultural practices have greatly reduced farmland bird faunas in most parts of northern Europe. Intensified cultivation, drainage of wet grasslands and ceased grazing all contribute to impoverished biodiversity (Donald et al. 2001, Newton 2004, Wretenberg et al. 2006). Many ground-nesting birds such as shorebirds (waders), have decreased drastically in recent years (Senner and Howe 1984, Chamberlain et al. 2000, BirdLife International 2004, Ottvall et al. 2008). Habitat loss is considered the major cause for the decline and fragmentation of the remaining habitats have led many wader species to breed in a small number of key breeding sites (e.g. Senner and Howe 1984, Donald et al. 2001).

Low reproductive success, through high predation rates of wader nests and chicks, has been suggested as an additional cause for the decline of wader populations. (Peach et al. 1994, Grant et al. 1999, Ottvall and Smith 2006, Bolton et al. 2007, reviewed in Macdonald and Bolton 2008). There are interactions between human-induced changes of the habitat and predation (e.g. Evans 2004). Habitat fragmentation may increase nest predation by predators attracted by habitat edges. Such edge effects on nest predation have been found in a wide range of habitat types (reviewed by Paton 1994, Batáry and Báldi 2004, but see Lahti 2001). Habitat deterioration can lead to higher predation rates through changes in sward height and therefore reduced nest concealment (Evans 2004, Newton 2004). In addition, non-lethal effects of predators may intensify their impact on prey populations (reviewed by Preisser et al. 2007, Cresswell 2008), for instance if prey species avoid otherwise suitable habitats near predator perches.

Whether or not predator populations and predation rates have increased in recent years is not easily quantified due to scarce data. However, the most important nest predators (e.g. corvids and the red fox *Vulpes vulpes*) are common in and near waders habitats and can be favoured locally by human-induced environmental changes (Evans 2004). The generalist feeding behaviour of these predators can also increase predation rates on specific species, independent of prey density, and can thus cause population declines (Newton 1998). Moreover, given the decrease in wader populations through the loss and fragmentation of suitable breeding habitats, predation rates, that were once considered normal, can now have a negative impact on wader populations.

Therefore, in addition to managing and creating habitats that attract breeding waders, predation management has also received increased attention (Reynolds and Tapper 1996, Teunissen et al. 2008, Macdonald and Bolton 2008). In order for successful predation management, we must know which factors affect predation rates and how they can be managed by effective and publicly accepted methods.

Habitat structures and predation

Waders breeding in open habitats show several adaptations for reducing nest predation, such as hiding their nests in vegetation and laying cryptically coloured eggs, in many species the incubating adults also have a cryptically patterned dorsal plumage (Gochfeld 1984). A lack of raised perches for predators in many open, flat habitats make these adaptations effective, since predators can then find eggs or chicks only through searching the area by foot or on wing.

Many farmland habitats, such as coastal pastures, are generally flat and lack trees. However, most grazed areas are small and surrounded by stone walls, fences, trees, electrical lines or buildings. These elevated structures are used by avian predators as lookouts in search for prey, and pose a high predation risk for eggs and young of many species (e.g. Preston 1957, Berg et al. 1992, Grant et al. 1999, Whittingham and Evans 2004). Trees and bushes in otherwise flat and open habitats are known to affect the spatial distribution of nests as well as the nest predation rates in waders. Forest edges and trees are sometimes avoided by nesting birds (Galbraith 1988, Stroud et al. 1990, Berg 1992, Berg et al. 1992), and nest survival sometimes increases with the distance from trees or bushes that are suitable as lookout perches for avian predators (Berg et al. 1992, but see Seymour et al. 2003, Ottvall et al. 2005).

Searching from a fixed position, instead of e.g. hovering, can increase the predator's ability to discover prey (see Kramer and McLaughlin 2001). Theory and tests show that predator perch height and distance to prey can strongly influence prey detectability and predator hunting success (e.g. Andersson 1981a, Carlson 1985, Getty and Pulliam 1991, 1993, Sonerud 1992, Malan and Crowe 1997). In an aviary experiment with two perch heights, Carlson (1985) found that the probability of prey detection increased with predator-prey proximity and perch height. However, although prey visibility, i.e. the proportion of the prey that is visible, is an important determinant of prey detectability (see below), there is no quantitative analysis of prey visibility in relation to predator search height and distance in open natural habitats (for forest, see Post and Götmark 2006). Such quantitative data are needed to better understand predator search behaviour and ecology, including habitat choice, space use and activity patterns, as well as anti-predator tactics in prey (Caro 2005). This knowledge can also be important for the management of threatened populations.

In paper I we measure prey visibility as a function of predator perch height, distance to prey, vegetation height and microtopography in coastal pastures. Theory suggests that the prey detection rate decreases with distance r approximately as r^{-d}, where d is the distance decay parameter (see Methods). Providing a first empirical estimate of d in natural habitats is therefore another purpose.

Man-made structures such as stone walls and barbed wire fences are common in coastal pastures in Sweden. How such raised man-made structures are used by foraging predators is poorly known, and so is the effect of such structures on wader nest site selection and the risk of nest predation. Perching on stone walls and fence posts, avian nest predators can get a good view of the surrounding areas, which may put nests near such structures at a greater risk of predation. Moreover, these raised structures may offer refuge for nest predators if attacked by waders defending their nests (Elliot 1985), or by other predators. Waders may also avoid nesting close to structures that reduce the view of surrounding areas (Koivula and Rönkä 1998, Amat and Masero 2004). Elevated structures might therefore have important effects on nest site selection and nest predation rates in waders and other ground-nesting birds.

In paper II we evaluate the effect of man-made elevated structures on the breeding success and nest site selection of waders on coastal pastures, and the extent to which the hooded crow *Corvus cornix* use these structures during the wader breeding season.

Predators and predation management

When predation is found to be of importance to a threatened prey population there are several possible managing methods. The most common include habitat management that favours the prey but not the predator. In pastures, adjusting grazing regimes can make nests less visible, and removing predator perches can reduce predation near such structures (see above). Other methods reduce the predator population by lethal control, which can increase the hatching and fledgling success of the prey. However, effects on breeding densities of the prey is less consistent (Coté and Sutherland 1997, Newton, 1998, Bolton et al. 2007). Moreover, lethal control has some drawbacks: (1) it may be considered unethical and protested against, (2) the predator may itself be threatened, and (3) removed territorial predators may quickly be replaced by new individuals (Goodrich and Buskirk 1995, Conover 2002, Roemer and Wayne 2003, Krajick 2005). Non-lethal methods can avoid these problems since the target individuals are not killed but can remain and defend their territories. Many of these methods are still at an experimental stage and require more field-based evaluations.

It is important that the pros and cons of any management action, such as predation management, are examined closely, since the protected species might be affected in many different ways. Conservation techniques that are not properly evaluated can cause damage (e.g. Ausden et al. 2001, Martínez-Abraín et al. 2004), which is particularly serious for threatened species. Yet, few reports have tested the effect of specific management actions (Fazey et al. 2005), possibly because of publication bias where negative results are seldom reported. Moreover, most results derive from practical management actions rather than research experiments, and are therefore seldom widely disseminated (Fischer and Lindenmayer 2000, Fazey et al. 2004, Pullin et al. 2004).

Nest exclosures

One non-lethal technique for reducing nest predation is the exclusion of predators from habitat patches or individual nests. Fencing of habitat patches has been used to decrease predation from mammalian predators (Jackson 2001, Conover 2002, Moseby and Read 2006). Fencing does not, however, protect nests from aerial predators, and it may even delay or hinder the exit of the broods unless carefully constructed. Protection of individual nests has been applied to ground nesting birds and turtles (e.g. Rimmer and Deblinger 1990, Ratnaswamy et al. 1997, Johnson and Oring 2002, Pauliny et al. 2008). These nest exclosures are placed as protective cages around the nests to prevent predators from reaching the eggs. In the case of turtles, cages only need to protect the eggs and allow the hatchlings to exit, whereas for birds, the incubating adult must have free access to and from the nest, accept the exclosure, and be able to incubate the eggs properly.

Nest exclosures have been used for more than two decades in threatened plovers (Charadriidae) in North America, and are receiving increased interest in Europe and Australia (Jönsson 1993, Garnett and Crowley 2000, Johnson and Oring 2002, Middleton 2003, Pauliny et al. 2008). Testing nest exclosures on three plover species in North America, Mabeé and Estelle (2000), and Johnson and Oring (2002) found conflicting results on the hatching success. This was attributed to differences in the predator communities, and the authors cautioned that increased adult predation can counteract positive effects of increased hatching success. Protective cages can potentially affect many more aspects. Incubation length, hatching synchrony and hatchability can be affected if incubating parents in protected nests become more wary and incubate unevenly. This could in turn lead to impaired chick condition, which ultimately may reduce the long-term survival of a population.

More exclosure studies of birds have dealt with plovers than with sandpipers (Scolopacidae). Many plovers and sandpipers are threatened regionally as well as globally (IUCN, 2006) and are potential target species for nest exclosures. It is therefore important to further evaluate this method in species of both families, which we do in Paper III.

Conditioned taste aversion

When the taste of a food is associated with illness, this can lead to a reduced consumption of that food (Garcia et al. 1955). This phenomenon is commonly called "conditioned taste aversion" (CTA), although many other terms have been used (see Cowan et al. 2000). CTA has been tested in wildlife management and conservation as a method of inducing aversion in predators by treating their prey, or mimics of their prey, with illness-inducing substances (Gustavson et al. 1976, Conover et al. 1977, Mason 1989, Nicolaus et al. 1989, Catry and Granadeiro 2006). The aim is to induce an aversion against the food itself, so that untreated food will also be avoided. This technique is particularly suitable for managing predation on eggs since mimic eggs, e.g. chicken and quail, are readily available. To be successful the predator should be induced with an aversion against the treated, mimic eggs and then generalize this aversion to the untreated real eggs based on visual cues. That is, the predator should not have to open and taste the real egg before avoiding it.

CTA has for many years been described as a promising non-lethal method for controlling predation. Tests using captive animals or free-ranging animals and artificial nests have shown that predation on untreated food can be reduced (Nicolaus et al. 1983, 1989). However, few studies have investigated the effect of CTA on real prey and a need for more field studies has been pointed out (Gustavson and Gustavson 1985, Cowan et al. 2000). Such an experiment is done in paper IV.

Public opinions

For success in nature conservation, we need biologically sound management methods, as well as public acceptance of these methods. The issue of acceptance is receiving increasing attention since conservation work is mostly funded by the public, directly or indirectly, and their opinion may affect the allocation of resources. Public attitudes can therefore be crucial for the success of conservation projects (Reading and Kellert 1993, Heinen 1996, Zinn and Manfredo 1998, Decker et al. 2001, Jacobson et al. 2006).

