Hazen in Nederland

Foto omslag: Sim Bróekhuizen en Frans Maaskamp

Promotor: dr. H. Klomp, hoogleraar in de dieroecologie.

Sim Broekhuizen

HAZEN IN NEDERLAND

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C. C. Oosterlee,
hoogleraar in de veeteeltwetenschappen,
in het openbaar te verdedigen
op woensdag 26 mei 1982
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

Stellingen

I

De hypothese van Rimathé, die stelt dat een positieve correlatie tussen de dichtheid van volwassen hazen en de reproductiesnelheid (aantal jongen per volwassen moerhaas per jaar) verklaard kan worden door een toename van het percentage superfoetatie, is onjuist.

Rimathé, R., 1977: Zur saisonalen Abundanzdynamik des Feldhasen (Lepus europaeus Pallas) im Schweizerischen Mittelland. Diss. Univ. Zürich.

II

De waargenomen variatie in de zoogtijden bij haasachtigen die hun jongen in speciaal gemaakte beschermende holen of nesten werpen, hangt samen met variatie in leeftijd van de betrokken jongen en niet met de vrije keuze van de moer.

III

De methode van Lloyd & McCowan, waarbij de duur van de zoogtijd bij in wentels geboren jonge konijnen wordt geschat door het registreren van de passages door de pijp van de wentel, is onjuist. De methode leidt tot een overschatting van de duur van het bezoek en een onderschatting van de duur van de periode waarin jongen in de wentel gezoogd worden.

Lloyd, H.C. & McCowan, D., 1968: Some observations on the breeding burrows of the wild rabbit *Oryctolagus cuniculus* on the island of Skokholm. J. Zool., Lond., 156: 540-549.

IV

Slechts een klein percentage van de zilvermeeuwen ontwikkelt zich tot rover van eieren en jongen van andere vogelsoorten. Een betere kennis van de factoren die tot dit roofgedrag leiden is noodzakelijk voor het nemen van beslissingen met betrekking tot de bestrijding van meeuwen om schade aan het broedsucces van andere vogelsoorten te beperken.

V

Indien plaatselijk het broeden van zilvermeeuwen moet worden bestreden, dan verdient het aanbeveling in het voorjaar met de actie te wachten tot het aantal nesten niet meer of nog maar weinig toeneemt en dan de bestrijding in zo kort mogelijke tijd uit te voeren. Op deze wijze kan het meest worden geprofiteerd van het feit dat het doden en vangen van zilvermeeuwen op het nest er toe leidt dat andere zilvermeeuwen hun broeden in de nabijheid opgeven.

VI

Bemesting met koperhoudende varkensmest leidt tot aantasting van de conditie van regenwormen. De mening van Eijsackers, dat de verminderde graafactiviteit van wormen in koperhoudende grond niet het gevolg is van beïnvloeding van de conditie van de wormen, blijkt niet uit het feit dat wormen zulke grond weten te mijden als daartoe de mogelijkheid bestaat.

Eijsackers, H., 1981: Effecten van koperhoudende varkensmest op regenwormen en op de kwaliteit van grasland. Landbouwk. Tijdschr./PT, 93: 307-314.

VII

In het studierapport 'Meerjarenvisie Landbouwkundig Onderzoek 1982-1986' van de Nationale Raad voor Landbouwkundig Onderzoek TNO wordt terecht opgemerkt dat er een achterstand is in het faunistisch onderzoek m.b.t. de eisen die organismen en levensgemeenschappen aan hun milieu stellen. Het voornemen het faunistisch onderzoek méér te richten op biotopen dan op afzonderlijke soorten en dan vooral op procesgerichte studies, mag niet leiden tot veronachtzaming van het inventariserende en het autecologische onderzoek.

Meerjarenvisie Landbouwkundig Onderzoek 1982-1986. 's Gravenhage, Nat. Raad Landbouwk. Onderz. TNO. 1981, 156 pp.

VIII

Het onvolledige inzicht in de invloed van de bodemmicroflora op de mate van bewegelijkheid van zware metalen in de bodem is een extra argument om verontreiniging van grond met zware metalen zo veel mogelijk te beperken.

IX

Het feit dat infectie van het Europese konijn met stammen van het myxomavirus met een hoge graad van virulentie leidde tot een relatief korte overlevingstijd van geïnfecteerde gastheren, waardoor deze stammen een kleinere kans op verspreiding en dus een hogere kans op uitsterven hadden dan stammen met een lagere graad van virulentie, wordt wel aangehaald als een voorbeeld van groepsselectie.Omdat bij deze interpretatie voorbij wordt gegaan aan het toenemen van de resistentie bij de gastheer, kan het voorbeeld niet worden opgevat als een ondersteuning van de hypothese over het bestaan van groepsselectie in het veld.

Barash, D.P., 1978: Sociobiology and behaviour. London, Heinemann. 378 pp.

X

Bij een ecologisch aangepast beheer kunnen zich in wegbermen tal van plante- en diersoorten vestigen die elders in het cultuurlandschap in hun verspreiding bedreigd worden. De nadruk die wordt gelegd op de mogelijke compensatiefunctie van wegbermen voor zulke soorten houdt het gevaar in zich dat de fatale invloed die doorsnijding van het landschap door wegen heeft voor andere diersoorten onvoldoende aandacht krijgt.

XI

Een groot deel van de inspanning die in Nederland wordt aangewend voor de bestrijding van predatoren en jagers ware beter besteed aan het behoud van de landschappelijke en natuurlijke variatie in dit land.

Stellingen behorend bij het proefschrift 'Hazen in Nederland'

S. Broekhuizen Wageningen, 26 mei 1982

Voorwoord

Dit proefschrift bevat een aantal artikelen met betrekking tot de populatieecologie van de haas in Nederland. De studie als geheel werd verricht in dienst van het Rijksinstituut voor Natuurbeheer. Bij het gereedkomen van dit proefschrift wil ik graag dank betuigen aan hen die mij bij deze studie hebben geholpen. Allereerst aan dr. A.D. Voûte, directeur van het ITBON, die het onderzoek initieerde en mij het vertrouwen voor de opdracht schonk, en aan de directeuren van het RIN, prof. dr. C.W. Stortenbeker, prof. dr. D.J. Kuenen en prof. dr. A.J. Wiggers, die mij veel vrijheid lieten ten aanzien van de uitvoering van het onderzoek. Daarnaast echter ook aan de vele medewerkers van het RIN, die niet alleen met elkaar voor een werksfeer zorgden waarin ik mij steeds bijzonder thuis voelde, maar ook daadwerkelijk meehielpen aan het onderzoek. Hoewel de hulp van velen van essentiële betekenis was, wil ik in het bijzonder noemen Herman de Vries, Johan de Wit en C.T. van Rijswijk, die allen gedurende een deel van het onderzoek aan dat helpen soms méér dan een dagtaak hadden. Het tragisch verongelukken van Johan de Wit was niet alleen voor het werk een verlies.

Dank ben ik ook verschuldigd aan Françoise Oomen-Kalsbeek, Karin Noordam, Rolf Kemmers, Ton Knijff, Pier Cnosse, Dick de Jong, Jaap van Egmond, Auke Petten, Ruud Crul en Wim van Kraaij. In het kader van hun doctoraalstudie biologie hadden ze een eigen inbreng in het onderzoek wat voor mij een grote stimulans was.

In de Nederlandse omstandigheden zijn hazen in het veld bezit van de grondeigenaren of de jachtgerechtigden. Zonder de medewerking van veel jagers en jachtopzichters zou een belangrijk deel van het onderzoek dan ook niet mogelijk zijn geweest. Mijn omgang met hen heeft me iets doen aanvoelen van hun ambivalente zorg voor het jachtwild. Het onderzoek van enkele aspecten van het gedrag van hazen zou niet mogelijk geweest zijn zonder de tolerantie en vaak ook medewerking van een aantal terreineigenaren, -beheerders en -gebruikers. In het bijzonder in het gebied rond Cortenoever mochten we een bijzondere mate van belangstelling en acceptatie ondervinden, nadat aanvankelijk 's nachts de politie nog wel eens gealarmeerd werd als we hazen volgden die onbekommerd steeds van eigenaar wisselden.

Veel collega's van andere instituten en laboratoria in binnen- en buitenland hebben me met raad en daad bijgestaan, waarvoor ik hun zeer erkentelijk ben. In het bijzonder Lise Martinet van het Station de Recherches de Physiologie Animale te Jouy-en-Josas, waarmee ik leeftijdgegevens van hazenembryo's kon uitwisselen en de Afdeling Ziektekunde Bijzondere Dieren van de Diergeneeskundige Faculteit te Utrecht, waar veel dood gevonden hazen bacteriologisch en zonodig parasitologisch werden onderzocht. Anneke en Carl König boden me de röntgenfaciliteiten voor het vaststellen van leeftijdscriteria, maar ook konden we steeds bij hen terecht als er weer iets mis dreigde te gaan met een van onze onderzoekdieren. Jane en Hans Kruuk hielpen me met de correctie van het Engels.

