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Levedyktighetsanalyser av skandinavisk jerv

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Tilgjengelighet: Åpen

Prosjekt nr.: 12970009

Signature of responsible person: *Norman S. Myklebust*

Oppdragsgiver:
Direktoratet for naturforvaltning

Referat

Basert på data fra Sarek og fra det norske overvåkningsprogrammet for jerv er det nå utarbeidet en levedyktighetsanalyse av Skandinavisk jerv. Med utgangspunkt i de data som er samlet over tid, blant annet på reproduksjon og overlevelse, kan man konkludere med følgende:

• Det er stor variasjon i tispenes evne til å rekruttere nye individer til bestanden (stor demografisk varians).
• Det er relativt stor variasjon fra år til år hvor god rekrutteringen er (stor miljømessig varians)

Jo større slike typer variasjon er i en bestand, jo flere dyr må til for å sikre at bestanden skal kunne overleve over tid. Er det for eksempel bare fem tisper i en bestand, kan det ved tilfeldigheter hende at ingen av dem klarer å fostre opp unger et år. Er bestanden større, vil slike "tilfeldigheter" ha mindre effekter på veksten i bestanden og dermed bestandens evne til å overleve på sikt. I bestander hvor slike "tilfeldigheter" påvirker bestandsutviklingen, slik som hos jerven, vil altså kravet til antallet dyr som er nødvendig for å sikre levedyktighet øke.

En annen faktor som er viktig, er hva som skjer med reproduksjon og overlevelse når bestanden blir tettere og nærmer seg bæreevnen i et område. Tettheten av dyr påvirker jervens tilgang på mat og areal, og påvirker dyras sosiale reguleringsmekanismer. **Tetthetsreguleringen for jerv i Sarek er svært sterk rundt bæreevnen.**

Det er av stor betydning å kjenne veksten i bestander med lav tetthet. Denne er beregnet for jerven i Sarek, og anslås å være ca 30 % årlig tilvekst. Dette er et optimistisk anslag, ettersom det forutsetter at alle tisper starter å reprodusere når de er 3 år gamle (fordi det er god tilgang på ulike typer ressurser for alle individer), og at tapet av unger i hiet er lavere enn det vi faktisk ser i dag (hvor vi ser eksempler på at "fremmede jerver" dreper unger).

På bakgrunn av disse forholdene, fant man følgende:

For at det skal være mindre enn 10 % sannsynlighet for at jerven skal dø ut i løpet av 100 år (IUCNs krav), må en norsk stamme bestå av minst 22 tisper som er gamle nok til å reprodusere. Med de antagelser som gjelder i rapporten skulle dette tilsi minimum 11 aktive reproduserende tisper. (Andelen aktivt reproduserende tisper er ikke godt kjent i de ulike områder.) Dette tilsvarer en bestand med totalt ca 90 dyr. Dette gjelder en sammenhengende bestand og vil si at den sør norske jervebestanden må telle minimum 90 dyr for å tilfredsstille IUCN sitt krav til levedyktighet forutsatt at det ikke skjer utveksling med andre bestander.

Dersom man ønsker å ta ut dyr anbefales det at det benyttes en terskelhøstings-strategi, der man ikke begynner å høste før bestanden har nådd et nivå hvor den er levedyktig selv om dyr tas ut. Man kan da ta ut 40 – 60 % av det som er over denne terskelen, hvor 40 % anbefales fordi usikkerheten i estimatene er stor. Med dagens kunnskap om bestandsstørrelse, betyr dette at det ikke bør høstes i Sør-Norge (registrert 8 ynglinger i 2002 = antatt 16 reproduksjonsdyktige tisper totalt), mens man kan høste i Nord-Norge (22 ynglinger = antatt 44 reproduksjonsdyktige tisper totalt). Disse beregningene forutsetter imidlertid at intet uttak skjer når bestanden er mindre enn 22 eldre tisper.

Bernt-Erik Sæther, Institutt for Biologi, Norges Teknisk Naturvitenskapelige Universitet, Realfagsbygget N-7491 Trondheim.

Steinar Engen, Institutt for matematiske fag, Norges Teknisk-Naturvitenskapelige Universitet, N-7491 Trondheim.

Jens Persson, Tomas Willebrand Dept. of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

Henrik Brøseth, Arild Landa, Norsk Institutt for Naturforskning, Tungasletta 2, N-7485 Trondheim.

Abstract

Based on data from Starek as well as the Norwegian monitoring programme of wolverine we have made a population viability analysis for the Scandinavian wolverine. We conclude that the population dynamics of this species is characterised by

- **large individual variation among the females in their ability to produce new   recruits to subsequent generations (large demographic stochasticity)** and
- **great annual variation in the number of recruits that are produced (large environmental stochasticity)**

Furthermore,
- **we recorded strong density dependence around the carrying capacity.**

The specific growth rate at small densities is a key parameter determining the viability of small populations. We calculated for the population in Sarek $r_1 = 0.27$. This is likely to be an

overestimate, e.g. because we assume all females to start reproducing at three years of age and low losses of litters during the denning period.

If a Norwegian population of wolverine should not be classified as vulnerable accoring to the criteria of IUCN, 22 adult ($\geq$ 3 years old) must be present. This corresponds to a total population size of approximately   90 animals. This implies that the population in Southern Norway (8   reproducing females in 2002) is currently below this critical population size. In contrast, the population northern Norway (11 reproducing females in 2002) can not be considered vulnerable if we assume that the number of active dens (11 in 2002) represents half of the number of adult ($\geq$ 3 years old) females in the population.

We recommend that if animals are going to be removed, a proportional threshold strategy should be applied. This means that no animals are removed below a given threshold, whereas a given proportion of the number animals above this threshold can be removed, conditioned on that the expected life expectance of the population should be so long that the population can not be classified a vulnerable even in the case of removal of animals. We find that the optimal proportion of the excess animals that can be removed is 40-60 % of the individuals above a threshold of 22 adult ($\geq$ 3 years old) . Because of the large uncertainty in the population estimates, we recommend that the harvest strategy is based on 40 %. A fundamental assumption for these recommendations is that no offtake occurs when the population is below the critical lower population size.

Forord

Innhold

1 Innledning

Ofte ønsker man å vurdere sannsynligheten for at en bestand i løpet av et gitt tidsrom skal dø ut eller reduseres til en forutbestemt nedre terskel. For å kunne foreta en slik vurdering må en derfor være i stand til å forutsi utviklingen til bestanden i de kommende år. I slike tilfeller må man gjennomføre en såkalt levedyktighetsanalyse. En av fordelene ved en slik analyse er at den gir muligheten for en objektiv klassifisering av bestander i forhold til graden av truethet. For å hjelpe til i dette arbeidet har IUCN (2001) angitt tre kategorier av truethet: kritisk, direkte truet og sårbar. I Tabell 1 har vi angitt kriteriene som gjelder for bestander som har vært gjenstand for slike analyser. Som vi ser, må en bestand som ikke skal anses sårbar i henhold til IUCN's kriterier ha mindre enn 10 % sjanse for å dø ut i løpet av 100 år. Eller sagt med andre ord, i 9 av 10 tilfeller vil en slik bestand overleve i mer enn 100 år, men vil allikevel anses for sårbar i henhold til de internasjonale retningslinjer for levedyktighet.

Tabell 1
Kategoriene for klassifisering av graden av sårbarhet ved hjelp av kvantiative bergninger i henhold til IUCN (2001).

Kategori	Definisjon
Kritisk (Critical)	50 % sjanse for utdøelse innen 5 år eller to generasjoner *
Direkte truet (Endangered	20 % sjanse for utdøelse innen 20 år eller 10 generasjoner*
Sårbar (Vulnerable)	10 % sjanse for utdøelse innen 100 år
* Generasjoner benyttes når denne perioden er lengst	

Analyser av levedyktighet krever selvsagt kunnskap om bestandens egenskaper. Eksempler på slike egenskaper er hvor mye avkom som produseres og dødeligheten av disse. Sentralt i en analyse av levedyktighet er å ha et mål på hvordan disse egenskapene påvirkes av:

a) variasjoner i selve bestands-størrelsen (også kalt tetthetsavhengige effekter) og
b) tilfeldige faktorer. Disse har vi to typer av:
   1) tilfeldige variasjoner som skyldes forskjeller mellom individene i deres evne til å overleve og reprodusere (også kalt demografisk stokastisitet) og
   2) tilfeldige variasjoner i miljøet som på et gitt tidspunkt påvirker alle individene eller en gruppe individer likt (også kalt miljøstokastisitet).

For nærmere beskrivelse av prinsippene bak levedyktighetsanalyser, se Sæther og Engen (1997).

Over store deler av Skandinavia er det knyttet sterke konflikter til forvaltningen av jerven. I første rekke er dette knyttet til at jerven er en skadegjører på sau og tamrein, noe som gjør det vanskelig å få aksept for oppbygging av bestander som er store nok til å sikre levedyktighet i tråd med de internasjonale retningslinjer. Formålet med denne studien har derfor vært å

benytte et matematisk analyse-apparat presentert i Lande et al. (2003) til å vurdere hvordan ulike forvaltningsstrategier vil påvirke den framtidige bestandsutviklingen og dermed levedyktigheten til bestanden. Et viktig moment i disse analysene vil også være å avdekke de faktorer som har størst betydning for estimatene av levedyktighet, samt skissere hvordan nødvendige data skal samles inn i framtiden for å bedre presisjonen i estimatene av disse faktorene.

I denne rapporten konsentrerer vi oss om de forvaltningsmessige konsekvensene av disse analysene. For lesere som ønsker en nærmere beskrivelse av modeller og for prosedyrene for estimering av de parametre som inngår i modellen, henvises til Vedlegg 1 i denne rapporten.

1.1 Jervebestanden i Sarek

1.1.1 Hvor store er de tilfeldige variasjonene?

Robuste analyser av levedyktighet krever en kombinasjon av lange tidsserier over bestandssvingninger og omfattende undersøkelser av individuelle forskjeller i reproduksjon og overlevelse. Slike data-sett fins bare for et fåtall arter. For jerv har vi imidlertid tilgang på slike individ-baserte data fra Sarek-området i Nord-Sverige, hvor det finnes data fra 37 forskjellige eldre tisper, samt tidsserier fra flere områder gjennom overvåkningsprosjekter i Norge og Sverige som viser antall kjente ynglende tisper i hvert område.

Våre analyser viste at det var stor variasjon i voksne tispers evne til å rekruttere nye individer til bestanden. (En rekrutt er her definert som et individ som var i live 1. februar året etter den var født). Basert på data fra radiomerkede tisper som var fulgt ett år etter merking fant vi at antallet nye hunndyr som ble rekruttert inn i bestanden varierte fra 0 til 4. Dette gav en høy s.k. demografisk varians $\hat{\sigma}_d^2$ = 0.571. Den store variasjonen i de enkelte hunndyrs evne til å bidra til veksten i bestanden, betyr at kravet til antall individer i en levedyktig bestand vil øke. Dette fordi sjansen for at en liten bestand består av svært dårlige produsenter er tilstede.

Ved å bruke en teknikk utviklet av Engen et al. (1998) kunne vi også utnytte variasjonen mellom år i rekrutteringssuksess til å estimere miljøvariasjonen. Også den ble funnet å være høy ($\hat{\sigma}_d^2$ = 0.154). Denne relativt store grad av variasjoner mellom år kan også være påvirket av tettheten av bestanden. Dette betyr at den estimerte verdi representerer en øvre skranke for miljøvariasjonen i området. En mindre grad av miljøvariasjon vil i så fall redusere kravet til størrelsen på en levedyktig bestand.