Conservation often involves managing animal populations that have a negative impact on threatened species by means of habitat destruction or predation (Reynolds and Tapper 1996, Campbell and Donlan 2005). Although the main focus has been on the effects of introduced non-native species (e.g. Mack et al. 2000, Blackburn and Gaston 2005), these problems are far from limited to introduced or invasive species; native species can also have negative effects. For example, ungulates and medium-sized predators have increased in numbers owing to reduced a decline of their predators (Crooks and Soulé 1999, Gordon et al. 2004, Elmhagen and Rushton 2007). Such changes can negatively impact other, threatened species that are sensitive to predation or overgrazing. In such situations animal control can be a biologically justified management option to increase the size of a threatened population (Goodrich and Buskirk 1995). Yet, there seems to be widespredpublic hesitation to animal control, in particular lethal control. For instance, actions to control or exterminate non-native species are sometimes protested against, especially by animal rights groups (Genovesi and Bertolino 2001, Krajick 2005, Perry and Perry 2008).

Also, given that a large part of the human population lives in cities, far away from nature, their opinions about nature and its management may have other bases than the actual experience of nature (Heberlein and Ericsson 2005). To ensure long-term success of conservation measures, and to help managers foresee where conflicts may arise, it is important to clarify public opinions towards management methods. Here we do so in a western European society with a long tradition of animal conservation, Sweden.

Most studies of attitudes towards animal control have focussed on large predators or ungulates (e.g. Williams et al. 2002, Fulton et al. 2004, Koval and Mertig 2004, Decker et al. 2006), finding that support for control depends on the situation. When a species affects human interests negatively, there is usually a higher support for control. A majority in Sweden supported lethal control of wolves if they threatened livestock, but not if they posed a threat to game species (Ericsson et al. 2004). Animal control for the protection of threatened species has received support in the U.S (Messmer et al. 1999, Koval and Mertig 2004).

As an alternative to traditional lethal control methods, several non-lethal techniques have been used (Conover 2002). Non-lethal methods may be more acceptable than culling, but previous studies have suggested that people's acceptance of control methods is influenced by their costs (Kellert 1985, Bowker 2003). Public attitudes towards non-lethal methods in relation to cost therefore need more attention.

Answers to such questions will be important for adequate allocation of information in connection with animal control for conservation purposes.

In this thesis I study the following:

Paper I. How does perch height and distance to prey relate to the visibility of prey in costal pastures? Here we measure prey visibility as a function of predator perch height, distance to prey, vegetation height and microtopography in coastal pastures. Based on the visibility measurements we also estimate how prey detection will depend on predator search height and distance.

Paper II. Here we study wader breeding tactics in relation to man-made raised landscape structures on coastal pastures, and the behaviour of a nest predator; the hooded crow. We examine the spatial distribution and hatching success of wader nests in relation to man-made structures such as stone walls and fences, and the extent to which hooded crows use these structures during the wader breeding season.

Paper III: Are nest exclosures effective for reducing predation on waders? We examine the effect of exclosures on the nesting success for two common and widespread waders in northern Europe; northern lapwing *Vanellus vanellus* (Charadriidae) and redshank *Tringa totanus* (Scolopacidae).

Paper IV: Can an aversion toward mimic eggs be induced in predators and lead to lower predation rate on real eggs? This study examines the effect of conditioned taste aversion on the nesting success of ground-nesting waders, comparing experimental and control areas.

Paper V: Via a large mail survey, we study Swedish public attitudes towards animal control for protecting threatened species. We compare this aim to other motivations for controlling animal populations and examine public attitudes to species that are, or could be, targets of such control. We also examine the attitudes of different parts of the public that might react to wildlife control operations.

METHODS

General methods *(Paper I, II, III, and IV)*

All field work in Papers I, II, III, and IV was carried out in coastal pastures in SW Sweden mid March - late June 2002 to 2005. For Paper II, III, and IV, northern lapwing and redshank nests were located by searching the pastures on foot, or by locating incubating adults with binoculars. Nest locations were plotted with a GPS receiver, for easy relocation of nests at return visits. Nest initiation day was determined in most cases by floating the eggs in water (van Paassen et al. 1984) or by recording addition of eggs between days. All nests were visited about every third day until they hatched or failed. They were considered preyed upon if the eggs disappeared a week or more before the estimated day of hatching. When eggs disappeared within a week of estimated hatching the nest was considered depredated if it did not contain any sign of hatching (such as small eggshell fragments in the nest cup, Green 2004) and we did not find adult birds tending newly hatched young in the vicinity of the nest. The daily survival rates for nests were calculated following the methods described in Mayfield (1961, 1975) and Johnson (1979).

Study areas (Paper I, II, III, IV)
These studies were conducted in coastal pastures in eight different areas on the Swedish west coast (between 56º55’N; 12º21’E and 57°24’N; 12°07’E). These were: Morups tånge,

Galtabäck, Getterön, Fyrstrandsfjorden, Båtafjorden, Löftaåns mouth, Ölmevalla and Tjolöholm. The study areas are flat, with short vegetation typical of coastal pastures. Altitude differences were usually < 2 m over distances of 0.5 km or more. The vegetation consisted mainly of grasses (Poaceae) and a few tufts of sedge (*Juncus* sp.) and all areas were grazed by cattle, horse or sheep.

Study species (Paper II, III, and IV)

Northern lapwing (lapwing hereafter) and redshank are the two most common waders (or "shorebirds" in America) on the coastal pastures studied in this thesis. They belong to two different families of wading birds, Charadriidae (lapwing) and Scolopacidae (redshank). We worked with these species because of their different incubation and anti-predator behaviours, representative of many other waders. Lapwings nest in short grass vegetation and redshanks concealed in higher vegetation. Lapwings are known for their vigilance and aggressive nest defence whereas redshanks sit tight on their nests and rely on crypsis (Cramp and Simmons 1983). Lapwings and redshanks lay four-egg clutches and start their nesting season at the end of March and mid April respectively.

Predators in the study areas

A number of potential nest predators are present in the study areas such as hooded crows, ravens *Corvus corax*, gulls (*Larus* sp.), and several mammalian predators, such as red fox, and mustelids (e.g. American mink *Mustela vison* and badger *Meles meles*). Up to 2005 we estimated the predator community by field observations (in Paper II, III, and IV). Due to the high number of empty eggs found at hooded crows' shell dumps and their frequent visits to the pastures, crows were considered the major nest predator (see Fig. 1 and Paper II).

Figure 1. Depredated lapwing and redshank eggs collected from a shell dump beneath a crow's nest.

For example, in 2003, we found 70 eggs, of which 61 came from lapwings and redshanks, in two shell dumps below two crow's nests. We located 60 wader nests of which 46 were later preyed upon within the territories of these two pairs. Loman and Göransson (1978) recovered only 17% of all eggs taken by crows in shell dumps. If this is also the case also in our study area, the real number of eggs taken by the crows was much higher than those found in the shell dumps.

However, such evidence and daytime sightings of nest predators are often biased toward avian diurnal predators, mainly corvids. A review (Macdonald and Bolton 2008) shows that the majority of predation on wader nests in Europe occurs at night by mammalian predators such as foxes and stoats. In 2005 and 2006, after the studies in paper II, III, and IV, we used temperature loggers, clay eggs (2005) and night-time observations (2006) for monitoring nest predation and nest predators.

Clay eggs

Using clay eggs can leave bite marks wherefrom one could detect which predator has been involved. For clay eggs to be the most effective, they should be placed in real nests. In wader nests, this means that one real egg must be removed from the nest so the incubation pattern is not disturbed. This may not always be feasible if the bird species is of conservation interest. Therefore, we used plastiline clay eggs painted to resemble lapwing eggs in 2005 and placed them some 30-50 cm from the nests. They were tethered to the ground by a steel wire. These eggs did not however give any useful information. The clay seems to have become soft when warmed by the sun and deformed. Flattening indicate that the clay egg had been incubated. Clay eggs should therefore be made of harder clay and, if possible left in the nest with the real eggs.

Temperature loggers

The time of predation can give some clue about which predator is responsible for it. Predation at night can be ascribed to mammalian species while diurnal predation is less reliably ascribed to avian predators. However, we rarely observed foxes, badgers or mustelids near the pastures during the day.

In 2005 and 2006 we used temperature loggers (TinyTag, Gemini Data Loggers) to monitor nests of redshanks and lapwings in Ölmevalla, Båtafjorden, Fyrstrandsfjorden and Getterön. These loggers were buried near the nest and a flexible thermistor probe was inserted in the nest, beneath the eggs. The logger collected temperature data every 2-3 minutes. Logger data was downloaded to a computer and analysed visually by EasyView 5 as a series of time/temperature diagrams.

Temperatures in the nest during incubation were stable, and predation events are detected as a steady drop (or rise) in temperature to the ambient temperature. All work with the loggers was done at night to avoid attracting attention from crows and gulls. No difference in the proportion of nests hatching or predated was found among nests with and without loggers (p = n.s., $\chi^2 = 0.003$, $n = 170$). This is similar to results using loggers on the island of Öland, Sweden (Richard Ottvall, personal communication). 67 predation events were recorded and the results (fig. 2) show that 65% of the nests were predated at night, contrary to our expectation. Only one locality had a majority of nests (56%) predated during the day, Ölmevalla. Here, one crow pair nested less than 100 m from the pasture in all years and egg shell dumps were seen every year 5 to 50 m away from this nest.

Night observations

In 2006 we observed two pastures in Ölmevalla and Fyrstrandsfjorden at night, searching for potential predators. Observations were done on six random nights in Ölmevalla and eight in

Fyrstrandsfjorden in May and June, from sunset to sunrise. All observations were made from cars with night-vision goggles (Leica BIM25). In Ölmevalla, a fox was seen in the pasture on four of the six nights. One badger and one cat were observed on a road alongside the pasture. Crows or gulls were never seen in the pasture during the observations. In Fyrstrandsfjorden, a fox was seen in the pasture every night, a badger on three occasions and a smaller animal (probably mustelid) on one occasion. Foxes were also observed in the pasture on two occasions when we were placing loggers in wader nests. When foxes were observed, intense alarm calls were given by the lapwings. On two occasions, lapwings were seen standing and running in front of the fox, raising their wings, probably to distract it and this warrants futher study . A fox den was also found in Fyrstrandsfjorden in 2006, 200 m from the pasture. When comparing night-time observations with the time of predation in Ölmevalla, we found two predation events occurring at the same time as a fox was spotted in the pasture.

From these data we now know that night-time, mammalian predation dominates in our study areas except for Ölmevalla. The impact of this on the results in Paper II and IV is discussed below.