Wie 'in het wild' dieren bestudeert die zich moeilijk laten manipuleren, moet het vrij vaak hebben van het gelukkig toeval. Hoewel het toeval wel kan worden voorbereid, blijft het moment van optreden ongewis en een zekere mate van flexibiliteit is dan ook noodzakelijk. Dat Grada Broekhuizen meer dan één maal bereid was de net gepakte koffers weer uit te pakken en de bedoelde buitenlandse vakantie op het allerlaatste moment in te wisselen voor slapeloze nachten in een observatiecaravannetje, illustreert iets van haar onzichtbaar aandeel in het onderzoek.

Dat het voor het gezin Maaskamp aanzienlijk moeilijker was alle onverwachte wisselingen in aard en tijd van het werk op te vangen, is begrijpelijk. Dat het meestal toch lukte werd zeer gewaardeerd. Frans Maaskamp te bedanken voor zijn hulp bij het onderzoek zou misplaatst zijn. Het onderzoek was immers voor een zeer groot gedeelte net zo zeer het zijne als het mijne. Voor de manier waarop we konden samenwerken mag ik hem echter wel bedanken. Althans uiterlijk verdroeg hij me altijd gelijkmoedig, ook als ik hem na te weinig slaap wakker maakte om de observatie over te nemen. Zelfs toen ik van een duistere en glibberige polderweg in een sloot reed en hem lichamelijk letsel veroorzaakte bleef elk verwijt achterwege.

Mijn promotor ben ik veel dank verschuldigd voor zijn bereidheid me bij het schrijven van dit proefschrift te begeleiden. Van de vele kritische kanttekeningen die hij plaatste heb ik veel mogen leren.

De uitgevers van de tijdschriften waarin de reeds gepubliceerde delen van dit proefschrift zijn verschenen ben ik erkentelijk voor hun toestemming tot opname van die delen in dit proefschrift.

Curriculum vitae

Sim Broekhuizen werd op 25 juni 1937 geboren in de gemeente Pynacker. Na het behalen van het diploma HBS-B aan het Utrechts Montessori Lyceum te De Bilt in 1956 ving hij in dat zelfde jaar aan met de studie biologie aan de R.U. Utrecht. Na het behalen van het candidaatsexamen in 1961 volgde een dienstplichtvervulling van 22 maanden bij de Geneeskundige Troepen. In 1964 werd hij door de Vereniging tot Behoud van Natuurmonumenten in Nederland - helaas tijdelijk - aangesteld als vogelwachter op het eiland Griend. De universitaire studie werd in 1966 'met lof' afgesloten met een doctoraalexamen dat als hoofdrichting had Vergelijkende Fysiologie, als nevenrichting Algemene Dierkunde en als bijvakken Toegepaste Entomologie en Plantengeografie. In 1966 ook trad hij in dienst van de Centrale Organisatie TNO bij het ITBON, waarbij een begin werd gemaakt met de studie van de populatie-ecologie van hazen. Het dienstverband werd in 1971 overgenomen door het Ministerie van Landbouw en Visserij, terwijl het ITBON in het zelfde jaar opging in het Rijksinstituut voor Natuurbeheer (RIN). Naast het onderzoek aan hazen werd ook enig onderzoek gedaan aan het foerageergedrag van de beverrat, het terreingebruik bij bunzing en steenmarter en het zooggedrag bij konijnen.

Inhoud

Art. I

Hazen in Nederland

door

Sim Broekhuizen

Hazen hebben een goede schutkleur en weten vaak uitstekend gebruik te maken van in het veld aanwezige dekking.

Foto: Sim Broekhuizen

HAZEN IN NEDERLAND

Trends in afschotgegevens

Hazen hebben een zeer goede schutkleur, weten vaak uitstekend gebruik te maken van in het veld aanwezige dekking en hebben een belangrijk deel van hun activiteit 's nachts. Hierdoor wordt het observeren aanmerkelijk bemoeilijkt. Informatie over de absolute aantallen hazen per terrein is dan ook zeer schaars. Omdat bij jagers de haas als kleinwild populair is, kunnen afschotgegevens echter een globaal inzicht geven in het verloop van de hazenstand door de jaren heen ten tijde van het jachtseizoen. Weliswaar kan niet aangenomen worden dat het afschot in omvang steeds evenredig is aan de hoogte van de stand, maar in het algemeen zal bij een hoge populatiedichtheid een groter afschot worden gerealiseerd dan bij een lage populatiedichtheid.

Bij beschouwing van reeksen afschotgegevens valt op dat van jaar tot jaar aanmerkelijke verschillen kunnen optreden, terwijl daarover gesuperponeerd trends waarneembaar zijn over perioden van tientallen jaren (fig. 1). Op regionale schaal worden de korte-termijn fluctuaties vooral bepaald door klimatologische factoren, die zowel de reproductie als de mortaliteit kunnen beïnvloeden (Andersen 1957, Puppe 1966, Bresiński 1976, Spittler 1976, Frylestam 1979a).

Ten aanzien van de trends op langere termijn moet naast de mogelijke invloed van klimaatsveranderingen ook rekening worden gehouden met veranderingen in de uitvoering van de jacht en met wijzigingen in de inrichting en het gebruik van het landschap. Welke factoren in concrete gevallen het belangrijkst zijn valt niet makkelijk aan te geven. Zo laat het afschot aan hazen in Denemarken gedurende de eerste helft van deze eeuw een toenemende trend zien, terwijl de trends in de afschotgegevens in Engeland, Zweden en Duitsland in die periode gelijkblijvend of afnemend waren (fig. 1).

Achteruitgang sinds 1960

In verschillende delen van Midden- en West Europa is sinds 1960 de dichtheid van de hazenstand teruggelopen. Zo laten naast de afschotgegevens uit Skåne en East Anglia (fig. 1b en e) ook gegevens uit Zwitserland, Beieren, Denemarken en Engeland als geheel (fig. 2c-f) sinds 1960 een dalende trend zien. Hoewel deze achteruitgang zich niet overal manifesteerde (fig. 2a-b), was in veel gevallen de teruggang zo opvallend dat in 1974 de Poolse jagersvereniging naar aanleiding daarvan een internationaal symposium organiseerde (Pielowski & Pucek 1976) en

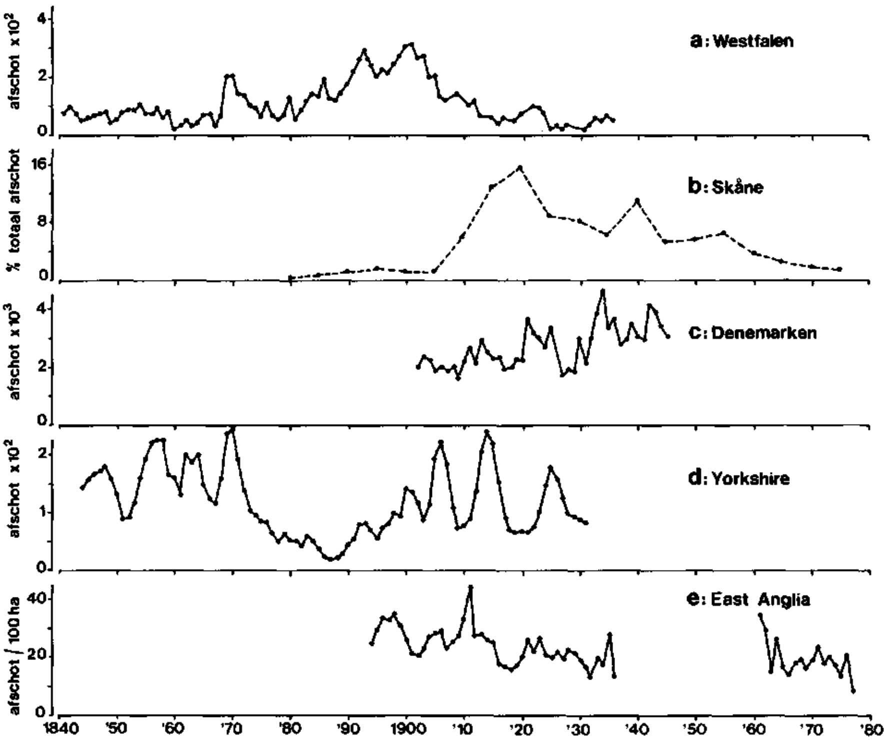


Fig. 1: Reeksen afschotgetallen die illustreren dat over de van jaar tot jaar optredende verschillen lange-termijn fluctuaties gesuperponeerd kunnen zijn.

a: afschot van een jachtveld in Westfalen, naar Rieck 1955.

b: afschot per perioden van 5 jaar van 10 landgoederen in Skåne, als percentage van het totale afschot in 100 jaar. Naar Göransson & Frylestam 1981.

c: totaal afschot van 22 districten in Denemarken, naar Andersen 1967.

d: afschot van een landgoed in Yorkshire, naar Middelton 1936.

e: afschot van 5 jachtvelden in East Anglia, naar Tapper & Parsons 1979.

de Conseil International de la Chasse in 1980 het zelfde deed (Coles 1981). In Zwitserland leidde de teruggang tot een omvangrijk onderzoekproject van de Allgemeiner Schweizerischen Jagdschutzverein en de Gruppe für Wildforschung van de Universiteit van Zürich (Merz 1973 & 1976, Fiechter 1975, Rimathé 1977, Pfister & Rimathé 1979). In Zweden startte het Department of Animal Ecology van de Universiteit van Lund in 1981 een onderzoekproject onder de titel 'Agriculture and Wildlife' (Göransson & Frylestam 1981).