1.1.2 Hvilken type tetthetsregulering finnes?

Varierende tetthet av dyr gir vanligvis varierende tilgang på mat og areal, noe som igjen gir seg utslag i varierende produksjon av avkom og overlevelse. Styrken på en slik tetthetsregulering påvirker tiden til utdøing (Sæther og Engen 2002a, under trykking) og må derfor estimeres for å få en pålitelig analyse av levedyktighet. Vi har her benyttet en nyere robust modell utviklet av Lande et al. (2003), Sæther og Engen

(2002a,b) og Sæther et al. (2002). Fordelen ved denne modellen er man kan beskrive mange forskjellige former for tetthetsregulering Gode beskrivelser av effekten av bestandstetthet krever lange tidsserier. Men selv om tidsserien over bestandssvingningene til jervebestanden i Sarek-området er relativt kort (Fig. 1), viste estimatet $\hat{\theta}$ = 12.46 en svært sterk tetthetsregulering rundt bæreevnen K.
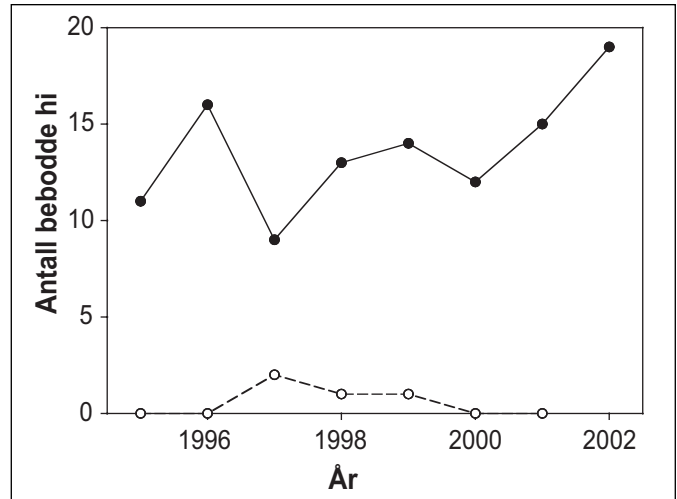
Figur 1
Variasjon i antallet aktive hi (heltrukken linje og svarte punkter) og antallet voksne (≥ 1 år gamle) hunner drept av ulike former for menneskelig aktivitet (prikket linje og åpne punkter) i Sarek-området.

For å forenkle analysene valgte vi å beskrive tetthetsreguleringen ved hjelp av en såkalt terskel-modell (Lande 1993). Denne antar eksponentiell vekst i bestanden opp til områdets bærevne K hvor videre vekst så blir null. For en grafisk representasjon, se Sæther og Engen (1997).

1.1.3 Vekstrate r_1 til bestanden i Sarek

Vekstraten r_1 er en svært vanskelig parameter å estimere fra tids-serier over bestandssvingninger fordi det også krever at man også må måle bestandsveksten når bestanden er fåtallig. Vi valgte derfor å estimere denne direkte fra data innsamlet fra kjente tisper i Sarek. Basert på en rekke antagelser (se Vedlegg 1) antok vi r_1= 0.27. Dette er med stor sannsynlighet et overestimat fordi vi blant annet. antar at ved små tettheter starter alle hunner å reprodusere ved 3 års alder og at tapet av unger i hiet er langt mindre enn det vi i dag finner i Sarek. Hvis den reelle bestandsveksten er mindre, vil dette øke kravet til størrelsen av en levedyktig bestand (Fig. 2).

Figur 2

Forventa tid utdøing av bestanden som en funksjon av bæreevnen for ulike verdier av vekstraten r_1. Andre parametre er som estimert for bestanden i Sarek (se Vedlegg 1). Den striplete linja viser forventa tid utdøing for en bestand som skal betrakes i henhold til IUCN's (2001) kriterier som 'sårbar'. De prikkete linjene viser estimatene for Sarek bestanden.

1.2 Levedyktigheten til bestanden i Sarek

Ved å ta utgangspunkt i de verdier vi hadde funnet for miljøvariasjon, individuelle variasjoner i rekrutteringsevne, og styrken på tetthetsreguleringen, kunne vi simulere den videre bestandsveksten til jervebestanden i Sarek-området. En vanlig måte å gjøre dette på er å kjøre modellen 1000 ganger. For hver enkelt kjøring av modellen får man ut bestandsstørrelsen på ulike tidspunkt. Ved å se på resultatet av de 1000 ulike kjøringene samlet, kan man få en oversikt over sannsynligheten for en bestemt bestandsstørrelse på et gitt tidspunkt.

Vi antok at antall hunner med ynglehi representerte halvparten av de reproduksjonsdyktige (≥ 3 år) hunnene som til enhver tid var til stede i området og at det høyeste antallet registreringer representerte bæreevnen *K* i området. Høyest antall ynglehi ble funnet i 2002, med 19 ynglehi. Dette betyr at vi antar at det fantes 38 eldre hunner i området. Tar vi så en utgangsbestand på *N = K =* 38 voksne (≥ 3 år gamle) hunner, viser modellen at bestanden i Sarek med 10 % sannsynlighet vil dø ut etter 137 år (Fig. 2), og videre at det bare var en 50 % sjanse for at bestanden ville være til stede etter 898 år. Dette betyr at bestanden i Sarek-omådet må i henhold til IUCN's (2001) kriterier klassifiseres som sårbar. Som det framgår i vedlegg 1, var utfallet følsomt ovenfor estimatet for miljøvariasjonen $\hat{\sigma}_e^2$. En lavere variasjon i miljøet mellom år vil gi generelt lengre levetid.

1.3 Jervebestanden i Norge

1.3.1 Beregning av områdenes bæreevne

Forvaltningen av jerv i Norge skjer i separat i Sør- og Nord-Norge, hvor forvaltningsopplegget blir bestemt av to jerven-

emder. Uttak av jerv anvendes som et regulært forvaltningstiltak (Fig. 3). For å kunne forutsi den framtidige bestandsveksten i disse to regionene må vi kjenne områdenes bæreevne – hvor mye jerv er det plass til? Vi antok at sammenhengende områder på over 50 km² som lå høyere enn 600 m over tregrensa (eller 300 m i de to nordligste fylkene) representerte egnet jervehabitat. Basert på studier av individmerkete dyr (se for eksempel Vangen et al. 2001, Persson upubl.) antok vi at hver hunn trengte et leveområde på 400 km². Et røft estimat for bæreevnen fremkommer da ved å dividere tilgjengelig areal med jervehabitat med størrelsen på det gjennomsnittlige leveområdet. Her antar vi at territorielle ikke-reproduserende 2 år gamle hunner (Vangen et al. 2001) utgjorde 30.5 % av 2 år eller eldre tisper i bestanden (Landa et al. 2001). Bæreevnen ble antatt å være 166 og 120 reproduksjonsdyktige (≥ 3 år) hunner i henholdsvis Sør- og Nord-Norge. Dette er selvsagt et svært grovt estimat, men ingen av de etterfølgende resultater er særlig følsomme for variasjon i denne parameteren.

1.3.2 Levedyktigheten til jerv i Norge

For å kunne forutsi bestandsutviklingen i Norge må vi også modellere uttaket av hunner som skyldes ulike former for menneskelig aktivitet. Vi antar at uttaket er konstant med et gjennomsnitt og en variasjon bestemt av uttaket de seinere årene (Fig. 3). Dersom dette uttaket fortsetter i framtiden viser våre simuleringer (Fig. 4) at bestanden i Sør- Norge må anses som sårbar, mens den nord-norske er truet i henhold til IUCN's (2001) kriterier. Faktisk vil det være større sannsynlighet for at jerven allerede om 243 år er borte i Nord Norge enn at den er til stede dersom tapet av dyr skjer i samme omfang som i de seinere årene.

Vi kan også benytte estimatene for bestanden i Sarek-området til å bestemme hvor stor bæreevnen må være for at bestand ikke skal anses sårbar i henhold til IUCN's (2001) kriterier. Vi antar da for enkelthets skyld at bestanden befinner seg på bærevnen *K*. Vi ser da fra Fig. 4 at bestander som lever i områder som har en bæreevne, *K,* mindre enn 48 3 år eller eldre tisper må anses som sårbare i henhold til IUCN's (2001) kriterier. Kravet til områdets bæreevne *K* øker kraftig bare med en liten reduksjon i vekstraten r_1 (Fig. 2).

1.4 Bærekraftige høstings-strategier

I Vedlegg 1 har vi foretatt omfattende analyser av ulike strategier for uttak av jerv som kan gjennomføres uten at dette fører til bestander som må karakteriseres som sårbare. I slike analyser må vi også ta hensyn til presisjonen i bestands-estimatene: kraftigere høsting tåles hvor vi kjenner bestandsstørrelsen med stor nøyaktighet. Vi anbefaler at en såkalt proporsjonal terskel strategi (Engen et al. 1997) benyttes til å fastsette kvoter. Dette innebærer at en nedre terskel, som vi kan kalle *c,* bestemmes hvor ingen høsting tillates når den estimerte bestandsstørrelsen er mindre enn *c*. Når den beregnede bestandsstørrelsen er større enn *c*, tas en viss andel *q* ut av differansen mellom den estimerte bestandsstørrelsen og terskelen *c*. Våre analyser viser at intet uttak kan skje før bestanden både i Sør- og Nord-Norge er på 22 reproduksjonsdyktige (≥ 3 år gamle) tisper. Med de antagelser vi tidligere har gjort, betyr dette altså at det må være minst 11 ynglehi. Videre bør *q* være rundt 0.4, hvor altså 40% av differansen mellom *c* og den kjente bestandsstørrelse kan tas ut.
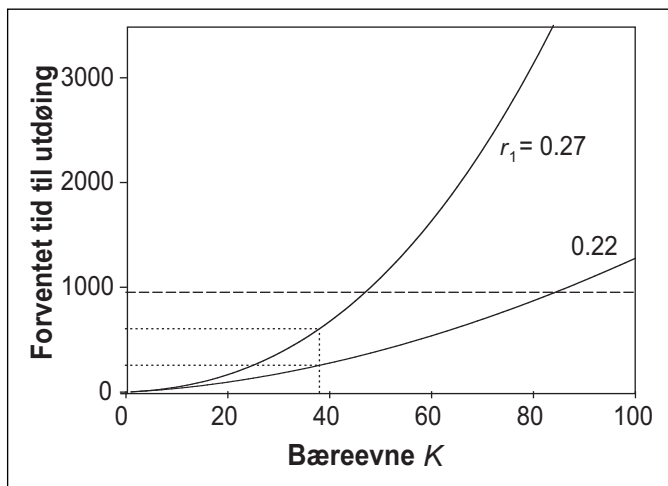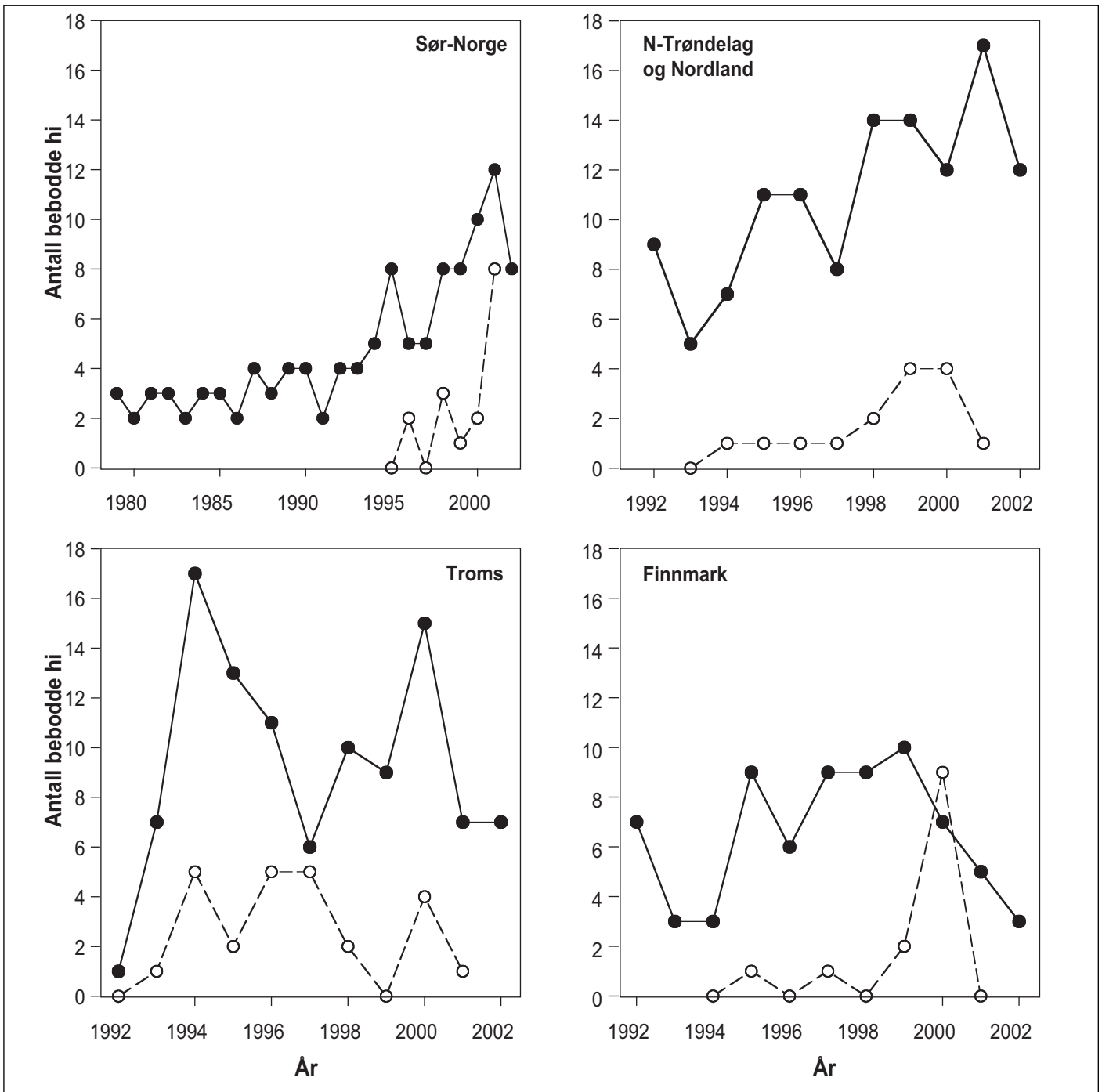
Figur 3
Variasjon i antallet aktive hi (heltrukken linje og svarte punkter) og antallet voksne (≥ 1 år gamle) hunner drept av ulike former for menneskelig aktivitet (prikket linje og åpne punkter) i ulike deler av Norge.

