Aldersbestemmelse, vækstudvikling og kohorteeffekter hos rådyr (*Capreolus capreolus* L.)

Specialerapport i Biologi

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Indholdsfortegnelse

Tak

At skrive dette speciale har engageret mig i gennem lang tid. Det har været både arbejde og fritid, socialt og ensomt, personligt og formelt. Mange forskellige mennesker har bidraget til, at det har været en god tid for mig. Tak til jer.

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Den vakre norske vinter og stilheden i de sene nattetimer på Fossheim har været en uvurderlig støtte frem mod afslutningen. Jeg kommer til at savne dem begge…

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Toke Thomas Høye

Baggrund

Fitnessforskelle mellem individer opstår på baggrund af genetisk variation og forskelle i forholdene oplevet gennem livet (Roff 1992)*. Studier af langtlevende arter som fugle og pattedyr har imidlertid vist, at en væsentlig del af den individuelle variation i fitnessrelaterede træk kan tilskrives miljøforhold i fødselsåret (se en gennemgang i Lindström 1999). For eksempel er det hormonale miljø i livmoderen, påvirket af de forhold moderen er udsat for, og dette influerer på individets livshistorie, således at individets reproduktive strategi delvis er styret af forhold i dets fosterstadie (Clark & Galef 1995).

Blandt pattedyr generelt og specielt hos hovdyrene er det kun moderen, som investerer i afkommet, og dets opvækstvilkår er derfor betinget af moderens allokering af ressourcer både under graviditet og opfostring (Clutton-Brock 1991). Omgivelserne i form af tæthedsafhængige og tæthedsuafhængige forhold har ligeledes betydning for opvæksten både direkte og indirekte gennem påvirkning af moderen (Forchhammer *et al.* 2001). Effekter af forholdene tidligt i livet, som er fælles for individer født i samme reproduktive periode, kaldes kohorteeffekter. Disse har fået speciel opmærksomhed hos iteropare arter i de senere år, hvilket blandt andet skyldes at ændringer i klimaet, har vist sig at have tydelige konsekvenser for vertebraters livshistorie. For eksempel er flere trækfuglearter i de seneste 30 år ankommet tidligere til deres ynglepladser, og padder og trækfugle har lagt deres æg tidligere end før. Denne generelle tendens og variationen mellem forskellige år kan forklares ud fra overordnede ændringer i klimaet (Forchhammer *et al.* 1998).

Konsekvenser af kohorteeffekter for danske rådyrs livshistorie (*Capreolus capreolus*) danner baggrunden for dette speciale. Jeg har undersøgt hvornår forskellige dele af rådyrs underkæber er fuldt udviklede for at finde et mål for omgivelsernes indflydelse på væksten tidligt i livet. Sammenholdt med et konditionsindeks ved dyrets død har jeg studeret betydningen af kohorteeffekter for rådyrs livshistorie i to danske bestande. For at kunne beskrive en variation betinget af fødselsåret er det dog nødvendigt at vide hvilket år, de enkelte individer er født i, derfor har en vigtig del af specialet været at udvikle en metode til aldersbestemmelse af rådyr.

Undersøgelserne i denne specialerapport bygger delvis på data indsamlet uden min deltagelse. Individuelle data på rådyr, i form af dødsdato, total og opbrækket vægt samt opsatstypen ved dødstidspunktet for bukke, er blevet stillet til rådighed for mig af

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* Litteraturliste følger efter introduktionskapitlet

Danmarks Miljøundersøgelser sammen med afkogte og rensede kæber fra de fleste af disse individer. Ligeledes var fangst af rådyrlam til øremærkning også afsluttet, før jeg begyndte dette specialeprojekt. Jeg har produceret data i de to papers om metoder til aldersbestemmelse af rådyr. Dette involverede blandt andet gennemgangen af op til 50 år gamle journaler og registreringshulkort fra lammefangster for at verificere at de anvendte kæber stammede fra individer med kendt alder. Endvidere har jeg registreret slidkarakterer på i alt 2.833 rådyrkæber med ukendt alder fra Borris og Kalø samt foretaget fem kæbemål på i alt 2.384 rådyrkæber. Nogle kæber er ikke blevet opmålt, fordi deres aldersestimat, baseret på metoden beskrevet i paper II, var for usikkert. Dette forklarer forskellen mellem de to antal.

Rapporten består af fire selvstændige dele. Jeg indleder med et introduktionskapitel, hvor jeg redegør for det teoretiske fundament som mine undersøgelser hviler på. Derefter følger tre udkast til videnskabelige papers, som kan læses selvstændigt og uafhængigt af denne introduktion. De er skrevet på engelsk med henblik på publikation i internationale fagtidsskrifter.

Introduktion

1. Indledning

På flere måder er rådyret specielt i Danmark en interessant art at studere kohorteeffekter hos. Den seneste forskning på kohorteeffekter og betydningen af klimaeffekter har hovedsageligt brugt krondyr og Soay sheep som modelorganismer, og de mest intenst studerede rådyrbestande ligger enten langt syd (Frankrig) eller langt nord (Midtnorge) for Danmark. Endvidere har rådyrbestande i Norden oplevet en kraftig stigning i bestanden, specielt i anden halvdel af det 20. århundrede (Madsen *et al.* 1996, Unsgård & Hægeland 1996). Der mangler derfor viden om rådyrs respons på danske klimaforhold.

I Danmark er det kun ræven, som spiller en betydningsfuld rolle som prædator på rådyrlam, og det er udelukkende på lam i den første sommer (Strandgaard 1972), mens voksne rådyr også har naturlige prædatorer i andre Skandinaviske lande (Unsgård & Hægeland 1996). Selvom jagten årligt tager ca. 100.000 stykker råvildt i Danmark (Asferg & Jeppesen 1996), vælges ikke selektivt efter dårlige individer. Dette kan indikere at kohorteeffekter spiller en større rolle her end i lande med flere prædatorer, som selektivt tager de svageste individer.

Jeg gennemgår her hovedtræk af de problemfelter mine undersøgelser relaterer sig til. Jeg koncentrerer mig om rådyr, men studier af andre hovdyrarter øger forståelsen af de forskellige temaer, hvorfor jeg også inddrager dem. Betydende faktorer for lammets opvækst såsom moderens investering i afkommet og omgivelsernes indflydelse behandles først. Derefter gennemgår jeg konsekvenser af forhold i opvæksten for forskellige livshistoriekarakterer med fokus på kohorteeffekter. Afslutningsvis behandler jeg brugen af forskellige konditionsindeks og gennemgår baggrunden for brugen af tænder til aldersbestemmelse af hovdyr. Jeg henviser undervejs til mine undersøgelser, men opsummerer ikke resultaterne af disse, siden de præsenteres og diskuteres udførligt i de tre papers, som følger denne sammenfattende introduktion.

2. Kohorteeffekter

De vilkår et individ vokser op under er betinget af samspillet mellem forældrenes investering i afkommet og omgivende faktorers indflydelse (Desai & Hales 1997). For hovdyr er forældrenes investering begrænset til moderens tildeling af ressourcer til fosteret under graviditet og opfostring. Jeg fokuserer her på hvilken konsekvens artsspecifik afkomsinvestering og omgivende faktorer har for omfanget af kohorteeffekter.

2.1. Moderens investering i afkommet

I studiet af reproduktiv investering hos pattedyr, skelner man mellem ”capital breeders” og ”income breeders”. Capital breeders udnytter oplagrede kropsreserver til afkomspleje mens income breeders i højere grad er afhængige af tilgængelige føderessourcer (Stearns 1992). Andersen *et al.* (2000) argumenterer for at rådyr ligner en income breeder, blandt andet fordi der ikke er forskel i vægttab mellem råer som har opfostret et lam, og råer der ikke har været gravide. Rådyr udviser ringe variation i kropsvægt igennem året (Hewison *et al.* 1996), hvilket er i modsætning til f.eks. krondyr (*Cervus elaphus*) (Mitchell *et al.* 1976) og Svalbard rensdyr (*Rangifer tarandus platyrhyncus*) (Nilssen & Ringberg 1980), som derfor i højere grad ligner capital breeders. For krondyr på Isle of Rum i Skotland, herefter kaldet ”Rum”, havde kalve født af socialt dominante hinder bedre overlevelseschancer i deres første sommer (Clutton-Brock *et al.* 1987a). Siden social dominans er afgørende for adgangen til specielt næringsrige græsningsområder (Clutton-Brock *et al.* 1984) og betinges af kropsstørrelsen hos hinder (Clutton-Brock *et al.* 1988), er hinders evne til at opfostre en kalv betinget af deres kropsstørrelse. Afkommets livshistorie forventes derfor at være mindre afhængigt af omgivende forhold end hos rådyr.

Fødselsvægten hos rådyr udgør op imod 15% af moderens vægt, hvilket er meget for hovdyr (Andersen *et al.* 1998), men selvom råer investerer relativt mange ressourcer i deres afkom i forhold til andre hovdyrarter, tyder ovenstående på at disse hovedsageligt kommer fra fødegrundlaget. Miljømæssige forhold under opfostring af afkommet spiller derfor en væsentlig rolle for lammenes opvækst, og kohorteeffekter kan umiddelbart forventes at være specielt tydelige hos rådyr.

Clutton-Brock *et al.* (1989) har gennem studier af totale livsforløb hos hinder af krondyr fundet at fitnessomkostningen under graviditeten er langt mindre end i dieperioden. Dette sandsynliggør, at hovdyr under dårlige forhold har mulighed for at justere ressourcetildelingen til reproduktion efter fødslen ved at afvise afkommet uden større konsekvenser for fremtidigt reproduktivt potentiale. Norske råer som var i stand til at investere mere i afkommet under graviditeten producerede flere men ikke større afkom (Andersen *et al.* 2000). Større kuld giver mulighed for at opfostre flere lam i gode år, og denne reproduktive strategi antyder at energiudgiften under graviditeten også er mindre end i dieperioden for rådyr. Samtidig indikerer den, at individuelle konditionsforskelle mellem råer ikke i sig selv producerer forskelle mellem afkom som er synlige ved fødslen. Moderens investering i afkommet efter fødslen var dog både afhængig af hendes kropsstørrelse (Andersen *et al.* 2000), og samspillet mellem miljøforhold og kuldstørrelse, idet søskende oftere oplevede samme skæbne med hensyn til vækst og overlevelse end ikke relaterede individer, men kun når forholdene var ufavorable (Gaillard *et al.* 1998a). Afkom født af lette mødre og afkom fra trillingepar havde generelt ringere overlevelseschancer end afkom fra tungere mødre og mindre kuld (Andersen og Linnell 1998).

2.2. Omgivende faktorer

Studier af kohorteeffekter hos hovdyr har ofte henført oprindelsen af disse til konsekvenser af bestandens egen tæthed (Clutton-Brock *et al.* 1987b) eller til variation i klimaparametre (Albon *et al.* 1987). Høj bestandstæthed forventes at øge konkurrencen om ressourcer og risikoen for spredning af parasitter, samt medføre en funktionel respons hos eventuelle naturlige prædatorer (Crawley 1992, Begon *et al.* 1996). I et omfattende eksperimentelt studie af rådyr ved forskellige bestandstætheder har Kjellander (2000) demonstreret tæthedsafhængighed i flere centrale livshistorieparametre. Omgivende faktorer har derimod indflydelse på tilgængelighed og næringsindhold i føden (Post og Stenseth 1999) samt øger energiudgiften til termoregulering (Hart *et al.* 1961) og bevægelse ved store snedybder (Cederlund *et al.* 1991a).

Flere studier har undersøgt betydningen af variation i fødegrundlag for populationer af større planteædende pattedyr (Langvatn & Albon 1986, Langvatn *et al.* 1996, Post og Stenseth 1999). Disse har blandt andet demonstreret, at kropsvæksten er mere følsom for variation i længden af planternes vækstsæson om foråret end af fødemængden senere på sommeren. Høj temperatur i planternes vækstperiode forkorter det tidsrum, hvor vegetationen er specielt næringsrig, hvilket er afgørende for opnåelse af høj kropsvægt (Langvatn & Albon 1986). En stor snemængde, eller topografisk variation øger den geografiske forskel i planteudvikling, så denne ”forårseffekt” forlænges (Albon & Langvatn 1992).

Nyere forskning i populationsøkologi har anvendt fluktuationer i et makrogeografisk vejrfænomen, North Atlantic Oscillation (NAO) som et mål for generelle vejrforhold i nordlige dele af Europa og Nordamerika (se nærmere beskrivelse i paper III). NAO indekset beskriver afvigelsen fra en normal tilstand, og giver derfor ikke samme vejrtype i forskellige dele af Nordatlanten. For eksempel giver et højt NAO indeks (relativt varmt, vådt og blæsende) i norske områder med fastlandsklima snerige vintre, som er meget energikrævende for større planteædere (Post *et al.* 1997). I kystnære områder i

Norge betyder et højt NAO indeks derimod snefattige vintre, fordi nedbøren hovedsageligt falder som regn. Lavt NAO indeks giver her ofte et islag over vegetationen, som begrænser fødetilgængeligheden for større planteædere (Loison *et al.* 1999). I et studie af krondyr var den mest fekunde kohorte i Norge også den mest fekunde kohorte på Rum og de to kohorter med lavest fekunditet i Norge var blandt de dårligste på Rum. Siden fekunditeten var korreleret med temperaturen i april-maj i fødselsåret, kunne noget tyde på at større vejrfænomener (NAO) spiller en rolle i dannelse af kohorteeffekter (Albon *et al.* 1992). NAO indeksets indflydelse på danske hovdyrbestande er ikke dokumenteret før, men dette undersøges i paper III.

For hjortevildt i Danmark står jagt for en væsentlig del af dødeligheden (Madsen *et al.* 1996). Denne kan til dels være tæthedsafhængig, men normalt beror den på en forvaltningsplan, som ikke udelukkende forholder sig til tætheden af bestanden. Såvel jagt som ændringer i arealanvendelse vil have mere langsigtede konsekvenser, som kan spores i kohorteundersøgelser af lange tidsserier. I mine undersøgelser, der strækker sig over en periode på 44 år fra 1956 til 1999, kan den øgede udbredelse af vintergrønne marker spille en væsentligt rolle, gennem større fødetilgængelighed i vintermånederne.

Moderens investering og omgivende faktorer virker sammen ind på opvækstvilkårene. Som income breeder med høj afkomsinvestering forventes forholdene omkring fødslen at være specielt afgørende hos denne art. Tæthedsafhængighed er dokumenteret hos rådyr, men også klimavariable forventes at være afgørende for opvækstvilkårene.

3. Kohortevariation i livshistorieparametre

Kohorteeffekter virker proksimalt ind på fødselstidspunkt, fødselsvægt, vækst og voksen kropsstørrelse, men ultimativt kan både overlevelse og reproduktion påvirkes af hæmmet vækst (Kjellander 2000, Forchhammer *et al.* 2001). Derfor er det naturligt at dele en gennemgang af kohorteeffekters konsekvenser på livshistorien op i afsnit om fødsel, vækst, reproduktion og mortalitet. Jeg berører også konsekvenser for seksuel størrelsesdimorfisme, kønsratio og opsatsudvikling, fordi disse aspekter relaterer sig til mine undersøgelser.

3.1. Fødselsdato

Rådyr udviser en høj grad af synkroni i fødselsdato uafhængigt af bestandstætheden (Gaillard *et al.* 1993b). Dette kan være særegent for denne art, fordi brunstperioden ligger allerede sidst på sommeren (Liberg *et al.* 1998), og der derfor er kort tid mellem energiudgiften forbundet med dieperioden og parringen. Bestandstætheden i vinteren inden fødslen spillede derimod ind på fødselsdatoen både hos ”bighorn sheep” (*Ovis canadensis*) (Festa-Bianchet 1988), ”Soay sheep” (*Ovis aries*) (Forchhammer *et al.* 2001) og krondyr på Rum (Clutton-Brock *et al.* 1987b). Strandgaard (1999) har vist, at danske rålam i gennemsnit fødes 13 dage senere i Borris end på Kalø men brunsten er også tilsvarende senere i Borris. Kohortevariation hos rådyr opstår tilsyneladende ikke ud fra forskelle i fødselstidspunkt, da dette er nøje synkroniseret med tidspunktet for brunsten, som antages at være styret af daglængden (Sempéré *et al.* 1998).

3.2. Fødselsvægt

Siden rådyrets livscyklus tvinger råerne til at føde på et bestemt tidspunkt (Gaillard *et al.* 1993b) er den tydelige kohortevariation i fødselsvægt både i Frankrig (Gaillard *et al.* 1993a) og i Norge (Andersen & Linnell 1997) forståelig. I dårlige år opnår fostrene ikke optimal størrelse, men råerne er tvunget til at føde afkommet på et bestemt tidspunkt for at kunne afslutte den energikrævende dieperiode før brunsten. Variation i fødselsvægten kunne delvis forklares ud fra klimaparametre sidst i graviditeten, hvilket også er tilfældet for andre hovdyrarter. For eksempel var fødselsvægten for krondyr på Rum hovedsageligt betinget af produktionen af højkvalitetsføde sidst i graviditeten (Albon *et al.* 1983), der er afhængig af temperaturen i april og maj på Rum (Albon *et al.* 1992).

Post & Stenseth (1999) har vist, at højt NAO indeks i fødselsåret giver lette men fekunde kohorter af krondyr i det norske indland, men tunge og mindre fekunde kohorter på Rum. Højt NAO indeks i Norge er i indlandet ensbetydende med dyb sne, hvilket påvirker moderen så ressourcetildelingen til fosteret reduceres. Dette forventes at være årsagen til den observerede lave fødselsvægt, der ikke senere kan kompenseres for. Til gengæld giver et højt NAO indeks en lang sæson med højkvalitetsføde, som fører til høj kondition og derfor høj fekunditet. På Rum er højt NAO indeks ensbetydende med milde vintre og god vækst af fosteret. Dette bliver derfor stort, men efter fødslen oplever kalven en kort sæson med højkvalitetsføde. Det er altså et samspil mellem flere faktorer, som bestemmer forskellen mellem de to områder.

Disse resultater giver en indikation af klimaets betydning for individets tidlige vækst. Længden af, og eventuelt konkurrencen i perioden med højkvalitetsføde i foråret er afgørende for det nyfødte afkoms opvækstvilkår. Den høje grad af synkroni i fødselstidspunktet kan være årsag til tydelig kohortevariation i fødselsvægten hos rådyr. Råerne kan ikke udskyde fødslen, og i dårlige år bliver lammene derfor små.

3.3. Vækst

Væksten hos rådyr i den første måned efter fødslen er tilnærmet lineær (Andersen & Linnell 1997, Portier *et al.* 2000). Vægten en måned efter fødslen er derfor korreleret med fødselsvægten. Hos lam fra trillingekuld var vækstraten mindre, men selvom tætheden øgede til det firedobbelte, kunne denne ikke forklare variationen i vækstraten efter fødslen (Andersen & Linnell 1997). I sammenhæng med ovenstående tyder dette resultat på at der er rigeligt føde i planternes vækstsæson, således at konkurrencen betyder mindre end længden af planternes vækstsæson. Fødselsdatoen påvirkede ikke væksthastigheden hos rålam i Frankrig (Gaillard *et al.* 1993a), mens lam født senere end flertallet voksede langsommere i Norge (Andersen & Linnell 1997). Dette kan muligvis forklares ud fra forskelle i spiringstidspunkt for fødeplanter i forhold til fødselstidspunktet mellem Norge og Frankrig. For en fransk rådyrbestand var vintervægten større efter kølige somre med lav bestandstæthed, og bukkelam havde højere vægt om vinteren, når nedbørsmængden i april-maj året før havde været lav (Gaillard *et al.* 1996). Dette skyldes sandsynligvis at sommertemperaturen var mest afgørende for næringsindholdet i planterne, mens nedbørsmængden i foråret udøvede et direkte fysiologisk stress på mødrene i slutningen af graviditeten.

Man har traditionelt antaget, at sammenhængen mellem fødselsvægt og vægten i den efterfølgende vinter er tydeligere, hvis bestanden er ressourcebegrænset i den første sommer. Blandt andet er evnen til at kompensere en ringe fødselsvægt påvist hos en bestand af franske rådyr i god stand (Gaillard *et al.* 1993c). En høj grad af polygyni er imidlertid blevet fremsat som en alternativ hypotese til at forklare fravær af kompenserende vækst hos velnærede dådyr (*Dama dama*) i fangenskab (Pélabon 1997). Hos polygyne arter, forventes kropsstørrelsesforskelle at blive opretholdt gennem seksuel selektion af de største hanner. For at nå en stor voksenstørrelse må vækstraten for hanner være høj og potentialet for kompenserende vækst forventes derfor at være ringe (se f.eks. Post *et al.* 1999a). Pélabon (1997) foreslår at kompenserende vækst hovedsageligt forekommer hos arter med ringe grad af polygyni og at ressourcebegrænsning kan have en reducerende effekt.