In het algemeen worden de oorzaken van de teruggang van de hazenstand gezocht in veranderingen in het milieu, met name in de intensivering van de landbouw en de daarmee samenhangende veranderingen in de inrichting van het landschap. In Engeland is wel gesuggereerd dat de toename van de hazenstand daar in de periode 1954-'60 (fig. 2f) het gevolg zou zijn geweest van de enorme teruggang van de konijnenstand ten gevolge van het uitbreken van de myxomatosis. Als gevolg daarvan zou voor de hazen de voedselconcurrentie kunnen zijn verminderd als ook de predatiedruk, wanneer met de konijnen ook het aantal vossen afnam (Tappert & Parsons 1979). De afname van de hazenstand na 1960 zou dan mede het gevolg kunnen zijn van het herstel van de konijnenpopulaties.

Ook in Nederland is in enkele gebieden met een oorspronkelijk hoge konijnenstand vastgesteld dat in de jaren na de eerste myxomatosis-golf de hazenstand toenam, en in het begin van de jaren zestig weer afnam. Ook kon worden aangetoond dat bij hazen de besmettingskans voor de voor hazen schadelijke maagworm *Graphidium strigosum* vooral bepaald wordt door de aanwezigheid van konijnen (Broekhuizen 1975, Broekhuizen & Kemmers 1976). Toch lijkt het onwaarschijnlijk dat de teruggang van de hazenstand sinds 1960 in zijn algemeenheid het gevolg is van het herstel van de konijnenstand na de eerste myxomatosis-epidemieën. Zo komen in Oostenrijk konijnen weliswaar maar op enkele plaatsen voor en is het hazenafschot in dat land in de vijftiger- en zestiger jaren vrij stabiel gebleven (fig. 2a), maar konijnen ontbreken ook in de meeste kantons van Zwitserland waar de hazenstand wel achteruit ging. In Denemarken komen konijnen maar op enkele plaatsen voor, zodat ook daar de invloed van de konijnen op de jachtresultaten is uit te sluiten. In Nederland is de teruggang van de hazenstand ook niet beperkt gebleven tot gebieden met een hoge konijnenstand. Ook in een aantal gebieden met grootschalige akkerbouw op kleigrond is de hazenstand na 1960 teruggelopen. Het best is de teruggang gedocumenteerd voor de Noordoostpolder (fig. 3a). Helaas is men in Nederland pas sinds enkele jaren tot een landelijke jachtstatistiek gekomen (Leeuwenberg 1981). Een goed overzicht van de ontwikkeling van de hazenstand in de verschillende delen van het

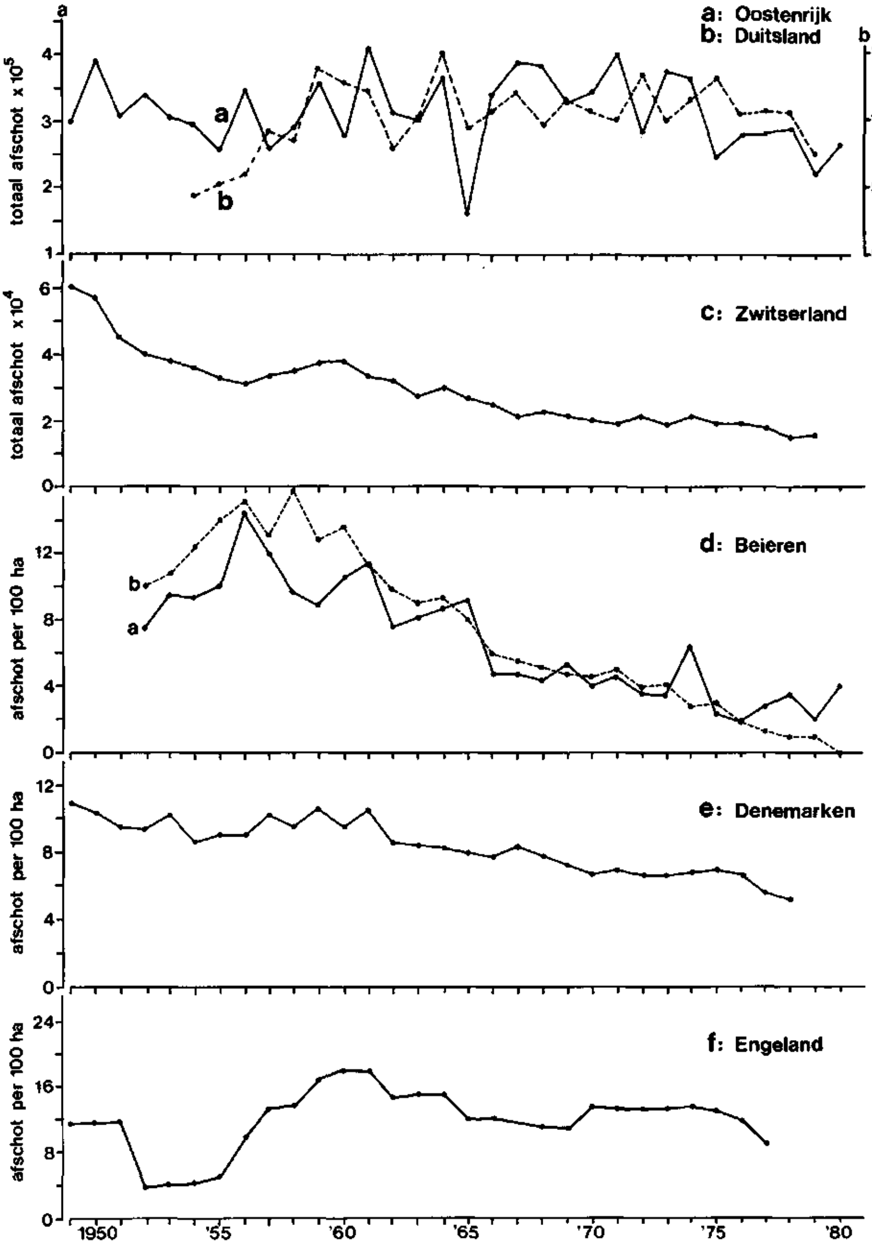


Fig. 2: (zie voor onderschrift volgende pagina).

land in de zestiger jaren ontbreekt dan ook. Uit wat over die periode wel bijeen is gebracht (Leeuwenberg, ongepubl.), blijkt dat ook landelijk gezien het afschot aan hazen een duidelijk dalende trend vertoonde (fig. 3b).

De teruggang van het hazenafschot in Nederland heeft tot nu toe betrekkelijk weinig aandacht gekregen. Doordat het afschot altijd aan fluctuaties onderhevig is geweest en de teruggang zich ook in Nederland niet overal in dezelfde mate voordeed, is het klaarblijkelijk structurele karakter van de achteruitgang slechts geleidelijk aan onderkend. De geringe aandacht kan ook samenhangen met het feit dat de haas de laatste zoogdiersoort is waarop de jacht in hoofdzaak nog als oogst- of recreatiejacht wordt uitgeoefend. De zorg van de jagers voor jaagbaar wild wordt vaak als hypokriet ervaren, omdat achter de wens naar een hogere wildstand de wens naar een groter afschot wordt gezien. De gedachtengang is vaak: als jagers bezorgd zijn over de teruggang van de wildstand, laten ze dan maar eerst ophouden er op te schieten. Dit kan jagers weerhouden hebben veel aandacht voor de teruggang van de hazenstand te vragen. De wens naar onderzoek naar de oorzaken van de teruggang kwam dan ook pas naar voren in een stadium van teruggang, waarbij het voor de jagers vaak al onaantrekkelijk was om nog een deel van de geslonken stand voor onderzoek beschikbaar te stellen, terwijl herhaalde bemonstering van de vereiste omvang de populatiegegevens zelf zou hebben beïnvloed.