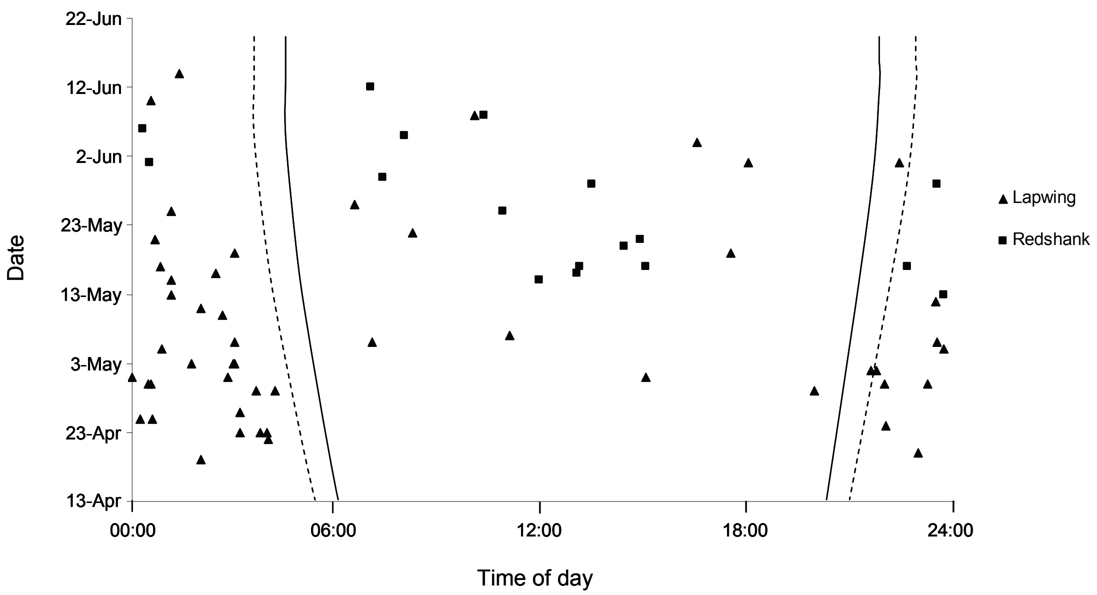

Figure 2. Time of day and date of failures of depredated lapwing and redshank nests monitored by temperature-time data loggers in 2005 and 2006. Data was collected at four of the study areas; Ölmevalla, Fyrstrandsfjorden, Båtafjorden and Getterön. The curves show the times of sunrise and sunset (solid lines) and of civil twilight (the geometric centre of the Sun is 6° below the horizon; dotted lines).

Specific methods

Predator perches and prey visibility (Paper I)

We studied seven coastal pastures 17-24 May 2005. We measured (prey) visibility *T* from artificial perches in the pastures. Target visibility was measured along 120 m transects from each perch at 5, 10, 20, 40, 80 and 120 m distances, and from each of five perch heights: 0.2, 1, 2, 4 and 8 m. We estimated grass sward height and topography for every 5 m along a 120 m transect starting from each perch. To estimate prey visibility we used two targets: a graduated rectangular plate for high accuracy of visibility readings, and a more natural target, a taxidermic mount of the ringed plover *Charadrius hiaticula.*

The probability of visually detecting a distant target is proportional to the solid angle Ω it subtends in the observer's visual field (e.g. Koopman 1980). For a given prey at distance *r*, the probability that the predator will detect it in a short time interval of length dt is given approximately by dt K/r^d. The quantity K/r^d, called prey detection intensity (or instantaneous rate of detection; see Koopman 1980, Andersson 1981a, Getty and Pulliam 1991), is composed of two main parts: (i) prey detectability K, which depends on aspects such as light, atmospheric conditions, sensory ability of the predator, and size, shape, visible area, coloration, background matching, movements and sounds of the prey; and (ii) the exponential distance dependence r^{-d} of the solid angle Ω subtended by the prey in the visual field of the predator (Fig. 1 in Paper I), where d is the distance decay parameter. For a fully visible prey, the distance decay rate of Ω is inverse quadratic, r^{-2}, for purely geometric reasons (Fig. 1 in Paper I). But in most natural habitats, Ω also decreases because concealing vegetation and uneven ground reduce the proportion of the target that is visible (Fig. 1 in Paper I). How much d is larger than 2 in natural habitats is unknown. Because its magnitude is expected to be important for predator hunting success, predation rate and prey risk, d is of primary interest for empirical tests (Andersson 1981a, Getty and Pulliam 1991). We estimated the distance decay of prey detection by calculating, for each perch height and predator-target distance r, the product Tr^{-2} between target visibility T and the geometrical distance-dependent decay (r^{-2}) of the solid angle Ω subtended by the target (see Paper I).

Nest distribution and crow behaviour in relation to elevated man-made structures (Paper II)
This study was carried 2002-2004 in Båtafjorden and Ölmevalla and 2003-2004 at Tjolöholm, Löftaåns mouth, and Fyrstrandsfjorden. The position of all lapwing and redshank nests was plotted on aerial photographs of the study sites. The distance between each nest and the nearest man-made structure was measured directly on the aerial photographs. We included in the analyses all man-made elevated structures at least 30 cm high, which is enough to provide some view of the surrounding area, and cover for crows or to obscure the view for incubating waders. To test whether wader nests are randomly distributed in relation to these raised structures we compared the distance to these structures between real nests and random nest coordinates. To compare survival rates for nests in relation to distance from raised structures, we performed a logistic regression with nest outcome (surviving, not surviving) as dependent variable, and distance from structures and number of exposure days as independent variables.

Observations of the crows' distance to the nearest structure were carried out mid March to the end of May in 2003 and late March to the end of May 2004 on the same pastures that we searched for wader nests. On each plot instantaneous sampling was conducted on the first crow seen in the plot. The crow's distance to the nearest raised, man-made structure was estimated every 10 s (2004) or every minute (2003). To test for a seasonal change in crow distance from structures, the crows' median distance from these structures in the early part of the season was compared to that in the latter part. We also tested whether the distribution of crows in the pastures was random with respect to these structures, comparing the time they spent on or ≤ 1 m from such structures with the time expected from a random distribution. The expected time was proportional to the area covered by these structures in each study plot.

Nest exclosures (Paper III)
We studied the effects of exclosures on redshank nests in 2002 and on lapwing nests in 2002 and 2004 at three coastal pastures: Ölmevalla, Båtafjorden, and Fyrstrandsfjorden. We found 190 lapwing nests in 2002 and 2004, and 68 redshank nests in 2002. Of these, 37 lapwing nests and 34 redshank nests were protected by exclosures. Nests receiving an exclosure (protected) were assigned randomly among the nests found; nests not receiving an exclosure were used as controls. We measured daily nest survival rate, nest abandonment, incubation length, hatchability, partial clutch loss, hatching synchrony, and chick condition and compared protected and control nests.

Our exclosures were smaller than most previously used (Fig. 3), similar in size to those of Estelle et al. (1996). In our study areas there are cattle and some predators (e.g. badgers) that might tilt the exclosure, so we used a firm construction from plastic-coated steel bars designed by Mikael Larsson, Värö, Sweden. Before using the construction in the field, we tested and modified it using captive red foxes, badgers and hooded crows.

Figure 3. Male lapwing incubating in the nest exclosure. Photo by Mikael Larsson

Conditioned taste aversion (paper IV)

This study was carried out April-June 2003 at nine coastal pastures in five areas: Tjolöholm, Ölmevalla, Löftaåns mouth, Båtafjorden and Fyrstrandsfjorden. Five of the pastures were randomly assigned as experimental sites and four as control areas. Quail eggs and small chicken eggs were painted and used to mimic the eggs of redshank and lapwing. As an aversive agent we used the emetic carbachol (carbamyl choline chloride), a water-soluble, widely available cholinergic agonist. Carbachol has been used to induce an aversion to eggs in both captive and free-ranging animals and it produces illness shortly after consumption (Nicolaus and Nellis 1987, Nicolaus et al. 1989, Bogliano and Bellinato 1998). The doses used were adjusted for crows and gulls and followed recommendations by Nicolaus et al. (1989) and Bogliani and Bellinato (1998). Eggs were placed in artificial nest scrapes on two occasions with one week's interval in the beginning of April, before the onset of egg-laying in lapwings and redshanks. No eggs were planted in control areas.

We compared the daily survival rate of lapwing and redshank nests in experimental and control sites**.** Besides presenting results for the nesting season as a whole we also divided the season into one period that is more likely to be influenced by an aversion to eggs and one period that is not. Previous studies have found that the duration of aversion is highly variable, ranging from two weeks to a year, but most are in the lower end of that range (Nicolaus and Nellis 1987, Dimmick and Nicolaus 1990). Our mimic eggs with carbachol were planted in the first week of April, and differences in daily survival rate for nests were examined for April and May-June respectively. For clarity, we also show the weekly survival rate for nests in both experimental and control areas. We looked at differences between the first and second round of CTA-nests in: predated nests, nests with fully eaten eggs, nests with partially eaten eggs, and partially predated nests. The presence of opened but uneaten eggs, eggs thrown out of the nest, and partial depredation indicate that an aversion has been formed (Nicolaus and Nellis 1987, Avery and Decker 1994, Catry and Granadeiro 2006).

Public opinion to predator control and conservation (Paper V)

We participated in a nationwide mail survey sent out annually to 3000 randomly drawn individuals (aged 15 to 85) in the Swedish public (implemented by Kinnmark Information AB, 20 September, 2004 - 4 February, 2005) described by Nilsson (2005).

An excerpt of the questionnaire showing the main questions can be found in Appendix 2 in Paper V. Our questions were developed in collaboration with the SOM Institute (a research centre studying society, opinion and media at the University of Gothenburg). The questionnaire, in which people were asked about politics, society, media consumption and the environment, was 25 pages long and had 101 questions (see Appendix 2 for an excerpt of the questionnaire in Swedish and English). Five questions were constructed for our purpose, and they were pre-tested by the SOM Institute and the authors. After pre-testing, we changed the wording in the questions dealing with animal control from "control of" to "limit the range and number of" to make the questions unambiguous to the respondents. For the sake of brevity, we use "control" in this thesis.

We asked our questions in a section called *Animals and Nature,* and first asked about the interest in animals and nature. We then provided three statements dealing with conservation of threatened species, control of animals in general and all animals' equal right to exist. Support or opposition to these statements was measured on a five-point Likert scale (1 = *strongly disagree* to 5 = *strongly agree*) and a *no opinion* option. The next question dealt with potentially important reasons for controlling an animal species. We gave eight arguments and used four response alternatives (*very important reason*, *somewhat important*, *not particularly important*, and *not at all important*) and a *no opinion* option. The arguments for controlling an animal species were that it poses a threat to (1) game species, (2) cattle, (3) the survival of threatened animal species, that it (4) was introduced to Sweden by humans, (5) has increased in range and numbers due to human activity, (6) can pose a threat to humans, (7) poses a threat to traffic, and (8) contributes to damages in gardens and plantations.