Alternativt har en ”weeding out” effekt været fremsat som en forklaring til at forstå sammenhængen mellem fødselsvægt, og vægt senere i livet (Begon *et al.* 1996, Rose *et al.* 1998). Individer som er født med en lav kropsvægt har mindre overlevelseschancer og bliver efterhånden ”luget ud” af bestanden. Sammenhængen mellem fødselsvægt og voksenvægt blandt de tilbageværende individer øges derfor, uden at der er tale om kompenserende vækst. Denne effekt er blandt andet blevet påvist hos rensdyr (*Rangifer tarandus*) (Rognmo *et al.* 1983, Skogland 1984). Endvidere havde kohorter med høj juvenil mortalitet modsvarende lav adult mortalitet hos krondyr (Rose *et al.* 1998) og Soay sheep (Forchhammer *et al.* 2001). Weeding out effekter skyldes ikke nødvendigvis differentieret dødelighed, men kan også havde sin årsag i sociale reguleringsmekanismer, hvilket jeg argumenterer for i paper III.

En signifikant kohorteeffekt i vægt og vægttab i løbet af den første vinter er fundet for norske krondyr, og variationen i vinterkropsvægt kunne i nogen grad forklares af NAO indekset for den vinter hvor kohorten var i fosterstadiet (Loison *et al.* 1999). Post *et al.* (1997) viste ligeledes at norske krondyr, født efter vintre med højt NAO indeks (streng vinter), havde lav fødselsvægt og mindre veludviklet skeletstørrelse, og at denne forskel mellem kohorter var signifikant hos voksne individer. Klimaet i fødselsåret og dermed fødselsvægt har også vist nær sammenhæng med både voksenstørrelse og afkommets fødselsvægt for krondyr på Rum (Albon *et al.* 1987), hvilket illustrerer den store indflydelse kohorteeffekter kan have på individuel livshistorievariation. Hos rensdyr er fødselsvægten korreleret med moderens vægt ved afkommets fødselstidspunkt, og denne kohorteeffekt forsvinder ikke ved kompenserende vækst senere i livet (Skogland 1983). Omfanget af kohorteeffekter i vækstrelaterede træk kan ud fra ovenstående påvirkes af forskellige mekanismer afhængig af arten. I paper III undersøger jeg hvorvidt kohortevariation i væksten omkring fødslen hos rådyr er tydelig i vægt og kondition blandt voksne individer.

3.4. Reproduktion

Kohorteeffekter forventes at kunne spores direkte på væksten, mens reproduktionen påvirkes indirekte gennem kropsstørrelsen (Loison & Langvatn 1998). Blandt toårige råer kunne vintervægten forudsige sandsynligheden for at råen var drægtig (Gaillard *et al.* 1992), hvilket støtter denne antagelse. Eksperimentelt manipuleret tæthed af en svensk rådyrbestand har også vist, at fekunditeten er tæthedsafhængig, men at effekten indirekte styres af kropsvægten (Kjellander 2000). Rådyr har potentialet til jævnligt at få trillinger (Andersen *et al.* 1998), og når disse oftest kommer fra de største mødre (Andersen *et al.* 2000), må forhold, som spiller ind på mødrenes vægt, forventes at have potentialet til at skabe kohorteeffekter i kuldstørrelsen. Hos Soay sheep i Skotland medførte høj tæthed og højt NAO indeks i vinteren inden kohorten blev født blandt andet færre tvillingefødsler (Forchhammer *et al.* 2001).

Livstidsbaseret reproduktiv succes, målt som totalt antal afkom et individ får opfostret til reproduktiv alder, kan deles op i kuldstørrelsen i hver reproduktiv periode og antallet af reproduktive perioder (Begon *et al.* 1996). Clutton-Brock *et al.* (1988) har vist at for krondyr er en væsentlig del af variationen i reproduktiv succes bestemt af længden på deres reproduktivt aktive livsperiode. Derfor er konsekvenser for alderen ved kønsmodning helt centralt i studiet af kohorteeffekter. Hos førstegangsfødende hinder af krondyr var sandsynligheden for at få en kalv negativt relateret til antallet af daggrader over 6°C i maj og juni i samme år som parringen (Langvatn *et al.* 1996) og aldersspecifik fekunditet var signifikant positivt relateret til gennemsnitstemperaturen i april og maj (Albon *et al.* 1992). I april er tilgængeligheden af højkvalitetsføde stadig så ringe, at en øget temperatur forøger energioptaget hos mødrene, mens der i maj og juni er rigeligt føde tilgængeligt og kvaliteten derfor er vigtigere end kvantiteten (Langvatn *et al.* 1996). Når hinder i Norge havde nået 4-årsalderen reproducerede de hvert år, og undslap dermed en kohorteeffekt i fekunditeten. Den maksimale vægt blev opnået i 5 års alderen (Langvatn & Albon 1986), og noget tyder på at alle kohorter havde en voksen vægt som lå over grænsen for reduceret fekunditet (Albon *et al.* 1992). For hjorte varierede den livstidsbaserede reproduktive succes mellem kohorter og var signifikant korreleret med april-maj nedbørsmængden i deres fødselsår (Rose *et al.* 1998). Kohorter af Soay sheep født efter vintre med højt NAO indeks havde større chance for at få lam som årsdyr og større fekunditet som 2-4 årige, mens tætheden i det år kohorten blev født havde negativ indflydelse på alder for kønsmodning (Forchhammer *et al.* 2001).

Jeg undersøger ikke reproduktiv succes hos rådyr direkte i dette speciale, men nylige studier bekræfter betydningen af kohorteeffekter for årlig og livstidsbaseret reproduktiv succes hos denne art (Kjellander 2000).

3.5. Mortalitet

Juvenil mortalitet har vist sig at være en mere følsom demografisk parameter for forringede kår end adult mortalitet i bestande af hovdyr (Gaillard *et al.* 1998b), hvilket understreger betydningen af forholdene tidligt i livet for resten af livshistorien. Antallet af dødfødte lam af rådyr viste sammenhæng med bestandstætheden i Norge (Andersen & Linnell 1998). Efter fødslen var mortaliteten størst i dyrets første fem levedage og udgjorde 50-80% af dødeligheden i de første tre måneder (Andersen *et al.* 1995). Derimod døde ingen lam i deres anden og tredje levemåned i gennem en fire års periode (Andersen *et al.* 1995). For to franske bestande af rådyr havde kohortevariation i lammedødeligheden forskellige konsekvenser. En bestand havde stabil størrelse, og kohortevariationen var begrænset til omfanget af lammedødeligheden. I den anden bestand med sommertørke og tæthedsafhængig begrænsning af bestanden var lammedødeligheden ligeledes høj i dårlige år, men vægten blandt de overlevende individer var ydermere signifikant lavere end blandt individer født i gode år. Denne forskel holdt sig igennem de to første vintre og medførte ringere chance for at overleve vinteren og reproducere tidligt (Gaillard *et al.* 1997). I Norge opgives et eller flere af lammene muligvis tidligt efter fødslen, hvis moderen ikke vurderer mulighederne for at kunne opfostre dem som gode. I Frankrig hvor kuldene generelt er mindre (Andersen *et al.* 1998), sker optimeringen af afkomsinvesteringen sandsynligvis i højere grad gennem differentieret ressourcetildeling til afkommene.

På trods af markante forskelle i forholdene mellem de to franske rådyrbestande var mortaliteten blandt voksne individer dog af samme omfang (Gaillard *et al.* 1993d). Hos norske krondyr var kalvenes overlevelseschance relateret til kropsvægten (Loison *et al.* 1999), mens voksenmortalitet var tilnærmet konstant mellem år (Loison & Langvatn 1998). Derimod varierede både kondition og kropsvægt signifikant mellem årene for voksne individer. Sæther (1997) foreslog, at det er kropsvægten som påvirkes af omgivelserne, og at betydningen for reproduktion og mortalitet medieres gennem ændringer i kropsvægten. Derfor forventes kropsvægten at fungere som en buffer for ændring i demografiske parametre (Gaillard *et al.* 1998b). Voksenoverlevelse blandt 2-8 årige krondyr på Rum var dog signifikant korreleret med temperaturen i april og maj i deres fødselsår (Albon *et al.* 1987), og sent fødte kohorter havde højere mortalitet som årsdyr og voksne (Rose *et al.* 1998). Dette kunne indikere at den norske bestand er i bedre forfatning end den skotske, noget som også fremgår af evnen til at kompensere en lav fødselsvægt blandt norske krondyr, som nævnt ovenfor.

Kohorter af Soay sheep på øen Hirta i Skotland født efter vintre med højt NAO indeks havde større dødelighed som juvenile, men mindre som 2-4 årige (Forchhammer *et al.* 2001). Denne umiddelbare modsætning kan skyldes, at et højt NAO indeks påvirker mødre og fostre i negativ retning i graviditeten og dermed produceres små afkom. Til gengæld oplever lammene en lang periode med højkvalitetsføde efter fødslen, som kommer dem til gode gennem moderens øgede mælkeproduktion. En sådan effekt på vegetationen er fundet som en konsekvens af højt NAO indeks i Norge (Post & Stenseth 1999). Den fulde forståelse af dette samspil af faktorer bremses dog af resultater fra Rum, som klimatisk minder om Hirta. Her kunne resultater på vækst og fekunditet bedst forklares hvis højt NAO indeks giver kraftig fostervækst men kort periode med tilgængelighed af højkvalitetsføde i foråret efter fødslen (Post & Stenseth 1999). Disse resultater illustrerer vigtigheden af at kunne kvantificere aldersspecifik mortalitet for at forstå den observerede variation i livshistorietræk indenfor arten. I Paper III diskuterer jeg betydningen af en differentieret udvandring eller mortalitet mellem individer med forskellig kondition for tydeligheden af kohorteeffekter hos rådyr.

3.6. Seksuel størrelsesdimorfisme

Hos polygyne arter opnår hanner gennem seksuel selektion på stor kropsstørrelse en reproduktiv fordel ved hurtig vækst frem til alderen for kønsmodning, mens hunner forventes at prioritere kondition højt i denne periode (Stearns 1992). Hos krondyr i Norge, som i de sidste 30 år har oplevet stadigt varmere klima, har hjortene vist sig at vokse hurtigere og større end tidligere, mens størrelsen på hinderne er blevet mindre. Dette har forstærket en størrelsesdimorfi som i udgangspunktet var skabt af seksuel selektion (Post *et al.* 1999a). For bighorn sheep ved lav tæthed udviklede størrelsesdimorfien mellem kønnene sig dog først efter dieperiodens afslutning, og variationen kunne derfor i mindre grad tilskrives en kohorteeffekt (Festa-Bianchet *et al.* 1996). Hos rådyr er størrelsesdimorfien lille (Gaillard *et al.* 1993a, Andersen *et al.* 1995), hvilket kan forventes ud fra den ringe grad af polygyni. Potentialet for kohorteeffekter i denne karakter for rådyr forventes derfor at være begrænset.

3.7. Kønsratio

Blandt polygyne arter er variationen i livstidsbaseret reproduktiv succes større for hanner end for hunner, og dominante mødre i god stand forventes derfor at producere flere hanner end hunner i afkommet, ifølge en hypotese fremsat af Trivers og Willard (se f.eks. Clutton-Brock *et al.* 1984, Hewison & Gaillard 1999). Højt NAO indeks (streng vinter) i de senere år har imidlertid ført til kuld med flest hanner blandt norske krondyr (Post *et al.* 1999b), hvilket ikke kan forklares ud fra denne hypotese. Forchhammer (2000) har foreslået, at tidspunktet for miljøstress er afgørende for kønsspecifik overlevelseschance i fosterstadiet. Hanner vokser mest i slutningen af fosterstadiet (Post *et al.* 1999b), og forventes derfor at have lavere overlevelseschancer ved miljøstress oplevet sent i fosterstadiet. Hunner har derimod størst væksthastighed tidligt i fosterstadiet (Post *et al.* 1999b), og miljøstress i denne periode sandsynliggør dermed en overvægt af hanner i afkommet. Høj tæthed medfører imidlertid en lavere andel af hanner i afkommet (Kruuk *et al.* 1999), hvilket umiddelbart modsiger ovenstående. Er miljøpåvirkningen på moderen en effekt på kønsspecifik mortalitet efter befrugtningen, mens moderens kondition og dominans er af betydning for afkommets kønsratio ved befrugtning, kan man dog alligevel forklare denne tilsyneladende inkonsistens.

Hos rådyr, som er mindre polygyne, har ”local resource competition” hypotesen om kønsratiovariation været grundlag for en række studier (Wauters *et al.* 1995, Hewison & Gaillard 1996, Hewison *et al.* 1999a). Den forudsiger, at mødre som oplever dårlige forhold producerer flest hanner, fordi de forlader moderen før hunner, hvilket mindsker konkurrencen om føde. Der er ikke enighed om hvorvidt Trivers og Willard hypotesen er forklarende for observationerne hos rådyr, men variation i afkommets kønsratio har betydning for forståelsen af livshistoriekonsekvenser af kohorteeffekter.

3.8. Opsatsudvikling

Ifølge handicapprincippet om interseksuel selektion (bl.a. beskrevet i Cockburn 1991), forventes hanner med veludviklede sekundære kønskarakterer (f.eks. gevirer og horn hos hovdyr) at opleve højere reproduktiv succes end hanner med mindre veludviklede træk. Graden af asymmetri i opsatsen hos bukke var korreleret med kropsvægt for forskellige bestandstætheder, og for bukke med samme vægt var der negativ sammenhæng mellem opsatsstørrelse og graden af asymmetri (Pélabon & Breukelen 1998). Hvis en stor og symmetrisk opsats udgør en reproduktiv fordel må dets udvikling være betinget af en afvejning af ressourcer med andre energiudgifter forbundet med overlevelse og reproduktion. Unge dyr med store opsatser forventes derfor at have det største overskud af ressourcer, mens bukke i perioden med højest reproduktivt potentiale – typisk midt i livet

(Strandgaard 1972, Clutton-Brock *et al.* 1988) med små opsatser forventes at være i dårligst stand. Denne hypotese undersøges i paper III.

Gennem adfærdsstudier har Wahlström (1994) fundet at etårige bukke med store opsatser oplevede mere fysisk aggression fra adulte bukke end etårige bukke med små opsatser. Da energiudgiften dermed er størst for bukke som udviser høj fænotypisk kvalitet kan dette være med til at reducere deres kondition gennem fysisk stress eller, som Wahlström (1994) foreslår, øge udvandringen blandt etårige med store opsatser. Dette fungerer da som en modificeret weeding out effekt. En eventuel kohorteeffekt i opsatsudvikling må derfor forventes at være tydeligst, hvis man inddrager individer, som er udvandret fra bestanden.

4. Konditionsindeks

En lang række konditionsindeks har været anvendt til at kvantificere kondition hos hovdyr (Hanks 1981, Huot 1988). Nyrefedtindeks og benmarvens fedtprocent er traditionelle mål, men der er stadig uenighed om i hvor stor grad de beskriver fitnessforskelle mellem individer (se f.eks. Anderson *et al.* 1990). Huot (1988) skelner blandt andet mellem indeks som er følsomme overfor sæsonvariation i kondition, og indeks som integrerer hele vækstperioden. Mål på skelettet er ikke følsomme overfor sæsonvariation og er derfor specielt velegnede som indeks for vækstforhold tidligt i livet.

Mål på underkæbebenet er blevet brugt i en række hjortestudier som et fitnessrelateret indeks (Frampton & Nugent 1992, Bertouille & Crombrugghe 1995, Hewison *et al.* 1996, Post *et al.* 1997). Fordelen med mål på skelettet er at disse færdigudvikles relativt tidligt i livet og kraniet antages at være noget af det først færdigudviklede (Langvatn *et al.* 1977). Den anteriore del af kæben hos krondyr har vækstprioritet over den posteriore del under fostervæksten og det første år efter fødslen (Langvatn & Post *in prep.*). Post *et al.* (1997) har brugt forholdet mellem længden på den anteriore del og total kæbelængde (mandibular skeletal ratio) som et indeks for vækstforholdene oplevet i det første leveår. Et sådant indeks gør det muligt at vurdere forholdene i en kohortes fødselsår ud fra kæber fra voksne individer. Afhængigt af evnen til at kompensere for reduceret vækst tidligt i livet, kan kropsstørrelse og relaterede livshistorietræk som alder ved kønsmodning og juvenil mortalitet blive påvirket. For eksempel fandt Clutton-Brock *et al.* (1988) en signifikant sammenhæng mellem kæbelængden og kampegenskaberne hos hjorte. Dette skyldes sandsynligvis at kæbens længde er relateret til voksen kropsstørrelse, hvilket jeg undersøger i paper III.

Residualerne fra regressionen mellem kropsvægt og skeletstørrelse er blevet brugt som konditionsindeks i flere populationsbiologiske undersøgelser (Bandy *et al.* 1956, McEwan & Wood 1966, Loison & Langvatn 1998). En stor kropsvægt i forhold til skeletstørrelse forventes at indikere et højt fedtindhold. For hinder antages dette at være afgørende for høj reproduktionsevne (Loison & Langvatn 1998). I paper III undersøger jeg sammenhængen mellem vækstudviklingen tidligt i livet og kondition hos voksne individer.

5. Aldersbestemmelse

Indenfor populationsbiologien er studiet af kohorteeffekter specielt afhængigt af sikker aldersbestemmelse hvis man analyserer data fra individer, som ikke er observeret gennem hele livet. Hvis alderen vurderes en reproduktiv periode forkert, placeres individet i en forkert kohorte, og analysen svækkes. Specielt i studiet af langtlevende arter, såsom større pattedyr, er præcis aldersbestemmelse vigtig. Behovet for pålidelige aldersestimater hos pattedyr har medført udviklingen af en lang række metoder (se en oversigt i Morris 1972). To overordnede fremgangsmåder har fået speciel opmærksomhed, i forbindelse med aldersbestemmelse af hovdyr. Den ene baserer sig på studier af tandcement og sekundær dentin, som lægger sig i lag rundt om roden (cement) eller i hulheden inde i molaren (sekundær dentin). Den anden udnytter graden af slitage på kindtænderne, og kvantificerer dette som et mål for individets alder.

5.1. Tandcement

Princippet med at studere årringslignende strukturer i tænder blev først udviklet til aldersbestemmelse af søelefant (*Mirounga leonina*) af Laws (1952). Han argumenterede for at cyklisk variation i dannelse af tandcement var korreleret med den årlige metaboliske cyklus, og at antallet af linjer derfor svarede til dyrets alder i år. Hos små pattedyr og rovdyr har man oftest brugt snit af fortænder fra afkalkede tænder. Disse farves, monteres på objektglas og undersøges i mikroskop (Morris 1972). Cementlinjer hos hovdyr er oftest blevet studeret i delte blankslebne kindtænder, typisk den første molar (Fancy 1980). Metoden er justeret til anvendelse hos en lang række hovdyrarter: elg (*Alces alces*) (Sergeant & Pimlott 1959, Wolfe 1969), pyrenæisk gemse (*Rupicapra pyrenaica parva*)

(Pérez-Barberia & Fernandez-López 1996), grønlandsk rensdyr (*Rangifer tarandus groenlandicus*) (Miller 1974), dådyr (Moore *et al.* 1995), "mule deer" (*Odocoileus hemionus*) (Erickson & Seliger 1969, Erickson *et al.* 1970), krondyr (Lowe 1967, Mitchell 1963, 1967, Douglas 1970, Almasan & Rieck 1970), rensdyr (Reimers & Nordby 1968), rådyr (Almasan 1972, Szabik 1973, White 1974, Aitken 1975, Ashby & Henry 1979, Ueckermann & Scholz 1986, Hrabe & Koubek 1987, Cederlund *et al.* 1991b, Kovács & Felek 1991) og "white-tailed deer" (*Odocoileus virginianus*) (Gilbert 1966, Ransom 1966, Gilbert & Stolt 1970, Lockard 1972).