Fig. 2: Verloop van het hazenafschot in verschillende delen van Europa gedurende de laatste decennia.

a: totaal afschot in Oostenrijk, naar Kutzer & Frey 1977.

b: totaal afschot in West-Duitsland, naar Spittler 1981.

c: totaal hazenafschot (*Lepus europaeus* + *L. timidus*) in Zwitserland zonder de kantons Ticino en Genève, naar Anderegg 1979 en voor 1976-'79 aangevuld met gegevens uit jaaroverzichten van het Oberforstinspektorat, Sekt. Jagdwesen und Wildforschung (stencils).

d: afschot per 100 ha in twee jachtgebieden in Neder-Beieren.
  a: Eging, waar gedurende de jaren '60 een ruilverkaveling werd uitgevoerd; b: Kirchberg, waar alleen 'autonome ontwikkeling' het landschap beïnvloedde. Naar Passberger 1981.

e: gemiddeld afschot per 100 ha voor geheel Denemarken, naar Strandgard & Asferg 1980 en Asferg 1980.

f: gemiddeld afschot per 100 ha voor Engeland.
De lijn is afgevlakt door steeds het gemiddelde van drie opeenvolgende jaren te nemen. Naar Tapper & Barnes 1981.

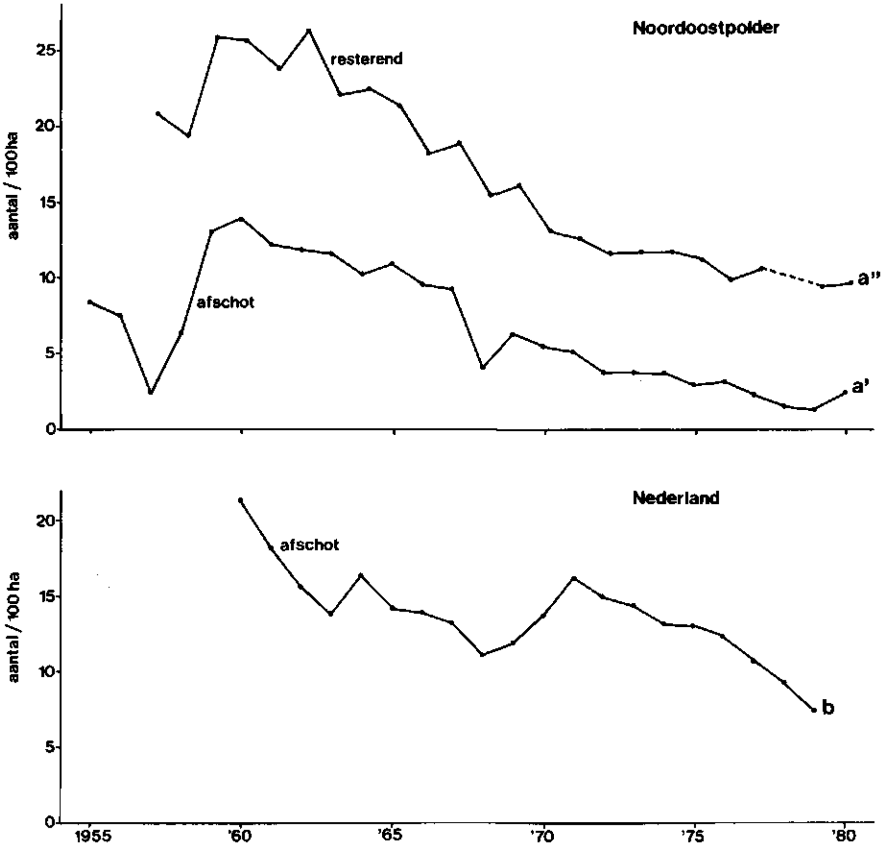


Fig. 3: Verloop van het gemiddelde afschot van hazen per 100 ha voor de Noordoostpolder (a') en Nederland als geheel (b, zie tekst). In de Noordoostpolder is sinds 1957 ook de populatiedichtheid in de maanden januari-februari bepaald (a''), door in ieder jachtperceel een aantal landbouwkavels af te drijven (gegevens Rentambt Noordoostpolder).

Achteruitgang en leeftijdsopbouw

Ondanks het feit dat de teruggang van de hazenstand vrij algemeen in verband werd gebracht met de toenemende intensivering van de landbouw, was de oorzaak allerminst duidelijk. Onder de indruk van de grootschalige neveneffecten van het gebruik van persistente pesticiden in de tweede helft van de zestiger jaren, werd ook voor hazen gesuggereerd dat de teruggang het gevolg kon zijn van een verhoogde mortaliteit, veroorzaakt door deze bestrijdingsmiddelen. Het feit dat inderdaad vergiftiging door pecticiden plaatselijk op enige schaal optrad, versterkte dat idee. In Nederland werd hierover door van Klingeren et al. (1967)

bericht. Het droeg bij tot een toename van inzendingen van in het veld dood aangetroffen hazen. Voor de meeste van deze hazen kon echter worden vastgesteld dat ze gestorven waren aan bacteriële of parasitaire infecties (Broekhuizen & Poelma 1969, 1970). In hoeverre er van een toename van zulke infecties sprake was als gevolg van een door pesticiden veroorzaakte conditievermindering, is niet duidelijk geworden.

Naast aan toename van de mortaliteit door de toepassing van bestrijdingsmiddelen, kon ook gedacht worden aan een verminderde reproductie daardoor en aan een verhoogde zuigelingensterfte als gevolg van intensievere landbewerking. Bij de analyse van de verschillende oorzaken wreekt zich het feit dat in het veld geen 'blanco' situaties ter vergelijking worden aangetroffen, ten opzichte waarvan de invloed van een enkele faktor bestudeerd kan worden, en óók dat vóór de jaren zestig in Nederland geen gegevens over de leeftijdsopbouw van de hazenstand zijn verzameld. In die tijd ontbrak een bruikbare methode om de leeftijd te bepalen, zodat tijdens het jachtseizoen geen onderscheid kon worden gemaakt tussen de aanwas van dat jaar en de oudere hazen. Ten aanzien van de soms gebruikelijke methode om dat onderscheid te maken aan de hand van het al dan niet aanwezig zijn van de distale epiphysaire kraakbeenschijf in de ulna, was twijfel gerezen. De mogelijkheid om ook bij hazen het gewicht van de ooglens voor leeftijdsbepaling te gebruiken, was juist door Rieck (1962) naar voren gebracht. Omdat een bruikbare leeftijdsbepaling ook van belang was bij de studie van de invloed van mortaliteitsfaktoren en de reproduktie, was het zaak voor de Nederlandse situatie referentiewaarden te verzamelen en de bruikbaarheid van leeftijdskriteria te toetsen. De resultaten hiervan zijn weergegeven in het artikel 'Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands', dat hier is bijgevoegd en verder wordt aangeduid als Art. II.

Sterfte onder volwassen hazen

In een aantal jachtvelden is gedurende één of meerdere jaren aan de hand van het hazenafschot de verhouding tussen de dieren uit voorgaande jaren en de aanwas bepaald. Als vóóronderstelling gold, dat het geschoten deel van de populatie representatief was voor de aanwezige populatie. Daar uit de jachtliteratuur bekend was dat dit waarschijnlijk het meest het geval is bij drijfjachten waarbij ook 'geweren' tussen de drijvers meelopen, werden jachtvelden gekozen waar deze vorm van bejaging plaatsvond. Samen met terugmeldingen van gemerkte hazen leverde het onderzoek informatie over de levensverwachting voor volwassen hazen. Deze informatie is neergelegd in het artikel 'Survival in adult European hares', dat hier is bijgevoegd en verder wordt aangeduid als Art. IV. Het bleek dat de berekende levensverwachting voor een volwassen haas ruim één jaar bedroeg, wat inhoudt dat de hazen gemiddeld slechts één seizoen aan de voortplanting deelnemen. Het betreft hier dus een levensverwachting bij bejaagde populaties.

Een groot nadeel van het onderscheiden van aanwas (eerstejaars) en oudere hazen door middel van het ooglensgewicht is dat deze methode niet door amateurs gehanteerd kan worden. Hierdoor bleef de informatie beperkt, en in het kader van dit onderzoek was het niet mogelijk om voldoende materiaal te verzamelen om regionale gemiddelden te kunnen vergelijken. Spijtig is ook dat geen onbejaagde populaties bemonsterd konden worden om het effect van exploitatie op de leeftijdsopbouw te kunnen nagaan.