We then asked to what extent twelve animals or animal groups should be controlled. We used four response alternatives to measure the control (to a very large extent, to quite a large extent, to quite a small extent, and not at all) and a no opinion option. The animals were badger *Meles meles*, red fox *Vulpes vulpes*, American mink *Mustela vison*, roe deer *Capreolus capreolus*, moose *Alces alces*, grey wolf *Canis lupus*, mice and rats, snakes, seals, gulls, corvids, and birds of prey. We choose these animals since they either are under control or may be considered for control due to their negative impact on other species in need of protection. The American mink was the only introduced species, but this was not mentioned in the questionnaire. The final question in the *Animals and nature* section concerned non-lethal methods for controlling animals. The respondents were told that the control of an animal species is often done by shooting, but that there are other methods where the animals are not killed. We asked if the respondents found it important to use such non-lethal methods even if they are much more expensive to society. The six answer categories were: 1) *Yes, use the more expensive methods that do not involve killing*; 2) *Yes, maybe*; 3) *No, hardly*; 4) *No, keep the present, cheaper methods of shooting* and 5) *no opinion*. We also included a final answer category: *Mankind should under no circumstances limit the range and number of animal species*. This was done to provide an answer for those who oppose all forms of animal control.

The response rate was 63 % and the sample is representative of the Swedish population as a whole (described in Nilsson 2005).

RESULTS AND DISCUSSION

Predator perches and prey visibility (Paper I)

As theoretically expected in open habitats (Andersson 1981a), target visibility *T* increased greatly with predator perch height and proximity (Fig. 4). For short distances (up to 10 m) most of the increase due to perch height took place already from 0.2 to 2 m. At longer distances there was also a considerable increase in target visibility also from 2 to 4 and 4 to 8 m. The increase in visibility with perch height is very consistent. For any given perch height, targets became less visible with increasing distance (Fig. 4) because of concealing vegetation and uneven ground. At the lowest perches, the visibility of both targets declined steeply to low values with increasing distance, for instance to < 20% at 40 m for the bird target and perch height ≤ 2 m (Fig. 4). For the plate target, visibility was generally higher and declined less strongly with increasing distance due to its higher stature. From the highest perch (8 m), target visibility at 120 m was still > 60% for the plate and 40% for the bird, demonstrating the importance of search height for prey visibility at long distances. The results show that prey visibility increases greatly with predator search height, helping explain why high perches offer a great search advantage for predators of partly concealed terrestrial prey in open habitats, such as avian predators of insects and small rodents in grassland (e.g. Sonerud 1992, Widén 1994, Malan and Crowe 1997, Leyhe and Ritchison 2004), and piscine predators of benthic prey (e.g. McLaughlin and Grant 2001). Attacking from a higher position can also give the predator several other advantages, such as greater prey capture success (e.g. Götmark and Post 1996; Jenkins 2000). The great increase in prey visibility with search height over long distances is important, because it increases the number of potential prey that can be discovered from the perch. Predators are therefore expected to discover increasing proportions of prey at longer distances with increasing search height (see also Andersson 1981a, Sonerud 1992).

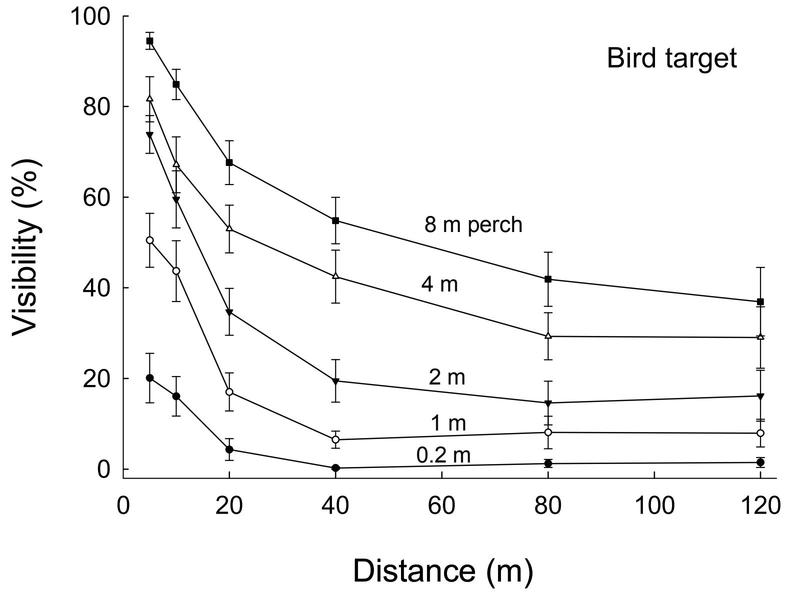

Figure 4. The visibility of the bird target increases strongly with perch height, and decreases with increasing predator-target distance. The curve for each of the five perch heights is based on means ± SE for the 20 transects (see Methods). Standard errors can be multiplied by 2.1 to obtain approximate 95 % confidence limits, but for visual clarity this has not been done in the figures.

In accordance, 10 of 12 field studies found a positive correlation between the predator perch height and the distance to prey attacked (reviewed by Sonerud 1992, see also Malan and Crowe 1997). The advantage of greater prey visibility at longer distances from high perches may be reduced, however, by lower capture success for long strikes (Sonerud 1992, Malan and Crowe 1997). And increased search height also increases the predator-prey distance, which counteracts the effect of increased prey visibility and tends to reduce prey detectability. Therefore, many different and partly counteracting factors may influence optimal search height (Andersson 1981b). Controlled experimental tests with different perch heights and standardized prey, for example, combining and extending the approaches of Carlson (1985) and Sonerud (1992), can help clarify these aspects.

Visibility followed similar trends in relation to perch height and distance in both targets, but the bird target was less visible. Compared to the plate, the bird is lower (10 vs. 7 cm), and in lateral view has more of its area at low levels. This makes it more likely to be concealed by vegetation and uneven ground as distance increases, the distance decay of its visibility therefore being more rapid (higher values of d).

The distance dependence of target detection is an important aspect of the predator search process (e.g. Andersson 1981a, Getty and Pulliam 1991, 1993). The estimates of the distance decay parameter d range from 2.13 to 2.39. With predator search heights, habitats and prey types for which visibility-distance relationships are similar to those found here, a distance decay parameter d of magnitude 2.1-2.4 therefore appears realistic. For similar prey types in less even habitats with higher vegetation, such as clear-cuts studied by Sonerud (1992, 1997), higher values of d are likely to apply. The parameter d was highest for the bird target at all five perch heights, as expected because it is smaller than the plate target, and therefore declines more rapidly in visibility with increasing distance.

The relationships found here seem likely to apply reasonably well in a range of open habitats with similar proportions between predator search height, prey size, vegetation height and topography. Our results also show that when prey (target) stature is in the same range as vegetation height, the latter may be of critical importance for prey visibility. Increased predator perch height can then render the prey much more visible, also at long distances. On the other hand, if the prey are much taller than the vegetation they will usually be visible above it in an even habitat, rendering perch height less important. In contrast, prey that are much smaller than grass sward height are only visible from almost directly above. Grazing regimes that lead to suitable sward height is therefore important for the conservation of threatened grassland birds (e.g. Ausden 2007, Tichit et al. 2007), by reducing predation and increasing reproductive success. But sward height can only partly counteract the effect of perches: even in twice as high vegetation, prey may still be visible at short to medium distances from perches. Thus the removal of perches can therefore reduce the predation risk (see also Quinn and Cresswell 2004).

Our results suggest that the availability of sufficiently high perches can greatly increase predator hunting success and prey risk, and many observations and experiments show that perches attract hunting predators (e.g. Sheffield et al. 2001, Leyhe and Ritchison 2004, Dzialak et al. 2007). The addition of perches, even if only a few metres high, can therefore substantially improve habitat suitability for some predator species in areas where perches are rare or lacking (e.g. Widén 1994, Chandler et al. 1995, Malan and Crowe 1997, Sonerud 1997, Sheffield et al. 2001). Predator preferences for perches can in turn lead to higher predation risk in their vicinity (e.g. Erikstad et al. 1982, Berg et al. 1992, Kay et al. 1994, Söderström et al. 1998), which may therefore be avoided by prey.

Nest distribution and crow behaviour in relation to elevated man-made structures (Paper II)

Many previous studies have examined nest predation and nest distribution relative to habitat edges (see Lahti 2001, Batáry and Báldi 2004 for reviews), corvid lookouts (Berg et al. 1992, Ottvall et al. 2005) and corvid nests (Loman and Göransson 1978, Erikstad et al. 1982). Few studies, however, have examined nest predation and nest distribution in relation to elevated man-made structures and how these structures are used by potential predators (Fig. 5).

In both years studied, the time spent by crows on or near these raised structures was significantly higher than expected by chance. The crows spent approximately 25-35% of their time on such structures, although they on average only constitute < 4% of each pastures on average. In 2003, but not 2004, the crows' average distance to raised structures decreased significantly between the early and late part of the season.

The proximity to potential corvid lookout perches and corvid nests may negatively affect nest survival (Berg et al. 1992, Söderström et al. 1998). Both Preston (1957) and Erikstad et al. (1982) suggested that crows, when perched on elevated objects, find nests by watching ground-nesting birds approaching or leaving their nests. Elevated perches for predators may therefore offset some of the advantages of anti-predator behaviour in ground-nesting birds, especially in flat open pastures. If crows use elevated structures to find birds' nests, theory and Paper I suggest that nests close to these structures are most likely to be detected and depredated (Andersson 1981a).

Figure 5. Crows perching on fence posts on a coastal pasture. Several available perches are seen such as stone-walls, trees and an electric post.

We did not, however, find evidence for a higher predation risk to nests close to elevated man-made structures. This result was surprising, given the large proportion of time (~30%) that crows spent close to man-made structures, and the strong effect of proximity to natural lookout perches on predation rates in other studies (Berg et al. 1992, Söderström et al. 1998). In accordance with our study, however, Ottvall et al. (2005) found no effect of distance to natural or man-made lookout perches on nest predation rate in redshanks in SE Sweden, neither did Seymour et al. (2003) in a study of lapwings in England. The effect of lookout perches on hatching success therefore seems to vary, and more research is required to identify crucial aspects.

There are several possible reasons for a lack of correlation between predation rate and proximity to elevated man-made structures. The stone-walls and fences in our study area were usually <1.5m high, lower than most natural perches in the form of trees and bushes examined in other studies. On the other hand, if crows use birds' movements as cues to find nests (Preston 1957, Berg et al. 1992), they might discover nests by observing incubation shifts or birds being flushed from the nest, e.g. by cattle. Nests relatively far away could then also be found and preyed upon, making predation rates similar over large parts of the pastures. Secondly, differences in the predator communities between studies may have a noticeable effect on the results. Therefore, it is desirable to establish the importance of different nest predators in an area (Seymour et al. 2003, Maconald and Bolton 2008). Our data from crows'

Figure. 6. A crow waiting out a lapwing attack on a stone-wall next to a fence.

shell dumps pointed to crows as important nest predators. However, data obtained after this study suggest that mammalian predators are more important than we expected (see Methods). Foxes and badgers may search the whole pasture for prey, increasing the likelihood that nests placed far away from elevated structures will also be preyed upon. This might mask any elevated nest predation risk by crows near these structures. Thirdly, and perhaps most importantly, crows may use raised structures for reasons other than in search of prey. Smedshaug et al. (2002) found that crows usually alternated foraging with periods when perched on elevated structures watching for territory intruders or predators. On pastures, crows might use raised man-made structures in a similar way. Albeit low compared to trees and bushes, most raised man-made structures in our study area are still the highest objects in the pastures. Therefore, crows may use them as lookouts not only in search for prey but also to look for predators and territory intruders, and for announcing their own presence in the territory. To separate between these explanations a combination of experimental tests and behavioural studies of potential nest predators are needed.