Reimers & Nordby (1968), Lockard (1972), Cederlund *et al.* (1991b) og Moore *et al.* (1995) er imidlertid de eneste af ovennævnte studier som baserer sig på mere end 25 individer med kendt alder, og de beskriver varierende succes med at tildele dyrene den rigtige alder ved hjælp af cementlinjeteknikken. Rådyr har vist sig som specielt vanskelig at aldersbestemme, idet tydelige linjer ofte ikke er synlige (Borg 1970, Grue & Jensen 1979, Kaluzinski 1982, Cederlund *et al.* 1991b, Paper I). Selvom et nyt studie af amerikanske hovdyrarter giver tandcementteknikken noget medhold, bekræfter det også, at nogle arter og bestande er vanskelige at aldersbestemme med denne teknik (Hamlin *et al.* 2000). Den udbredte brug af metoden på trods af vanskeligheder med at bekræfte dens pålidelighed kan skyldes det objektive resultat man får ved at tælle et antal linjer, også selvom det ikke svarer til alderen i år. Der er altså brug for en aldersbestemmelsesmetode, som er objektiv og pålidelig, og som kan bestemme alderen på en stor del af en bestand. Denne metode må, som Dapson (1980) påpeger, være udviklet på baggrund af studier af individer med kendt alder. Det er dette behov som jeg prøver at dække ved den metode jeg præsenterer i paper II.

På trods af de mange studier af tandcement er årsagen til deres dannelse endnu ikke klarlagt (Grue & Jensen 1979, Lieberman 1994). Det er generelt accepteret at afsætning af tandcement er en vækstproces, hvor materialet reflekterer lyset ved langsom vækst og er gennemsigtigt ved hurtig vækst (Lieberman & Meadow 1992). Bestande som oplever kraftig sæsonvariation i ressourcetilgængeligheden forventes derfor at have de tydeligste linjer. Mange studier som ikke har haft succes med metoden har ofte brugt manglende sæsonvariation som argument (f.eks. Fruzinski *et al.* 1982, Moore *et al.* 1995). McCullough (1996) rapporterede at synligheden af cementlinjer forsvandt ved lav bestandstæthed, og argumenterede for at ressourcebegrænsningen blev mindre og derfor ikke svingede tilstrækkeligt til at skabe årstidsvariation i tandcementvæksten. Denne hypotese er desværre aldrig blevet testet på individer med kendt alder. Det mest alvorlige problem er dog, at nogle studier har rapporteret at cementlinjer deler sig i to eller mødes nogle steder i tandrødderne (Rice 1980). Dette sætter spørgsmålstegn ved den grundlæggende antagelse at der er sammenhæng mellem antallet af linjer og individets alder i år. Denne antagelse kan kun bekræftes ved at lave blindtests på individer med kendt alder, som jeg har gjort i paper I.

5.2. Tandslid

Hos drøvtyggere har den vedvarende nedslidning af kindtænderne gennem lang tid været brugt som et mål for alderen (Robinette *et al.* 1957, Quimby & Gaab 1957). Når den lyse emalje er slidt ned bliver det mørkere dentin synligt og der opstår karakteristiske mønstre i kindtænderne. Disse mønstre ændrer sig med alderen efterhånden som tænderne bliver mere og mere slidt. Det har været udbredt at bruge en ”ekspert” til at forestå aldersvurderingen, men dermed er aldersbestemmelsen baseret på erfaring (Kovács & Felek 1991). Alternativt har man brugt et såkaldt ”jaw board”, som er en samling af kæber i forskellige aldre, hvor man har kendt den nøjagtige alder på hvert enkelt individ. Dette har da fungeret som et søgebillede man har kunnet sammenligne med slidmønstrene på kæber med ukendt alder (Cederlund *et al.* 1991b). Begge fremgangsmåder er tvivlsomme på grund af personafhængigheden.

Flere faktorer har været hævdet at influere på graden af slid så som individuelle forskelle i hårdheden af tandemaljen (Kierdorf & Becher 1997), forskelle i fødesammensætning mellem individer eller bestande (Morris 1972) eller fødeknaphed, som resulterer i at vegetation bides tættere ved jordoverfladen og dermed øger tandsliddet ved indtagelse af mineralske jordpartikler (Skogland 1988). Ikke desto mindre har kun et enkelt studie nærmet sig disse hypoteser ved at sammenligne tandsliddet mellem forskellige bestande ud fra individer med kendt alder (Hewison *et al.* 1999b).

Dapson (1980) diskuterede statistiske og metodiske udfordringer ved vurdering af aldersbestemmelsesteknikker, og understregede at kendt alder materiale er nødvendigt for at kunne vurdere en tekniks præcision. Desuden er objektive kriterier nødvendige for at eliminere personafhængigheden. Dette har været forsøgt ved at kvantificere sliddet i forskellige målbare indeks: tandhøjde (Severinghaus 1949, Robinette *et al.* 1957, Lowe 1967, White 1974, Aitken 1975, Ashby & Henry 1979, Cederlund *et al.* 1991b, Fandos *et al.* 1993, Moore *et al.* 1995, Morrison & Whitridge 1997, Hewison *et al.* 1999b) ”molar tooth ratio” (summen af bredden på buccale tandrygge/summen af højden på linguale tandrygge) (Robinette *et al.* 1957, Erickson *et al.* 1970) og slidindeks (maksimal bredde på dentinbåndet på den mesiobuccale slidflade/total bredde af kronen) (Kierdorf & Becher 1997). Alle disse indeks udnytter mål på enkelte tænder, hvilket antyder, at risikoen for alvorlige måleusikkerheder ikke kun er teoretisk, specielt når man tager problemet med at definere målet helt præcist i betragtning. Mitchell (1967) brugte vægten på den molare krone og argumenterede for at dennes vægt vil aftage med alderen efterhånden som den blev slidt ned, mens roden vil øge i vægt på grund af afsættelse af tandcement. Denne metode lider dog under samme afhængighed af ekstrem præcision i præparering og vejning af prøverne. Quimby & Gaab (1957) og Brown & Chapman (1990, 1991) baserede deres aldersestimater på objektivt beskrevne slidkarakterer på individuelle tænder, som enten fandtes eller ikke fandtes i hvert enkelt individ, hvorved måleusikkerheden elimineredes. Desværre brugte de ikke et frekvensbaseret aldersbestemmelsessystem, hvilket muligvis forklarer den begrænsede præcision i systemet. I paper II kvantificerer jeg tandslid ved hjælp af den frekvens hvormed individuelle slidkarakterer forekommer i hver enkelt aldersklasse og undgår dermed personafhængigheden. Dette udnyttes til udvikling af en objektiv metode til aldersbestemmelse af rådyr ud fra tandslid på kindtænderne.

6. Afrunding

En række aspekter af rådyrets biologi er blevet behandlet i denne introduktion. Sammenfattende kan man sige, at kategoriseringen som income breeder og den høje afkomsinvestering blandt hovdyr indikerer en stor afhængighed af forholdene under graviditet og opfostring for dannelsen af kohorteeffekter hos rådyr. Potentialet for at variere kuldstørrelsen efter fødslen kan reducere kohorteeffekten gennem differentieret afkomsinvestering, men det er usikkert hvor udbredt dette er. Fødselsdatoen er nøje synkroniseret med brunsten og udviser derfor ikke markant kohortevariation, mens fødselsvægten varierer mellem år i flere bestande. Vækstraten er afhængig af kuldstørrelsen, men påvirkes ikke af tætheden, og længden af planternes vækstsæson kan være hovedårsagen til dannelsen af kohorteeffekter hos rådyr.

Evnen til at kompensere en ringe vækst tidligt i livet kan være høj hos rådyr på grund af den ringe grad af polygyni, men ved ressourcebegrænsning er der observeret kohorteeffekter i kropsvægten. Vægten menes at blive påvirket før overlevelse og reproduktion når forholdene er dårlige, men alligevel er der fundet tydelige kohorteeffekter hos rådyr i overlevelseschance og reproduktiv succes. Ringe grad af polygyni mindsker omfanget af seksuel størrelsesdimorfisme og den forventede mindre variation i livstidsbaseret reproduktiv succes blandt bukke reducerer ydermere fordelen ved en overvægt af hanner i afkommet.

Underkæben udvikles tidligt hos hovdyr og specielt længden af den forreste del forventes at afspejle vækstforholdene tidligt i livet, og mål på underkæben af voksne dyr kan derfor bruges som et indeks for opvækstvilkårene tidligere i livet. Sammenholdt med mål for kondition ved individets død kan man på denne måde vurdere evnen til at kompensere for reduceret vækst tidligt i livet. Denne type undersøgelser kræver naturligvis en præcis aldersbestemmelsesmetode. Tandcementundersøgelser giver brugbare resultater i nogle tilfælde, men ikke i andre. Aldersbestemmelse ud fra tandslid har hidtil været afhængigt af undersøgerens erfaring, men den større tilgængelighed af materiale fra individer med kendt alder muliggør udviklingen af metoder, som sikrer objektive aldersestimater.

Denne gennemgang af den teoretiske baggrund for mine undersøgelser har vist, at der er væsentlige forskelle mellem hovdyrarter, men også en betragtelig variation mellem bestande af samme art. Rådyrets livshistorie er speciel blandt hovdyrene med den særegne reproduktive cyklus, evnen til jævnligt at få op til tre afkom i hvert kuld og den ringe størrelse blandt hovdyr i tempererede områder. Dette særpræg har betydning for forståelsen af kohorteeffekters rolle og må tages i betragtning, når man studerer rådyrets økologi.

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Paper I

Failure of the molar cementum ageing technique on known age Danish roe deer (*Capreolus capreolus*)

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Running head: Failure of the cementum ageing technique

Introduction

The counting of dental cementum layers as an ageing technique was first described in studies of marine mammals (Laws 1952) and has since been refined and used to age an increasing number of mammalian species (Morris 1972). In small mammals, incisors or molars have most frequently been decalcified, sliced on a microtome and stained to produce microscope slides for examination (Fancy 1980). Cementum layers in larger mammals like ungulates have more frequently been studied in polished halved first molars using a dissecting microscope (e.g. Stallibras 1982). White (1974) and Aitken (1975) described this technique as reliable for use on roe deer (*Capreolus capreolus*). However, as inferred by Dapson (1980) evaluation of age estimation techniques must be based on known age material. Aitken (1975) used only nine known age individuals as reference and White (1974) did not use any.

Grue & Jensen (1979) reviewed early literature on the background for the formation of incremental lines and concluded that no single factor could cause the formation, as related individuals exhibited very different visibility of lines. Recently, Lieberman (1994) addressed the issue again, but it still awaits a fulfilling explanation. It is generally accepted that the appearance of cementum material varies over time; deposition of cementum is a growth process wherein the cementum is opaque during slow growth and translucent during rapid growth (Lieberman & Meadow 1992). Therefore, regular seasonal changes in overall growth rate, caused for example by seasonal environments, may lead to the formation of cementum lines (Grue & Jensen 1979). Unfortunately, this hypothesis has not yet come to test using known age animals, and for roe deer a growing body of evidence exists, indicating that the method is not generally applicable (Borg 1970, Grue & Jensen 1979, Kaluzinski 1982, Cederlund *et al.* 1991). However, the most serious problem is that studies have reported cementum lines sometimes splitting into two or fusing together in some areas of the root (Rice 1980). This questions the underlying assumption of correspondence between age in years and number of incremental lines.

Since most studies, analysing cross-sectional data on populations of ungulates, uses age estimates based on the cementum ageing technique, it is surprising that the method is not better confirmed. The only way to reach a reliable conclusion is by performing blind tests on material of known age animals, which so far have been scarce. Furthermore, in order to age individuals with confidence the period of formation of new lines must be known (Grue & Jensen 1979). Here I use jaws from 83 roe deer of known age obtained from a geographically limited area to investigate at what time of year cementum layers form and test the reliability of the cementum ageing technique.

Materials and methods

A total of 83 first molars M1 (see Langvatn 1977) was obtained from jaws of roe deer with known age from Kalø, Denmark. All animals were ear tagged as fawns and recovered as dead (Strandgaard 1972a). Sex and date of shooting was recorded and individuals were assigned to whole year age classes with first of June as date of birth, corresponding with parturition dates observed at Kalø (Strandgaard 1972b). The molars were cut in halves perpendicular to the axis of the jaw while *in situ*, using a fine hack saw. The cut was made posterior of the molar arch between the two roots of the tooth. Thereby, the cementum in the molar arch was left undamaged on the anterior part of the tooth. Abrasive papers with different grain sizes were used to polish the cut surface (finest grain size was p1200). The pad of molar cementum was examined using a dissecting microscope under reflecting light.

If cementum layers formed before the first of June, where age classes were set to shift, individuals that died in the period between formation and the first of June, would have been overestimated by one year. Therefore, an increased number of overestimated individuals that died in the period before June would indicate that cementum layers form right before this period.

A sub sample of 23 jaws was used in blind tests of cementum line counts on two test persons. The age composition was not known to the test persons, but they were presented with a picture of cementum layers and allowed to examine five molars before assigning the first age estimate. Deviations from known age were calculated for estimates from each blind test and average deviation was compared for difference in accuracy between test persons using t-test. Correlation analyses were performed for each blind test between known age and blind test estimates and between deviations from known age in estimates from the two blind tests. A high degree of correlation between estimates from blind tests would indicate that test persons agreed on the number of lines in the molars of the sample, even if estimates did not correspond with known age.

Results

The number of cementum lines was unclear in most samples and impossible to count in several instances. For individuals that died in March through May more were overestimated than correctly aged whereas this was fewer in the rest of the year (figure 1). When individuals were grouped in age classes using first of March as date dividing separate age classes, the result was improved considerably (figure 2).

The degree of correlation between blind test estimates and known age was low for both test persons (figure 3), and the equally low correlation between deviations from known age in estimates from the two blind tests show that the same individuals are assigned to different age classes by the two test persons (figure 4). Furthermore, the average deviation did not differ between test persons (t-test: $t_{44} = 0.348$, $p = 0.73$).

Discussion

Formation of cementum layers during the winter will lead to a general overestimation of individuals in the months preceding the first of June where age classes were set to shift when using the cementum ageing technique. As a larger proportion of individuals were in fact overestimated in March through May this indicates that cementum layers may form in February or March, which corresponds with the months, were roe deer forage is of low quality (Selås *et al*. 1991, Mysterud *et al*. 1999).

Incremental lines in dental cement are believed to form as a response to energy constraints usually experienced during winter (Grue & Jensen 1979). They appear as dark bands in reflected light and are usually not visible until some lighter cementum forms on the outside (Lieberman 1994). It is in agreement with this hypothesis that my results suggest February and March to be the months where the new line becomes visible. However, the low percentage of correctly aged individuals cannot be ignored, and may have influenced the results on month of formation of cementum layers. Three proximate causes explain why the use of the cementum ageing technique proved unsatisfying results:

a) No lines were clear in the dental cement of some individuals and obviously, no age estimate could be made. The sample size reduction influences the power of statistic testing, but not the reliability of the result.

b) The number of lines in the dental cement was clear in some individuals, but may not have corresponded with age in years, and a wrong reading was taken.

c) The number of lines in the dental cement was unclear in some individuals. Either no estimate was made or the estimate may have been wrong.

Two different causes can therefore explain the deviation between true and estimated age based on the cementum ageing technique. The number of layers may not correspond with the age of the animal in years. This can be caused either by ”rutting lines” formed by slower growth rate during the energetically demanding rut (Grue & Jensen 1979) or by physical damage of the tooth during life, or by cementum layers not forming every year. This implies that the method is not reliable, regardless of the observer. Alternatively, the ability to recognise samples where the estimate should be considered unreliable is not adequate, indicating that deviation is caused by the selection criteria or the experience of the observer.

In order to eliminate observer bias, several observers can evaluate the same samples, thereby producing blind tests. If all observers agree on individual estimates, but these do not correspond with known age, the first cause explains the result. In contrast, if some blind tests produce accurate results while others do not, the first cause can be ruled out. The low degree of correlation in deviations from known age between the blind tests in this study clearly illustrates that different number of lines were counted by test persons and that lines were unclear in the random sample (figure 4).

However, some drawbacks of blind testing in the cementum ageing technique do exist. Cementum layers can be more or less visible in different parts of the molar pad, and finding the clearest view of the cementum lines involves successive rounds of polishing and examination under dissecting microscope. During this process, it is possible to destroy what would later appear to have been the clearest part of the molar pad. The final visible surface may indicate a different number of lines, than what had been visible at an earlier stage. Hence, blind tests suffer from only testing visibility of cementum lines in the final visible surface. Furthermore, inexperienced test persons have not developed a detailed “search image”, thereby reducing the chance of a good estimate.

The poor accuracy obtained in this study seriously questions the applicability of the cementum ageing technique on roe deer. I cannot exclude that the number of cementum layers does not correspond with age in years, because the blind tests produced very different results. However, this could also have been caused by unclear number of cementum layers. Indeed the low percentage of correctly aged individuals confounded the evaluation of these two different causes in explaining the failure of the technique in this study.

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Figure legends

Figure 1

The number of individuals overestimated, correctly aged and underestimated by the cementum ageing technique according to month of death.

Figure 2

The percentage of correctly aged individuals, incorrectly aged individuals and individuals where cementum lines were uncountable are presented using either first of June or first of March as grouping date for age classes.

Figure 3

Correlation between known age and the number of cementum lines counted by A) 1. test person and B) 2. test person. Age classes are set to shift at first of March.

Figure 4

Correlation between deviations of the number of cementum lines counted from known age for 1. test person and 2. test person. Deviations are based on age classes shifting at first of March.

Figure 1

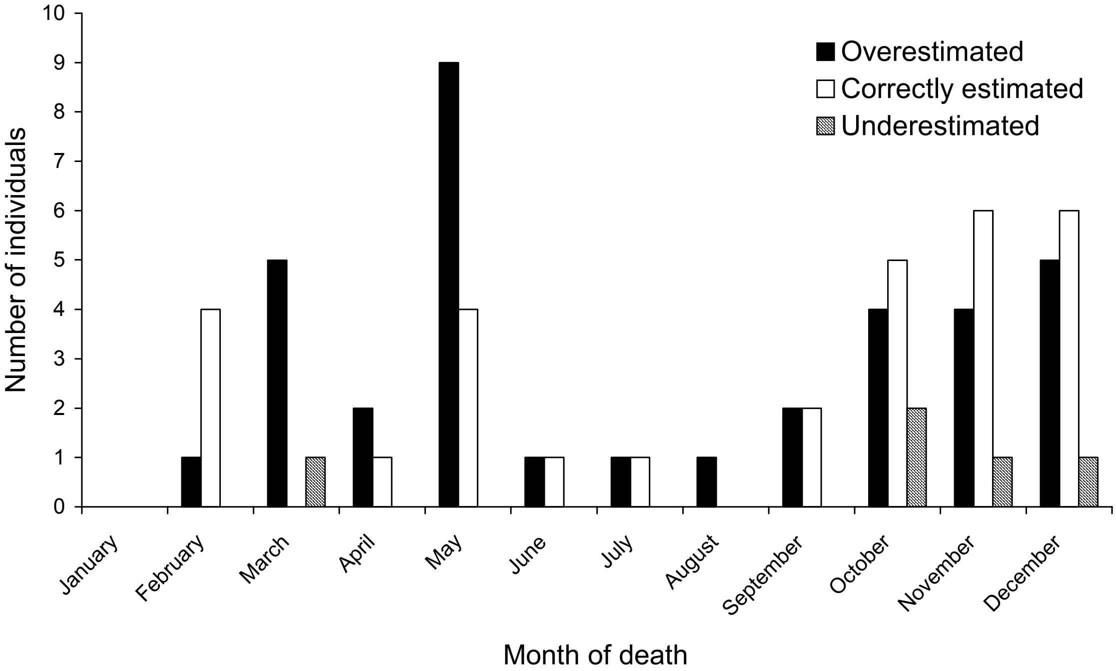

Number of individuals
10
9
8
7
6
5
4
3
2
1
0
Overestimated
Correctly estimated
Underestimated
January
February
March
April
May
June
July
August
September
October
November
December
Month of death