Bij het bepalen van de leeftijdsverwachting hebben we ons moeten beperken tot volgroeide hazen. Dit als gevolg van het feit dat verreweg de meeste hazen die gemerkt werden aan het einde van of kort na het jachtseizoen werden gevangen en dan reeds volgroeid waren. Jonge hazen zijn veel moeilijker te bemachtigen en meldingen anders dan door jacht zijn spaarzaam. Het is ook aannemelijk dat de vind- c.q. meldkans voor jonge hazen afhankelijk is van de lichaamsgrootte en dus van de leeftijd.

Sterfte onder jonge hazen gedurende hun zoogperiode

Om iets naders te kunnen zeggen over de overlevingskans bij pasgeboren haasjes, diende eerst meer inzicht te worden verkregen in hun levenswijze. Dit leidde tot uitvoerige observaties gedurende de zoogperiode, waarvan de resultaten zijn neergelegd in het artikel 'Behaviour of does and leverets of European hares (*Lepus europaeus*) whilst nursing', dat hier is bijgevoegd en verder wordt aangeduid als Art. V. De observaties toonden aan dat jonge haasjes soms al na één of enkele dagen zelfstandig de geboorteplaats verlaten, maar er ongeveer drie kwartier na zonsondergang weer terugkomen om er gemiddeld één kwartier later door de moerhaas te worden gezoogd. De wetenschap dat de jongen gedurende de zoogperiode op een vrij vaste tijd teruggaan naar de plaats van geboorte, maakt het mogelijk op eenmaal vastgestelde geboorteplaatsen gedurende de zoogperiode op eenvoudige wijze 'appèl van overlevenden' te houden, en op die manier inzicht te krijgen in de overleving gedurende de zoogperiode. Er zijn echter twee beperkingen: het aantal geboren haasjes moet bekend zijn en het bijeenkomen van de zuigelingen moet te observeren zijn.

Af en toe wordt een worp jonge haasjes gevonden waarvan het aannemelijk is dat hij nog compleet is. Meestal is dat echter onzeker. Als het oorspronkelijke aantal jongen niet bekend is, kan daarvoor in de plaats als referentie het gemiddelde aantal embryo's per drachtige moer gebruikt worden. Dit gegeven werd ontleend aan onderzoek van drachtige moerhazen uit verschillende delen van het land dat zich over meerdere jaren uitstrekte, en waarvan de resultaten zijn samengevat in het artikel 'Annual production of young in European hares (*Lepus europaeus*) in the Netherlands'. Dit artikel is hier bijgevoegd en wordt verder aangeduid als Art. VI. Substitutie van het gevonden gemiddelde aantal embryo's per drachtige moerhaas voor het oorspronkelijke aantal geboren jongen per in het veld gevonden worp betekende zeker een aanmerkelijke vergroving, omdat voorbij moest worden gegaan aan mogelijke verschillen in de gemiddelde worpgrootte per terrein en per jaar.

De gegevens met betrekking tot de worpgrootte bij hazen, zoals bijeengebracht in Art. VI, zijn gebaseerd op het aantal normale embryo's dat bij de onderzochte moerhazen werd aangetroffen. Over het jaar bleek het gemiddelde aantal per drachtige moerhaas niet constant, maar gedurende de eerste maanden van het voortplantingsseizoen toe te nemen en in april-mei het maximum te behalen. Als gevolg van deze verandering van de gemiddelde worpgrootte was het voor de vergelijking van het gemiddelde aantal waargenomen embryo's per moeder en het gemiddelde aantal waargenomen zogende jongen per worp nodig beide gegevens te betrekken op één tijdstip. Van de geobserveerde zogende jongen werd aan de hand van visuele schattingen van de grootte de leeftijd bepaald en op grond daarvan de vermoedelijke datum van geboorte. Om ook bij de onderzochte drachtige moerhazen de leeftijd van de embryo's en de daarbij behorende datum van geboorte te kunnen bepalen, zijn de daarvoor beschikbare referenties samengebracht in het artikel 'Growth of embryos of the European hare (*Lepus europaeus* Pallas)', dat hier is bijgevoegd en verder wordt aangegeven als Art. III. Daar pas in een latere fase van het onderzoek de embryo's voldoende nauwkeurig werden opgemeten, is voor de embryo's gesteld dat ze zich gemiddeld halverwege hun ontwikkeling bevonden en gemiddeld drie weken later geboren zouden zijn. Door van de geschatte geboortedata van de geobserveerde jongen drie weken terug te gaan, werd de maand gevonden waarvan het gemiddelde embryo-aantal als vergelijking diende.

De hierboven aangegeven vergelijking tussen het aantal embryo's per drachtige moerhaas en het gemiddelde aantal waargenomen jongen per worp aan het einde van de zoogtijd, is weergegeven in fig. 4. De zoogtijd is hier gesteld op één maand, wat voor de laatste worpen van het seizoen strikt genomen niet opgaat (Art. V p. 496). Indien we de maandgemiddelden voor het aantal gespeende jongen uit fig. 4 substitueren voor de worpgrootte in Tabel VI van Art. VI, waarin de productie van jongen per gezonde moerhaas per jaar werd berekend aan de hand van het aantal embryo's, dan blijkt dat van de gemiddelde productie van 11 jongen

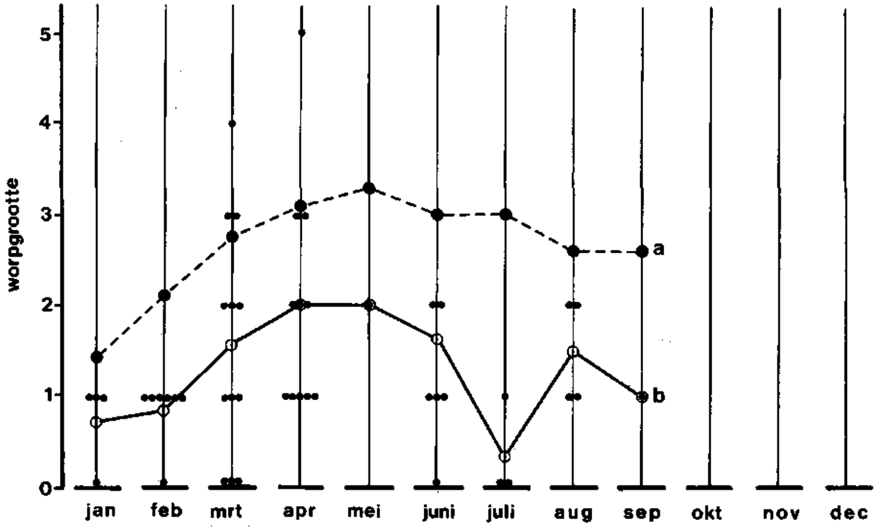


Fig. 4: Het verloop van het maandelijkse gemiddelde van het aantal embryo's bij drachtige moerhazen (a), de daarbij behorende aantallen geobserveerde jongen per nest die ouder werden dan één maand (stippen) en het verloop van het maandelijkse gemiddelde daarvan (b).

Tabel 1: Netto productie van gespeende jongen (voor de worpen uit augustus en september jongen van één maand oud) in de loop van het jaar per volwassen, gezonde moerhaas.

maand	percentage drachtige moerhazen')	aantal jongen dat gespeend wordt (fig. 4)	maanden tussen opeenvolgende worpen')	productie aan zelfstandige jongen
jan.	68	0,75	1,6	0,32
feb.	86	0,86	1,6	0,46
maart	73	1,58	1,6	0,72
april	100	2,0	1,6	1,25
mei	89	2,0	1,6	1,11
juni	80	1,67	1,6	0,83
juli	62	0,33	1,6	0,13
aug.	78	1,50	1,6	0,73
sept.	22	1,0	1,6	0,14
okt.	0	-	-	-
nov.	0	-	-	-
dec.	0	-	-	-
Totale productie per jaar				5,69

'): ontleend aan tabel 4 van Art. V.

per jaar er slechts 5,7 ouder worden dan één maand, wat een sterfte van 48% zou betekenen voor de eerste levensmaand (tabel 1). Verdisconteerd moet echter worden dat deze berekening stoelt op observaties van het zogen van worpen waarvan bij de eerste observatie tenminste nog één jong in leven was. Worpen die in een vroeg stadium geheel verloren gaan hebben een kleine kans geobserveerd te worden, zodat de sterfte van 48% in de eerste levensmaand wat dat betreft een onderschatting van de werkelijkheid zal zijn. Doordat grote worpen eerder zullen opvallen dan kleine, kan ook daardoor een te optimistische schatting van de overleving verwacht worden. Anderzijds moet in aanmerking worden genomen dat de zoogwaarnemingen gedaan zijn op plaatsen met weinig dekking. Het is mogelijk dat in gebieden met méér dekking en een minder intensief grondgebruik de jeugdmortaliteit aanmerkelijk lager ligt.