I Sør-Norge ble det i 2002 registrert 8 ynglehi (Fig. 3). Dette innebærer at ingen høsting kan skje i Sør-Norge. I Nord-Norge ble det i 2002 registrert totalt 22 ynglinger. Siden vi antar at andelen eldre tisper som reproduserer utgjør halvparten av totalt antall reproduksjonsdyktige (≥ 3 år gamle) hunner i bestanden, kan et begrenset antall eldre hunndyr dyr tillates tatt ut. Dette forutsetter at bestandsstørrelsen er eksakt kjent, noe som ikke er tilfelle og at ikke noe uttak har skjer når den beregnede bestanden har vært mindre enn *c.* Så har hittil ikke vært tilfelle, noe som har medført at den vekstraten ved lave tettheter som har vært anvendt i beregningene da blir for høy. Bare en liten reduksjon i denne vekstraten som for eksempel som en følge av irregulær felling vil gi langt høyere terskler.

Figur 4.
Simulering av effekten av det nåværende uttaket av jerv på den framtidige bestandsveksten N i Sør- og Nord-Norge. $f_{0.50}$, $f_{0.20}$ and $f_{0.10}$ viser 50 %, 20 % og 10 % kvantilene i fordelingen av simulert bestandsstørrelse.

2 Anbefalinger

Våre analyser viser at

- fortsatte langtidsstudier som kombinerer både individuell-baserte undersøkelser og bestandssvingninger er viktige for å oppnå mer presise estimater av den spesifikke vekstraten r_1, miljøvariasjon $\hat{\sigma}_e^2$ og formen på tetthetsreguleringen. Dette er alle parametre som sterkt påvirker estimatene for levedyktighet.
- Det er et sterkt behov for å kjenne usikkerheten i bestands-anslagene.
- Det er av spesiell betydning å kjenne andelen eldre hunner som hvert år går i hi, og hvordan dette avhenger av bestandsstørrelsen og mattilgang.

Den store betydningen av nøyaktige bestandsanslag for et bærekraftig uttak

- nødvendiggjør også individ-baserte bestandsanslag, for eksempel basert på DNA-analyser, som kan gi informasjon om kjønns- og alderssammensetning i stammen.

Nøkkelparameteren i mange av analysene er den spesifikke vekstraten ved små tettheter.

- Innsats må derfor rettes mot innsamling av nøye bestand-sestimater fra små isolerte bestander slik at denne parame-teren kan estimeres mer presist.

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Vedlegg 1

Management Strategies for the Scandinavian Wolverine: Practical Application of Stochastic Models in Population Viability Analysis

Bernt-Erik Sæther
Institute for Biology
Norwegian University of Science and Technology
Realfagsbygget
N-7491 Trondheim
Norway

Steinar Engen
Department of Mathematical Sciences
Norwegian University of Science and Technology
N-7491 Trondheim
Norway

Jens Persson
Dept. of Animal Ecology
Swedish University of Agricultural Sciences
SE-901 83 Umeå
Sweden

Henrik Brøseth
Norwegian Institute for Nature Research
Tungasletta 2
N-7485 Trondheim
Norway

Arild Landa
Norwegian Institute for Nature Research
Tungasletta 2
N-7485 Trondheim
Norway

Tomas Willebrand
Dept. of Animal Ecology
Swedish University of Agricultural Sciences
SE-901 83 Umeå
Sweden

Author for correspondence:
Bernt-Erik Sæther
Institute for Biology
Norwegian University of Science and Technology
Realfagsbygget
N-7491 Trondheim
Norway

Email: Bernt-Erik.Sather@bio.ntnu.no
Telephone: +47 73 59 05 84
Telefax: +47 73 59 13 09

Abstract

Strong conflicting interests are involved in the development of management strategies for the Scandinavian wolverine. Environmentalists would like an increase in current population sizes to improve their viability, whereas other groups advocate reduction in numbers to reduce the losses of free-ranging sheep and semi-domestic reindeer from wolverine predation. Here we use the insight gained from analyses of stochastic population models to quantitatively analyze different management options, based on data from an individual-based demographic study in the Sarek National Park, Sweden, as well as data from monitoring schemes in Norway and Sweden. The stochastic components in the population dynamics of the wolverine are large. Strong density regulation occurs around the carrying capacity. The carrying capacity of populations that should not be considered vulnerable according to the classification of IUCN (2000) must at least exceed 46 sexually mature ($\geq$ 3 years old) females. Continuation of the current levels of offtake in Norway will lead to rapid extinction of the species over larger parts of the country. Hence, prolongation of the current rate of killings of female wolverine makes the northern population being considered according to IUCN's (2000) criteria as 'endangered' whereas the southern population is classified as 'vulnerable'. Management plans allowing offtake of individuals should be based on proportional threshold harvest strategy. This means that only 40-60 % of the surplus individuals exceeding a certain threshold for harvesting can be removed. Such a management strategy will also require knowledge of the precision in the population estimates.

1 Introduction

Population Viability Analysis (PVA) has got a wide application in the management of threatened and vulnerable species (see reviews in Beissinger and Westphal 1998, Groom and Pascual 1998, Sjögren-Gulve and Ebenhard 2000 and Beissinger and McCullough 2002). The predictions from such analysis have recently received severe criticism (e.g. Ludwig 1996, 1999, Fieberg and Ellner 2000). The major problems with many PVAs can be summarized as:

(1) For most threatened or vulnerable species little demographic data are often available. Even when long (e.g. 20-30 years of data) series of high quality data are available, the uncertainties in the parameter estimates still become large (Sæther et al. 2000, Sæther and Engen 2002a, b).

(2) In many cases the data available is inappropriate for estimating crucial parameters for describing the dynamics and may even result in biased estimates. For instance, the specific growth rate at small densities is often difficult to estimate in many time series of population fluctuations because interpolation over a wide range of population sizes is often necessary (Taylor 1995, Aanes et al. 2002).

(3) The stochastic effects on the population dynamics have not been properly estimated and modeled (Sæther and Engen 2002a), resulting in biased estimates of the risk of extinction. As a consequence, the validity of predictions based on PVA has been seriously questioned (Ludwig 1999).

Recently, great advances have been made in our understanding of stochastic effects on the dynamics of fluctuating populations (Lande et al. 2003). An important step was the development of precise definitions of the stochastic components (Engen et al. 1998) that permitted estimation of demographic and environmental stochasticity from field data (see Sæther et al. 2000, Engen et al. 2001 and Sæther et al. in press). Demographic stochasticity is due to random variation in individual fitness, whereas environmental stochasticity arises from random variation that affects the whole or parts of the population similarly. These methods allow us to separate the stochastic effects on the population dynamics from the deterministic components, e.g. due to density dependence or life history variation.

In PVA, development of projections for the future population fluctuations is necessary for calculating the risk of extinction or the probability for reaching some critical lower population size. Such analyses must necessarily model both the deterministic influence and the stochastic effects on the population dynamics as well as taking into account the uncertainty in the population parameters (Sæther and Engen 2002a).

Many large carnivores have become vulnerable or threatened because of human persecution (Swenson et al. 1994). For instance, the Scandinavian wolverine *Gulo gulo* L. population followed this path of persecution from the mid-19th century,

when harvest increased due to the introduction of state boun- ties. Hunting statistics indicate that the population declined dramatically from about 1870 until they became protected in Sweden (1969) (Landa et al. 2000). The main reason for this intense persecution was predation by wolverines on domestic sheep and reindeer, a conflict still present today in many parts of Scandinavia. As a consequence, offtake of individuals is therefore important to consider as an option in management plans of large carnivores such as the wolverine and is often a prerequisite for local acceptance. In such cases, stochastic factors must be estimated and modeled to obtain a proper understanding of the effects on the viability of the population (Lande et al. 1995, 1997, 2001, Tufto et al. 1999).

The purpose of this study is to utilize the recent advances in the theory of stochastic population ecology to perform a popu- lation viability analysis of the Scandinavian wolverine. We com- bine data from long-term population studies with data on individual variation in reproductive success and survival to obtain estimates of the stochastic components in the popula- tion dynamics. We then provide analyses of factors influencing the time to extinction. We use this insight to quantitatively analyze different management strategies, especially focusing on, by means of sensitivity analysis, how uncertainty in para- meter estimates as well as imprecise population estimates should affect the choice of management actions.

2 The Wolverine

The wolverine is a medium-sized carnivore where the female is smaller ($\bar{x}$ = 11.0 kg, SD = 1.1, n = 63) than the males ($\bar{x}$ = 14.1 kg, SD = 1.6, n = 75) (data from Landa and Skogland 1995). It has a circumpolar distribution, inhabiting boreal coniferous forests and arctic tundra on the northern hemi- sphere (Pasitschniak-Arts and Larivière 1995). Historically, wolverines were found throughout mountainous and forested areas in Norway and from the south-central to the northern parts of Sweden (Johnsen 1929, Lönnberg 1936). From the mid 19th century the Scandinavian wolverine population decreased due to human persecution until they became pro- tected in Sweden in 1969, in southern Norway in 1973 and in the remaining parts of Norway in 1982 (Landa et al. 2000). At that time, the distribution of the wolverine was limited to the mountain range along the Swedish-Norwegian border. The population increased in both countries slowly during the first decades after protection. The estimates of the total population size in 1998-2000 were 326 (± 45) individuals in Sweden, and 269 (±32) individuals in Norway (Landa et al. 2001). The Swedish population is protected, whereas offtake of individu- als is an important tool in the management of the Norwegian wolverine population.