Figure 2

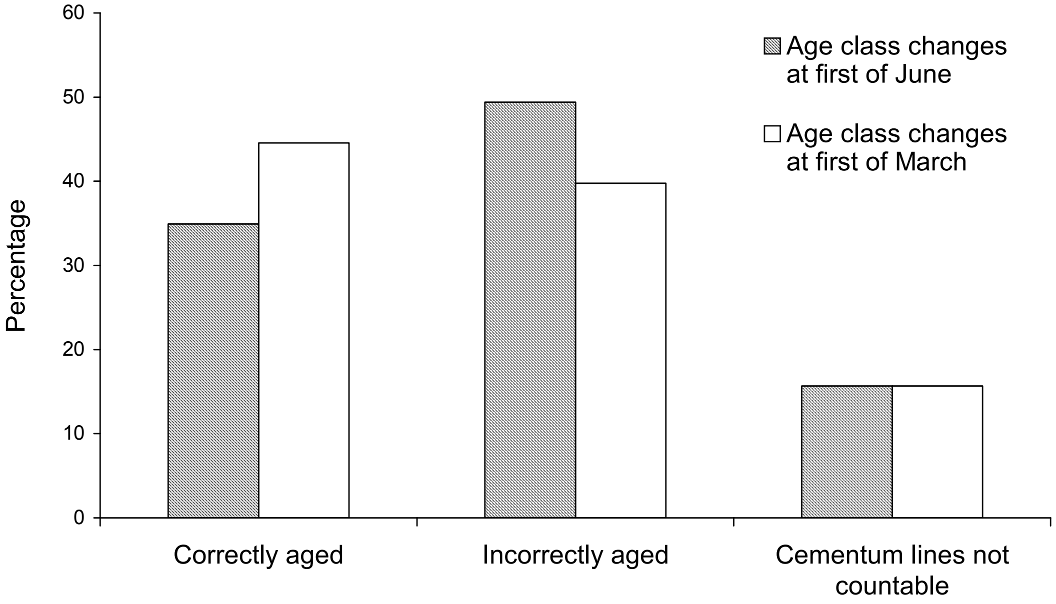

60
50
40
30
20
10
0
Percentage
▨ Age class changes at first of June
☐ Age class changes at first of March
Correctly aged
Incorrectly aged
Cementum lines not countable

Figure 3

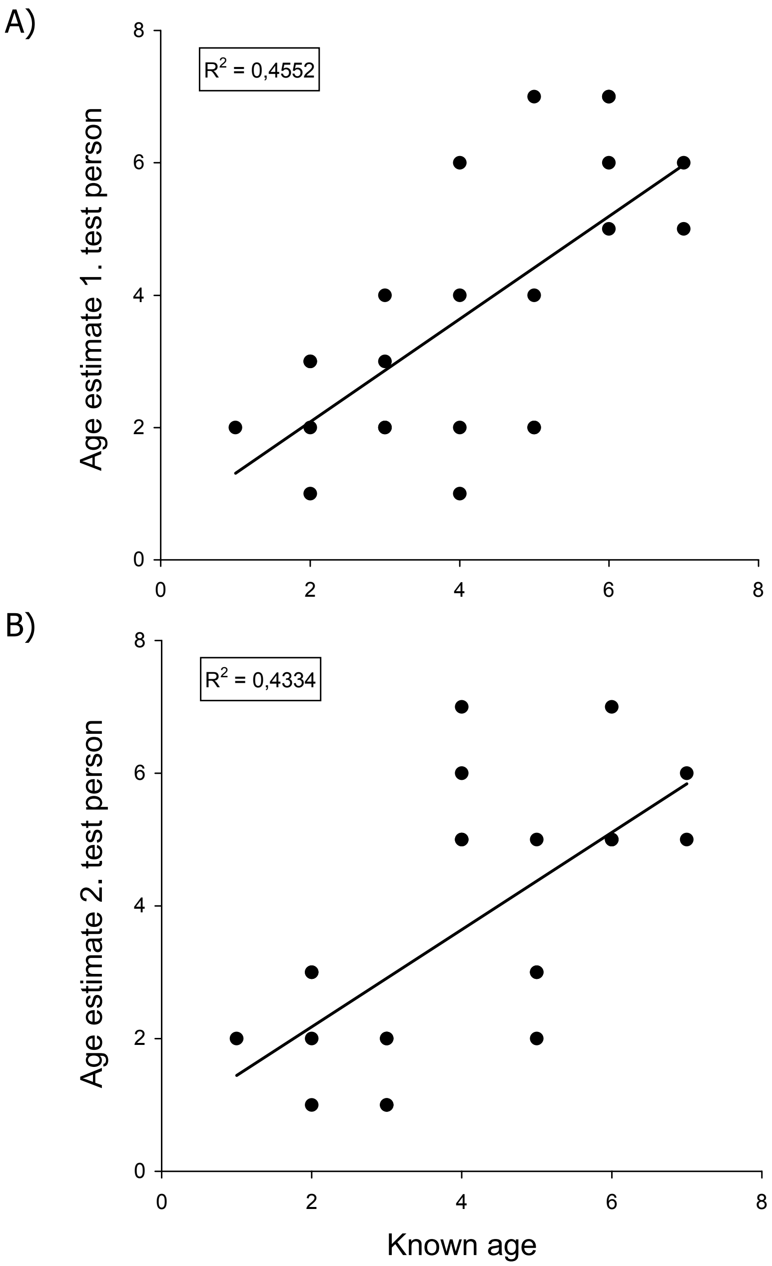
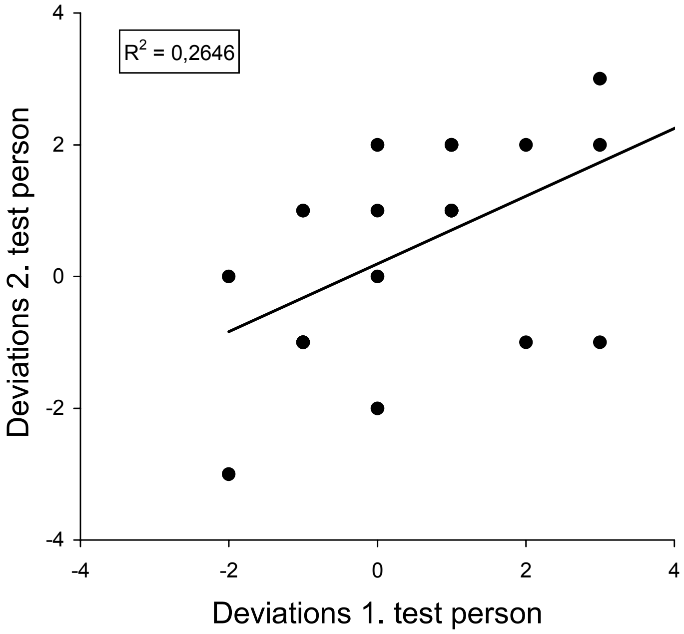

A)
R² = 0,4552
Age estimate 1. test person
0
2
4
6
8
0
2
4
6
8
B)
R² = 0,4334
Age estimate 2. test person
0
2
4
6
8
0
2
4
6
8
Known age

Figure 4


R^2 = 0,2646
4
2
0
-2
-4
-4
-2
0
2
4
Deviations 2. test person
Deviations 1. test person

Paper II

Age determination in roe deer. A scoring system based on objective wear characters of populations in contrasting environments

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Running head: Objective age determination in roe deer

Abstract

Observer bias is a serious drawback of age determination methods based on the general wear pattern of ruminant cheek teeth. However, the more commonly used alternative of cementum annuli counting has produced various degrees of success in roe deer (*Capreolus capreolus*). Here, I present a novel, simple, and objective method for ageing roe deer based on 493 jaws from individual roe deer of known age. The method uses present/absent wear characters on permanent molars and premolars incorporated in a scoring system and provides the correct age of 88 % of all animals 3 years old or younger. Precision in the estimate was influenced by the choice of wear characters, indicating that the ability to evaluate the descriptive power of individual wear characters strengthens the method. The data originate from two Danish populations of roe deer exposed to contrasting environments, but no differences in wear rates were found either between populations or between sexes. The development of the permanent cheek teeth took place between March and July in the second calendar year, which enabled the precise age determination of all individuals with deciduous premolars. These results show that by using the right set of wear characters, age determination based on tooth wear can provide useful data to population studies. This is in contrast to most other studies on tooth wear in ruminants, and the causes for this are discussed.

Keywords

Molar wear patterns, objective age criteria, *Capreolus capreolus*, age determination

Introduction

Knowledge of the age of animals is an important prerequisite to understand life history evolution and population dynamics (Stearns 1992, Charlesworth 1994). For example, the benefit of investing resources in either growth or reproduction is dependent on life stage or age (Promislow & Harvey 1990). Since this choice of investment influences survival and reproduction, it has consequences for population dynamics (Gaillard *et al.* 1998). Obviously, in the study of long living, iteroparous animals like large mammals, accuracy in age determination is of vital importance.

The need for reliable age determination of mammals has developed a number of different methods (see Morris 1972 for a review). However, since animals of known age so far have been scarce, it has proved a great challenge to evaluate the accuracy of these methods (Dapson 1980). In ruminants, the progressive wearing of the cheek teeth has been used as a measure of age for several decades (Robinette *et al.* 1957, Quimby & Gaab 1957). This method has been criticised because variations within and among populations in molar wear rates confound precise age determination. The causes of this variation are believed to be individual differences in hardness of tooth enamel (Kierdorf & Becher 1997), individual or population differences in diet composition (Morris 1972) or food shortages, resulting in animals eating vegetation closer to the ground and thereby increasing intake of mineral soil causing higher wear rates (Skogland 1988). However, so far only one study has approached these hypothesises by comparing progressive dental wear between populations of known age roe deer (Hewison *et al.* 1999).

To avoid observer bias in age estimation techniques, metric variables have been used to quantify dental wear: tooth height (e.g. Moore *et al.* 1995), molar tooth ratio (sum of width of buccal crests/sum of lingual cusp heights) (e.g. Erickson *et al.* 1970), wear index (maximal width of the dentine band on the mesiobuccal cusp/total width of crown)

(Kierdorf & Becher 1997), and weight of molar root and crown (Mitchell 1967). However, all these indices are dependent on precise measurement and the potential for measurement errors may not be negligible, considering the difficulties in defining these measurements.

Quimby & Gaab (1957) and Brown & Chapman (1990, 1991) based their age assessment on objectively described characters being either present or absent, and form a promising alternative, but the descriptive power of individual characters was not evaluated, which may explain the moderate accuracy achieved.

Finally, the cementum annuli counting (CAC) method first developed for elephant seal (*Mirounga leonina*) by Laws (1952) has been adjusted for use on most ungulate species e.g. moose (*Alces alces*) (Sergeant & Pimlott 1959), fallow deer (*Dama dama*) (Moore *et al.* 1995), reindeer (*Rangifer tarandus*) (Reimers & Nordby 1968) and roe deer (Aitken 1975). This method may be termed objective, because it relies on the counting of lines in the dental cement. However, few studies have investigated the applicability of the CAC-method using more than 25 individuals of known age (Reimers & Nordby 1968, Lockard 1972, Cederlund *et al.* 1991, Moore *et al.* 1995). In addition, these studies report varying success in assigning animals to their known age class. A recent paper by Hamlin *et al.* (2000) does give some support to the CAC-method for American ungulates, but at the same time confirms the difficulties in ageing some species and populations. Roe deer have been particularly difficult to age using the CAC-method (Borg 1970, Grue & Jensen 1979, Kaluzinski 1982, Cederlund *et al.* 1991, paper I).

Here I develop a scoring system applicable for ageing roe deer by using objective present/absent characters on molars and premolars as quantification of dental wear. The data embrace 493 individual roe deer of known age from two Danish populations exposed to contrasting environments, enabling the comparison of wear rates between populations and between sexes.

Study areas

The study area at Borris in western Jutland (55°55'N, 8°40'E) is a military shooting terrain. It consists of 5.000 ha of sandy and nutrient poor soil within a flat heath plain traversed by a considerable river valley (250 ha). Heather moors (2.400 ha), grassy plains with wetlands (1.600 ha), willow shrubs (200 ha), and conifer plantations (600 ha) constitute the major vegetational elements (Tønsberg *et al.* 1972, Petersen & Strandgaard 1992, Strandgaard 1999). In contrast, the study area at Kalø (1000 ha) in east Jutland (56°17'N, 10°30'E) has fertile soil with two small forests - Hestehaven and Ringelmosen comprising 350 ha and farmland with hedges of 650 ha. Terminal moraines dominate the rolling landscape with a general southward slope towards the sea. The vegetational composition of the forested area is two-thirds deciduous and one-third coniferous trees and the surrounding fields are subject to intense cultivation with mainly wheat, barley, rape, beets and seed grass (Strandgaard 1972a, Petersen and Strandgaard 1992)

Materials & methods

Jaws

The data material of the study consisted of 258 known age roe deer jaws obtained from the Kalø population in the years 1956-1987 and 235 known age roe deer jaws obtained from the Borris population in the years 1963-1984. An additional sample of 997 jaws from roe deer of unknown age from the Borris population obtained in the years 1966-1992 were integrated in the analysis of tooth replacement during the first year of life. All known age jaws were from animals ear tagged in their first year of life either as newborns or during annual winter catchings (Strandgaard 1972a). Juveniles caught during their first winter were checked for the presence of deciduous premolars indicating that they were born in the preceding summer. Most animals were either shot or died in traffic accidents, but a few animals were included, which had died from natural causes. These were all estimated to have died less than 30 days before they were found, thereby minimising the risk of grouping them to the wrong age class. Obvious damage to the jaw caused during the life of the animal or lack of teeth lead to the exclusion of twelve jaws from Kalø and ten jaws from Borris. The remaining jaws with permanent cheek teeth formed the basis for the study of molar wear patterns, including 177 jaws from Kalø and 174 jaws from Borris. The age of animals varied between less than a month and more than thirteen years. In order to quantify wear on the finest possible time scale without making sample sizes too small, individuals were grouped in age classes spanning six months (table 1).

Roe deer in the two populations have their mean parturition date close to the first of June (Strandgaard 1972b), and in order to group animals as close to their date of birth or "date of birth plus six months" the first of June was set as the median date of age classes of animals aged 1 year, 2 years, 3 years etc., and the first of December as the median of the age classes of animals aged 1.5 years, 2.5 years, 3.5 years etc. Hence, animals that had died in the period March through August were grouped in age classes according to the number of years between birth and death (x). Animals that had died in the period September through December were grouped in age classes x + 0.5, and animals that had died in January or February were grouped in age classes x – 0.5.

Tooth development

The development of the permanent cheek teeth was investigated in all known age individuals from Borris and Kalø. Among known age individuals with deciduous premolars (n = 120), none were older than one year. Hence, all individuals in an additional sample of jaws from 997 animals of unknown age from Borris with deciduous premolars present were considered either six months or one year old, dependent on the month of death. Using the population-specific scoring table for Borris described below, individuals with permanent cheek teeth estimated to be one year old were aged with an accuracy of 100% (figure 4a). Therefore, the jaws from individuals of unknown age estimated to be one year old or younger were in effect of known age. Jaws from animals that had died in the calendar year after their birth were grouped according to their month of death, and the frequency of jaws with at least one deciduous premolar present was calculated for each month.

The scoring system

In order to describe dental wear objectively, I used wear characters that were either present or absent on individual premolars and molars. Detailed study of jaws grouped in age classes formed the basis for the choice and description of individual wear characters. Only characters on individual teeth which were evidently present or absent were used, i.e., where no intermediate wear stages existed. A total of 21 characters were described on five of the six cheek teeth of the lower jaw (appendix A). As jaws may vary in the degree of wear between the left and right halves, I consistently used the right half to prevent bias. Only when teeth were lacking on the right side, the left side was used.

The wear characters described are only present in a certain period of the life of an individual, and the percentage of individuals displaying a given character is expected to either increase asymptotically with age to one hundred or decrease to zero, depending of the nature of the character. Within age classes where the percentage shifts between zero and one hundred, a second order polynomial approximates this relation for each character (figure 1). I calculated the percentage of individuals in each age class displaying the character and performed second order polynomial regression on percentages with age class as independent variable. This was done for all known age individuals together and for

Borris and Kalø populations separately (table 2). The smoothed percentages calculated from the regression polynomials of each character, were put together in scoring tables for the total sample (table 3) and for Borris (table 4) and Kalø (table 5) separately. Each score represents the probability that an individual in the given age class displays the character. A score of 25 for a character in a given age class indicates that there is a 25% chance that an individual of that age displays the character.

When ageing an animal, the presence or absence of each character is recorded. For each present character, a score equal to the percentage in the scoring table is given to each age class. For characters not present, a score equal to 100 minus the percentage in the scoring table is given, i.e., the probability of an individual not displaying the character. Hence, an animal gets a score for each character in each age class even if it does not display all characters. If the presence or absence of a character results in a score of zero for a certain age class, the animal cannot possibly belong to that age class and the age class is not considered for the age estimate. When scores have been assigned for all characters to all age classes, they are summed for each age class, and the age class with the highest summed score being the most probable, is the age estimate. Animals are grouped in six months age classes as described above, and though they receive a score in all age classes, only those to which they can theoretically belong are considered for the age estimate.

As an example, individual number 193/78 from Borris died on October 21st 1978 and displayed characters number 4, 6, 8, 11, 15 and 19. Because of its date of death it belongs to the group x + 0.5 and can not possibly belong to age class 1, 2, 3, 4, 5, 6 or 7. For the rest of the age classes scores are assigned. It receives a score equal to the value in table 3 for all characters present, and a score equal to 100 minus the value in table 3 for the rest of the characters. Age classes 1.5, 4.5, 5.5, 6.5, 7.5, 8-8.5, 9-9.5 and >9.5 can be excluded, because the individual displayed character number 19 which is not present in any known age animals younger than 2 years, and character number 6 which is not present in any known age animals older than 4 years. The remaining two age classes 2.5 and 3.5 scored 1662 and 1589 respectively, and since 2.5 received the highest score, it is the most likely age of the individual. Indeed, this is the age of individual 193/78 from Borris.

Population differences in dental wear and food selection

In order to test for general differences in wear rate between the Kalø and the Borris population, the percentages of character number 2, 4, 5, 6, 8, 9, 10, 11, 13, 14, 17 and 18 were transformed to 100 minus the original score in the sample making high scores indicate high degrees of wear. Percentages of all characters in all age classes were aligned for the two populations and tested for differences in rank, using the normal approximation of the Wilcoxon signed rank matched pairs test. Differences in wear between sexes were tested in the same way as differences between populations, using the normal approximation of the Wilcoxon signed rank matched pairs test. The percentage of each character in each age class was calculated for both populations together. Only age classes with percentages based on three or more individuals were used including the following age classes: 1, 1.5, 2, 2.5, 3.5, 4, 4.5 and 6.5.

Detailed analyses of rumen content of 1104 individual roe deer from Borris and 146 roe deer from Kalø have demonstrated marked differences in food choice between the two habitats, probably because of differences in vegetational composition (Petersen & Strandgaard 1992). Food items presented as volume percentages were divided into the following categories: Anemone (*Anemone nemorosa*), cereal grains, herbs, apples, fungi, graminids, dwarf shrubs – mainly heather (*Calluna vulgaris*), conifers and deciduous tree species. Anemone was further divided into two categories: rhizomes and leaves/flowers. I grouped food items arbitrarily in two categories – hard and soft items, and tested whether the abundance of hard food items differed between the Kalø and Borris populations, using one-way ANOVA with month as factor.

Results

Tooth development

In the Borris population, the first animals to loose deciduous premolars died in March of the calendar year after their birth, and the oldest animals with deciduous premolars died in July one year after their birth. For Kalø the shift to permanent cheek teeth took place in May, June or July. Tooth replacement was slightly later in Kalø than in Borris (figure 2).

The scoring system

Regression analyses of frequency distributions of individual wear characters on age classes clearly demonstrate, that wear characters in permanent cheek teeth are well described by second order polynomials (table 2). The choice of characters used in the scoring system influenced accuracy in the age estimates. If characters with R^2-values less than 0.85 for the second order polynomials presented in table 2 were excluded, estimates of older individuals improved (figure 3). The accuracy among younger age classes was improved by excluding five wear characters that were almost equally frequent for younger age classes or present only in intermediate age classes (figure 3). The specific characters in this selection are marked by § in table 2. Using the population-specific scoring tables, the highest accuracy among younger age classes was obtained by including only characters with R^2-values higher than 0.85 (figure 4), resulting in 12 characters for Kalø and 11 for Borris likewise marked by § in table 2.

Using the selection of characters in the general scoring table based on all individuals with permanent cheek teeth, it was possible to age individuals with permanent cheek teeth with 80% accuracy up to the age of 3 years (figure 3). Furthermore, if jaws with deciduous teeth were included, the accuracy of age estimate of individuals up to the age of 3 years increased to 88%. For the population-specific scoring tables, 80% accuracy was achieved among individuals with permanent cheek teeth up to the age of 3.5 years from Borris and 3 years from Kalø and all estimates of one year were correct (figure 4).