Even though nest predation rates were not related to distance from raised man-made structures, such structures may still have a negative effect if they enable nest predators to stay in otherwise inaccessible areas (for a similar argument concerning the importance of hedgerows for passerines see Hinsley and Bellamy 2000). Both Lemmetyinen (1971) and Elliot (1985) noted that crows hid behind elevated structures when attacked by birds aggressively defending their nests. Crows were often excluded from areas close to lapwing nests, probably because of the nest defence by lapwings. The only areas where crows maintained a high activity in pastures were near fences, where they could quickly take cover if attacked by lapwings (Elliot 1985).

In 2003 (but not in 2004, perhaps due to the later start of crow observations in that year), crows' mean distance from the structures decreased significantly with time of the season. This coincided with the progress of the lapwings' breeding season and was probably a result of their attacks on crows. However, crows did not leave the pastures completely: we often observed how crows when attacked by lapwings retreated and hid behind stone walls or fence posts, only to reappear on the pastures once the lapwings were no longer attacking (Fig 6).

Raised man-made structures therefore may have negative effects on nest survival even if predation is not directly related to distance from such structures. Their presence probably makes it easier for crows and other predators to remain on the pastures. This idea can be tested by experimental removal of raised structures, comparing crow presence and predation rate before and after such removal. High levels of nest predation may affect the spatial distribution of nests since territories associated with increased risk of predation might be abandoned (Newton 1998, Roos and Pärt 2004). For example, low densities of some open-country ground-nesting birds at habitat edges may depend on high nest predation rates in such areas (Boström and Nilsson 1983, Møller 1989, Stroud et al. 1990). Although we did not find an elevated predation risk for nests close to the raised structures, wader nests tended to be farther away from these structures compared to random nests in two out of three years (2002: real nests 45.1 m, random nests 32.3 m; 2003: real nests 49.6 m, random nests 42.3 m.). In 2004, there was no significant difference (real nests 52.4 m, random nests 53.8 m). We cannot explain the lack of an effect in 2004, but it might have been due to the dry spring of that year. An important aspect of nest site selection in waders is proximity to water-holding depressions and rills (Milsom et al. 2003) and the reduced wetness in 2004 may thus have had an affect on the distribution of waders that differed from previous years.

Proximity to predator perches could be more dangerous at the chick stage, which was not analysed in this study. Nearness to raised structures could also be dangerous for adults. Mammalian and avian predators may use linear habitat structures such as fence lines and stone walls as corridors when moving between habitat patches (e.g. Wegner and Merriam 1979). Increased predator density near such structures thus raises the predation risk for both adults and nests, and breeding birds may therefore shun these areas. Moreover, nest site selection in many birds seems to involve a trade-off between concealment of the eggs and enhancement of the incubating bird's view of the surrounding areas (Götmark et al. 1995, Koivula and Rönkä 1998). Breeding close to man-made structures may limit the view of surrounding areas, making the incubating bird more vulnerable and less likely to detect an approaching predator in time for safe escape. Predators may also increase their hunting effort in areas where prey is most vulnerable (Newton 1998, Quinn and Cresswell 2004). Breeding close to obstacles that obscure the view may therefore jeopardise adult survival. If so, the areas of suitable breeding habitat may be considerably reduced by the presence of raised structures such as stone walls and barbed wire fences.

Managing predation with nest exclosures (Paper III)

Nest exclosures have been used for more than 20 years and can sometimes be an important non-lethal management tool in threatened ground-nesting birds. However, the method needs further evaluation since exclosures have been used mostly on one group of waders, plovers (Charadriidae). In this study, we compare one charadriid and one scolopacid shorebird, and measure several aspects of breeding performance.

In accordance with other studies, we found positive effects of exclosures on hatching success in both lapwing and redshank. In addition, when we include the several other variables measured, the net effect of exclosures on hatching success was positive for both redshank and lapwing. On average, in the lapwing nests, 2.6 eggs hatched in the protected nests and 1.4 in the unprotected nests. In redshanks, 3.6 eggs hatched in the protected nests and 1.6 in the unprotected nests.

A major drawback was increased predation on adult redshank, which reached such proportions that we decided not to use exclosures on redshanks in the second year. In all, nine adults were depredated in 8 out of 37 protected redshank nests, whereas only one adult was depredated in 31 unprotected nests. Increased adult mortality at protected nests has also been found in some other exclosure studies (e.g. Johnson and Oring 2002, Murphy et al. 2003).

Since both plovers and sandpipers are long-lived, markedly increased rates of adult mortality are unacceptable in a management program. Increased predation on adult redshanks is probably related to the incubation behaviour of redshanks and many other sandpipers. Redshanks usually sit tight on their well-concealed nests, and flush only at close distance when approached by a predator (Cramp and Simmons 1983). When flushed from a protected nest they might have flown into the top of the cage, and may not have gotten out of the cage fast enough to escape the predator. Although we did not observe predation on redshanks directly, we suspect that hooded crows learned how to catch redshanks when trying to leave the exclosures. Therefore, the incubation behaviour of the protected species must be examined before applying nest exclosures. They should be used only with extreme caution, or not at all in species with incubation behaviour similar to that of the redshank. Niehaus et al. (2004) found that long-tailed skuas *Stercorarius longicaudus* learned to associate exclosures with nests of western sandpiper *Calidris mauri*. Such learning has also been observed in corvids (M. Marriot cited in Liebezeit and George 2001) and needs to be carefully controlled in the use of nest exclosures.

The protected lapwing nests took one day longer to hatch compared to control nests but this did not seem to affect chick condition. The increase in incubation time could be due to several causes. Lapwings nest in short vegetation in open areas and rely on early visual detection of predators (Cramp and Simmons 1983). An exclosure may reduce the visibility and induce a more vigilant behaviour. This could result in adults leaving the nest more often or for longer periods, leading to later hatching. Exclosures could also affect incubation behaviour differently in males and females. If one sex is more reluctant to incubate in exclosures and the other sex cannot fully compensate, incubation time may increase. Moreover, predators and domestic livestock might be attracted to cages and increase disturbance to the incubating adult (Picozzi 1975, Beintema and Müskens 1987), leading to less efficient incubation. We cannot separate between these possibilities. There was no clear effect of nest exclosures on incubation time in redshanks which, in contrast to lapwings, lay their eggs in well-concealed nests and rely on crypsis while incubating. They may therefore be less disturbed by the exclosure. Even though we did not find any effect on chick condition it is important to monitor since in both lapwing and some Scolopacidae, heavier chicks survive better than smaller chicks (e.g. Grant 1991, Blomqvist et al. 1997).

Most lapwings and all redshanks accepted the exclosure within 30 min. Some lapwings were more reluctant to enter the cage, but all birds finally accepted it and incubated. Although all adults accepted the exclosure initially, they led to increased nest abandonment in lapwings later on. Vaske et al. (1994) analysed the impact of several types of predator exclosure on nest abandonment in piping plover (Charadrius melodus), concluding that exclosures with a roof might increase abandonment. Omitting the roof is not a realistic option when avian predators are present or when exclosures are small, as in this study, since mammals might be able to enter the cage from above. Nest abandonment in protected lapwings might also be related to disturbance, since increased disturbance at protected nests might cause an increase in nest abandonment. Although nest abandonment increased in protected lapwing nests, on average they still hatched more eggs than unprotected nests.

These nest exclosures have been used on lapwings elsewhere with mixed results (Grønstol et al. 2003, 2005). The main problem in these studies was that the exclosures could not be fixed to the ground due to the thin soil layer on the limestone bedrock. This made it possible for badgers to remove the cage and reach the eggs. It has also been suggested that jackdaws *Corvus monedula* or small mustelids are responsible for predation inside cages of the threatened southern dunlin *Calidris alpina schinzii* (Richard Ottvall, personal communication). This shows that the effect of exclosures varies depending on the local conditions. Negative effects can occur even after years of successful usage (e.g. Grønstol et al. 2003, 2005, Pauliny et al. 2008) when for example, a new predatory species enters the pasture or the stationary predators learn how to depredate the adults or nests in the exclosures. The exclosures we used can be modified, making them both wider and higher and changing the distance between the sidebars. If, however, the predator is smaller than the species being protected it will be able to enter the cages, thus rendering them ineffective.

It is therefore important to monitor the success (or failure) of this and other management methods. As for all predation management this includes monitoring the predator community by e.g. temperature loggers and nest cameras (MacDonald and Bolton 2008).

Lapwings and some other Charadriiformes have aggressive antipredator behaviour that offers some protection from nest predators, even for prey species nesting nearby (Eriksson and Götmark 1982, Cramp and Simmons 1983, Elliot 1985). We suggest that further research should be conducted to see if nest exclosures could be used at nests of these aggressively nest-defending species. In such a scheme, threatened species might benefit from the protective umbrella formed by the aggressive species (e.g. Dyrcz et al. 1981), at the same time avoiding the potential negative side effects from exclosures on incubation.

Managing predation using conditioned taste aversion (CTA) (Paper IV)

The prospect of allowing predators to remain as part of the ecosystem and defending their territory from non-conditioned intruders is an attractive idea. Using CTA as a tool in wildlife management to reduce predation has been suggested for decades but tests have yielded different results on its effectiveness (e.g. Gustavson et al. 1976, Conover et al. 1977, Mason 1989, Nicolaus et al. 1989, Catry and Granadeiro 2006).

In this experiment there was a significantly higher survival rate for wader nests in experimental areas in April, but not in May-June. This difference in survival rate is greatest during the first three weeks after the final round of CTA-eggs. Such reduced predation after an aversion period has been found in yellow-legged gulls *Larus michahellis* predating roseate tern *Sterna dougallii* eggs and ravens predating California least tern nests *Sterna antillarum browni* (Avery et al. 1995, Neves et al. 2006). Most other studies have tested the effectiveness of CTA either in captivity or by using artificial nests in the field. Previous studies using carbachol in artificial nests in a field setting have found that the substance can reduce predation by American crows and mongoose on untreated eggs that smell or look different from treated eggs (Nicolaus and Nellis 1987, Nicolaus et al. 1989).