Sterfte onder de opgroeiende hazen tot de winter

Bij onderzoek van het ooglensgewicht van hazen die waren geschoten op drijfjachten waarbij tenminste 20 hazen konden worden onderzocht, bleek dat gemiddeld 63,1% van de geschoten hazen een ooglensgewicht van minder dan 280 mg had en dus (Art. II) tot de aanwas van het betreffende jaar behoorde (fig. 5). Van de oudere hazen bleek 50,95% vrouwelijk te zijn. De geringe maar significante meerderheid van moerhazen blijkt het gevolg te zijn van een grotere overleving onder de oudere moerhazen (fig. 6), zoals ook werd gevonden door Flux (1967), Pielowski (1971) en Möller (1975).

Met inachtneming van de geslachtsverhouding blijkt dat ten tijde van het jachtseizoen (15 oktober - 31 december) per volwassen moerhaas gemiddeld nog een aanwas van 3,4 resteerde. Omdat bij een gemiddelde productie van 11 jongen per gezonde, volwassen moerhaas en een zuigelingensterfte van 48% er per gezonde moerhaas gemiddeld 5,7 jongen zelfstandig worden, wijst de teruggang tot 3,4 jongen per moerhaas tijdens het jachtseizoen er op dat tot die tijd en nadat de jongen onafhankelijk van de moer zijn geworden, de sterfte onder de zelfstandige jongen hoger is dan onder de oudere hazen.

Gezien de lage levensverwachting van maar iets meer dan één jaar voor volwassen hazen (Art. IV) en de hoge reproductiesnelheid (Art. VI), lijkt het voor de hand liggend dat de populatiegrootte tijdens het jachtseizoen, en ook de 'breeding stock' aan het einde daarvan, in hoge mate wordt bepaald door het reproductiesucces in het afgelopen jaar. Inderdaad hebben meerdere onderzoekers de aandacht gevestigd op de relatie tussen het percentage jongen (= aanwas) in de populatie omstreeks het einde van het jaar en de omvang van het afschot of van de 'breeding stock' voor het volgende voortplantingsseizoen (Jezierski 1965,

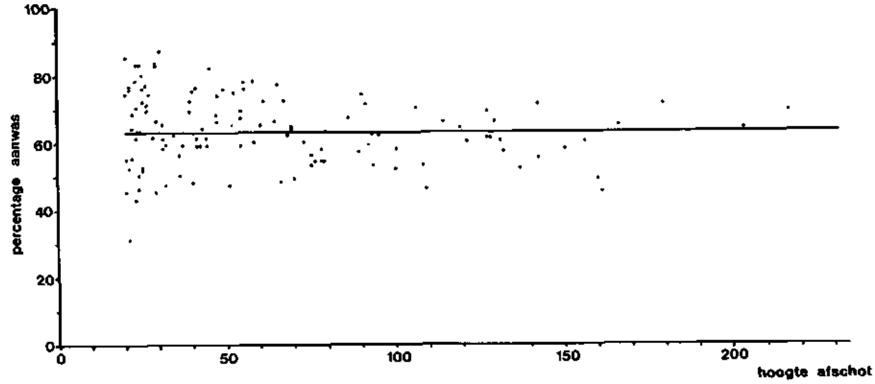


Fig. 5: De relatie tussen de aanwas (het percentage hazen met een ooglensgewicht van 280 mg en minder in het afschot) en de omvang van het afschot bij drijfjachten tijdens het jachtseizoen, waarbij tenminste twintig hazen werden geschoten.

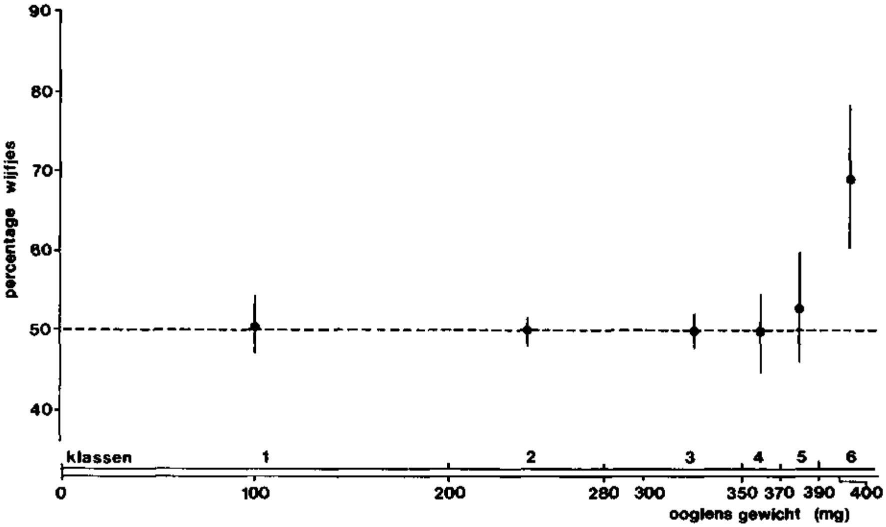


Fig. 6: Percentage wijfjes en de 90% betrouwbaarheidsintervallen in het afschot van de onderzochte drijfjachten per ooglensgewichtsklasse. De verdeling van de hazen over de ooglensgewichtsklassen is 1: 744, 2: 3557, 3: 2132, 4: 401, 5: 206, 6: 107. Ze werden in de jaren 1966-'76 geschoten in 32 jachtvelden.

Pielowski 1968, Petrusewicz 1970, Adamczewska-Andrzejewska & Szaniawski 1972, Möller 1975, Frylestam 1979). Het gevonden verband maakt niet duidelijk in hoeverre fluctuaties in de omvang van de winterstand bepaald worden door fluctuaties in de nataliteit en in hoeverre door fluctuaties in de overleving van geboren jongen.

Literatuurgegevens met betrekking tot de overleving van jongen tot aan de winter vertonen een opmerkelijke overeenstemming. In Polen kwam Petrusewicz (1970) op ongeveer 26%, Pielowski (1975) op 23% en Pielowski & Raczynski (1976) meldden 20-30%. Voor Bulgarije gaven Petrov & Dragoev (1962) 25% aan en voor zijn onderzoekterreinen op het Zweedse vasteland vond Frylestam (1979b) een gemiddelde van 22%. Möller (1975) vond echter verschil in overleving van jongen in gunstige en ongunstige biotopen: 12-33% en 5-15% respectievelijk.

Pielowski (1975 & 1976) vond in zijn onderzoekterrein ten zuiden van Poznań dat de sterfte onder de jonge hazen van jaar tot jaar weinig verschilde. Omdat hij echter wel een hoge positieve correlatie vond tussen het percentage aanwas in de herfstpopulatie en de hoogte van die populatie, concludeerde hij dat de populatieschommelingen in overwegende mate het gevolg waren van verschillen in nataliteit, en niet van verschillen in overleving van de jongen. Dit is opmerkelijk, omdat andere onderzoekers (o.a. Andersen 1952 & 1957, Rieck 1956, Nováková & Hanzl 1966, Möller 1967, Brezinski 1976, Petrov 1976, Spittler 1976) wel verschillen in de reductie van de aanwas vonden als gevolg van veranderde milieufactoren als temperatuur en neerslag. Naast een directe invloed hebben deze factoren ook een belangrijke indirecte invloed op de overleving van de jongen, omdat ze in sterke mate bepalend zijn voor de ontwikkeling van coccidiosis, een ziekte veroorzaakt door infectie van de darmepitheelcellen met ééncellige parasieten van het geslacht *Eimeria* (Bouvier et al. 1954, Kötsche & Gottschalk 1972). Jonge hazen zijn voor deze infectie aanzienlijk gevoeliger dan volwassen hazen (zie ook fig. 7).