Female wolverines may attain sexual maturity at about 15 months, but previous studies have reported varying propor- tions of 2-year old females that are pregnant (Rausch and Pearson 1972, Liskop et al. 1981, Banci and Harestad 1988). Information from reproductive tracts has shown that a very high proportion of adult females (≥ 3 years) are pregnant each year, but observations of radio-collared wolverines indicate that the proportion of actually reproducing females is much lower (Banci & Harestad, 1988). The mean litter size at wean- ing is typically about 2 (Magoun 1985, Copeland 1996).

In relation to their body size, wolverines have very large home ranges and the females occupy distinct home ranges that over- lap to a small extent (Powell 1979, Magoun 1985, Copeland 1996). Adult males occupy larger home-ranges than females and can encompass several female home ranges (Banci 1994). Dispersal in wolverines is male-biased, often resulting in long distance movements (Vangen et al. 2001). However, the dis- persal rate and the reproductive success of those long distance dispersers are currently unknown.

The average first year survival of Scandinavian wolverine is around 70 % (Persson et al. in press), whereas adult survival is approximately 90% (Willebrand et al. 1999). However, these rates will be strongly influenced by human killings.

3 Study Populations

3.1 Individual-based study: Sarek

Sarek National Park and surrounding areas in the County of Norrbotten (hereafter called 'Sarek'), northern Sweden (67° 00'N 17° 40'E) (Fig. 1) was the location of the study of individual variation in reproductive success and survival. The climate of this area is continental with cold winters (-10 to -13°C in January) and the annual precipitation is 500-1000 mm. Snow usually covers the ground from October to May. The area is characterized by deep valleys, glaciers and mountain plateaus with peaks reaching above 2000 m a.s.l. In the valleys forests are dominated by mountain birch *Betula pubescens* or Scots pine *Pinus sylvestris*. The tree line is formed by the mountain birch and reaches to a maximum of 600-700 m a.s.l. Semi-domesticated reindeer managed by the indigenous Sámi are numerous in Sarek.
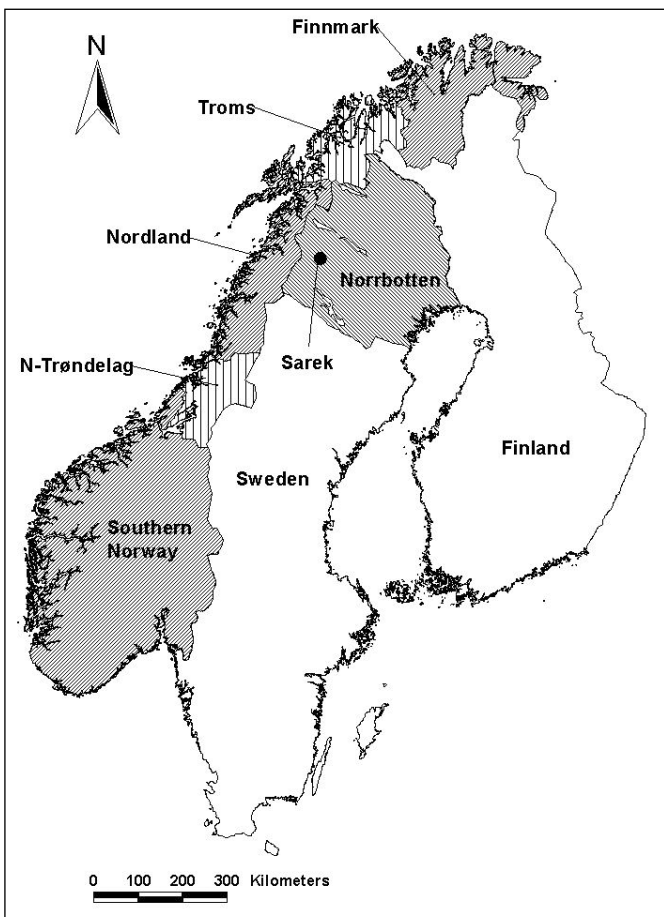

Figure 1.
The location of the study areas.

The analysis is based on data from 37 radio-collared adult females. The females were equipped with an intraperitoneally implanted transmitter. The individuals were radio-tracked from the ground or from the air approximately once every second week. In this way we could determine whether the female and

her offspring survived to the following season, assumed to start on March 1.

In addition to the study of radio-collared individuals, an area of approximately 6000 km² in Sarek was during the years 1995-2002 carefully searched for dens during winter and spring by the use of helicopters and snow-mobiles. We assume that this extensive field work in combination with a large number of radio-collared individuals has given accurate estimate of the annual variation in the breeding population in Sarek. During this period the number of dens fluctuated in the study area between 9 and 19 active dens (Fig. 2).
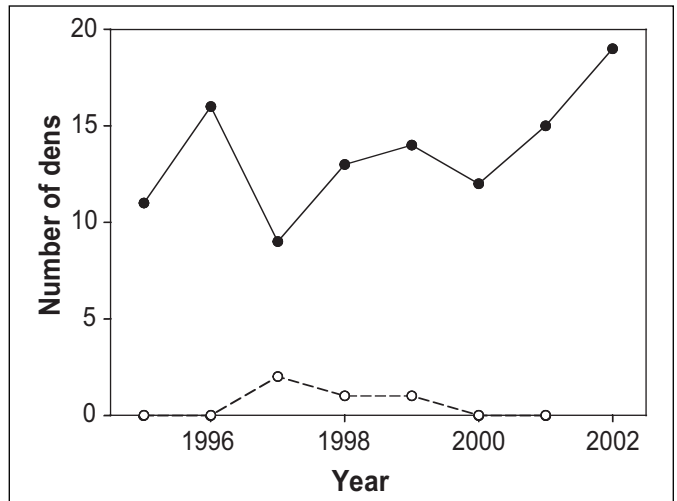
Figure 2.
Fluctuations in the number of active dens (solid line) and female (≥ 1 year old) killed by humans (dotted line) in the Sarek area

3.2 Population census

Over larger parts of its distributional range of the wolverine in Scandinavia annual censuses of the breeding population have been done (Fig. 1). Likely den localities are visited several times during late winter and early spring by experienced persons to search for typical characteristics of a natal den (for a closer description of the den characteristics, see Magoun and Copeland 1998 and Andersen et al. 2001). In addition, in many areas fixed tracks were also driven by snow-mobiles to search for wolverine tracks. When a track was detected, it was followed to see whether it leads to a denning area. In this way an estimate of the size of the minimum number of reproductive females is obtained.

Unfortunately, not all sexually mature females reproduce each year. In Sarek, the mean proportion of the radio-collared adult females that bred each year was 0.57 (*n* =6 year). Thus, the number of active dens represents an underestimate of the actual number of sexually mature females present in the population (Fig. 2).

In the southern part of Norway (Fig. 1) an increase in numbers

has occurred during the last years (Fig. 3). In the other parts of the country no clear trend was present in the population fluctuations. In contrast, the number of recorded dens has declined in Sweden during the study period (Fig. 4), mainly due to a decline in the county with the largest number of wolverine (Norrbotten county).

In recent years, females (≥ 1 year old) have been killed by humans on a regular basis over larger parts of its current distributional range (Figs. 2-3).
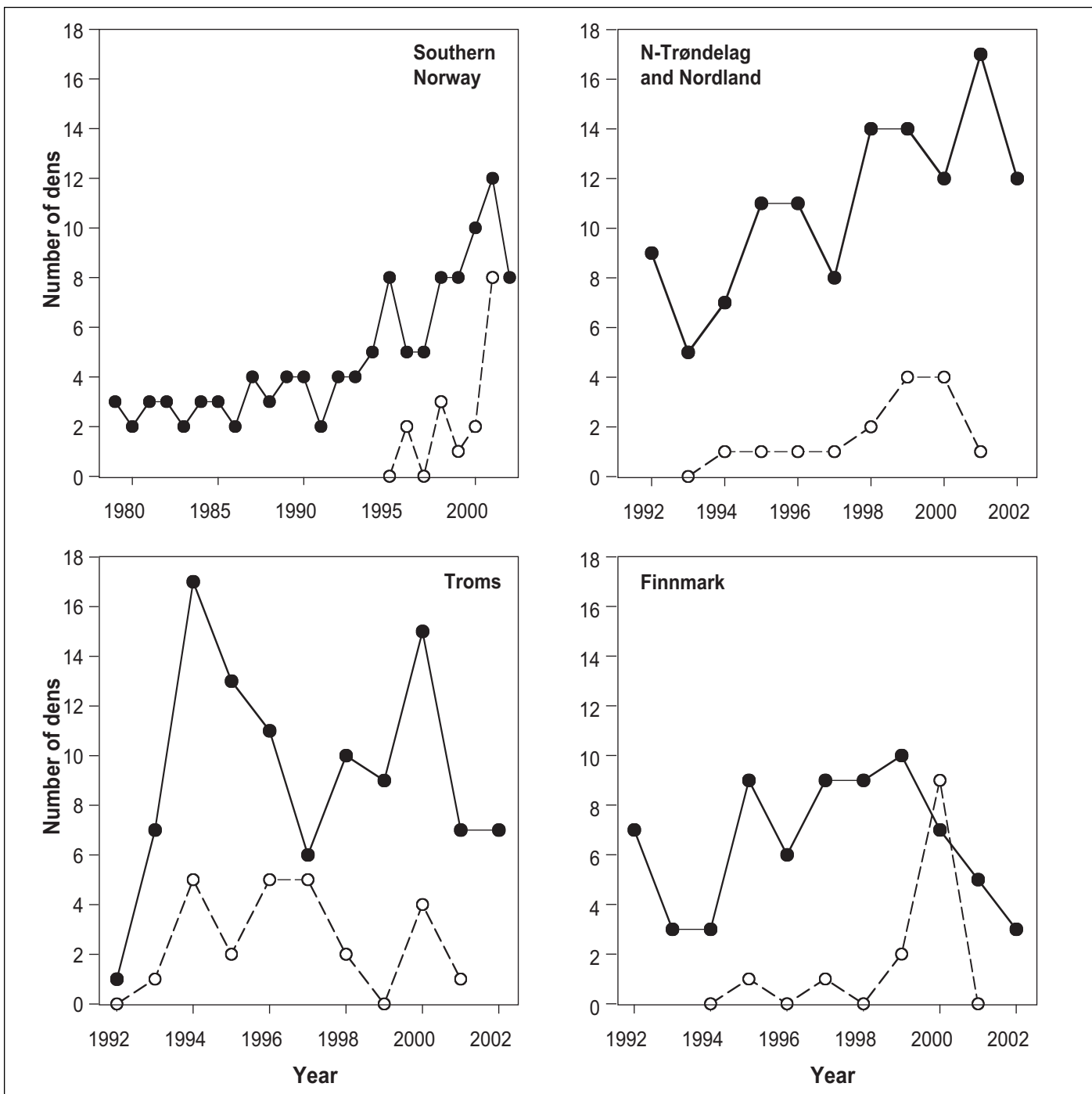

Figure 3.

Fluctuations in the number of dens (solid line and black circles) and number of females (≥ 1 years old) known to be killed in different types (hunting, illegal killing, road accidents etc.) of human activities (dotted lines and open circles) in different parts of Norway (see Fig.1). March 1 is used as initial date of the year.