Population differences in dental wear and food selection

No differences in dental wear were found in the comparison of frequency distributions of wear characters among age classes between populations (Wilcoxon signed rank matched pairs test: $z_{119} = -0.705$, $n = 120$, $p = 0.481$) or sexes ($z_{72} = -0.913$, $n = 73$, $p = 0,361$). The volume percentage of “hard” food items (small shrubs, conifers and deciduous tree species) in rumen content were larger in Borris than in Kalø although not significantly ($F_{2,11} = 3.244$, $p = 0.085$). At Kalø, rhizomes of anemone constituted a considerable part of the diet in winter and early spring. Because of expected intake of soil when foraging rhizomes it can be argued, that these should be included as hard food, and in doing so the difference in volume percentage of hard food items disappeared ($F_{2,11} = 0.524$, $p = 0.48$). However, if intake of mineral soil is more important than abrasion caused by the forage itself, the sandy soil expected to cover smaller shrubs in Borris may increase dental wear in this population. Indeed, the volume percentage in rumen content of heather at Borris differed from the volume percentage of anemone rhizomes at Kalø ($F_{2,11} = 14.36$, $p = 0.001$).

Discussion

The need of accuracy in age determination is dependent on the research purpose. For example, in studies on population dynamics from cross-sectional data, overestimation of ages will underestimate mortality leading to calculated population increases, when population size is actually decreasing (Vincent *et al.* 1994). However, as long as individuals can be correctly aged up to a certain age class, they can provide reliable data to cohort effect analyses. In order to recognise persistent cohort effects reported for many species (Lindström 1999), an accurate ageing technique is required.

Here I have presented a novel and accurate technique that can easily be applied to large samples of roe deer jaws. It is based on objective wear characteristics of the cheek teeth, and tested on 493 roe deer jaws of known age. The use of present/absent wear characters makes the method simple to use, and the calculations involved can easily be automated by a computer, but more importantly, the estimates are not biased by the observer. Among individuals of known age estimated to be 3 years old or younger, 88% were aged correctly and for younger individuals accuracy was even higher.

The high correlation coefficients from the regression analyses of percentages of individuals displaying wear characters on age indicate, that no individual wear character or individual jaw can describe the wear pattern of animals in a certain age class. This implicates that small collections of known age jaws are of little value as reference material, which may explain the lack of success in studies based on such jaw boards (e.g. Cederlund *et al.* 1991, Hewison *et al.* 1999).

The absence of significant population differences in dental wear for two populations of roe deer exposed to very different habitats found in this study is important for the understanding of wear patterns in ungulate cheek teeth. It indicates that by using a frequency-based scoring system, individual variations in wear rates are largely controlled for. As population-specific scoring tables differ, there are differences between populations, but the high accuracy obtained by using the general scoring table based on individuals from both populations suggests that the differences may be caused by small sample sizes.

Differences in forage composition between populations did not seriously affect dental wear. However, the abrasive potential of various food items and the amount of mineral soil ingested with these must be quantified in order to properly evaluate the importance of forage composition for dental wear. This evaluation is confounded by seasonal and geographical variation in forage composition as well as differences in abrasive potential between plant parts. Intuitively, the diet of roe deer at Kalø is expected to induce less wear of teeth than the coarser food items (heather) and sandy soil at Borris (Strandgaard 1999), although the results on forage composition were inconclusive.

A distinction has been made between “attrition”, which refers to wear caused by the friction of the teeth against teeth, and “abrasion” referring to wear caused by friction between teeth and food (Fandos *et al.* 1993). My results indicate that for roe deer, the process of attrition is more important than abrasion, something that could stem from roe deer being selective feeders. Due to their relatively small size for ruminants, roe deer are forced to select forage of high nutritious value, expected to be softer and inducing less wear on cheek teeth (Duncan *et al.* 1998) thereby reducing inter-population wear rate differences.

Differences in dental wear between the sexes, as investigated here for two roe deer populations have only recently been quantified in ungulates species. Van Deelen *et al.* (2000) found subtle but significant sex differences in dental wear of white-tailed deer (*Odocoileus virginianus*) when the effect of observer variation was controlled. They argued that size dimorphism and hence selection on size in males may increase mortality by inducing higher priority on growth than condition. The shorter life span expectancy may reduce selection on tooth conservation in males leading to the observed higher wear rates for males. As size dimorphism is smaller in roe deer (Andersen *et al.* 1998), this difference in molar robustness between the sexes is expected to be less pronounced in this species, explaining my results.

Individual variation in wear characters within age classes displayed by the large number of known age animals used in this study confirms that individual variation in wear patterns exists. However, the use of objective wear characters and the frequency of their appearance in different age classes does facilitate reliable estimates of younger animals.

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Table 1

The number of jaws of known age with fully developed permanent cheek teeth in each population, separated in sexes and age classes.

	Kalø			Borris		
Age	n_{Male}	n_{Female}	n_{Total}	n_{Male}	n_{Female}	n_{Total}
1	9	2	11	14	1	15
1.5	11	12	23	11	11	22
2	14	3	17	16	2	18
2.5	8	9	17	5	7	12
3	15	1	16	46	-	46
3.5	2	9	11	3	7	10
4	6	3	9	15	2	17
4.5	-	6	6	1	3	4
5	5	1	6	6	-	6
5.5	2	17	19	1	2	3
6	4	-	4	3	1	4
6.5	1	4	5	2	1	3
7	1	4	5	1	-	1
7.5	1	3	4	1	1	2
8	4	1	5	-	2	2
8.5	1	1	2	-	1	1
9	-	5	5	-	1	1
9.5	-	5	5	-	2	2
10	-	-	-	-	1	1
10.5	-	1	1	-	2	2
11	-	3	3	-	1	1
11.5	-	1	1	-	1	1
12	-	-	-	-	-	-
12.5	-	1	1	-	-	-
13	-	-	-	-	-	-
13.5	-	1	1	-	-	-
Total	84	94	177	125	49	174

Table 2

Second order polynomial regression of percentage of individuals displaying each wear character with age class as independent variable. Characters marked by § were used in the improved scoring systems.

	Total		Borris		Kalø	
Character number	**2nd order polynomial**	**R^2**	**2nd order polynomial**	**R^2**	**2nd order polynomial**	**R^2**
1	$-3.56x^2 + 43.07x - 35.76$	$0.84^{\S}$	$-3.82x^2 + 44.15x - 39.87$	0.77	$-4.54x^2 + 49.29x - 39.5$	0.69
2	$11.66x^2 - 81.11x + 137.24$	$0.90^{\S}$	$10.9x^2 - 78.29x + 140.05$	$0.90^{\S}$	$23.72x^2 - 143.87x + 192.89$	$1.00^{\S}$
3	$0.18x^2 + 8.63x - 14.12$	$0.86^{\S}$	$0.51x^2 + 5.31x - 13.5$	0.67	$-0.31x^2 + 14.09x - 19.52$	0.80
4	$-0.61x^2 - 9.77x + 116.66$	0.91	$0.2x^2 - 17.87x + 127.79$	$0.86^{\S}$	$-1.56x^2 - 1.46x + 106.64$	$0.89^{\S}$
5	$130.56x^2 - 479.17x + 436.11$	$1.00^{\S}$	$-200x + 300$	$1.00^{\S}$	$53.04x^2 - 229.13x + 246.09$	$1.00^{\S}$
6	$11.14x^2 - 92.33x + 190.54$	$0.96^{\S}$	$10.69x^2 - 88.77x + 185.17$	$0.97^{\S}$	$6.17x^2 - 73.24x + 175.72$	$0.96^{\S}$
7	$0.13x^2 + 10x - 23.3$	$0.86^{\S}$	$-0.14x^2 + 13.64x - 28.05$	0.64	$-1.24x^2 + 30.08x - 93.15$	$0.85^{\S}$
8	$-0.23x^2 - 15.47x + 129.23$	$0.89^{\S}$	$0.68x^2 - 25.92x + 146.34$	$0.86^{\S}$	$-1.23x^2 - 6.34x + 115.89$	$0.86^{\S}$
9	$105.81x^2 - 405.9x + 388.55$	$1.00^{\S}$	$-186.67x + 280$	$1.00^{\S}$	$24.51x^2 - 155.34x + 212.65$	$1.00^{\S}$
10	$9.67x^2 - 71.82x + 134.69$	0.94	$1.56x^2 - 23.16x + 89.62$	$0.90^{\S}$	$11.03x^2 - 77.98x + 140.59$	$0.93^{\S}$
11	$-0.98x^2 - 0.35x + 49.51$	$0.51^{\S}$	$-9.7x^2 + 48.76x - 6.14$	0.78	$-0.7x^2 - 1.13x + 50.02$	0.30
12	$-3.85x^2 + 49.9x - 69.45$	$0.92^{\S}$	$0.38x^2 + 24.48x - 35.88$	$0.98^{\S}$	$-4.32x^2 + 52.34x - 72.6$	0.76
13	$16.07x^2 - 113.2x + 199.13$	$0.98^{\S}$	$19.89x^2 - 130.92x + 214.89$	$0.98^{\S}$	$13.53x^2 - 99.52x + 186.39$	$0.97^{\S}$
14	$-6.16x^2 + 32.37x - 13.78$	$0.56^{\S}$	$-8.01x^2 + 39.78x - 21.26$	0.50	$-6.93x^2 + 37.08x - 18.2$	0.53
15	$-6.2x^2 + 51.30x - 54.81$	0.73	$-8.22x^2 + 63.55x - 67.62$	0.44	$-6.11x^2 + 52.93x - 61.84$	0.71
16	$0.55x^2 + 12.71x - 22.3$	$0.89^{\S}$	$0.8x^2 + 13.26x - 25.3$	0.62	$0.8x^2 + 9.48x - 18.49$	0.83
17	$56.36x^2 - 229.09x + 232.73$	$1.00^{\S}$	$78.79x^2 - 303.03x + 290.91$	$1.00^{\S}$	$27.27x^2 - 131.82x + 154.55$	$1.00^{\S}$
18	$25.57x^2 - 148.89x + 211.87$	1.00	$27.68x^2 - 161.56x + 229.06$	$0.99^{\S}$	$20.34x^2 - 123.63x + 182.61$	$1.00^{\S}$
19	$-4.72x^2 + 53.07x - 52.34$	0.95	$-4.37x^2 + 47.33x - 42.86$	0.70	$1.23x^2 + 26.34x - 28.05$	$0.91^{\S}$
20	$-0.04x^2 + 11.25x - 31.57$	$0.63^{\S}$	$1.02x^2 - 9.39x + 32.26$	0.20	$-0.21x^2 + 15.9x - 44.02$	0.62
21	$-0.34x^2 + 21.23x - 94.62$	$0.71^{\S}$	$1.47x^2 - 11.03x + 21.71$	0.45	$-0.79x^2 + 30.06x - 127.94$	0.71

Table 3

Scoring table for the general scoring system based on all known age animals. The scores are percentages of individuals in each age class which display individual wear characters, smoothed by using calculated values from second order polynomial regression in table 2. Character numbers refers to descriptions in appendix A.

AGE CLASS CHARACTER	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8-8.5	9-9.5	>9.5
1	0	21	36	50	61	71	79	86	90	100	100	100	100	100	100	100	100
2	68	42	22	7	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	4	9	13	18	23	28	33	39	44	49	55	61	69	81	96
4	100	100	95	88	82	75	68	60	53	44	36	27	18	0	0	0	0
5	88	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	100	77	50	29	14	4	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	3	8	13	19	24	30	36	41	47	53	59	68	80	96
8	100	100	97	89	81	72	64	55	46	37	28	19	10	0	0	0	0
9	88	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	73	49	30	16	6	2	2	0	0	0	0	0	0	0	0	0	0
11	48	47	45	43	40	36	32	28	23	18	12	6	0	0	0	0	0
12	0	0	15	31	46	58	68	77	84	88	91	92	100	100	100	100	100
13	100	65	37	17	4	0	0	0	0	0	0	0	0	0	0	0	0
14	12	21	26	29	28	24	17	7	0	0	0	0	0	0	0	0	0
15	0	0	23	35	43	49	51	51	47	40	30	17	0	0	0	0	0
16	0	0	5	13	21	29	37	46	55	64	74	84	100	100	100	100	100
17	60	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	89	46	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	17	35	51	64	76	84	91	95	97	96	93	100	100	100	100	100
20	0	0	0	0	2	7	13	18	24	29	34	40	45	50	58	69	82
21	0	0	0	0	0	0	0	0	3	12	20	29	37	45	57	72	90

Table 4

Scoring table for Borris based on known age individuals from this population. The scores are percentages of individuals in each age class which display individual wear characters, smoothed by using calculated values from second order polynomial regression in table 2. Character numbers refers to descriptions in appendix A.

AGE CLASS CHARACTER	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8-8.5	9-9.5	>9.5
1	0	18	33	47	58	68	76	81	85	100	100	100	100	100	100	100	100
2	73	47	27	12	3	0	1	0	0	0	0	0	0	0	0	0	0
3	0	0	0	3	7	11	16	21	26	31	37	42	49	55	65	79	98
4	100	100	93	84	76	68	59	51	43	35	28	20	0	0	0	0	0
5	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	100	76	50	30	15	5	1	0	0	0	0	0	0	0	0	0	0
7	0	0	0	5	12	18	24	31	37	43	49	55	61	67	75	87	100
8	100	100	97	86	75	64	54	44	34	24	15	7	0	0	0	0	0
9	93	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	74	49	29	14	5	1	3	0	0	0	0	0	0	0	0	0	0
11	33	45	53	55	53	46	34	17	0	0	0	0	0	0	0	0	0
12	0	0	15	28	41	54	68	82	100	100	100	100	100	100	100	100	100
13	100	63	33	12	1	0	0	0	0	0	0	0	0	0	0	0	0
14	0	20	26	28	26	20	10	0	0	0	0	0	0	0	0	0	0
15	0	0	27	40	49	54	55	52	45	33	18	0	0	0	0	0	0
16	0	0	0	13	22	31	41	51	61	72	83	100	100	100	100	100	100
17	67	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	95	49	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	34	48	60	69	77	82	85	85	84	80	100	100	100	100	100
20	0	0	0	0	0	12	11	11	11	11	13	14	16	19	24	33	46
21	0	0	0	0	0	0	0	0	3	6	8	12	17	22	31	45	68

Table 5

Scoring table for Kalø based on known age individuals from this population. The scores are percentages of individuals in each age class which display individual wear characters, smoothed by using calculated values from second order polynomial regression in table 2. Character numbers refers to descriptions in appendix A.

AGE CLASS CHARACTER	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8-8.5	9-9.5	>9.5
1	0	24	41	55	67	77	85	90	100	100	100	100	100	100	100	100	100
2	73	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	7	14	20	26	32	38	43	49	54	59	64	69	76	84	100
4	100	100	97	93	88	82	76	68	60	51	42	31	20	0	0	0	0
5	70	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	100	80	54	31	11	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	7	17	26	35	43	50	57	63	70	79	86
8	100	100	98	92	86	79	71	63	54	44	34	23	11	0	0	0	0
9	82	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	74	48	29	15	6	3	0	0	0	0	0	0	0	0	0	0	0
11	48	47	45	43	40	37	34	31	27	23	18	13	0	0	0	0	0
12	0	0	15	31	46	58	68	75	81	85	86	85	100	100	100	100	100
13	100	68	41	22	10	4	0	0	0	0	0	0	0	0	0	0	0
14	0	22	28	31	31	27	19	8	0	0	0	0	0	0	0	0	0
15	0	0	20	32	42	49	52	53	50	44	36	24	0	0	0	0	0
16	0	0	4	10	17	25	32	40	49	58	67	77	100	100	100	100	100
17	50	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	79	43	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	14	30	45	62	79	100	100	100	100	100	100	100	100	100	100	100
20	0	0	0	0	2	9	16	23	30	37	44	50	57	63	73	85	100
21	0	0	0	0	0	0	0	0	3	14	24	34	44	53	67	83	100

Figure legends

Figure 1

Percentages of known age individuals displaying two characters (no 9. and no. 16) are plotted against age to exemplify how frequencies of individuals displaying a given character change with age. Characters are described in appendix A. Second order polynomial trend lines are shown.

Figure 2

The fraction of individuals that died in the calendar year after their birth from Borris and Kalø, which still had at least one deciduous premolar present in the lower jaw. Data from Kalø are from individuals of known age calculated separately for each month of the year. From Borris, data on individuals of known age were pooled with data on unknown age individuals, aged with 100% accuracy using the population-specific scoring system for the Borris population and calculated separately for each month of the year.

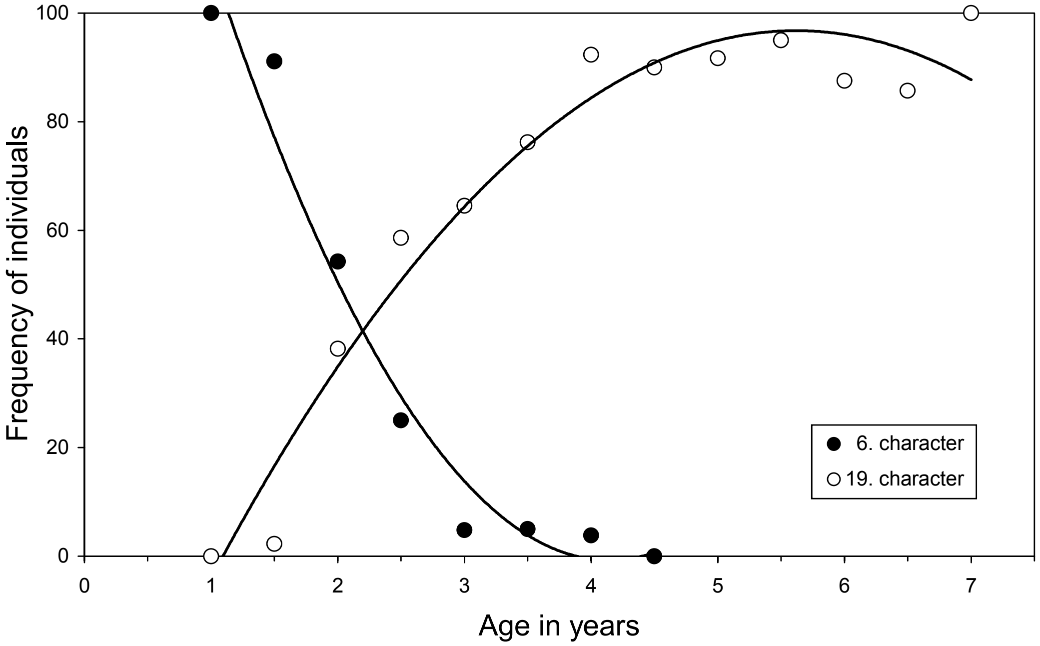
Figure 3

The percentage of correctly aged individuals among those assigned to a given age class or younger. Age estimates are based on the general scoring table developed from data on all known age jaws from both populations using: □ all characters, ▨ all characters with $R^2 \geq 0.85$ for second order polynomial regressions presented in table 2 or ■ a selection of 16 characters based on criteria explained in the text.

Figure 4

The percentages of correctly aged individuals among those assigned to a given age class or younger. Age estimates are based on scoring tables developed separately for: A) Borris and B) Kalø, using all characters and all characters with $R^2 \geq 0.85$ for second order polynomial regressions presented in table 2.