Dichtheidsafhankelijke sterfte

Behalve waarnemingen van positieve correlaties tussen het percentage aanwas in de winterpopulatie en de omvang van het afschot c.q. hoogte van de winterpopulatie of van de breeding stock (in tabel 2 is dat de correlatie d/c), zijn er ook waarnemingen die duiden op een negatieve correlatie tussen het percentage aanwas in de winterpopulatie en het aantal oudere hazen in de winterpopulatie (Petrusewicz 1970) of tussen het percentage aanwas in de winterpopulatie en het aantal oudere moerhazen daarin (Abildgard et al. 1972). In de opzet van tabel 2 gaat het in beide gevallen om een negatieve correlatie d/a, wanneer de geslachtsverhouding onder de oudere hazen niet aan aanmerkelijke verandering onderhevig is. Deze negatieve correlatie zou zowel het gevolg kunnen zijn van een dichtheidsafhankelijk negatief effect op de nataliteit, als ook het gevolg van jeugdsterfte die in haar omvang afhankelijk is van de dichtheid van de oudere hazen. Wanneer de nataliteit en/of de overleving van de jongen niet al te sterk afnemen met toenemende dichtheid draagt de relatie bij tot een stabilisatie van de aantallen binnen populaties.

Binnen bepaalde dichtheidsgrenzen kan een positieve correlatie tussen het percentage aanwas en de hoogte van de totale stand (tabel 2: d/c) alléén door de negatieve correlatie tussen het percentage aanwas in de populatie en de dichtheid van de oudere dieren (tabel 2: d/a) veroorzaakt worden. Het dichtheidsafhankelijke effect zou dan echter buitengewoon sterk moeten zijn en het zou dan zeker algemeen zijn onderkend. Daar dat niet het geval is wijst een positieve correlatie d/c op de werking van dichtheids*on*afhankelijke factoren. Deze kunnen betrekking hebben op de nataliteit, als ook op de jeugdmortaliteit wanneer er in de populatie een numeriek overwicht van de aanwas is. Dat laatste is in het algemeen het geval (zie ook fig. 5 en tabel 2).

Van de door ons in de jaren 1966-'76 onderzochte jachttableaus van 24 plaatsen met elk meer dan 20 voor onderzoek geschikte hazen, is de relatie tussen het percentage aanwas en de omvang van het afschot weergegeven in fig. 5. De gegevens laten géén positieve correlatie zien tussen het percentage aanwas en de omvang van het tableau. Hoewel de onderzochte tableaus alle het resultaat waren van een hele dag drijfjacht en als zodanig zeker reflecties vormden van de populatiedichtheden ter plaatse, is de omvang van het afschot ook afhankelijk van de aard van het terrein, het jachtgezelschap en de jachtmethode. De relatie tussen het percentage aanwas in de populatie en het afschot (c.q. de populatiedichtheid) laat zich dan ook beter beoordelen aan de hand van afschotresultaten in verschillende jaren uit terreinen waarin de jacht op min of meer constante wijze werd uitgeoefend. Van drie terreinen waar dat laatste het geval was, konden we over tenminste vijf jaren gegevens verzamelen, te weten het eiland Tiengemeten (ZH), het Balloërveld (D) en de luchthaven Schiphol. De betreffende gegevens zijn samengevat in tabel 2. Op Schiphol was het niet steeds mogelijk om alle geschoten hazen op leeftijd te onderzoeken. Sommige hazen waren daarvoor te veel beschadigd, soms ook ontbrak daartoe de tijd. Aangenomen wordt dat het wel onderzochte deel van het afschot in samenstelling niet afweek van het niet onderzochte deel.

Op grond van de gegevens van tabel 2 blijkt dat alleen voor Schiphol een positieve en significante correlatie aanwezig was tussen het percentage aanwas in

Tabel 2. Gegevens m.b.t. het percentage aanwas in het afschot in relatie tot de hoogte van het afschot en m.b.t. de hoogte van de aanwas in relatie tot het aantal oudere hazen, ontleend aan drijfjacht-tableaus van Tiengemeten, het Balloërveld en Schiphol.

	Tiengemeten				Balloërveld				Schiphol					
									onderzocht		in totaal afschot			
	oudere hazen (a)	aanwas (b)	totaal (c)	perc. aanwas (d)	oudere hazen (a)	aanwas (b)	totaal (c)	perc. aanwas (d)	oudere hazen (a')	aanwas (b')	oudere hazen (a)	aanwas (b)	totaal afschot (c)	perc. aanwas (d)
1967	55	109	164	66,5										
1968	51	88	139	63,3	17	45	62	72,6						
1969	49	82	131	62,6	53	81	134	60,4						
1970	40	88	128	68,8	69	77	146	52,7	121	256	168	354	522	67,8
1971	46	119	165	72,1	64	88	152	57,9	165	360	168	365	533	68,6
1972	63	109	172	63,4	90	82	172	47,7	123	159	131	169	300	56,4
1973	70	94	164	57,3					121	148	122	150	272	55,0
1974	39	73	112	65,2					121	219	124	225	349	64,4
1975	89	94	183	51,4					152	254	160	268	428	62,6
1976	76	94	170	55,3					163	340	167	349	516	67,6

	Tiengemeten		Balloërveld		Schiphol	
d/c (Spearman's rangcorr.'))	r_s=-0,45	p>0,05	r_s=-0,9	p=0,05	r_s=0,90	p<0,01
d/a (Terpstra's toets voor dichot. pop.'))	$\underline{T}$=3,02	p<0,01	$\underline{T}$=3,30	p<0,01	$\underline{T}$=0,36	p=0,36

') zie tekst

het afschot en de omvang van het afschot (in tabel 2 de correlatie d/c). Voor Tiengemeten en het Balloërveld was géén positieve correlatie d/c aanwezig. Omdat het percentage aanwas in tabel 2 niet geheel onafhankelijk is van het totale afschot, kan de correlatie tussen beide grootheden m.b.v. de rangcorrelatietoets van Spearman wel worden geschat, maar niet worden getoetst. De aangegeven overschrijdingskansen hebben daarom alleen indicatieve waarde.

Voor het nagaan van een mogelijke negatieve correlatie tussen het percentage aanwas in het afschot en het aantal geschoten oudere dieren (in tabel de correlatie d/a), kan om dezelfde reden geen gebruik gemaakt worden van Spearman's rangcorrelatietoets. Wel kan met behulp van de toets van Terpstra voor aselecte steekproeven uit dichotome populaties het verband getoetst worden tussen het aantal oudere hazen in het afschot (a) en het aantal geschoten eerstejaars dieren (b). Bij deze toets is er bij een positieve waarde van de toetsingsgrootheid $\underline{T}$ sprake van een negatief verband en bij een negatieve waarde van $\underline{T}$ sprake van een positief verband. Een negatieve correlatie b/a houdt een negatieve correlatie d/a in. Omdat geldt $d=b/(a+b)$, wordt bij constante b de waarde van d kleiner als a toeneemt en wordt voor constante a de waarde van d bovendien kleiner als b toeneemt. Een significant negatieve correlatie b/a en dus ook d/a blijkt aanwezig in het materiaal van Tiengemeten en het Balloërveld, maar niet in dat van Schiphol (tabel 2).

Tijdens de periode van onderzoek onderscheidde de situatie m.b.t. Schiphol zich van die in de beide andere terreinen in die zin, dat op Schiphol het terreingebruik in de loop van de onderzoekperiode aanmerkelijk veranderde. Tot en met 1971 werd het gras tussen de start- en landingsbanen als veevoer gebruikt en daartoe gemiddeld drie maal per jaar gemaaid. Voor 1972 werd besloten het gras kort te houden, wat betekende dat het in het groeiseizoen tenminste één maal per twee weken werd gemaaid. Door het achterwege blijven van bemesting nam vanaf 1973 de maaifrekwentie weer af. In 1975 werd bovendien als proef het gras langs één van de landingsbanen weer twee of driemaal gemaaid, welke proef in 1976 tot een tweede baan werd uitgebreid. Door de droogte van dat jaar liep overigens ook de maaifrekwentie op de rest van het grasland terug: het maaien begon niet voor half april en bleef tussen half juni en begin september achterwege.

Omdat jonge haasjes zich vooral de eerste weken van hun leven bij naderend onraad 'drukken', is het aannemelijk dat een verhoogde maaifrekwentie een toename van de zuigelingensterfte onder de hazen op Schiphol veroorzaakte en dat vooral deze dichtheidsonafhankelijke factor bepalend was voor de positieve correlatie tussen het percentage aanwas tijdens het jachtseizoen en de hoogte van het afschot c.q. dichtheid van de populatie.

Regulatie en fluctuatie

De negatieve correlatie tussen het percentage aanwas in de november-december populatie en het aantal hazen in die populatie die ouder is dan één jaar, zoals we die vonden voor Tiengemeten en het Balloërveld (tabel 2) en welke ook werd aangegeven door Petrusewicz (1970) en te vinden is in het materiaal van Abildgard et al.(1972), zou kunnen betekenen dat de dichtheid van de geslachtsrijpe hazen remmend werkt op de netto-productie aan jongen. Uit de verzamelde gegevens valt niet op te maken of dit het gevolg is van remming van de ovulatie, verhoging van prenatale sterfte of verhoging van de jeugdsterfte.