4 Population model

The dynamics of all populations have both a deterministic (predictable) and a stochastic (unpredictable) component that operate simultaneously. Writing N_t for the population size and $X_t = \ln N_t$ for the logarithm of the population size in year t, the deterministic component can be formalized mathematically as the expected change of the log population size during the next year, the mean value of $\Delta X_t = X_{t+1} - X_t$ conditioned on X_t, or, alternatively, as the mean change in population size. Now, first ignoring stochastic effects, a very general class of models specifying the determinstic component is the theta-logistic model (Gilpin and Ayala 1973, Gilpin et al. 1976, Sæther et al. 1996, 2000, 2002, Lande et al. 2003)

$$\Delta N = rN\left[1 - (N/K)^\theta\right]$$

(1)

where the time index is now omitted to simplify the notation. For a positive value of the parameter θ, we see that r is the specific growth rate at small population sizes, formally the growth rate obtained in the limit as N approaches zero. The carrying capacity for this model is K, which means that the expected change in population size when $N = K$ is zero. For small and moderate changes between two years, we have $\Delta N / N \approx \Delta \ln N = \Delta X$ giving

$$\Delta X \approx r\left[1 - (N/K)^\theta\right]$$

(2)

Because all methods for parameter estimation from data is based on the use of log population size, we prefer to use eq. 2 rewritten as an exact equation as our basic model. If we define extinction to occur at $N = 1$, the smallest possible specific growth rate is actually the growth rate at $N = 1, r_1 = r\left[1 - K^{-\theta}\right]$. Using r_1 rather than r in eq. 2, the model may be rewritten as

$$X = r_1\left[1 - (N^\theta - 1)/(K^\theta - 1)\right] = r_1\left[1 - h(N,\theta)/h(K,\theta)\right],$$

(3)

where $h(N,\theta) = (N^\theta - 1)/\theta$. An advantage with this formulation of the theta-logistic model is that a well defined model is obtained as θ approaches zero and even when θ is negative. Considering the limit as θ approaches zero we find $h(N,0) = \ln N = X$. Hence, for $\theta = 0$ we obtain a form of density regulation that is linear on the log scale,

$$\Delta X = r_1(1 - X/k)$$

(4)

where $k = \ln K$ is the carrying capacity on the log scale. This is

called the Gompertz type of density regulation. Alternatively, this may also be written as

$$X_{t+1} = r_1 + (1 - r_1/k)X_t,$$

(5)

a linear model frequently used in time series analysis of population fluctuations (Royama 1992). Another special case is the logistic model obtained as $\theta = 1$, giving a second-degree polynomial on the right side of (1) and a linear expression in N in eq. 2.

When studying small fluctuations around the carrying capacity a simple linear approximation on the absolute scale, that is, a linearization of $E(\Delta N | N)$ is often used (e.g. Lande et al. 2002). It is interesting to notify that such a linear form also is a special case. By inserting $\theta = -1$, we find

$$\Delta N = r_1 \frac{K}{K-1}\left[1 - N/K\right]$$

(6)

A fourth special case of the theta-logistic model that is often used especially for territorial species is the ceiling model (Lande 1993), with no density regulation (exponential growth) for population sizes smaller than K. The ceiling at $N = K$ is then a reflecting barrier preventing the population size to exceed K. By inspection of eq. 3, we see that this is exactly the model we obtain in the limit as θ approaches infinity.

The expected time to extinction is computed by adopting the diffusion approximation to the process on the logarithmic scale (Lande et al. 2003). The infinitesimal mean and variance is then $\mu(N) = r_1 N\left[1 - h(N;\theta)/h(K;\theta)\right]$ and $\nu(N) = \sigma_e^2 + \sigma_d^2/N$. The expected time to extinction is calculated numerically by first calculating the Green function for the diffusion process (Karlin and Taylor 1981, Lande et al. 1995, 2003)

$$G(N, N_0) = \begin{cases} 2m(N)S(N) \text{ for } 1 \le N \le N_0 \\ 2m(N)S(N_0) \text{ for } 1 \le N_0 \le N \end{cases}$$

(7)

where $S(N) = \int^N s(z)dz, s(N) = \exp\left[-2\int^N \frac{\mu(z)}{\nu(z)}dz\right]$ and

$m(N) = \dfrac{1}{\nu(N)s(N)}$. We then integrate this function numerically from the extinction barrier at $N = 1$ to infinity. For the ceiling model of Lande (1993) we consider the limiting form as θ approaches infinity. This is equivalent to a model with reflecting barrier, a ceiling, at population size K, and exponential growth with stochastic growth rate r_1 below K. The Green function (eq. 7) for this process must be equal to zero for

Expected time to extinction can then be written

$$\mathrm{E}T = \int_1^K G(N, N_0)\,dN$$

From this we get

$$\frac{d\mathrm{E}T}{dK} = \frac{1}{K}\frac{d\mathrm{E}T}{d\ln(K)} = G(N, N_0)/K.$$

(8)

For $N_0 = K$ eq. 8 simplifies to

$$\frac{d\mathrm{E}T}{dK} = \frac{1}{K}\frac{d\mathrm{E}T}{d\ln(K)} = G(N, N_0)/K.$$

(9)

where , $r_0 = r_1 - \frac{1}{2}\sigma_e^2$, $\gamma = 2r_0/\sigma_e^2 - 1$ and $\delta = \sigma_d^2/\sigma_e^2$

(Lande et al. 2003). This expression can easily be integrated numerically to give E T.

5 Estimation of parameters

5.1 Demographic and environmental variance

Let $R_{i,j}$, $i = 1\ldots n_j$, $j = 1, 2, \ldots t$, denote observations of the contribution by the females to the following generation, where j is the year and n_j is the number of females for which data is available a given year. The total contribution of a female i in year j ($R_{i,j}$) is the number of female offspring born during the year that survive for at least one year plus 1 if the female survives to the next year (Sæther et al. 1998a). If Z is a stochastic vector describing the environment influencing R, the variance in R can be partitioned into two components (Engen et al. 1998)

$$\mathrm{var}(R) = \mathrm{E}\,\mathrm{var}(R|\mathbf{Z}) + \mathrm{var}(\mathrm{E}R|\mathbf{Z})$$

(10)

where $\mathrm{E}\,\mathrm{var}(R|\mathbf{Z}) = \sigma_d^2$ and $\mathrm{var}\,\mathrm{E}(R|\mathbf{Z}) = \sigma_e^2$ is the demographic and the environmental variance, respectively. For a given population size N the variance in the change in population size to the next year will then be

$$\mathrm{var}(\Delta N|N) = \sigma_d^2 N + \sigma_e^2 N^2$$

(11)

Let $\overline{R}_j$ denote the mean value of the contributions in year j, and $\overline{R}$ let be the mean of all recorded contributions. The major part of the information in the environmental variance comes from the variation between years, whereas the variation in $R_{i,j}$ within years contain information about the demographic variance. Sæther et al. (1998a) showed that

$$\hat{\sigma}_d^2 = \frac{1}{n-t}\sum_{j=1}^t\sum_{i=1}^{n_j}(R_{ij} - \overline{R}_j)^2$$

(12)

is a unbiased estimator for the demographic variance.

Usually σ_e^2 is estimated from time series of fluctuations in ΔN (Sæther et al. 1998a, Sæther et al. 2000, Sæther et al. in press). A problem with this approach is that the environmental stochasticity is extremely difficult to separate from the effects of sampling errors in the population estimates (De Valpine and Hastings 2002). Thus, in many cases it will be better to estimate σ_e^2 from the individual variation in fitness. Engen et al. (1998) has shown that the fitness contributions can be written on the form $R_{ij} = \mathrm{E}R + e_j + d_{ij}$, where e_j and d_{ij} are independent, $\sigma_e^2 = \mathrm{var}(e_j)$ and $\sigma_d^2 = \mathrm{var}(d_{ij})$. In general, we have the relationship

$$\operatorname{var} \overline{R}_j - \overline{R} = \left(\operatorname{var}(\overline{R}_j)\right) + \operatorname{var}(\overline{R}) - 2\operatorname{cov}(\overline{R}_j, \overline{R})$$

(13)

From eq. 10, it then follows

$$\operatorname{var}(\overline{R}_j) = \sigma_e^2 + \sigma_d^2 / n_i$$

(14a)

$$\operatorname{var}(\overline{R}) = \sigma_d^2 / n + \sigma_e^2 \sum n_j^2 / n^2$$

(14b)

and

$$2\operatorname{cov}(\overline{R}_j, \overline{R}) = 2(\sigma_d^2 + n_j \sigma_e^2) / n$$

(14c)

This gives

$$\mathrm{E}\sum_{j=1}^t (\overline{R}_j - \overline{R})^2 = \sigma_e^2 (t - 2 + t \sum n_j^2 / n^2) + \sigma_d^2 (1 / n_j - t / n)$$

This leads to the estimation equation

$$\sum_{j=1}^t (\overline{R}_j - \overline{R})^2 = \hat{\sigma}_e^2 (t - 2) + t \sum n_j^2 / n^2) + \hat{\sigma}_d^2 (\sum 1 / n_j - t / n)$$

(15)

that combined by eq. 12 determines $\hat{\sigma}_e^2$. We use equal weights on $(\overline{R}_j - \overline{R})^2$ because this will be optimal for large values of n_j that gives $\overline{R}_j \approx e_j$.

Estimation of the variance components for the wolverine in Sarek is also complicated by the fact that the radio-collared females do not represent a random sample of the population because only females that have a den are captured in the first year. We therefore did not include the results from the year of capture in the analyses. In this way we obtained data from 28 females covering the years 1995-2001. The range of variation in the individual contributions of females R was from 0 to 4, with 1 as the modal value (Fig. 5). The estimated demographic variance was $\hat{\sigma}_e^2 = 0.571$, whereas the environmental variance was $\hat{\sigma}_e^2 = 0.154$.

A problem with this approach using eq. 15 is that variation in R will also be dependent on fluctuations in population size through the effects of density regulation. Thus, our estimate of

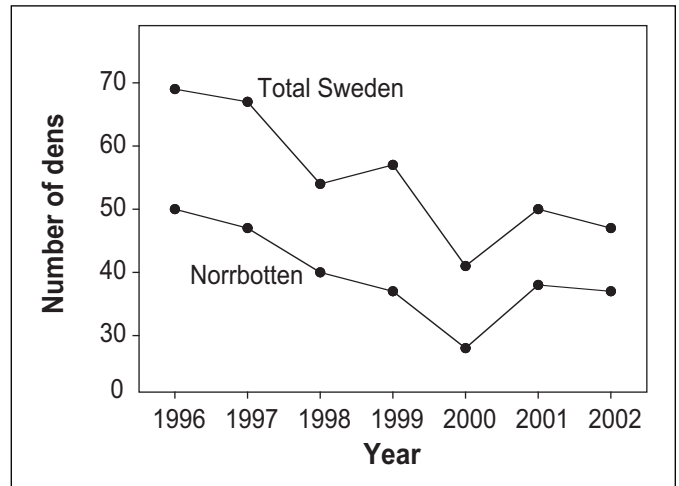$\hat{\sigma}_e^2$ may represent an upper level for the environmental variance in Sarek.

Figure 4.
The number of active dens recorded in Sweden and in the county of Norrbotten
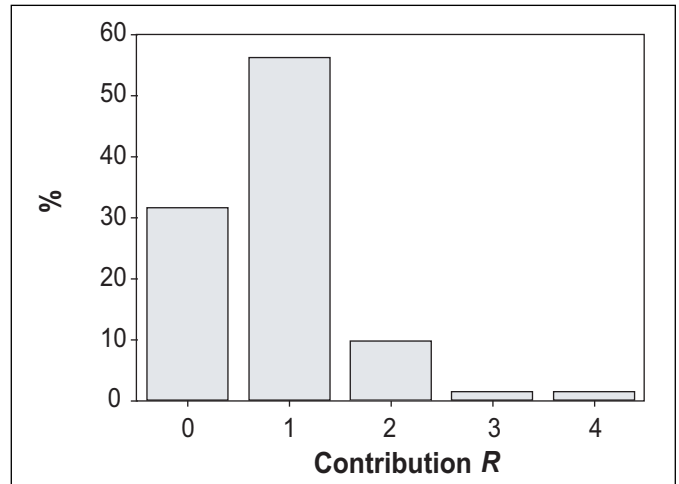
Figure 5.
*The distribution of the fitness contribution **R** of adult wolverine females in Sarek.*

5.2 The specific population growth rate r_1

The specific population growth rate is a problematic parameter to estimate because the population must spend periods at low population sizes to avoid interpolation over a large range of population sizes (Taylor 1995, Sæther and Engen 2002a, Aanes et al. 2002). Thus, we follow Sæther et al. (2002) and used demographic data to get information about this parameter. In an area where the females were given supplemental food, 83 % of the females gave birth to a litter (Persson in prep.). The mean litter size of litters digged out close after birth was 2.77 (Pulliainen 1968), which was significantly higher than the litter size at the time of radio marking in Sarek

($\bar{x}$ =1.9) (Persson in prep.). This reduction was probably due to losses from infanticide, starvation, predation or disease (Persson et al. in prep). At low population densities we assumed that these losses were reduced by 25 %, giving a litter size at weaning of 2.12. Assuming a slightly female biased sex ratio at birth (55 % females; Persson et al. in prep) and a juvenile survival rate of 0.81, this represents an annual recruitment rate of 0.78 juvenile females to the next generation. If we assume reproductive onset at 3 years and an adult survival rate of 0.92 (Willebrand et al. 1999), the specific population growth rate at low density was r_1=0.27.