Figure 1



Frequency of individuals
100
80
60
40
20
0
0
1
2
3
4
5
6
7
Age in years
● 6. character
○ 19. character

Figure 2

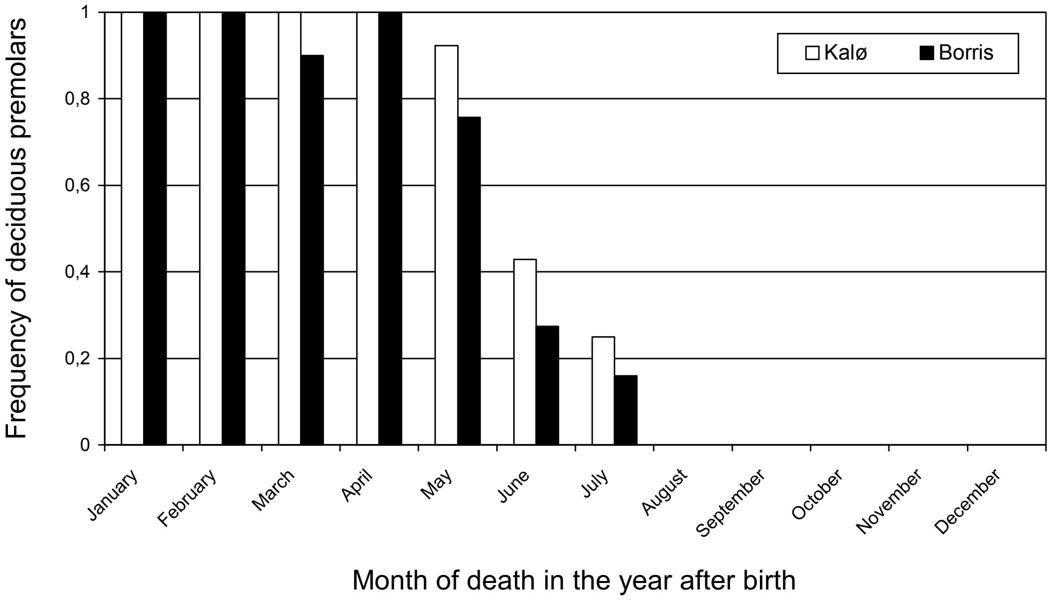

Frequency of deciduous premolars
1
0,8
0,6
0,4
0,2
0
☐ Kalø
■ Borris
January
February
March
April
May
June
July
August
September
October
November
December
Month of death in the year after birth

Figure 3

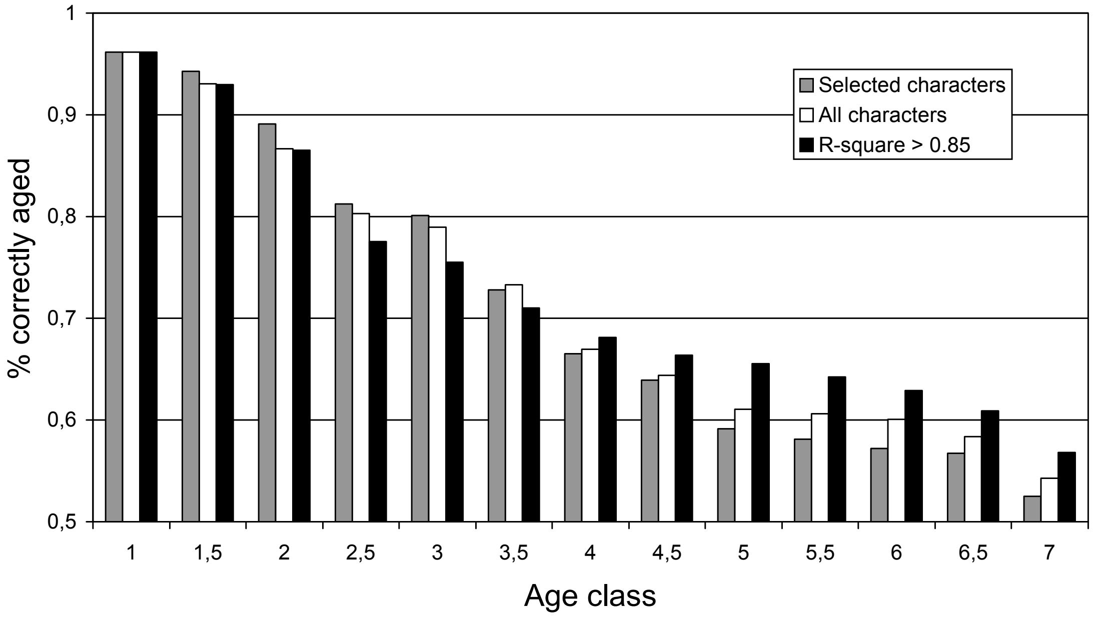
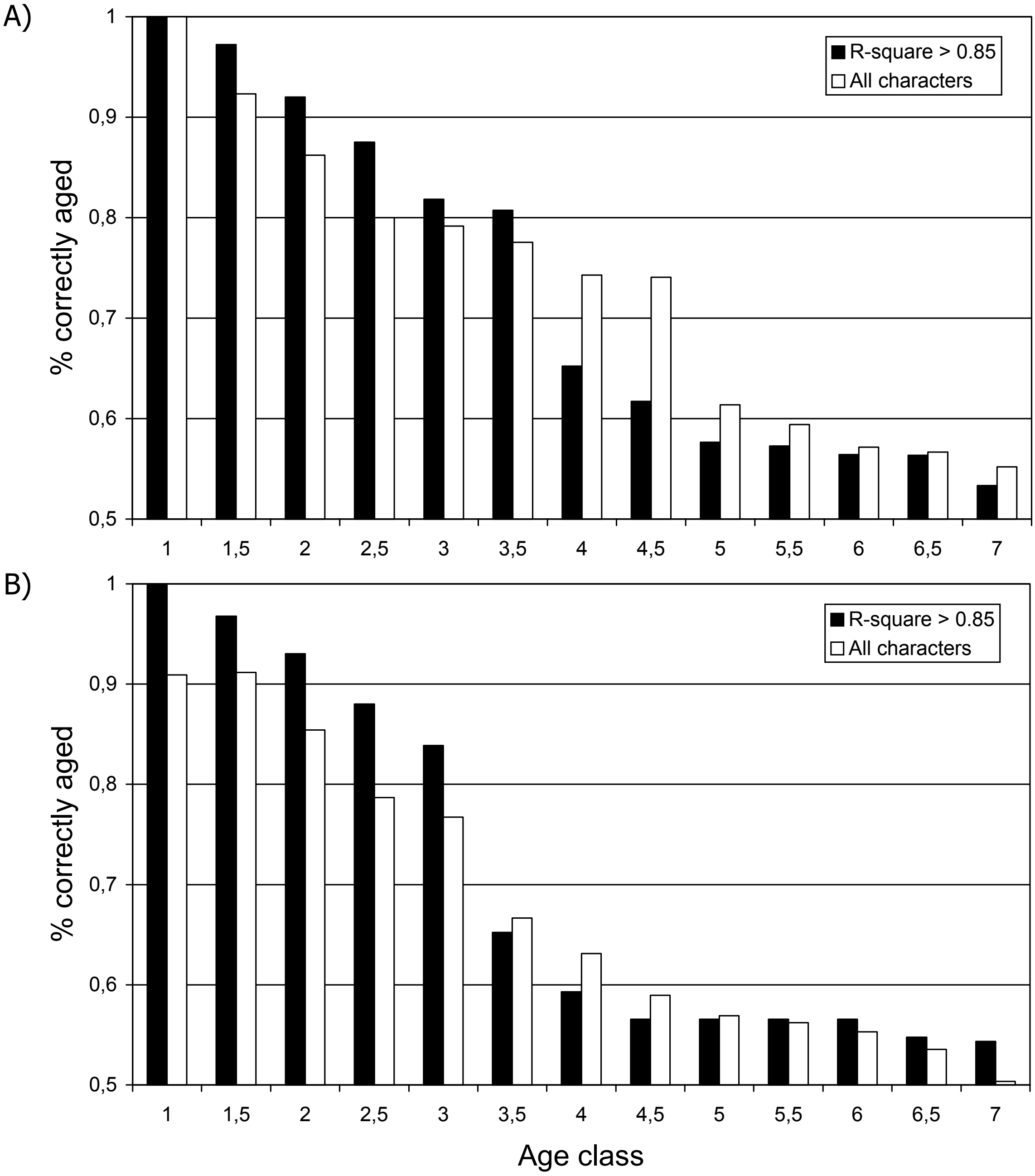

Selected characters
All characters
R-square > 0.85
% correctly aged
1
0,9
0,8
0,7
0,6
0,5
1
1,5
2
2,5
3
3,5
4
4,5
5
5,5
6
6,5
7
Age class

Figure 4


A)
B)
% correctly aged
1
0,9
0,8
0,7
0,6
0,5
■ R-square > 0.85
□ All characters
1
1,5
2
2,5
3
3,5
4
4,5
5
5,5
6
6,5
7
Age class

Appendix A - description of wear characters

Characters are grouped according to the cheek teeth to which they refer. PM2 is the second premolar, PM3 is the third and PM4 is the third. Likewise, M2 is the second molar and M3 is the third (Langvatn 1977).

PM2

1. character
Wear on the tooth is evident from the posterior edge of the tooth, and at least to the highest point of the ridge.

2. character
No signs of wear evident at all, either on the top or on the side.

PM3

3. character
The anterior infundibulum closed[1] lingually.

4. character
The posterior infundibulum open[1] lingually.

5. character
The central line of dentin is not visible lingually, anterior to the highest point of the ridge. The dentin is often slightly visible if wear is evident, and the tooth does therefore not display the character.

PM4

6. character
The anterior infundibulum open[1] anteriorly.

7. character
The anterior infundibulum closed[1] lingually. This either can be at buccal edge or almost centrally, were wear is often profound.

8. character
The posterior infundibulum open[1] lingually.

9. character
The central line of dentin is not visible lingually, anterior to the highest point of the ridge. The dentin is often slightly visible if wear is evident, and the tooth does therefore not display the character.

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[1] Closed or open refers to whether the wear surface is smooth all around the infundibulum. By pressing a sharp object against the wear surface and moving it around the infundibulum any inequalities are easily registered

Paper III

Growth dynamics and cohort variation in phenotypic traits – evidence of a silver spoon effect in roe deer

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with 5 tables, 8 figures and 53 references

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Running head: Cohort effects in roe deer

Abstract

Early environmental conditions experienced by cohorts while *in utero* have profound life history consequences for several ungulate species. The variability of an early-developed skeletal part (the anterior jaw length) is analysed in relation to adult fitness-related phenotypic traits (body weight and condition) among roe deer cohorts in Denmark. Two populations (Borris and Kalø) differing in density and vegetational composition both showed that anterior jaw length is full-grown within the first few months after birth. Cohort variability was pronounced in both sexes at Borris, but only for bucks at Kalø. Cohorts of males experiencing favourable early conditions (large anterior jaw lengths) were larger and in better condition as yearlings and adults but this persistent cohort effect was more evident at Borris than at Kalø. In addition, females born with small anterior jaws were lighter as juveniles and adults at Borris, but only as juveniles at Kalø indicating that individuals at Kalø were able to compensate for adverse growth conditions in early life. Furthermore, there was a tendency for larger-born males to allocate more resources to antler growth, as juvenile males with large antlers had experienced better skeletal growth *in utero* than prime aged adult males with small antlers. However, both skeletal size and body weight were significantly larger at Borris suggesting higher performance in this population. The potential of using skeletal indices in studies of cohort variability and the life history consequences of early development are discussed in relation to density and density-independent processes.

Keywords

Cohort effects, *Capreolus capreolus*, skeletal development, anterior jaw length, density dependence, North Atlantic Oscillation

Introduction

Individual variation in lifetime reproductive success is shaped by genetic variation and environmental conditions experienced from conception to death (Roff 1992). However, conditions during early life have received special attention in birds and mammals because of their potential to affect long-term survival and fecundity through impact on birth weight and consequently growth (see Lindström 1999 for a review). For example, in red deer (*Cervus elaphus*), juvenile survival is related to birth weight and birth date (Clutton-Brock *et al*. 1987) and maturity is reached earlier by individuals born in years with temperatures, which favour forage digestibility (Langvatn *et al*. 1996). Furthermore, Clark and Galef (1995) have stressed the importance of prenatal conditions for the development of life history strategies through hormonal exposure and, ultimately, conditions experienced in early life have a potential impact on population dynamics (see Sæther 1997 and Gaillard *et al*. 1998 for recent reviews). Therefore, a good start in life may be more important for individual fitness, than benign conditions experienced later as adult (Forchhammer *et al*. 2001).

Early development is determined by the combined effect of maternal investment and environmental constraints. Although individual differences in maternal investment between mothers are pronounced (Andersen *et al*. 2000) and fecundity may have a genetic basis (Hewison 1997), conditions experienced by all individuals within a breeding season creates documented cohort effects in ungulates arising from density-dependent and density-independent processes (Albon *et al*. 1987, Clutton-Brock *et al*. 1987, Albon *et al*. 1992, Rose *et al*. 1998). The proximate cause of fitness differences between cohorts is retarded growth, but the resulting effect on survival and reproduction may differ according to climatic regimes and population density (Post *et al*. 1999).

Density dependence has created long-term cohort effects through resource limitation in wild reindeer (*Rangifer tarandus*) (Skogland 1983), Soay sheep (*Ovis aries*) (Robertson *et al.* 1992) and roe deer (*Capreolus capreolus*) (Kjellander 2000). Density-independent effects act either directly as energetic constraints experienced by pregnant mothers while cohorts are *in utero* (Forchhammer *et al.* 1998, Forchhammer 2000) or through impact on forage quality (Albon & Langvatn 1992). Recent changes in a large-scale atmospheric phenomenon, the North Atlantic Oscillation (NAO) have a documented effect on skeletal growth of red deer while cohorts are *in utero* (Post *et al.* 1997) and plant phenology (Post and Stenseth 1999), indicating the potential of large-scale climatic fluctuations in shaping cohort effects. Indeed, climatic impact on pregnant females has been demonstrated to persist throughout the life span of their offspring in red deer (Albon *et al.* 1992) and Soay sheep (Forchhammer *et al.* 2001).

Of the numerous condition indices, which have been proposed for ungulates (see Hanks 1981 and Huot 1988 for reviews), skeletal parts have received some attention in cohort studies, because their early development minimises compensatory growth later in life (e.g. Hewison *et al.* 1996a). In particular, the anterior portion of the jaw in red deer has growth priority over the posterior in prenatal life, while the posterior part has growth priority *post-partum* (Post *et al.* 1997 and Langvatn & Post *in prep.*). This facilitates the evaluation of conditions experienced by a cohort in the year of birth from data on individuals of various ages.

This paper explores and evaluates the use of skeletal parts in the analysis of cohort variability in roe deer and focuses on three perspectives. First, I investigate the growth pattern of different parts of the jaw in order to evaluate their potential as condition indices of perinatal life. Second, the relationship between cohort mean anterior jaw length and body weight/condition in different age classes is investigated. A high degree of correlation for juveniles and a less pronounced correlation for adults is expected, because conditions experienced progressively during adult life reduce cohort variation through weeding out and catch up effects (see e.g. Rose *et al.* 1998). Finally, I analyse the underlying causes of variation in cohort mean anterior jaw length focusing on both density-dependent and density-independent processes.

The analyses presented are based on data from two unusually long time-series on roe deer in Denmark (44 years for Kalø and 30 years for Borris) with different population developmental histories.

Materials & methods

The material used originates from a long-term study of two populations of roe deer in Denmark, Borris and Kalø (Strandgaard 1972a, Strandgaard 1999) and includes data on 3538 individuals. Data was collected by the National Environmental Research Institute in the period 1956-1999 for the Kalø population and in the period 1963-1992 for the Borris population. Each individual was assigned a record number and date, year of death, total weight, eviscerated weight (without internal organs), sex and the type of antlers for bucks were registered and mandibles were collected. Autumn densities of roe deer in the two different counties to which the study areas belong were inferred from hunting statistics (Strandgaard & Asferg 1980, Madsen *et al.* 1996).

Study areas and populations

The study area at Borris in western Jutland (55°55’N, 8°40’E) is a military shooting terrain. It consists of 5000 ha of sandy and nutrient poor soil. Half of the area is heath and the remaining area is two-thirds grassland and one-third woodland and shrubs (Tønsberg *et al.* 1972). Since 1956, ear tagging of fawns has been carried out and from 1969, adult animals have been captured and marked with collars. Based on these markings and field observations spring densities of roe deer in this population were calculated for the years 1970-1979 using capture-mark-resighting (CMR) methods (Strandgaard 1999). Density increased dramatically until 1976 where a population size of 1680 individuals was estimated within the study area. In 1979, density was almost halved and is believed to have stabilised at that level in subsequent years after the CMR-procedures were terminated (Strandgaard 1999).

The other study area at Kalø consists of 1000 ha of fertile land in east Jutland, Denmark (56°17'N, 10°30'E) of which two small forests, Hestehaven and Ringelmosen comprise one third, while the remaining area is farmland with hedges. Terminal moraines dominate the rolling landscape with a general southward slope towards the sea. The composition of the forested area is two-thirds deciduous and one third coniferous trees and the surrounding fields are subject to intense agricultural management (Strandgaard 1972a, Petersen and Strandgaard 1992). The total population of roe deer was exterminated in 1950 (Andersen 1953). In 1951, a new population was released and from 1955, it has been followed by a marking project (Strandgaard 1972a) in part of the study area (Ringelmosen forest and adjacent farmland - 400 ha.). Population densities were calculated from CMR-data obtained for Ringelmosen forest in the years 1956 and 1958-68 and were roughly constant in this period (Strandgaard 1972a).

Winter climate

General climatic variability in northern Europe can be described by fluctuations in the North Atlantic Oscillation (NAO). It is a quantification of the annual winter deviation from the average difference in sea level pressure between the Azores and Iceland (Lamb and Peppler 1987). The NAO determines the speed and directions of across-Atlantic westerly winds between the subtropical and sub-polar regions of the North Atlantic, which strongly influence winter weather conditions in the coastal parts of Northern Europe. When the NAO is in a high state (mass balance centred over the Azores), strong, warm and moist westerly winds are driven far into Northern Europe. In contrast, low NAO indices reflect weakened westerly winds resulting in low winter temperature and reduced precipitation in Northern Europe (Hurrell 1995).

Ageing method and jaw measurements

A total of 990 roe deer jaws were aged from the Kalø population and 1843 from the Borris population using the scoring system of tooth wear characters described in paper II. This method assigns the ages of individuals younger than 4 years with an accuracy of about 90%. Accuracy in estimates of older individuals was lower, and therefore these were excluded. Additionally, 258 individuals of known age from Kalø and 235 from Borris were included in the analyses. Ages in these samples ranged from one month to thirteen years. A birth date of first of June is assumed whenever age in months is used. This approximates the mean birth date in the two populations (Strandgaard 1972b).

Five measurements were taken to the nearest 0.01 mm on each lower jaw using a digital vernier caliper (figure 1). The exact descriptions of these measurements are taken from Langvatn (1977) and Nugent & Frampton (1994). However, the total length of the mandible (AD in figure 1) was measured as described by Crombrugghe *et al.* (1989) from the most posterior point of the socket of the corner incisor to the most posterior point at *processus angularis* as a considerable number of jaws were damaged anteriorly. The right half of the jaw was consistently chosen for measurements, only in case of damage was the left half used (21% of the sample).

Statistical analysis

I used linear regression of total weight on eviscerated weight to interpolate missing values of eviscerated weight for each sex in each population. Ten repetitions of measurements on six jaws of different size and age measured in random order were used to quantify measurement error, and the average coefficient of variance was calculated from these repetitions. Difference between anterior jaw length from left and right halves of the jaw was tested in t-tests for both sexes in both populations. Individual jaw measurements and eviscerated weights are ln-transformed in all analyses used in this study.

Jaw measurements

Jaws of individuals older than 48 months were expected to be full-grown (Angibault *et al.* 1993), and in order to compare differences in growth pattern between individual parts of the lower jaw, measurements on individual jaws were standardised to fractions of full-grown size for each measure. The average length of each skeletal measure for all animals of each sex older than 48 months was used as denominator, and standardised values were plotted against age in months for Borris (figure 2) and Kalø (figure 3) separately. It is evident from the plots that BC, hereafter termed "anterior jaw length" showed the least dependency of age. I tested whether mean anterior jaw length was dependent on age in months for both sexes and populations by one-way ANOVA with age in months as factor and anterior jaw length as dependent variable. By successively excluding the youngest age classes, it was possible to find the age where individual variation showed no dependency on age in months.

Since roe deer are slightly sexually dimorphic (Andersen *et* al. 1998) and size may vary between populations (Klein & Strandgaard 1972) it was tested whether anterior jaw length was dependent on sex or population. For all individuals older than the age where anterior jaw length was age dependent, anterior jaw length was used as dependent variable in a two-way ANOVA according to sex and population. Based on the results of this test, cohort variation in anterior jaw length was calculated separately for each sex in each population using one-way ANOVA with year of birth as factor.

Body mass and condition index

I used eviscerated weight of adults as dependent variable and month of death as factor in a one-way ANOVA for each sex in each population in order to test for seasonal variation in body mass. To account for seasonal body mass changes present in both populations (see test results below) and documented in other studies (Holand 1992, Hewison *et al.* 1996b), I used only data from individuals that died within the hunting seasons (16th of May – 15th of July for bucks and 1st of October – 31st of December for both sexes), which included the majority of individuals. Males were grouped in “juveniles” (died during the autumn hunt in their first year of life), “yearlings” (died during the spring hunt as one year olds) and “adults” (all older individuals that died during either spring or autumn hunts). Females were grouped in “juveniles” (died during the autumn hunt in their first year of life), and “adults” (all older individuals that died during the autumn hunt).