Several signs of an aversion were seen at the artificial CTA nests. These include partially eaten eggs, partial predation and eggs thrown out of the nest. 10 out of 29 partly depredated nests that still contained whole eggs remained intact for at least a month, indicating that the predators avoided CTA-eggs. A higher proportion of nests was partially predated and contained partially eaten eggs in the second round. These nests were found in all experimental areas indicating an aversion being formed. These types of predation (partial eaten eggs or eggs thrown out of the nest) were not seen in any of the real nests in experimental areas, so the predators either developed a search image for the treated eggs and focussed their search on these eggs, or reduced their overall hunting activity on eggs during the three weeks following the aversion period.

In the present study, the effect of reduced predation only lasted 2-3 weeks and there still was a high predation rate. This is similar to studies on mongoose and hooded crow (Nicolaus and Nellis 1987, Bogliano and Bellinato 1998). Since the nesting season for waders is approximately three months, a more long-lasting and stronger aversion is needed. This weak and short effect can be due to several reasons. Predation by larger mammals such as foxes could have masked a greater effect on crows and other avian predators. Based on the timing of predation (presented in Methods) we believe that the impact of red fox predation was underestimated when using only day-time sightings and crow egg shell dumps as evidence.

The doses of carbachol used were adjusted for crows and similar-sized birds. If foxes can form an aversion at a similar dose per bodyweight as rats and mongooses they could also have been affected if instantly consuming all eggs in an artificial CTA nest with three or four eggs in the second round (L.K. Nicolaus unpublished data 1986 in Nicolaus et al. 1989). However, foxes caching behaviour makes this less likely (Macdonald 1976, Macdonald et al. 1994).

To increase the strength and duration a longer acquisition period and/or higher dose could be tested. We placed the treated eggs with a one week interval and most eggs were depredated after two weeks. Since others have dissuaded the use of presenting both treated and untreated eggs simultaneously, the treated eggs should be placed one or two weeks earlier than we did (Conover 1990). This could be coupled with replacing predated eggs with new treated eggs and hence deploy more eggs. This would also give the researcher more time to determine if an aversion has been formed and, if necessary increase the dose. If the conditioned predators abandon the site and new unconditioned predators enter it, it could be necessary to keep the treatment also during egg-laying, or use traps baited with eggs to remove any unconditioned predator (Conover 1990). This calls for a thorough monitoring of the predators and predation during a conditioned taste aversion experiment.

Recent studies on crows have suggested a higher dose of carbachol for field trials (Cox et al. 2004). However, since this is intended to be a non-lethal method one must also consider the lethal effects of carbachol, which has been seen in studies on captive crows and mongooses (Nicolaus and Nellis 1987, Cox et al. 2004). An increased dose is not a guarantee for a stronger aversion. If the dose causes a very rapid vomiting, less is absorbed and the emesis, and thus aversion, might be weaker (Nicolaus et al. 1989). Doses effective to foxes should be tested and if these are lethal to crows one might consider using CTA on crows and other methods for managing fox predation in areas where both are present.

Even though we did find increased survival of real birds nest in experimental areas, was it a result of an aversion? We did not just experiment with carbachol but also with a large amount of eggs, a rich food source for predators. If an aversion was not formed, this extra food supplement could perhaps make the predators satiated on eggs and thereby reduce predation on real eggs and give the results we found. However, supplying predators with extra food has been tested to reduce nest predation on ground nesting birds but with mostly negative results (reviewed in Jiménez and Conover 2001, Conover et al. 2005, but see Redpath et al. 2001). Also, our treated eggs disappeared fast and showed several signs of an aversion being formed. Since eggs can be stored in caches for long periods of time it seems unlikely that predators would ignore collecting eggs due to satiation. On the contrary, supplementing food could lure (new) predators to a site. This has been seen at deer feeding stations that attract raccoons, leading to increased nest predation near such feeders (Cooper and Ginnet 2000). In future studies testing other doses or CTA-agents, one could include a second control area where only untreated eggs are placed. This would show any effect of supplying extra food.

Public attitudes toward wildlife conservation and control (Paper V)

The importance of communicating with the public and stakeholders in wildlife management is obvious. A plethora of species in need of protection, combined with limited funding, calls for well-planned management actions. Dissenting public views can greatly affect the outcome, as shown e.g. by frequent poaching of some large carnivores in Sweden (Brå 2007). Animal control is one method in the toolbox of wildlife managers that is likely to cause debate. It is a tool that may become more important in the future, because of the increasing undesired spread of organisms around the world, and because of increases in certain predators that may threaten endangered populations or species (e.g. Soulé 1990).

The results of the questionnaire indicate that there is a strong support for protecting threatened animal species. Even though we added a strong wording (…*actively* protect *all* threatened…), over fifty per cent of all the studied groups in society agreed with this statement (Fig. 7a). This support is not surprising given the long history of nature conservation and high level of environmental concern in Sweden and many other countries (Dunlap 1993, Lothigius 2006, Boman and Mattson 2008).

We also find that the Swedish public is negative or ambivalent when asked about controlling animal populations, if no reason is given for control (Fig. 7b). Such attitudes might originate from a negative outlook on human interference in nature, stemming from the idea of a fragile nature in delicate balance. The idea of balance in nature was prominent in ecology up to the late 1980's and early conservation, and still is so for many people (Coursey 2001, Wallington et al. 2005, Fischer and Young 2007, König 2008, Lindemann-Matthies and Bose 2008). For example, Uddenberg (1995) found that a vast majority of the Swedish public agreed with the following: (1) nature's own balance is the best for humans, animals and plants and should therefore not be disrupted by man; (2) it is wrong to divide animals and plants into useful and harmful since all species have a function in nature. Similar results have been found in many other countries, based on strong endorsement of the new environmental paradigm (NEP) attitudinal scale (Dunlap et al. 2000).

A majority agreed on animals' equal rights to exist (Fig. 7c), but they also agreed on controlling animals when faced with specific situations and animals (see below).

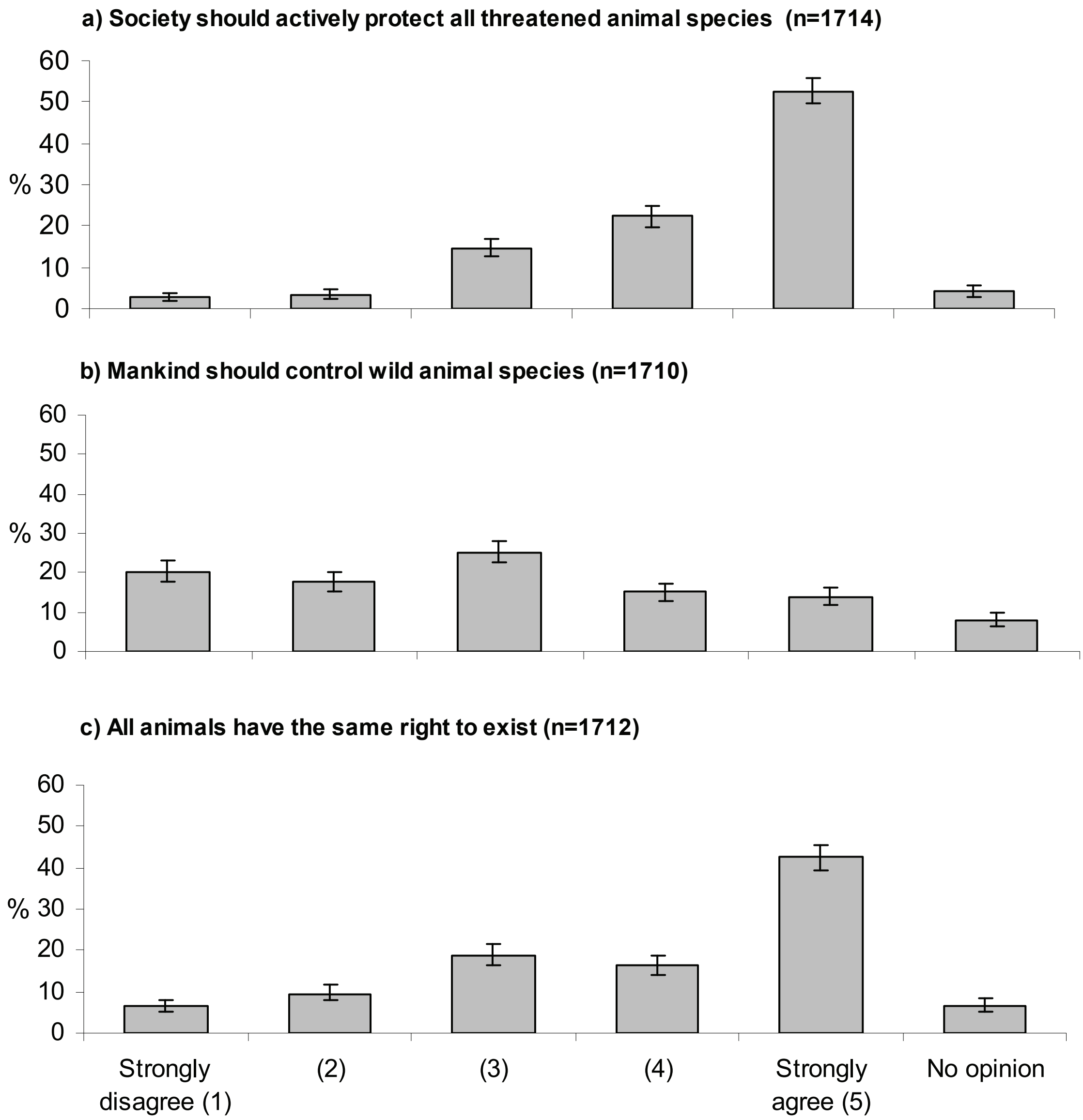

Figure 7. Respondents answers in percent with simultaneous 95%-confidence intervals to the general arguments about animals and nature. Number in parenthesis is number of respondents.

Arguments for controlling animals

Threats to humans, to traffic and to threatened species were considered the most important reasons for controlling animals (Fig. 8). Support for animal control in order to protect threatened species has been found elsewhere (Philips et al. 1998, Messmer et al. 1999, Koval and Mertig 2004, Bremner and Park 2007). By a majority of respondents, threats to gardens and plantations and to game species were not considered important reasons for using animal control by a majority of respondents. In Sweden, lethal control of wolves has been supported by the public in order to protect livestock and humans, but not game species (Ericsson et al. 2004).

We included two arguments in which animals had increased due to human activities or had been introduced to Sweden by humans. If people have an idealized view of humans as a disturbing factor in nature, they might support animal control for these reasons in order to restore a balance in nature. Indeed, over half of the respondents believed that an important reason for animal control is if the animal in question has increased in numbers due to human activities. However, a majority of respondents did not consider animals that have been introduced in Sweden by humans an important reason for animal control. The wording of this question, however, did not specify any negative effects these animals might have on native species. Given the small number of animals that have been introduced in Sweden and caused damage, this result is perhaps not surprising. This might also explain why a high proportion of respondents had no opinion on these reasons for control. In Scotland, respondents supported control of (introduced) non-native species if they cause economic damage or threaten other species (Bremner and Park 2007).