5.3 The form of density regulation θ

We estimated the form of density regulation for the population in Sarek, where the population estimates were assumed to be reasonably accurate. Estimation was performed by maximum likelihood, assuming that the population process is a Markov process and normally distributed with mean $\mu(N) = r_1 N \left[1 - h(N;\theta)/h(K;\theta) \right]$ and variance $\nu(N) = \sigma_e^2 + \sigma_d^2/N$

A large value of θ was estimated for the Sarek population ($\hat{\theta}$ = 12.46), which means a strong density regulation around the carrying capacity K and weak regulation below K. However, as expected from the short study period, the estimate of θ was very uncertain (Fig. 6), with a relatively high proportion of the bootstrap-replicates at very large values. This suggests that the ceiling model of Lande (1993) describes the form of the density regulation of the wolverine reasonably well. Hence, this model will be used in the following analyses.
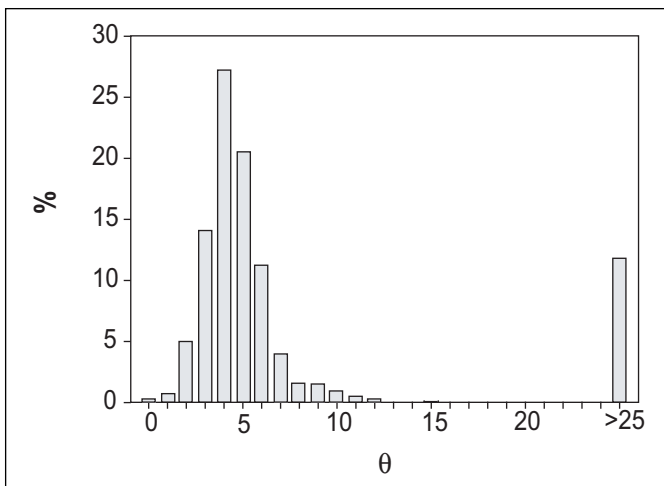

Figure 6
The distribution of the bootstrap-replicates of θ, describing the density regulation in the theta-logistic model (see text), for the wolverine population in Sarek.

6 Time to extinction

Assuming that the ceiling model of Lande (1993) is valid, and using the transformation formulas for diffusion (Karlin and Taylor 1981), the infinitesimal mean and variance for the process $X = \ln$ are $N\, r_1 - \frac{1}{2}\sigma_e^2 - \frac{1}{2}\sigma_d^2 e^{-X}$ is $\sigma_e^2 + \sigma_d^2 e^{-X}$, respectively, for . We examined the dynamical characteristics of the population in Sarek by simulating 1000 sample paths from this model (Fig. 7). We assume that the number of active dens recorded represents only 50 % of the sexually mature females actually present in the population (see p. 14). We see that a population at an initial population size of $N = K$ = 38 adult ($\geq$ 3 years old) females has a 10 % probability of being extinct after 137 years, and that it is only 50 % probability that the population will be present after 898 years. These results were very sensitive to the estimate of the environmental variance σ_e^2. If we assume σ_e^2 = 0.075, the population will not be considered vulnerable according to IUCN's (2000) classification.
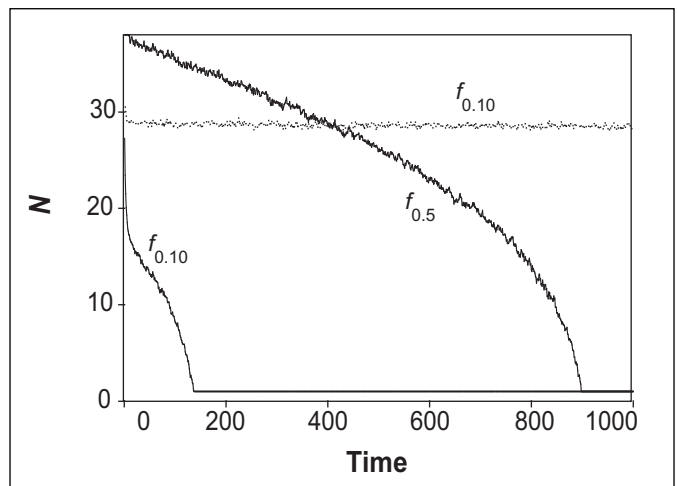

Figure 7.
Simulation of the ceiling population model with parameters estimated for the Sarek population (solid line) for σ_e^2= 0.154 and for σ_e^2= 0.075 (dotted line). $f_{0.50}$ and $f_{0.10}$ denote the 50 % and the 10 % quantiles in the distribution of the simulated population sizes. Initial population size was at K = 38 sexually mature ($\geq$ 3 years old) females, twice the highest value of active dens recorded during the study period (Fig. 2). Other parameters were r_1=0.27 and = 0.571.

The distribution of the time to extinction of the Sarek population, using the ceiling model, assuming an initial population size of K =38 ($\geq$ 3 years old) females, closely resembles an exponential distribution (Fig. 8). Thus, the probability of extinction will be highest during the first years for then to decline. Assuming the population parameters as estimated for the Sarek population, we find that the expected time to extinction increased curvilinearily with carrying capacity K (Fig. 9). The expected time to extinction of the Sarek population was 604 years (Fig. 9) when assuming a ceiling model with K equal to twice the highest number of dens recorded during the study period (K =38 ($\geq$ 3 years old) females) with r_1 = 0.27. This

means that the wolverine population in Sarek must be recorded vulnerable according to IUCN's (2000) classification. Only populations with a carrying capacity larger than 46 adult (≥ 3 years old) females can be considered not vulnerable according to this classification (Fig. 9). As expected (Lande 1993, Sæther et al. 1998a), this critical population size is strongly influenced by the value of r_1 (Fig. 9). A decrease in r_1 by 0.05 increased the necessary carrying capacity for the population not to be considered vulnerable to $K = 85$. In contrast, if $\sigma_e^2 = 0.075$ this critical carrying capacity was reduced to only $K = 18$.
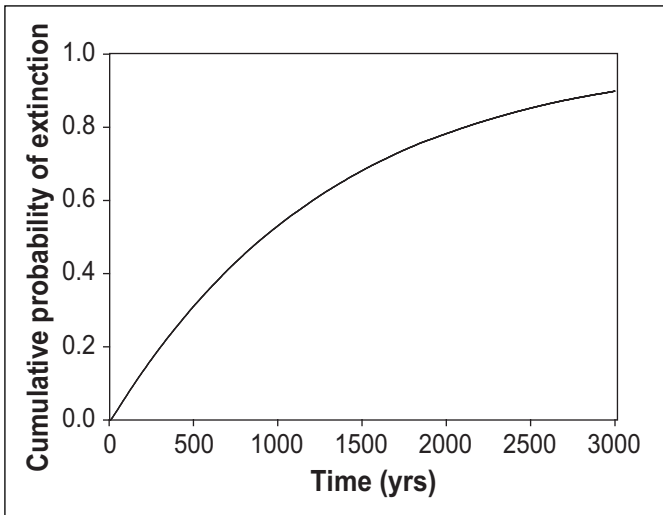

Figure 8.

*The cumulative distribution of the time to extinction for the ceiling model of Lande (1993) (solid lines), assuming an initial population size of **N** = 38. Other parameters were r_1=0.27, $\sigma_d^2 = 0.571$ and $\sigma_e^2 = 0.154$.*
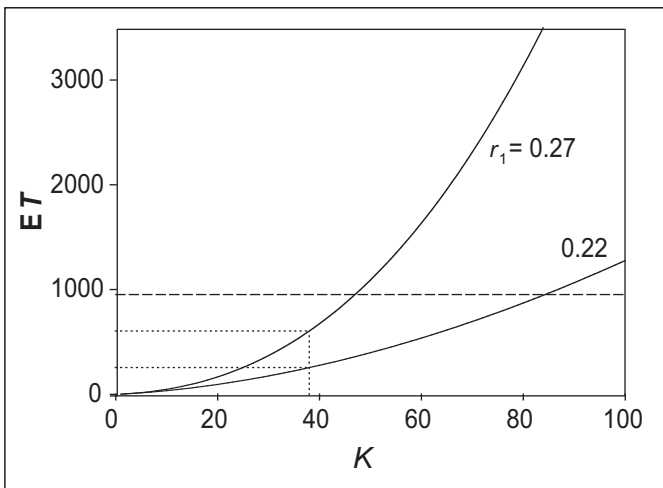

Figure 9

*Expected time to extinction E**T** in relation to the carrying capacity **K** in the ceiling model of Lande (1993) for different values of the specific growth rate r_1. The dashed line indicates the expected time to extinction for a population that is considered 'vulnerable' according to IUCN's (2000) classification. The dotted line indicates the estimates for the Sarek population.*

7 Harvesting strategies

In Scandinavia the wolverine kills domestic free-ranging sheep and semi-domestic reindeer that both use mountain ranges for grazing. As a consequence, the demand for reduction of wolverine population size through an offtake of individuals, e.g. through hunting, is strong in many areas of Scandinavia. A central aim when performing such actions is to minimize their effect on the expected time to extinction. We suggest that two types of harvest strategies should be considered: proportional harvesting and proportional threshold harvesting.

Proportional harvesting means removing a fixed proportion of the population each year, giving the annual yield

$$y = b\, N,$$

(16)

where **b** is the proportion harvested. In fisheries, this strategy is often carried out by assuming that a given harvesting effort leads to harvesting a given proportion (Quinn and Deriso 1999). The optimal proportion to harvest will depend on the dynamics of the populations, e.g. the form of the density regulation (Beddington and May 1977, May et al. 1978, Jonzén et al. 2002). Unfortunately, this commonly employed harvesting strategy leads to higher risk of extinction than threshold harvesting (Lande et al. 1995, 1997), i.e. harvesting occurs only when the population size exceeds a certain threshold **c**.

The population size of wolverines is difficult to assess. Uncertainty in population estimates should therefore be considered when choosing harvest strategy (Engen et al. 1997, Quinn and Deriso 1999). Engen et al. (1997) proposed that proportional threshold harvesting, defined as

$$y(\hat{N}, q, c) = \begin{cases} q(\hat{N} - c) \text{ for } \hat{N} > c \\ 0 \text{ otherwise} \end{cases}$$

(17)

will reduce the effect on population viability by overestimating the actual population size and thereby causing too high offtake of animals. Here is the estimated population size and **q** is the proportion of the estimated surplus individuals above the threshold **c** that can be removed.

A reasonable assumption about the sampling variance in the estimated population size is that it is proportional to the expected population size.

$$\operatorname{var} \hat{N} = \varepsilon^2 \operatorname{E} N$$

(18)

where ε determines the sampling error. The coefficient of variation in $\hat{N}$ $CV = \varepsilon / \sqrt{\operatorname{E}(N)}$ then becomes dependent on **N**. If we assume binomial sampling (Seber 1982) with probability **p** of detecting an animal, $\varepsilon = \sqrt{(1-p)/p}$. Thus, **p** = 0.5 corresponds to ε = 1.

The expressions for the infinitesimal mean and variance to be applied in the diffusion approximation for this process are given by Engen et al. (1997). The derivation of these functions was based on the assumption that the estimate of the population size is unbiased and normally distributed. When the population size is not known exactly, harvesting also introduces an additional term in the infinitesimal variance that must be incorporated (for further details, see Engen et al. 1997).