I used the residuals of the regression of individual values of eviscerated weight on total jaw length (BD in figure 1) in each sex and age group as condition index (CI) (Loison & Langvatn 1998). Significance tests of cohort variation in eviscerated weight and CI for each group were performed in ANCOVA with year of birth as independent variable and “date” (the day of the year between 1 and 365 the animal died) as covariate. For adult males, regression of eviscerated weights on date within each hunting season (autumn and spring) was performed first, and in case of significant regressions residuals were used. A binomial variable called “season” was used as covariate in the ANCOVA correcting for differences between the autumn hunt and the spring hunt. Seasonal change was corrected in this way because weights changed less within than between hunting seasons.

Cohort mean eviscerated weight and cohort mean CI was regressed against cohort mean anterior jaw length for each sex and age class that exhibited significant cohort variation in order to evaluate the persistency of cohort effects in body weight and condition through the life stages of roe deer. Anterior jaw length represents an index of conditions experienced in early life, whereas eviscerated weight and CI are respectively raw and size-adjusted indices of condition at death. Hence, high correlation between anterior jaw length and these two indices would demonstrate that cohort effects persist into adulthood.

Environmental variables

The effect of density and NAO on individual variation in anterior jaw length was analysed in stepwise multiple linear regressions for sexes and age classes in each population exhibiting significant cohort variation. I used densities in the year when cohorts were born (t) and the year cohorts were *in utero* (t-1) in separate analyses to avoid multicolinearity between independent variables. Since roe deer densities calculated from capture-mark-recapture procedures in the populations did not cover all years, separate analyses were performed with population-specific N(pop) and county-scale densities N(county). I used detrended values of the NAO winter index (December through March) for the year that cohorts were *in utero* (t-1) as a measure of climatic conditions.

All statistical analyses were performed with SYSTAT version 8.0 for WINDOWS. For parametric tests, normality in distributions of observations was checked graphically, and homogeneity of variances was confirmed in F-tests of samples with highest and lowest variance (Neter *et al*. 1990).

Results

There was a very strong linear relationship between eviscerated and total weight for both sexes tested separately in each population (Kalø females: $R^2 = 0.91$; $n = 356$; $p < 0.0001$; males: $R^2 = 0.95$; $n = 455$; $p < 0.0001$; Borris females: $R^2 = 0.91$; $n = 393$; $p < 0.0001$; males: $R^2 = 0.93$; $n = 908$; $p < 0.0001$), justifying the use of interpolated values of eviscerated weights. Ten repetitions of each skeletal measure showed that coefficients of variation did not exceed 0.25%, indicating that measurement error was very low (table 1). Anterior jaw length did not differ between left and right jaw halves in either females or males at Kalø (females: $t_{323} = -0.784$; $p = 0.434$; males: $t_{505} = 0.326$; $p = 0.744$). At Borris, the difference was marginally significant for females, but not for males (females: $t_{225} = 2.236$; $p = 0.026$; males: $t_{1019} = 1.698$; $p = 0.09$).

Jaw measurements

Individual skeletal parts of the lower jaw showed large variation in dependency of age at Borris (figure 2) as well as in the Kalø (figure 3) population. The fourth order polynomial trend lines clearly show that among measured parts of the jaw, the anterior jaw length (BC) is the first to reach full-grown size. The anterior jaw length showed no dependency on age in either sex in the Kalø population (males: $F_{49,504} = 1.11$; $p = 0.29$; females: $F_{63,316} = 1.166$; $p = 0.206$). At Borris, there was no dependency of the anterior jaw length on age above 6 months in males ($F_{45,1022} = 0.896$; $p = 0.668$) and above 4 months in females ($F_{48, 226} = 1.27$; $p = 0.135$).

Anterior jaw length was significantly larger for males than females and larger at Borris than at Kalø with an almost significant interaction between sex and population indicating that sexual size dimorphism was larger at Borris than at Kalø (sex: $F_{1,2112} = 111.601$; $p < 0.001$; population: $F_{1,2112} = 450.544$; $p < 0.001$; interaction sex$*$population:

$F_{1,2109} = 3.502$; $p = 0.061$). Hence, cohort analyses of anterior jaw length were divided into sexes and populations. Significant cohort variation of anterior jaw length was found in both males and females at Borris, and males but not females at Kalø (table 2). For males cohort mean anterior jaw length was consistently larger at Borris than at Kalø, although cohort variability is evidently more pronounced at Borris (figure 4).

Body mass and condition index

Eviscerated weight of individuals older than one year varied significantly between months of death for males ($F_{9,232} = 4.595$; $p < 0.001$) and females ($F_{9,160} = 4.367$; $p < 0.001$) at Kalø and for males ($F_{11,674} = 14.741$; $p < 0.001$) but not females ($F_{11,157} = 0.959$; $p = 0.486$) at Borris. However, data on females at Borris was clumped as 87% of the individuals in this group had died in October, November and December. Eviscerated weight of adult males was not dependent on date within hunting seasons, except for individuals at Borris that died during the autumn hunting season, where a significant negative relation was found ($R^2 = 0.056$; $F_{1,104} = 6.17$; $p = 0.015$). Using data from the hunting seasons only, cohort variation in eviscerated weight was significant for yearlings males at Borris and all adults, except for females at Kalø (table 3). This coincided with smaller sample sizes for younger age classes.

Regression analyses of individual values of eviscerated weight on total jaw length were significant for both sexes in all age classes at both Borris and Kalø at the 0.001 level. Residuals from the regressions were used as condition index (CI). No dependency of CI on date within hunting seasons was found for adult males. CI varied significantly among cohorts of males at Borris for juveniles, yearlings and adults. The same was true for adult females at Borris and adult males at Kalø (table 4).

Cohort mean eviscerated weight showed a high correlation with cohort mean anterior jaw length for yearling and adult males at Borris (figure 5) but only weak correlation for adult males at Kalø (figure 6). Because of lack of cohort variation in females, I regressed individual values of anterior jaw length on eviscerated weight after controlling for date of death for juveniles and adults and found a significant relationship for juveniles in both populations (Borris: $R^2 = 0.191$; $n = 79$; $p < 0.001$; Kalø: $R^2 = 0.227$; $n = 104$; $p < 0.001$) and for adults at Borris ($R^2 = 0.076$; $n = 133$; $p = 0.001$) but not at Kalø ($R^2 = 0.022$; $n = 127$; $p = 0.093$). This indicates that although inter-cohort variability in eviscerated weight of females was non-significant, individual variation in eviscerated weight in the autumn of the first year could be explained by the anterior jaw length. Furthermore, as for males the effect of early conditions persisted into adulthood at Borris, but not at Kalø. Cohort mean CI of juvenile, yearling and adult males at Borris was likewise highly correlated with cohort mean anterior jaw length (figure 7), whereas this was not true for adult males at Kalø (figure 8).

Causes of cohort variation

Cohorts born in, or following years with high county-specific population densities had small anterior jaw lengths at Borris. In addition, males born following relatively warm and wet winters (high NAO_t) where population-specific density was high in the year of birth [$N(pop)_t$] or the preceding year [$N(pop)_{t-1}$] also had small anterior jaw lengths. Although significant, no more than 4% of the variation was explained by any model. At Kalø, the only environmental variable explaining a significant proportion of variation in anterior jaw length was $N(county)_t$, and it showed a positive relationship with anterior jaw length. However, less than 1.5% of the variation was explained in this regression (Table 5).

Discussion

The analysis of skeletal growth development revealed that the lower jaw exhibited large temporal differences in growth for different parts at both Borris (figure 2) and Kalø (figure 3). The anterior jaw length (BC in figure 1) is full-grown within the first few months after birth and therefore, it can serve as a reliable index of early conditions experienced by individuals. Cohorts of males experiencing favourable early conditions (large anterior jaw lengths) were larger and in better condition as yearlings and adults (figure 5-8). However, this persistent cohort effect was more evident at Borris than at Kalø. Furthermore, females born skeletally small were lighter as juveniles and adults at Borris, but only as juveniles at Kalø, indicating different ability to compensate for adverse early growth conditions between populations in both sexes. Density-dependent processes seemed to be important in explaining up to 4% of the cohort variation in anterior jaw length at Borris and less than 1% at Kalø (Table 5).

Greaves (1991) argued that the observed 3:7 ratio between the distance from the jaw joint to the last tooth and the anterior part of the jaw, has the smallest demand of bone tissue and seems to be universal for attaining maximum bite force for forage mastication in ungulates independent of jaw length. Eruption of molars increases the anterior part of this ratio and in order to maintain the ratio at 3:7, additional growth must concentrate on the posterior part. The conservation of maximum bite force using a minimum of resources to structural body parts may explain why roe deer only increase size of the posterior part of the jaw after birth.

Studies on mandible growth pattern in ungulate species have demonstrated differences in growth priority between parts of the jaw: moose (*Alces alces*) (Sæther 1983) fallow deer (*Dama dama*) (Nugent & Frampton 1994) and red deer (Langvatn & Post *in prep.*). Although the anterior part of the jaw reaches mature size earlier than the posterior part in these species, full-grown sizes of all measurements were reached much later than the anterior jaw length of roe deer in the present study. For example, the anterior part of the jaw in red deer reaches maximum size at the age of nine years in stags and four years in hinds (Langvatn & Post *in prep*.), and for moose, growth of the anterior jaw increases through 4 years in bulls and 3 years in cows (Sæther 1983). This indicates that skeletal development differs considerably between ungulate species. The anterior jaw length in roe deer may be particularly suited for studies of environmental impact on early growth and its fitness consequences in adults, because it is not expected to exhibit compensatory growth after the first few months *post partum*. My findings show that by excluding the most anterior part of the jaw (AB in figure 1) from the anterior jaw length, age dependency was considerably reduced at both Borris (figure 2) and Kalø (figure 3). This measure differs from other studies, which to some degree may explain why anterior jaw length (BC) is developed earlier than other skeletal parts presented so far.

Post *et al*. (1997) demonstrated that cohorts of Norwegian red deer born following winters with high NAO index exhibited abbreviated size of an early-developed skeletal ratio and were smaller as adults. The lower explanatory power of environmental variables for cohort variation found in this study may indicate that the NAO index as such is not equally descriptive of the environmental constraints posed on cohorts in pre- and early postnatal life of roe deer in Denmark. Alternatively, the county-specific population densities may not reflect actual population sizes at Borris and Kalø as correlation coefficients between county-specific and population-specific densities were low and non-significant (Borris: $R^2 = 0.11$; $p = 0.35$; Kalø: $R^2 = 0.20$; $p = 0.15$), and the population-specific densities covers less than half of the time series. For example, threshold values in density above which NAO is important, may not have been recognised.

The energetic constraints posed by environmental conditions on cohorts while carried *in utero* has produced documented effects on lifetime breeding success in Soay rams (Coltman *et al.* 1999) and red deer stags (Rose *et al.* 1998) illustrating the importance of cohort effects for individual fitness of ungulates. Loison & Langvatn (1998) found inter-cohort variability in both dressed body weight and CI of red deer, and juvenile, but not yearling survival of males was negatively related to CI. Influence of density-dependent and density-independent factors on demographic parameters may therefore be mediated through effects on body weight and condition, implying that these traits vary before the demographic parameters themselves (Sæther 1997).

I showed that phenotypic variation among cohorts persisted into adulthood, but that this "silver spoon" effect was far more important at Borris where population density underwent dramatic changes. Although males at Borris born after years with high population densities (1974-78) experienced abbreviated skeletal growth compared to other years, they were consistently larger than corresponding cohorts at Kalø (figure 4). In addition, adult eviscerated weights were higher for adult bucks at Borris ($F_{1,1607} = 96.553$; $p < 0.001$), suggesting that cohort quality may actually be better at Borris than at Kalø. This surprising result may be caused by differences in dispersal patterns between the two populations. At Kalø, the only major reason for loss of one- and two-year-old males was emigration, and heavier bucks with larger antlers were more likely to emigrate as one-year-olds (Strandgaard 1972a). In contrast, higher hunting pressure on bucks may explain the lesser degree of emigration observed at Borris (Strandgaard 1999). Therefore, I hypothesise that males born skeletally large, being heavier and in better condition as yearlings are more likely to emigrate if born at Kalø as compared to Borris. This could explain both the more pronounced cohort variation in anterior jaw length, eviscerated weight and condition and the higher correlation of cohort mean adult eviscerated weight on cohort mean anterior jaw length at Borris. Through behavioural studies, Wahlström (1994) found that yearling roe bucks with large antlers experienced more agonism from adult bucks than those with small antlers. By posing large energetic costs on yearling bucks showing high phenotypic quality, this could increase dispersal among large antlered yearlings (Wahlström 1994).

According to theory on sexual selection (e.g. Cockburn 1991), large antlers infer a reproductive advantage, and a trade off is expected between resources needed for survival and antler growth (Stearns 1992). Young animals with large antlers are expected to be in best condition, whereas medium aged bucks with small antlers are presumed to be in worst condition, because old bucks are often observed with small antler irrespective of condition (Strandgaard 1972a). As dispersal is less pronounced at Borris I would expect antler size to be variable and related to anterior jaw length in this population. Indeed, bucks younger than twenty months with four or six antler points (tines) had significantly longer anterior jaws than bucks older than twenty months with spike antlers (two tines) ($F_{1,135} = 5.440$; $p = 0.021$). If spike bucks older than 40 months were excluded, reducing the risk of including old, high dominance bucks with reduced antler growth late in life, the difference was even more significant ($F_{1,132} = 6.507$; $p = 0.012$). In Kalø, only five bucks older than 20 months had ”spike” antlers, making comparisons impossible.

These results confirm that anterior jaw length is indicative of phenotypic quality, and illustrates the multiplier effects, which early conditions have on fitness-related phenotypic traits.

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Table 1

Coefficient of variation for ten repetitions of each measure averaged for six individual jaws. Measurements were taken on all jaws in each round of repetition before returning to the same jaw.

Jaw measurement	**Coefficient of variation in %**
AB	0.087
BC	0.096
CD	0.14
EF	0.24
GH	0.094

Table 2

ANOVA results of cohort variation in anterior jaw length presented for each sex at Borris and at Kalø. Only years with at least five individuals were included.

Sex/age class	n	Independent variable	F-ratio	d.f.	*p* - value
Borris					
males	1018	year of birth	2.996	29	**> 0.0005**
females	186	year of birth	2.516	8	**0.013**
Kalø					
males	489	year of birth	1.666	39	**0.009**
females	278	year of birth	0.925	30	0.583

Table 3

ANCOVA results of cohort variation in eviscerated weight at Borris and Kalø for three age classes in males and two in females. Only years with at least five individuals were included.

Sex/age class	**n**	**Independent variable**	**Significant covariates**	**F-ratio**	**d.f.**	***p* - value**
Borris						
males						
juveniles	128	year of birth		1.762	11	0.069
			date[†]	4.002	1	**0.048**
yearlings	350	year of birth		10.192	10	**> 0.0005**
			date[†]	7.265	1	**0.007**
adults	666	year of birth		9.963	29	**> 0.0005**
			season[†]	12.711	1	**> 0.0005**
females						
juveniles	64	year of birth		0.752	3	**0.525**
adults	122	year of birth		4.455	5	**0.001**
Kalø						
males						
juveniles	48	year of birth		2.067	6	0.078
yearlings	71	year of birth		0.624	6	0.711
adults	192	year of birth		1.947	23	**0.009**
			season[†]	12.991	1	**> 0.0005**
females						
juveniles	68	year of birth		1.721	8	0.112
adults	65	year of birth		1.406	8	0.214

[†] See definition in text

Table 4

ANCOVA results of cohort variation in condition index at Borris and Kalø for three age classes in males and two in females. Only years with at least five individuals were included.

Sex/age class	**n**	**Independent variable**	**Significant covariates**	**F-ratio**	**d.f.**	***p* - value**
Borris						
males						
juveniles	121	year of birth		2.209	10	**0.022**
yearlings	330	year of birth		6.124	10	**> 0.0005**
			date[†]	13.896	1	**> 0.0005**
adults	652	year of birth		6.505	29	**> 0.0005**
			season[†]	50.123	1	**> 0.0005**
females						
juveniles	58	year of birth		0.529	2	0.592
adults	120	year of birth		4.486	5	**0.001**
Kalø						
males						
juveniles	45	year of birth		1.211	6	0.322
yearlings	71	year of birth		0.485	6	0.817
adults	183	year of birth		1.878	22	**0.014**
			season[†]	8.188	1	**0.005**
females						
juveniles	62	year of birth		0.275	8	0.971
			date[†]	5.019	1	**0.029**
adults	60	year of birth		1.781	7	0.111

[†] See definition in text

Table 5

The most parsimonious models using multiple linear regression. Individual values of anterior jaw length (BC in figure 1) were used as dependent variable. Four models were designed to test the effect of population and county-specific population estimates and detrended NAO on variation in anterior jaw length. Full models included the following variables (Model I: $N(pop)_t$, NAO_t; Model II: $N(pop)_{t-1}$, NAO_t; Model III: $N(county)_t$, NAO_t; Model IV: $N(county)_{t-1}$, NAO_t). Only final models with significant independent variables are presented.

Sex/age class	**Model**	**Independent variables**	**Regression coefficient**	**Partial R^2**	***p* - value**
Borris					
males					
	I	$N(pop)_t$	>-0.0001	0.015	0.005
		NAO_t	0.005	0.011	0.014
	II	$N(pop)_{t-1}$	>-0.0001	0.017	0.005
		NAO_t	0.004	0.011	0.026
	III	$N(county)_t$	-0.093	0.036	> 0.0005
	IV	$N(county)_{t-1}$	-0.097	0.034	> 0.0005
females					
	III	$N(county)_t$	-0.085	0.029	0.01
	IV	$N(county)_{t-1}$	-0.117	0.035	0.005
Kalø					
males					
	III	$N(county)_t$	0.009	0.014	0.008

Figure legends

Figure 1

Lower jaw of roe deer with measures indicated: AB – the most anterior part of the jaw measured from the most posterior part of the socket of the corner incisor to the most posterior part of the nervehole. BC - the anterior jaw measured from the most posterior part of the nervehole to the posterior part of the fourth premolar. CD - the posterior part measured from the posterior end of the fourth premolar to the most posterior point at *processus angularis*. EF – the minimum height of the diastema. GH - the notch height.

Figure 2

Growth pattern of the five measures on the lower jaw described in figure 1 for the Borris population. Values are standardised to fractions of full-grown size of individual measures by dividing individual values by the mean of each measure among individuals older than 48 months. Fourth order polynomial trend lines are used to illustrate trends.

Figure 3

Growth pattern of the five measures on the lower jaw described in figure 1 for the Kalø population. Values are standardised to fractions of full-grown size of individual measures by dividing individual values by the mean of each measure among individuals older than 48 months. Fourth order polynomial trend lines are used to illustrate trends.

Figure 4

Cohort variation in anterior jaw length for males from Kalø and Borris. Only means for years with five or more individuals are presented, and standard error bars are indicated.

Figure 5

Cohort mean eviscerated weight of males from Borris correlated with cohort mean anterior jaw length for: a) yearlings and b) adults. Weights are corrected for seasonal changes.

Figure 6

Cohort mean eviscerated weight of adult males from Kalø correlated with cohort mean anterior jaw length. Weights are corrected for seasonal changes.

Figure 7

Cohort mean condition index (CI) of males from Borris correlated with cohort mean anterior jaw length for: a) juveniles, b) yearlings and c) adults. Values of CI are corrected for seasonal changes.

Figure 8

Cohort mean condition index (CI) of adult males from Kalø correlated with cohort mean anterior jaw length. Values of CI are corrected for seasonal changes.