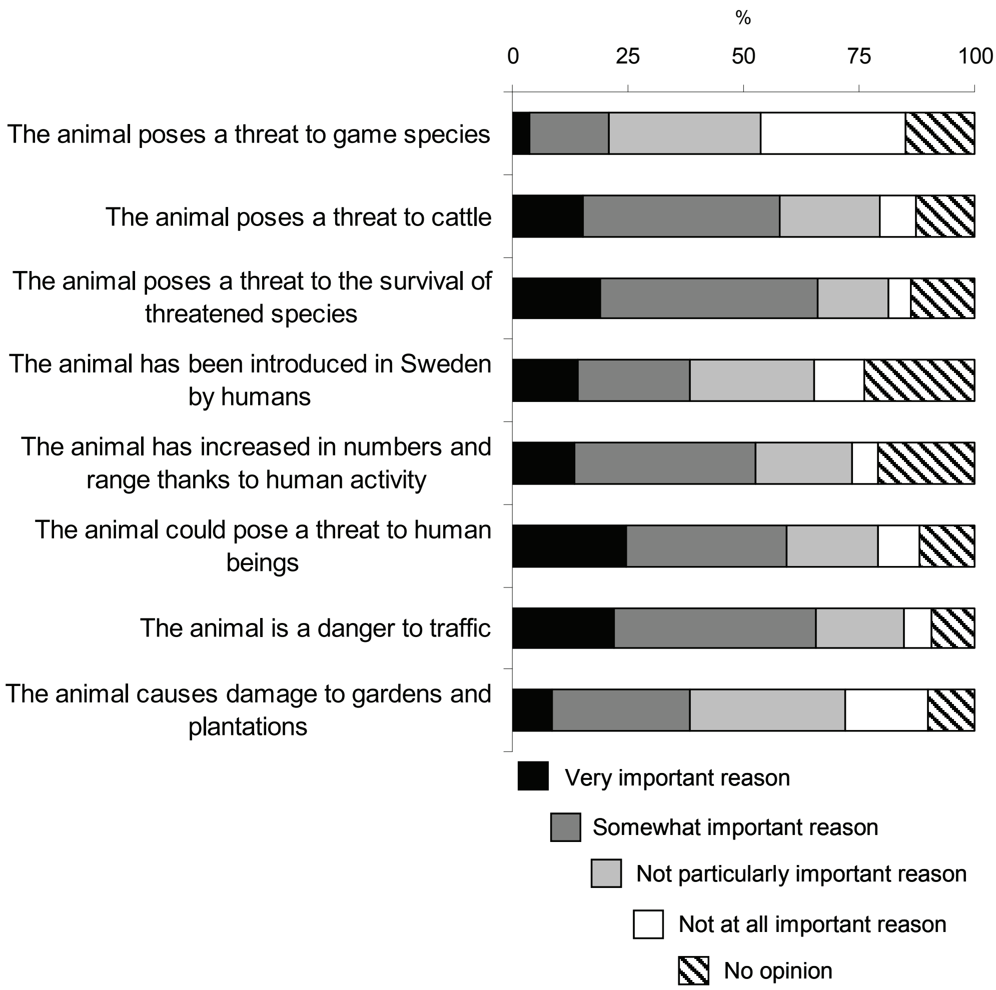

Figure 8. The importance of different reasons when using animal control. Number of respondents on each item varies from 1634 to 1667 due to non-responses.

Which animals should be controlled?

Attitudes towards wildlife management solutions depend on the species' characteristics (Kellert 1996). Even if the public accepts animal control to boost threatened animal populations, we need to know their attitudes towards controlling species that could be targets in such control. All of the twelve animals or animal groups we listed were well known to the public, although their impact on other species may not be. Since we did not give a specific reason for controlling these animals, answers probably reflect the respondents' general knowledge, attitudes to or valuation of these animals. Studies of how people value different species have shown several important factors. These include aesthetics, presumed threat to humans, cultural, historic and ecological importance, potential and actual economic value, perceived (over-)abundance, how the species is portrayed by the media, and if it is invasive and may disrupt a perceived balance of nature (Kellert 1985, DeKay and McClelland 1996, Czech et al. 1998, Fischer and van der Wal 2007). These factors play a part not only in forming attitudes towards the controlled animal but also to the animal being protected.

Mice and rats was the only animal group that over 50% wanted to control to a large or quite large extent, although control of eight of the twelve animals was supported to at least some extent (Fig. 9). Support for control was the lowest for birds of prey, seals and foxes. Among the respondents who replied to the question about the extent of control to at least one animal, 78% (n = 1304) supported control of at least one species to a very large or a quite large extent, i.e. many more than the 28% who agreed that humans should control animals in the general question in fig. 7b. This is also evident if we exclude mice and rats; 74% (n = 1120) agreed to control at least one of the other animals to a large or quite large extent.

It seems that people view mice and rats rather differently than they view other animals. This has been observed elsewhere and probably reflects the fear and dislike that mice and rats evoke in many people (Davey 1994, Bjerke and Østdahl 2004, van den Berg and Heijne 2005). A similar effect may explain the relatively high proportion of respondents that wanted to control snakes to a very large extent (Kaltenborn et al. 2006, Knight 2008). There are only two common snakes in Sweden, one of which is moderately poisonous, the viper *Vipera berus*, but 13% still support control to a very large extent. Low support for the control of seals and raptors is not surprising. Seals are aesthetically appealing and have had a prominent role in the Swedish environmental movement due to massive deaths of seals that occurred in 1988 and 2002 (Härkönen et al. 2006). However, seal populations have recovered and their impact on fishery is debated in both Sweden and elsewhere (Bosetti and Pearce 2003). Birds of prey also have great aesthetic value, and several species have been threatened by pesticides and persecution. Low support for their control has been seen elsewhere (e.g. Kellert 1985, Messmer et al 1999).

As already mentioned, red fox and badger are responsible for predation on threatened ground-nesting birds, and red fox competes with the threatened arctic fox (*Alopex lagopus*) in Scandinavia (Tannerfeldt et al. 2002, Teunissen et al. 2008). Red fox is also a target in game management. The low support for control of foxes may be due to their nocturnal behaviour (apparent rarity) and aesthetic appeal (König 2008). The red fox population in Sweden suffered from sarcoptic mange in the 1980s but has since recovered. We do not know if this decline is familiar to people in general and has influenced their attitudes. For the non-native American mink, also aesthetically appealing, we find a higher support for control. This has probably to do with greater media coverage of the mink's negative impact on animals in Swedish archipelagos. It is not known to what extent the public is aware that it is exotic to the Swedish fauna (in Swedish its common name is mink, not American mink). The low support for control of badgers may be influenced by the high number of road-kills seen (Seiler et al. 2004). In a Norwegian attitude study only 8% expressed negative attitudes to badgers (Bevanger 1990).

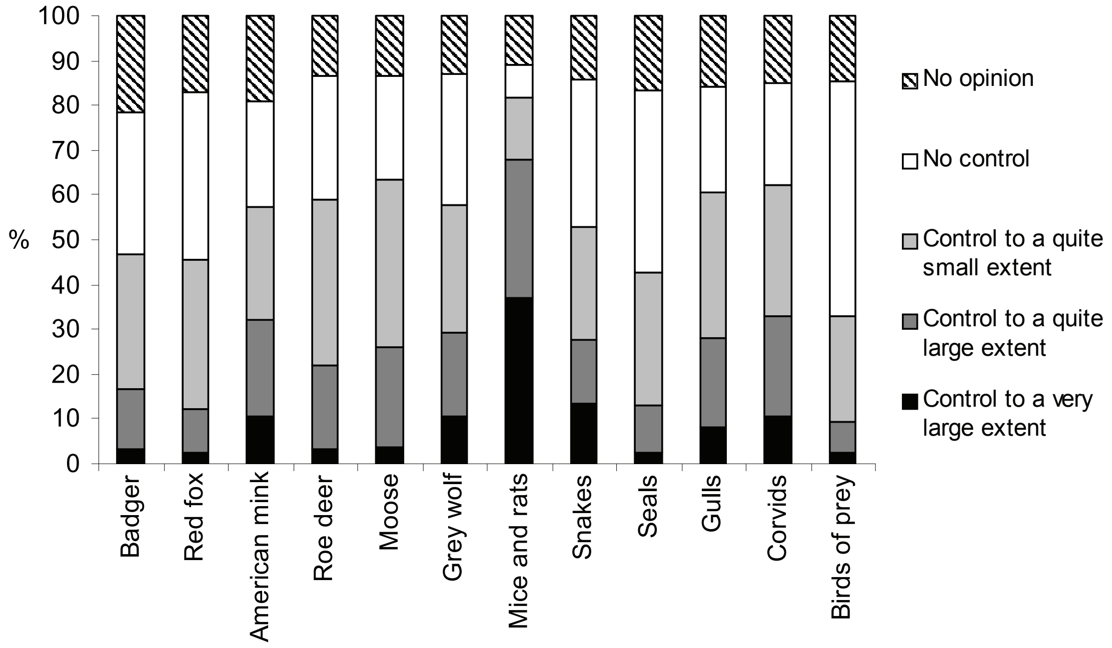

Figure 9. Responses in percent to the extent of control of twelve animal species. Number of respondents on each item varies from 1653 to 1668 due to non responses.

Will the low support for the contol of red fox and badger cause problems in wildlife control programs? If such a program were widely known among the public it might do so. However, considering that hunters shoot tens of thousands of foxes and badgers yearly in Sweden (Kindberg et al. 2008) without any major protests, it is doubtful whether the public would resist a fox control program aimed at protecting threatened species. In Germany, foxes are carriers of the small fox tapeworm *Echinococcus multilocularis* which can cause a serious zoonotic infection in humans. Here, urban residents agree on reducing the fox population, although not as much as on deworming them (König 2008). The German public view foxes favourably but still believe that the lack of natural enemies calls for actions to re-establish ecological equilibrium (König 2008).

About one third of the respondents believed that gulls and corvids should be controlled to a large or quite large extent. Both are widely distributed and are sometimes important predators of the eggs and chicks of threatened birds. Gulls and corvids can be considered as nuisance to people when nesting in urban areas. In an urban Norwegian population, 28% of the respondents claimed to have problems with wild animals, mostly gulls and crows (Bjerke and Østdahl 2004).

One third of the respondents supported the control of wolves to a large or quite large extent. The wolf was nearly extinct in Sweden when it became protected by law in 1966. It has since been allowed to increase in numbers, the present population size being 200-300. Attitudes toward wolf management have been studied in detail (e.g. Ericsson and Heberlein 2003, and Bisi et al. 2007). A majority of the Swedish public supports their existence but agrees to control wolves that threaten humans or livestock. There are regional differences, and support for wolves declines in areas where they are present (Ericsson and Heberlein 2003).