To examine the different harvest strategies we used the ceiling model and assumed an initial population $N_0 = K = 60$ sexually mature (≥ 3 years old) females. Furthermore, we also required that the harvest strategy should give an expected lifetime of the population larger than 952.3 years; thus, satisfying the criteria of IUCN for populations that are not considered vulnerable when the time to extinction is approximately exponentially distributed. No offtake is permitted when E T < 952.3 years. If T > 952.3 without harvesting we consider harvesting strategies (c, q) that keeps T constant equal to 952.3 years. When the population surveys are accurate, but environmental stochasticity is large, only small values of q can be permitted for relative thresholds c/K up to approximately 0.8, resulting in a very low annual offtake of individuals (Fig. 10). When c/K approaches 1, about half of the individuals in excess above the threshold can be removed, giving a low expected population size after the hunt, but with harvest only permitted a few years (Fig. 10). When the precision in the population estimates is improved, q is increasing for larger values of c/K (Fig. 10).

These patterns were extremely sensitive to the estimates of the environmental variance $\hat{\sigma}_d^2$, as expected from theoretical analysis of harvesting models (Sæther et al. 1996, Lande et al. 1997, 2001). When we assume a lower estimate of $\hat{\sigma}_d^2$, all individuals above the threshold can be removed for c/K > 0.37. With reduced bias in the population estimates, this critical threshold can be moved further down (Fig. 10). The amount of animals that can be removed and the expected population size after hunt depend on the particular combinations of c/K and q chosen (Fig. 10). Lowest expected population sizes after the hunt was found for values of c/K between 0.3 and 0.4, dependent on the census accuracy. In contrast, the highest offtake of animals occurred at c/K =0.59. We also find strong influence on the population dynamics when all excess individuals are being removed (Fig. 10).

The insight gained by analysis of the Sarek population was then applied to the development of management strategies of the Norwegian wolverine. The application of the ceiling model of Lande (1993) requires however an estimate of the carrying capacity for the different regions in Fig. 1. We assumed that continuous areas larger than 50 km2 situated 600 m or above the sea level (or 300 m above seal level in the two northernmost counties) represented suitable habitat for the wolverine. Scandinavian home range studies have shown that the mean size of a female annual home range varies from 274 km2 in Snøhetta in southern Norway (Landa et al. 1998) to 322 km2 in Sarek (Persson unpublished data). Because these estimates are obtained in areas likely to represent very suitable habitats

for wolverine, we assume that an average Norwegian wolverine female requires an area of 400 km2. Dividing the total area of available wolverine habitat with the mean home range size, the rough estimate of K is 166, 48, 26 and 46 sexually mature (≥ 3 years old) females in the regions (see Fig. 1) southern Norway, Nordland (inclusive Nord-Trøndelag), Troms and Finnmark, respectively. These estimates are based on that non-reproductive 2 years old females that occupy territories (Vangen et al. 2001) comprise 30.5 % of the adult (≥ 2 years old) females in the population (Landa et al. 2001).

The wolverine in Norway is currently managed by two regional management boards with heavy representation from various groups of end-users: one covering the four northernmost counties (Nord-Trøndelag, Nordland, Troms and Finnmark, see Fig. 1) and one for southern Norway. The quota is determined annually by these two boards. In all part of Norway, adult (>1 years-old) female wolverine were killed almost annually (Fig. 3) due to different forms of human activities such as regular hunt, illegal killing and offtake of individuals that do especially strong damage to semi-domestic reindeer or sheep.

The consequences of this offtake on the future population dynamics of the wolverine was examined by assuming removal of individuals during a period can be approximated by a constant harvest strategy where the number of animals removed each year has a constant mean and variance. We assume that the future harvest in each of the two regions (southern and northern Norway) would be equal to the offtake during the past years (Fig. 3). We also assumed that the number of active dens represented only 50 % of the sexually mature females present. In both regions, continuation of the current level of offtake of females will with 10 % probability cause extinction of the wolverine within 20 years (Fig. 11). In fact, the probability of absence of wolverine in northern Norway in 243 years is higher than the probability of presence. The simulations also showed that the time to extinction was relatively independent of the estimates of the carrying capacity. For instance, an increase in K by reducing the required home range size from 400 km2 to 200 km2 had in all regions only a small effect (less than 5 %) on the expected time to extinction. Thus, prolongation of the current harvest practice of wolverine in Norway is likely to cause extinction of the species in the near future. Hence, if the current rate of killings of female wolverine is continued the northern population is classified according to IUCN's (2000) criteria as 'endangered' whereas the southern population is considered 'vulnerable' (Fig. 11). Please note that the classification of the southern population is sensitive to the estimate of N_0. For instance, for N_0=20 the southern population will also be considered as 'endangered'.

To determine a sustainable strategy for offtake of wolverine we examined the threshold c/K in the different regions of Norway, under the constraints that the expected time to extinction should be longer than 952.3 years. Thus, the population should not be considered vulnerable according to the criteria of IUCN (2000). We used q = 0.4, representing a strategy to minimize expected population size after hunt, and q =

0.6, a strategy aimed to maximize the mean annual offtake of animals (Fig. 10). Using the parameter estimates from the Sarek population and an initial population size of $N_0 = K$, harvest could only be allowed in populations with $K > 47$ sexually mature females if the expected time to extinction should be long enough to consider the population as non-vulnerable. For increasing values of K the threshold could decrease, reaching 10-15 % of K in very large population (Fig. 12). These patterns were very sensitive to the environmental stochasticity. For lower estimates of σ_e^2 harvesting could start at much lower population sizes and lower thresholds could be chosen for a given q (Fig. 12).
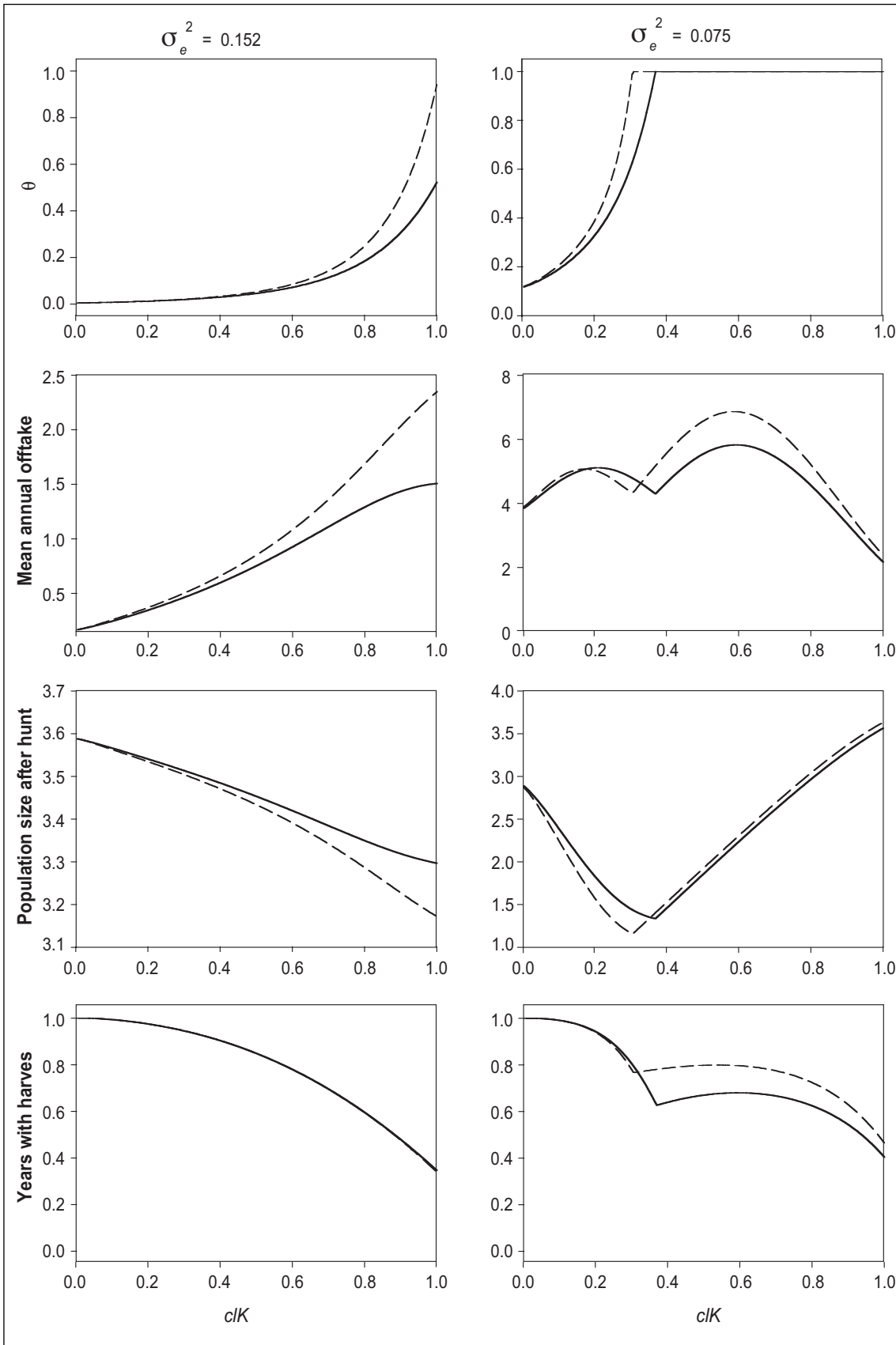

Figure 10.