Figure 1

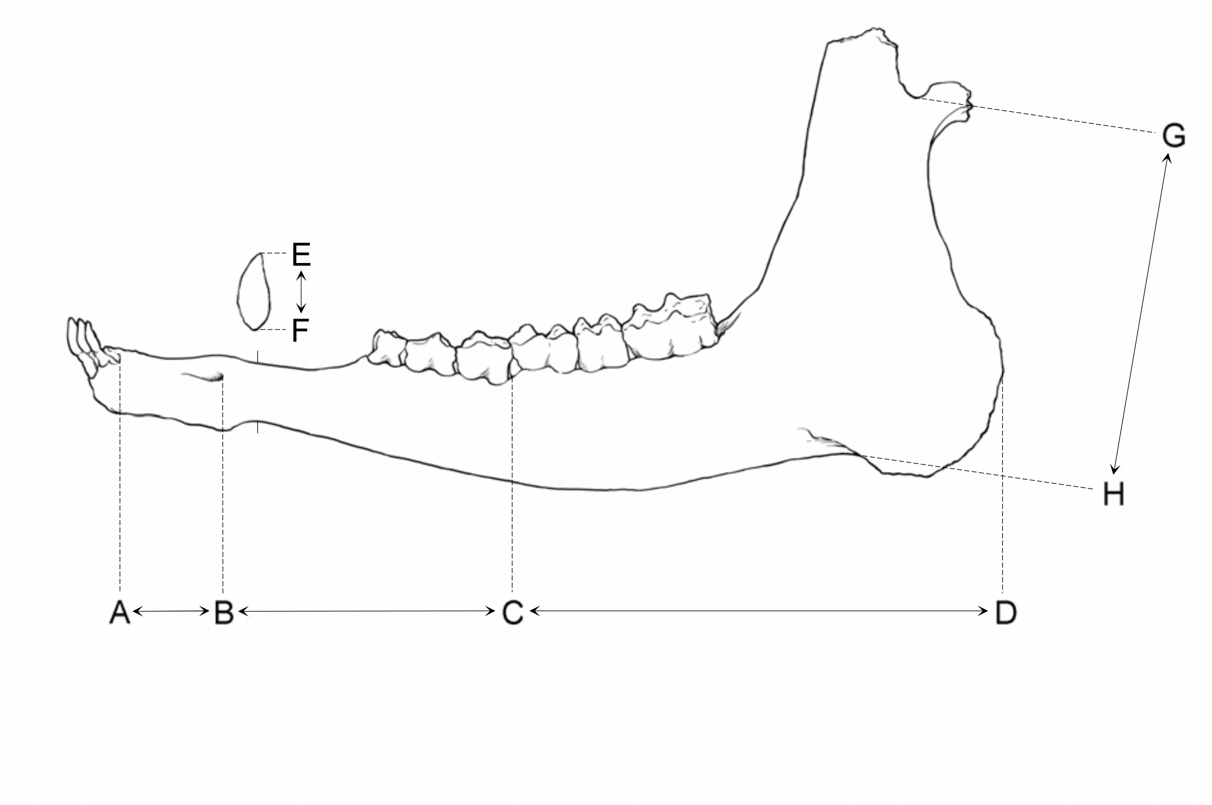


Figure 2

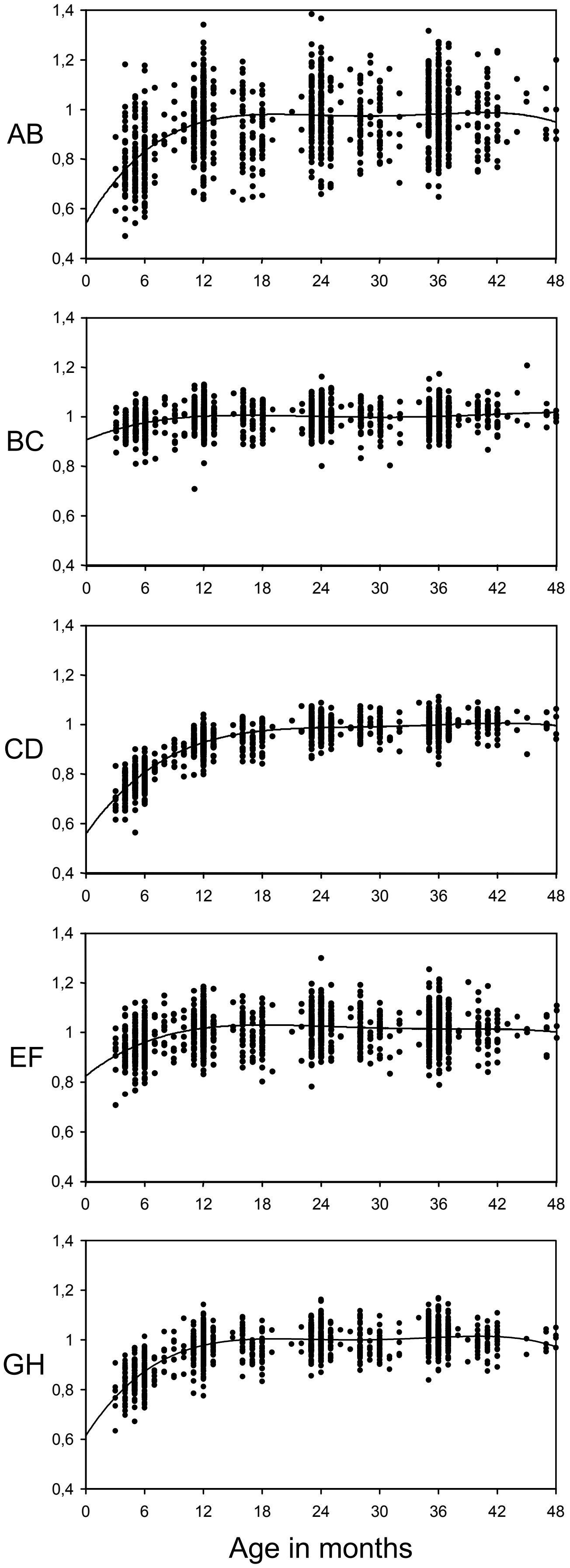


Figure 3

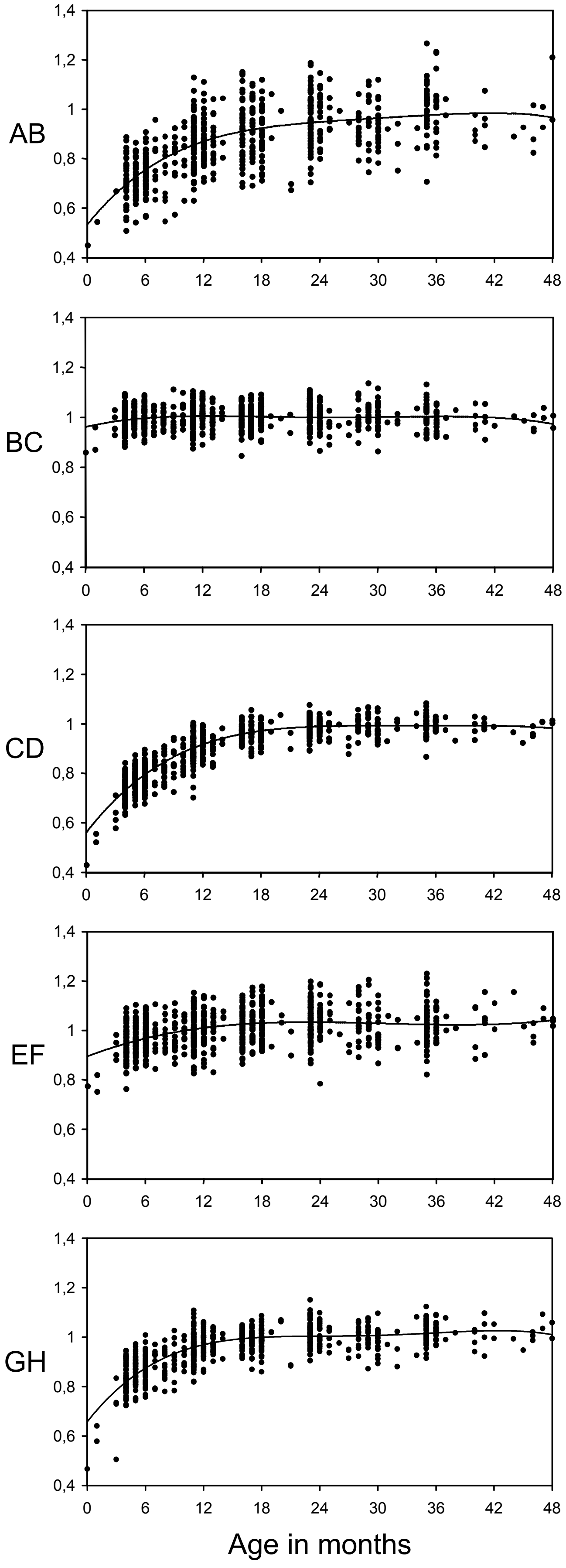


Figure 4

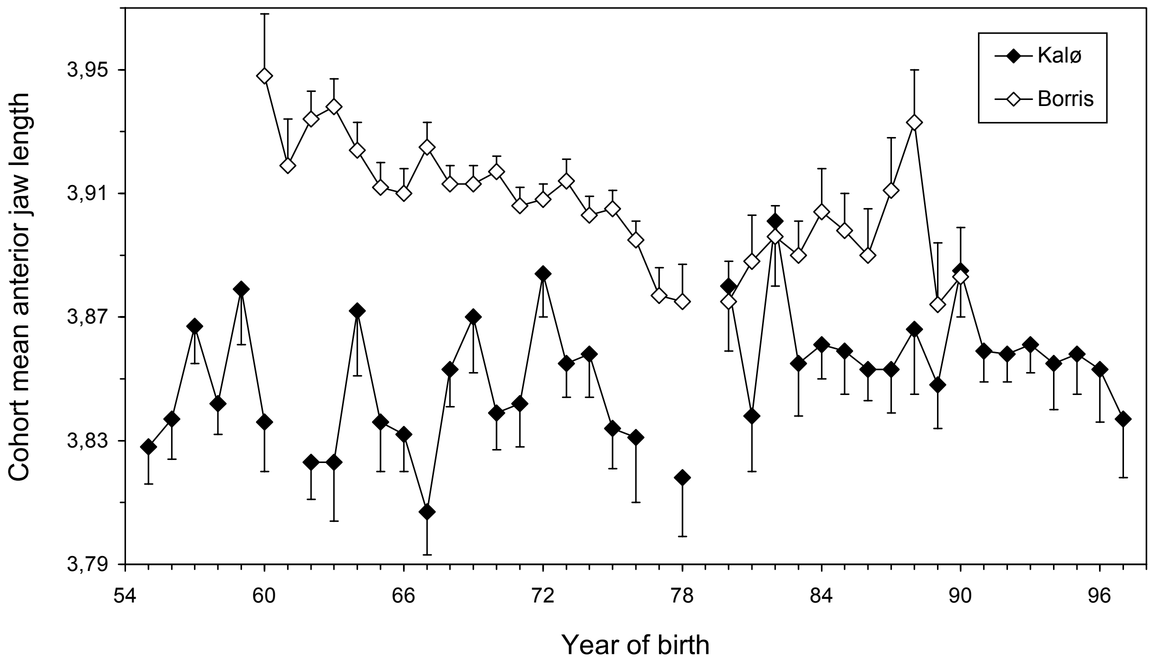

Cohort mean anterior jaw length
3,95
3,91
3,87
3,83
3,79
54
60
66
72
78
84
90
96
Year of birth
Kalø
Borris

Figure 5

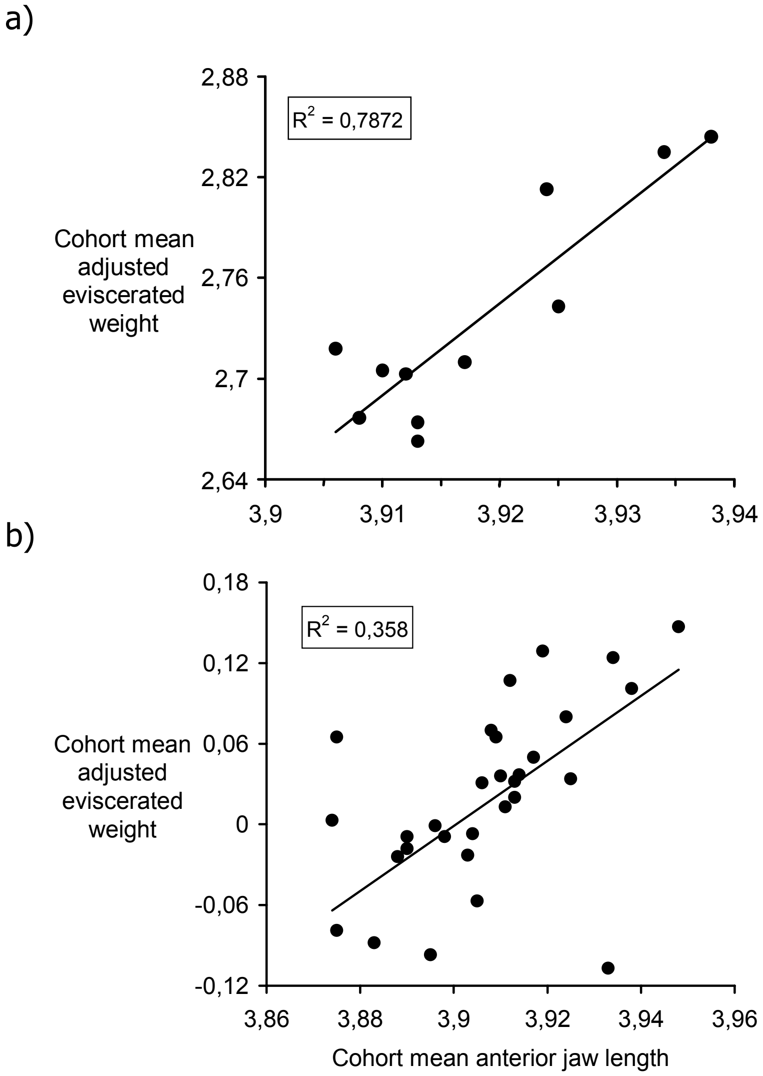

a)
R^2 = 0,7872
Cohort mean adjusted eviscerated weight
2,88
2,82
2,76
2,7
2,64
3,9
3,91
3,92
3,93
3,94
b)
R^2 = 0,358
Cohort mean adjusted eviscerated weight
0,18
0,12
0,06
0
-0,06
-0,12
3,86
3,88
3,9
3,92
3,94
3,96
Cohort mean anterior jaw length

Figure 6

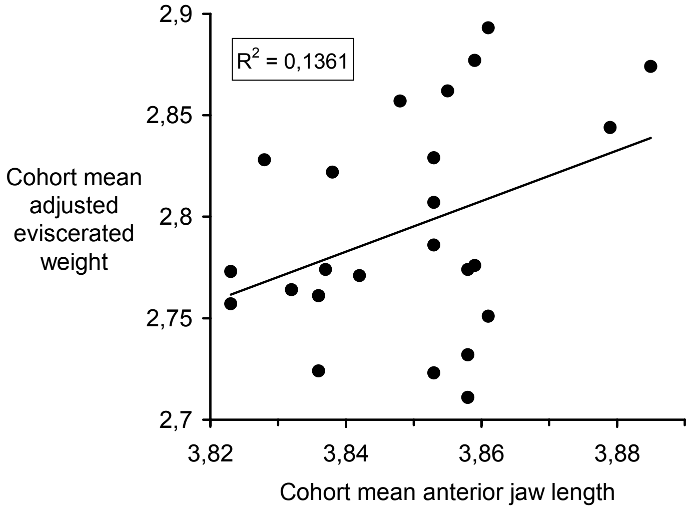

R^2 = 0,1361
Cohort mean adjusted eviscerated weight
2,9
2,85
2,8
2,75
2,7
3,82
3,84
3,86
3,88
Cohort mean anterior jaw length

Figure 7

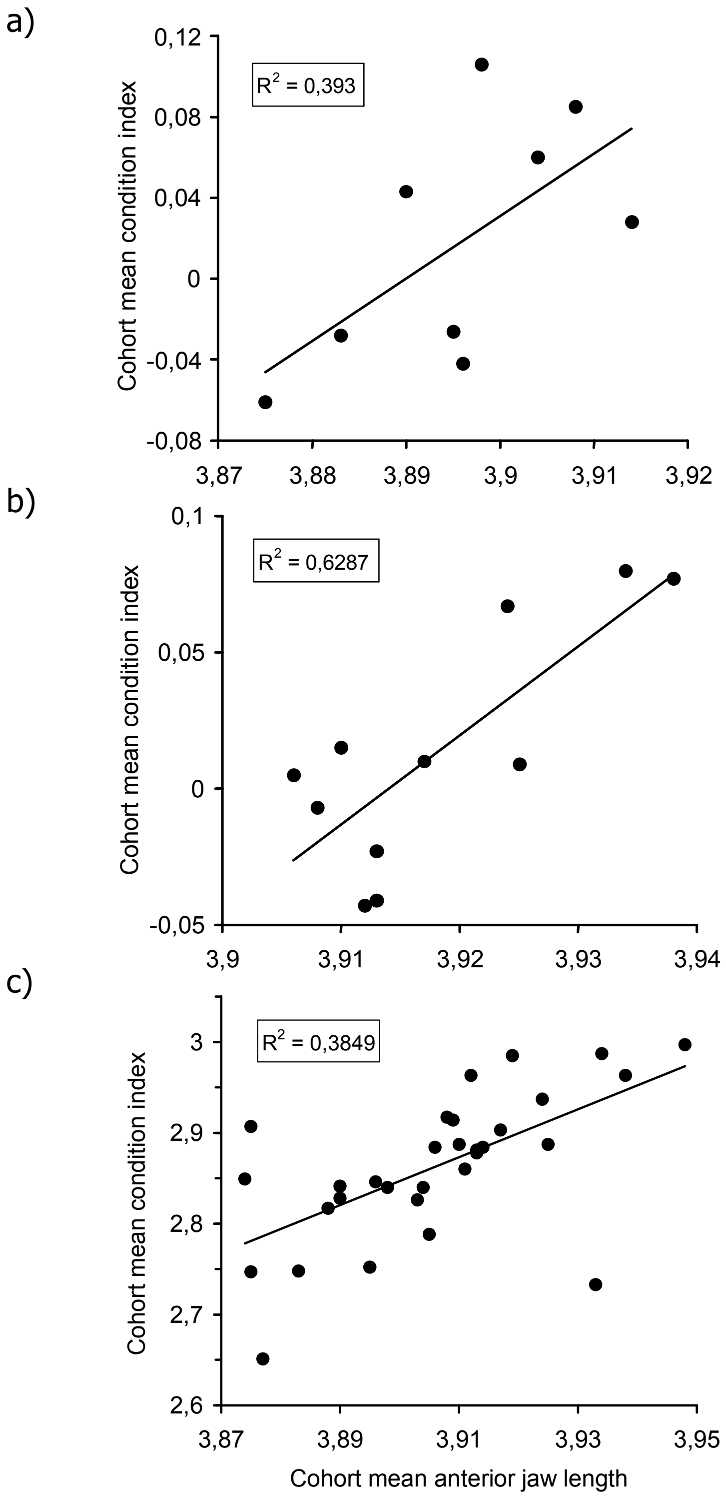
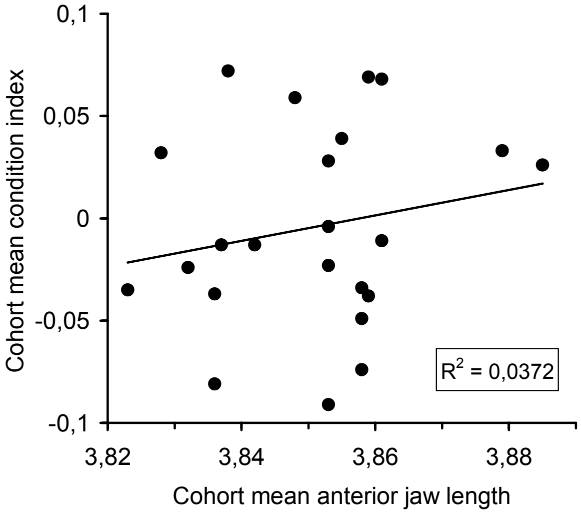

a)
R^2 = 0,393
0,12
0,08
0,04
0
-0,04
-0,08
Cohort mean condition index
3,87
3,88
3,89
3,9
3,91
3,92
b)
R^2 = 0,6287
0,1
0,05
0
-0,05
Cohort mean condition index
3,9
3,91
3,92
3,93
3,94
c)
R^2 = 0,3849
3
2,9
2,8
2,7
2,6
Cohort mean condition index
3,87
3,89
3,91
3,93
3,95
Cohort mean anterior jaw length

Figure 8


0,1
0,05
0
-0,05
-0,1
Cohort mean condition index
3,82
3,84
3,86
3,88
Cohort mean anterior jaw length
R^2 = 0,0372