Roe deer and moose are both important browsers that reduce the regeneration of pine (Pinus sylvestris) and broad-leaved trees in Sweden (Bergström and Bergqvist 1997, Götmark et al. 2005). They are also a hazard to human safety in traffic, and to forestry due to browsing damage. We found very little variation in attitudes to controlling these animals. Both are familiar species, and after the reduction of fox numbers through sarcoptic mange, roe deer have become more common and are often seen in urban areas, sometimes doing considerable damage to garden plants. Moose hunting is traditional and publicly well known, and a major yearly event for most hunters. There is also a great appreciation among the public for moose meat.

When looking at all these animals we find that respondents with a more rural residency, short education and higher age supported control of more animals. The effect of gender was different for different animals. For minks and seals, women were less supportive of a control compared to men. However, for wolves, rats and mice, snakes and birds of prey women were more supportive of control than men were. Wolf and its management are highest on the political agenda. Here, we also found the greatest difference between supporters of the two political blocks, right-wing supporters being more positive to control. The strongest proponents of animal rights were less supportive of controlling these animals, while over 40% of hunters agreed on controlling six or more of these animals. ‘No opinion’ answers to the question about the extent of control of these animals increased steadily from rural (range 3-11%) to urban residents (range 16-32%).

Non-lethal methods of control

Lethal control is not always the best management option from a biological or social point of view. Previous studies have found that people prefer control methods that are humane, and often considered non-lethal methods the most humane (Reiter et al. 1999). It has also been argued that a greater adherence to non-lethal methods might bridge the gap between wildlife managers and animal rights groups, which have opposed and even sabotaged animal control operations (Krajick 2005, Perry and Perry 2008). The inclusion of a greater cost for these non-lethal methods in our question was partly motivated by previous studies showing that people tend to prefer non-lethal over lethal methods (e.g. Reiter et al. 1999, König 2008). We wanted to see if this is the case also when non-lethal methods are more expensive. We did not specify how much more expensive these non-lethal methods were and did not mention possible differences in the efficiency of lethal and non-lethal methods.

Some 40% of the respondents were negative to the use of more costly non-lethal methods while one third was on the positive side (Fig. 10). Those negative also had stronger opinions than those positive given that most positive respondents answered *Yes, perhaps* and the negative respondents *No, keep the present, cheaper methods of control*. Twenty-two % had no opinion on non-lethal control; 5% thought that man should not control animals at all. However, of these 5%, over 40% supported limitation to a large or quite large extent of at least one animal group, mainly mice and rats. The ambiguity to non-lethal methods that are more expensive than lethal methods is perhaps not surprising. Previous studies in Sweden have shown that about 80% of the public accepts or are positive toward hunting in general, and hunting is seen as an accepted management method for controlling wolves if they threaten livestock or come too close to human settlement (Ericsson et al. 2004). Two thirds of the Swedish public also agree that hunting is necessary for maintaining a perceived ecological balance (Bråkenhielm 2001). In a U.S. population there was no support for a more costly non-lethal method of managing deer (Bowker et al. 2003) and, besides cost, the specificity and effectiveness of the control method are also important (Kellert 1985, Barr et al. 2002).

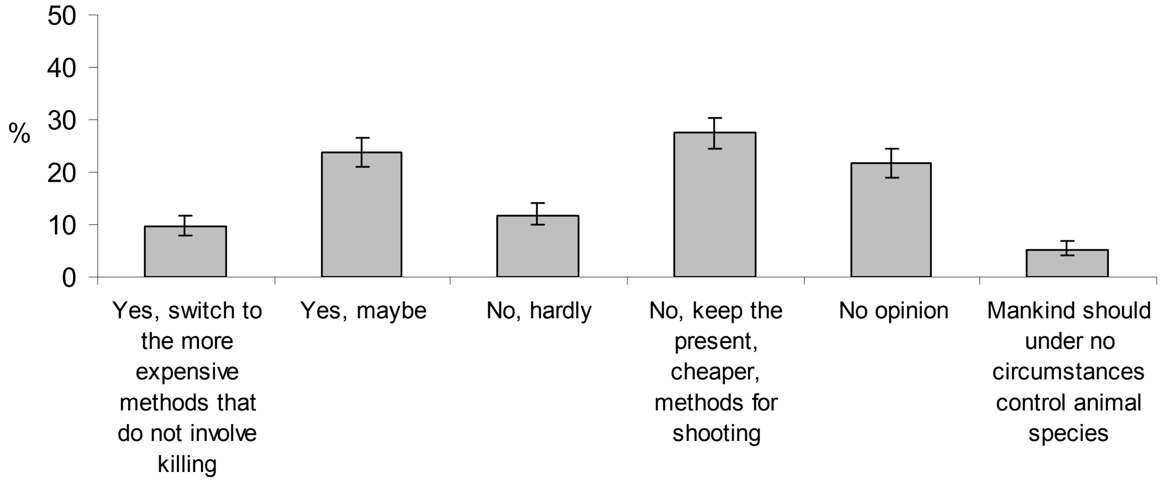

Figure 10. Answers in percent with 95% confidence intervals to the question: *Should we use non-lethal methods even if they are much more expensive to society?*

We find that women, younger people, urban residents and left-wing political supporters were more positive to the more costly non-lethal methods. Respondents who strongly agreed to strengthen animal rights were also more positive to non-lethal methods than those less supportive of animal rights. The lowest support for costly non-lethal methods was found among hunters, only 15 % being positive, whereas members of animal rights organisation were the most positive.

Engaging the public in wildlife management is an important issue for successful conservation. Doing so requires knowledge of public opinions on these issues.

The Swedish public agrees on protecting threatened species and using animal control in some situations, such as for protecting threatened species. This can be seen among the public and when looking at rural vs. urban residents and those who are more interested in and knowledgeable of animals and nature. It is, however, probable that the level of acceptance for protecting an animal, as well as controlling an animal, will depend on the characteristics of the animal. Since an animal’s status as threatened is important to the public, the protection of less liked animals might also be supported (Czech et al. 1998).

The major differences that emerge are noticed in the extent of the control of specific animals and the use of costly non-lethal methods. The use of non-lethal methods, if more expensive than lethal methods, was not supported by a majority of the respondents, and previous studies have shown an accepting attitude towards hunting in Sweden. However, near urban areas, where people are more positive to non-lethal than lethal control methods, wildlife managers should be more careful in using lethal control. Here, a greater emphasis should be placed on trying out non-lethal methods and explaining the efficiency and reasons for controlling animals.

About 15-25% of the public do not have an opinion on non-lethal control methods or the extent of control of the specific animals. These people might be more sensitive to particular incidents and media reports about these animals. Given that *no opinion* answer were more prevalent among urban residents we encourage wildlife managers to be aware of this when planning animal control operations in urban areas. Educating the public on these issues is not an easy task, but can be important. A communication strategy should build on information from credible sources, have a simple message that people can relate to, and make people feel relevance and become involved in the issue (Jacobson 2006).

We see no clear opposition to animal control among supporters of animal rights or members of animal rights organisations, especially if used to protect threatened species. So, it seems that having a positive attitude to animal rights does not exclude the possibility of controlling animals when given specific reasons or specific animals.

A deeper understanding of public attitudes towards wildlife management can be gained through postal or interview surveys that present different management scenarios including various animals being protected and controlled and choosing between different management methods (e.g. Messmer et al. 1999). These surveys should be directed at members of the public as well as representative samples of stakeholder groups such as hunters, farmers, bird watchers, and members of environmental and animal rights organisations. Surveys should include questions about the personal importance of the issue at hand, and people's views on balance and naturalness in nature. This could gain a deeper understanding of which persons or groups are more likely to be heard in wildlife related issues and how their attitudes are founded.

Wildlife managers should be encouraged by the present support that exists for protecting threatened species and for using invasive techniques, such as animal control, as a method of protecting them. However, the type of animal being controlled and protected will affect this support. Therefore, managers need to be aware of public views on these issues when animal control becomes a more frequently used tool.

CONCLUSION

Given the decline of many wader populations we need a better understanding of what factors affect survival and how these are to be managed in an effective and acceptable way. The papers presented in this thesis adds some new information about this.

The studies in Papers I and II suggest that the availability perches can greatly increase predator hunting success and prey risk, and that man-made perches attract one of the important nest predator, the hooded crow. Predator preferences for perches can in turn lead to higher predation risk in their vicinity (e.g. Berg et al. 1992), which may therefore be avoided by prey. In the coastal pastures we studied, nesting waders avoided the vicinity of even low, approximately 1 m high fence posts and stone walls. Predator perches, such as stone walls and fences, may therefore reduce areas of suitable habitat for prey species such as ground-nesting birds in open landscapes. These and other non-lethal effects of perching predators may have strong negative impact on prey populations (reviewed by Preisser et al. 2007, Cresswell 2008). Removal of perches could then be positive for nesting waders.

However, besides the cultural value of stone walls, these structures are also important to several organisms in the open landscape. Therefore, we propose that more comprehensive studies of the pros and cons of stone walls and fences are needed, preferably on a broader taxonomic level than only birds, before any action is taken to remove these structures. We also find in Paper I that vegetation of similar height as the prey has a strongly concealing effect at a long distance from even the highest perches, and at all but the shortest distances from low perches. Grazing regimes that lead to suitable sward height may therefore be important for the conservation of threatened grassland birds (e.g. Ausden 2007, Tichit et al. 2007), by reducing predation and increasing reproductive success. But sward height can only partly counteract the effect of perches: even in twice as high vegetation, prey may still be visible at short to medium distances from perches, the removal of which can therefore reduce predation risk (also see Quinn and Cresswell 2004). The effects of perch height could be further tested experimentally, by manipulating the availability of perches of various heights and recording the consequences for predators and prey as regards hunting success, predation risk and population consequences.

In addition to managing the habitat we also suggest that managers consider using more direct approaches in managing predation. Of the non-lethal methods tested here, the use of nest exclosures is the most promising, and could be used in ground-nesting birds that leave their nest early when approached by a predator. Given the positive, although weak, effect of conditioned taste aversion we encourage future studies before recommending it as a practical tool for predation management.

However, none of these non-lethal methods can be seen as a general solution for managing predation. Perhaps they are best suited near urban areas where there is a higher support for these methods, or when the predator itself is threatened. Except for perch removal, nest exclosures and conditioned taste aversion cannot protect the chicks of waders, only the eggs. Since chick predation is also important, additional methods are needed to managing this. Lethal predator control targeting the specific predator individuals responsible for the predation could potentially reduce both chick and nest predation, and there seems to be a support for using such methods if the prey species is threatened. Therefore, in order to protect our declining wader populations, a combination of lethal and non-lethal methods should be considered for managing predation.

As already pointed out, before any predation management is considered, the predator community should be thoroughly examined. In addition, management actions should be carried out so that the effects on the predator and prey populations as well as people's reactions, positive as well as negative, can be evaluated and disseminated to other managers and researchers.

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