The proportion of individuals in excess above the threshold c that can be removed (q), the mean annual harvest of individuals, the expected population size after the hunt, and the proportion of years when harvest is allowed in relation to the threshold c/K for different levels of uncertainty in the population estimates (dashed line: $\varepsilon = 0.01$, solid line: $\varepsilon = 1$, see eq. 18 in the text) for two values of the environmental stochasticity under the constraint of an expected time to extinction of 952.3 years; thus, satisfying the criteria that the population would not be classified as vulnerable according to IUCN (2000). The population model is the ceiling model of Lande (1993) (see text). Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$ and initial population size $N_0 = K = 60$.
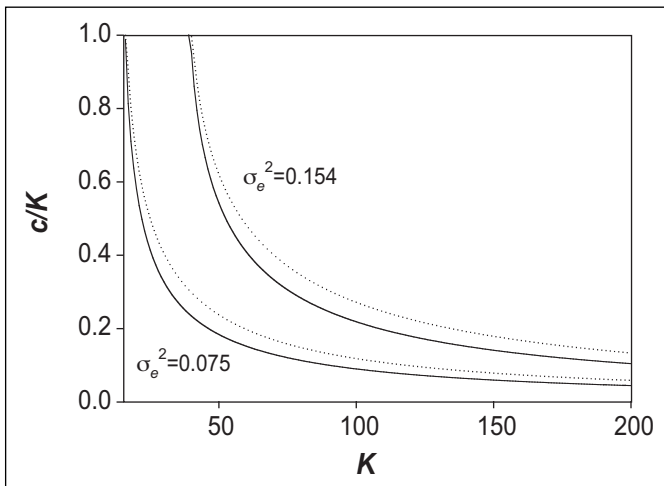
Figure 11.
Simulation of the effects of harvesting on wolverine populations in the two different parts of Norway (see Fig. 1) with parameters estimated for the Sarek population (solid line) for = 0.154. $f_{0.5}$, $f_{0.20}$ and $f_{0.10}$ denote the 50 %, 20 % and 10 % quantiles, respectively, in the distribution of the simulated population sizes. The population size of sexually mature (≥ 3 years old) females was set to twice the estimated number of active dens in 2002, assuming no sampling errors in the estimates. Because many killed females were not age-determined, we included the complete adult (≥ 1 years old) female segment of the population in the analyses. We assumed that 1 and 2 years old individuals comprised 50.5 % of the population (Landa et al. 2001). This gave $N_0 = 32$ and $K = 332$ in southern Norway and $N_0 = 88$ and $K = 240$ in northern Norway. A constant harvest was assumed, specified by the mean and variance in the number of adult females harvested in the region over the past years (see Fig. 3). The carrying capacity was determined from an assessment of the areas with available wolverine habitat (see text). Other parameters were $r_1 = 0.27$ and $\sigma_d^2 = 0.571$.
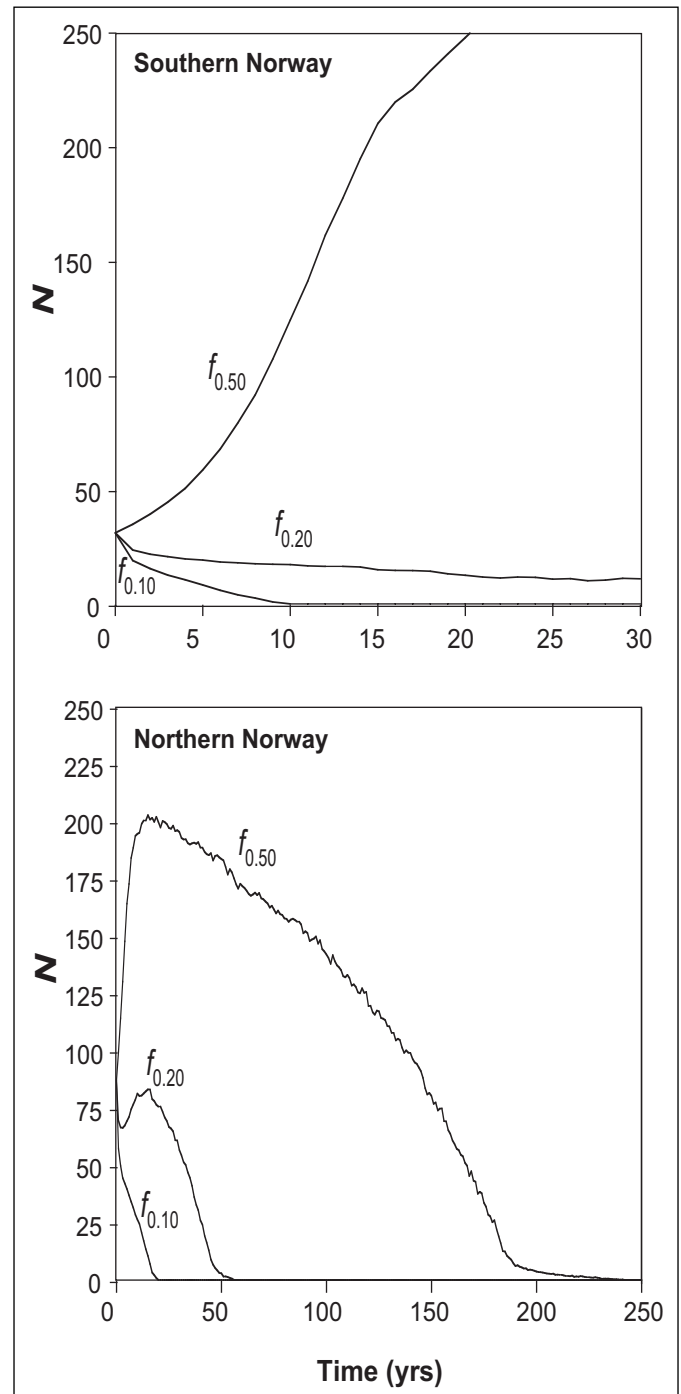
Figure 12.
The threshold c/K in relation to the carrying capacity K for different choice of q and environmental variance that gives an expected time to extinction of 952.3 years; thus, satisfying the criteria that the population would not be classified as vulnerable according to IUCN (2000). The solid lines represents $q = 0.4$ and the dotted line $q = 0.6$. Other parameters were $r_1 = 0.27$, $\sigma_d^2 = 0.571$ and initial population size $N_0 = 40$.

8 Discussion

We have demonstrated that the carrying capacity K of a Scandinavian wolverine population not be considered vulnerable according to the criteria of IUCN (2000) must be at least larger than 46 sexually mature ($\geq$ 3 years old) females (Fig. 9), assuming that the demographic characteristics of the Sarek population are typical for most populations in Scandinavia. This implies that the current population in Sarek can not be considered viable according to this criterion (Fig. 7) without immigration from surrounding areas. Furthermore, we also show that the rate of loss of wolverines in Norway due to various kinds of human activities is likely to lead to rapid extinction of the species (Fig. 11), provided that no immigration occurs from neighboring countries. According to IUCN's (2000) criteria the southern population in Norway is considered 'vulnerable', whereas the northern population is 'endangered' if no change in the rate of offtake of females occurs.

Our analyses are based on several simplifying assumptions. Our estimate of the specific growth rate r_1 = 0.27 is based on all females being mature at age of 3 years. In general, this is not the situation in Scandinavian populations where only 33% of 3-years old females reproduced. The average age at first reproduction among females monitored to their first reproduction was 3.4 years (Persson et al. in prep.). Similarly, we assume very small losses of offspring before weaning (see p. 8-19). Although these patterns are likely to be influenced by the fact that demographic studies of such difficult-studied species must necessarily be undertaken in dense populations likely to be close to K, our choice of parameter values for calculating the mean growth rate at small population sizes is likely to overestimate r_1. In general, a reduction in r_1 will have a strong effect on the time to extinction (Lande 1993, Sæther et al. 1998a, b, Lande et al. 2003, Sæther and Engen in press), as was also the case for the wolverine population in Sarek (Fig. 8). Furthermore, we have assumed that the recorded number of active dens represents only half of the number of sexually mature females present in the population. However, there was large annual variation in the proportion of the females breeding. If the large number of dens recorded in Sarek in 2002 (Fig. 2) was due to a high breeding propensity among the females that particular year, we may have over-estimated the carrying capacity for the area. This suggests that our estimates of the time to extinction of the Sarek population (e.g. Figs. 7,8, 9,10) is likely to represent over-estimates.

Reliable estimates of the form of density dependence requires long time series of precise population estimates (Sæther et al. 1998b, 2000, Sæther et al. 2002, in press), far longer than available for any Scandinavian population of wolverines. We have therefore in most of the analysis assumed the ceiling model of Lande (1993) with very simplified description of the density regulation. The uncertain estimates of θ in the Sarek population (Fig. 5) do indicate strong density regulation around K, supporting the choice of this model. This type of population dynamic seems typical for many solitary vertebrates that defend territories (Lande 1987, Sæther et al. 2002).

Stochastic factors were found to strongly influence the population dynamics of the wolverine. Our estimate of the demographic variance σ_d^2 in the wolverine population in Sarek is higher than those previously estimated in most vertebrate populations (Lande et al. 2003, Sæther et al. unpubl.). Similar values have only been recorded in some small passerine birds (Lande et al. 2003). This is related to the combination of relatively high survival rate of the adult females, but a very variable success in the production of new recruits (Fig. 5). Previous studies have indicated high losses of offspring after the denning period, probably related to intra-specific predation (Persson et al. in press). However, these estimates of recruitment can also be an artifact of the sampling procedure because the first year only breeding females are radio-collared. Accordingly, we included only females that already had been followed one year in the estimates of the recruitment success. However, including all adult females or selecting only females followed over two years gave a small change (< 5 %) in σ_d^2. This suggests that large demographic stochasticity is an important characteristic of the population dynamics of the wolverine. Theoretical analyses have shown that the demographic stochasticity strongly influences the time to extinction of small populations (Lande 1993, Lande et al. 1998, 2003, Sæther and Engen in press). Thus, the results of our calculations of the expected time to extinction (Figs. 9), the simulations of future population trajectories (Figs. 7, 11) and our analysis of different harvest strategies (Fig. 10, 12) all are likely to be influenced by such a high estimate of σ_d^2. This illustrates the importance of incorporating analysis of demographic stochasticity especially when considering management options for small populations (Sæther and Engen 2002a).

Environmental stochasticity is another important stochastic component of the population dynamics of the wolverine. Usually, we estimate this from time series of population fluctuations (Sæther and Engen 2002b, Sæther et al. 2000, 2002). In the Sarek population, we used the among-year variation in the individual fitness contributions, using the method of variance partitioning described in Engen et al. (1998). We then assume that the annual fluctuations in population size are only due to stochastic fluctuations around K and are not related to density dependence. Thus, σ_e^2 probably represents an upper limit for the environmental variance σ_e^2. However, large environmental stochasticity is expected in the population dynamics of the wolverine, because the demography is presumably influenced by highly variable food availability by e.g the cyclic abundance of rodents (Landa et al. 1997). All analyses are therefore performed using both σ_e^2=0.154 and σ_e^2 = 0.075. As expected from theoretical analysis (Lande 1993, Lande et al. 1998, 2003, Sæther et al. 1998a, Sæther and Engen in press), variation in this parameter strongly influenced the expected time to extinction, and the choice of harvest strategy for larger populations (Fig. 10). However, predictions of the future development of the Norwegian wolverine populations were relatively independent of the estimates of σ_e^2 (Fig. 11), probably because the offtake of individuals (Fig. 3) affected the deterministic dynamics through an effect of reducing r_1. It is therefore important to continue the long term individual-based pop-

ulation studies of the wolverine to improve the precision in the estimates of r_1 and σ_e^2.

Theoretical analysis of harvesting models have shown that proportional threshold harvesting has some useful properties in reducing the variance in the annual yield, compared to a pure threshold strategy (Engen et al. 1997, Lande et al. 1997, 2001). We are then left with two options, determining the threshold as well as determining the proportion of individuals above the threshold that can be removed, q. When we kept the expected time to extinction constant, we found for large values of the environmental stochasticity that the annual yield was maximized and the expected population size after hunt was minimized for high thresholds c/K (Fig. 10, see also Fig. 12). In contrast, when the environmental stochasticity was smaller, the chosen values c and q will depend on the optimization criteria. If the expected population size after the hunt should be minimized, a smaller threshold c/K should be chosen than for maximization of the annual offtake as optimization criterion. Irrespective the value of σ_e^2, higher values of q could occur when the precision in the population estimates is improved (Fig. 10). Thus, larger offtakes were permitted for small sampling errors than for larger sampling errors (Tufto et al. 1999), strongly emphasizing the need for the investment in precise population censuses for a sustainable harvest strategy of wolverine. A central focus for such schemes should be to obtain estimates of the non-breeding part of the population, for instance by using modern DNA techniques to obtain individual identification from samples of faeces or urine samples collected from tracks. Such data can be analyzed by capture-recapture techniques to give data on the precision in the censuses (Seber 1982) as well as estimates of important demographic variables (Lebreton et al. 1992).

In Norway, decisions on an eventual offtake of wolverines are made by two regional boards, whose members are politically appointed. Our analyses have shown that these boards have given too high quotas to secure wolverine populations in Norway that are viable according to IUCN's (2000) criteria (Fig. 11). Thus, if the current practice is continued, this is likely to lead to extinction of the wolverine over the larger parts of Norway within a relatively short period of time (Fig. 11). Assuming the demographic characteristics of the Sarek –population is typical also for most Norwegian populations, our estimates of K, though admittingly very rough, suggest that harvest can not be permitted before the populations exceed 22 sexually mature females in both northern and southern Norway. This calculation is based on $q = 0.4$ and an initial population size of sexually mature (≥ 3 years old) females twice the number of active dens in the two regions in 2002 (see Fig. 3). When the estimated population size exceeds this value, 40-60 % of the excess individuals can be removed (Figs. 10). Thus, before harvesting should be permitted in the southern management region for wolverine in Norway the current population size must be increased. In northern Norway a limited offtake can be permitted. However, this assumes a strong regulation of the offtake, with no harvest below the threshold.

A central element in a management strategy for the wolverine would be to reduce the number of animals killed illegally that is even likely to occur in the protected Sarek area (Fig. 3). A consequence of this will be an increase in the specific growth rate and a reduction in the stochastic influences on the population dynamics. This will strongly increase the expected time to extinction (Fig. 8), and hence improve the viability of the species.

Acknowledgements

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