Ten aanzien van de ovulatiesnelheid en de prenatale sterfte hebben we onvoldoende gegevens kunnen verzamelen om zicht te krijgen op de ruimtelijke en jaarlijkse variatie. Ook de variatie in de jeugdmortaliteit viel niet te kwantificeren. De mate waarin dode dieren werden gevonden, gemeld en voor onderzoek werden aangeboden werd in belangrijke mate bepaald door motivatie van mensen in het veld, terwijl de dichtheid van de hazenstand niet bekend was. Het onderzoek van de in het veld dood gevonden hazen die waren gestorven tengevolge van bacteriële of parasitaire infecties heeft wel de aandacht gevestigd op de betekenis van coccidiosis als sterftefactor onder jonge hazen met een zekere negatieve dichtheidsafhankelijkheid met betrekking tot de volwassen hazen. Bij darmcossidiosis vindt de vermeerdering plaats in de cellen van het darmepitheel. Door de beschadiging van deze cellen wordt de stofwisseling gestoord, wat meesal gepaard gaat met gasvorming in de darmen en diarree. In het onderzochte materiaal werden ernstige gevallen van coccidiosis, waarbij de ziekte als belangrijke doodsoorzaak werd aangemerkt, vooral aangetroffen bij hazen met een ooglensgewicht tussen de 81 en 160 mg (fig. 7). Deze ooglensgewichten komen ongeveer overeen met leeftijden tussen de 1,5 en 3,5 maand (Art.II). Bij 81% van deze hazen was coccidiosis in ernstige mate aanwezig. Bij hazen met ooglensgewichten van 161-220 mg (3,5-6,0 maand oud) was coccidiosis in 37% in ernstige mate aanwezig, en bij hazen met ooglensgewichten van meer dan 220 mg (ouder dan 6 maand) in slechts 7% (fig. 7). Toch bleek bij contrôle van 1 mm^3 mest uit de anus bij 2445 tijdens het jachtseizoen geschoten hazen met een ooglensgewicht van méér dan 220 mg, dat tenminste 20,4% van deze dieren oocysten uitscheidden. Het lijkt daarom aannemelijk dat de dichtheid van de volwassen hazen van invloed is op de besmettingskans van de jongen.

De besmettingskans voor jonge hazen m.b.t. coccidiosis hangt overigens niet alleen af van het aantal oocysten-uitscheidende dieren in het veld. Van groot belang is ook de sporulatie van de oocysten. Hierbij spelen factoren als tempe-

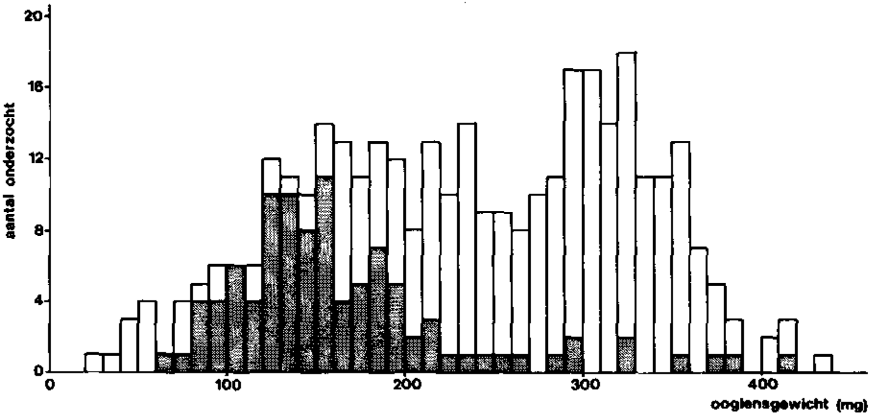


Fig. 7: Verdeling over klassen van 10 mg van ooglensgewichten van de in het veld dood gevonden hazen, die gestorven waren aan bacteriële of parasitaire infecties en waarvan de ooglenzen nog gaaf waren. Indien mogelijk werd het gemiddelde gewicht van beide ooglenzen van een dier genomen. Gearceerd zijn aangegeven de ooglensgewichten behorend bij hazen die in ernstige mate aan coccidiosis leden.

ratuur en luchtvochtigheid een belangrijke rol (Davies et al. 1963). Deze factoren zijn uiteraard niet dichtheidsafhankelijk, en dragen daardoor bij tot de positieve correlatie tussen het percentage jongen in de populatie en de totale omvang van die populatie (in tabel 2 de relatie d/c). Als zodanig zijn de uitkomsten van de bemonsteringen van de hazenstanden op Tiengemeten en het Balloërveld enerzijds en die op Schiphol anderzijds niet strijdig, maar illustreren ze verschillen in de verhouding tussen dichtheidsafhankelijke en dichtheidsonafhankelijke factoren.

Achteruitgang: mogelijke oorzaken en consequenties

De langdurige achteruitgang van de hazenstand, zoals die zich zowel in Nederland als in verschillende andere Europese landen sinds 1960 voordoet, duidt op een toenemende negatieve invloed van een of meer dichtheidsonafhankelijke factoren. Hoewel die factoren worden gezocht in het complex van veranderingen die vooral de modernisering van de landbouw de laatste decennia in het landschap teweeg heeft gebracht, is het nog steeds niet duidelijk welke aspecten van die veranderingen het zijn die tot de achteruitgang van de hazenstand hebben geleid en hoe die achteruitgang tot stand is gekomen. In de jachtliteratuur wordt de meeste aandacht gericht op een toename van de sterftesnelheid door mechanische grond- en gewasbewerking, door de toepassing van chemische middelen en door de afname van dekking en de daaraan gekoppelde toename van predatie op jongen. Weinig aandacht wordt besteed aan een mogelijke verlaging van de reproductiesnelheid. In Art. VI is geïllustreerd dat er een samenhang is tussen de lichamelijke conditie van de moerhazen en de fertiliteit.

Indien de teruggang van de hazenstand inderdaad een gevolg zou zijn van een mindere conditie van de hazen, zou er reden zijn meer aandacht te schenken aan hun voedselsituatie. Uit onderzoek van Brüll (1973) is gebleken dat hazen zeer selectief zijn bij hun voedselkeuze, met voorkeur voor kiemplanten, jonge plantedelen met een relatief laag celwandgehalte en voor bloeiwijzen van akkeronkruiden als paardebloem, viooltjes en soorten klaverachtigen. Nader onderzoek naar de invloed van de kwaliteit van het voedsel op de fertiliteit is daarom zeker gewenst, evenals naar de invloed die de kwaliteit van het voedsel kan hebben op de weerstand tegen ziekten. Zo is van de bacterie die de ziekte pseudotuberculosis veroorzaakt (*Yersinia pseudotuberculosis*) bekend dat hij alleen ziekteverwekkend wordt indien de gastheer in een mindere conditie geraakt terwijl de bacterie in de natuur zeer verbreid is, vooral onder woelmuizen (Kerschagl 1965). In dit verband is het opmerkelijk dat van de 45 hazen die in de herfst en de winter (oktober t/m maart) van de jaren 1966-'74 in de Noordoostpolder dood in het veld werden gevonden en voor onderzoek werden opgestuurd, 62% leed aan pseudotuberculosis, tegen slechts 29% van de 481 hazen die in dezelfde perioden uit de rest van het land werden ontvangen. Dit verschil zou er op kunnen wijzen dat de hazen in de Noordoostpolder in de herfst en de winter in een slechtere conditie verkeerden dan gemiddeld in de rest van het land. Voor een gericht beheer van de hazenstand zou het van betekenis kunnen zijn te weten in hoeverre de kwaliteit van het voedselaanbod in de Noordoostpolder hierbij van invloed was.

In hoeverre in Nederland na het jachtseizoen de sterfte onder de hazen nog dichtheidsafhankelijk is, is niet bekend. Daardoor is ook onbekend in welke mate het effect van jacht op de 'breeding stock' door het minder intensief optreden van andere sterftefactoren wordt gecompenseerd. De vraag kan zelfs gesteld worden of daar, waar een soort een structurele achteruitgang in aantal vertoont, recreatiejacht op die soort nog wenselijk of verantwoord is. Vooropgesteld moet dan worden dat er geen evidentie is om aan te nemen dat de jachtdruk zelf de primaire oorzaak is van de gemiddelde achteruitgang. Waarschijnlijk is het wel zo, dat de jacht een negatief effect heeft op de hoogte van de 'breeding stock' en dat daardoor méér dan de natuurlijke wintersterfte moet worden gecompenseerd door dichtheidsafhankelijke reproductie en -mortaliteit. Als dat compensatievermogen niet meer in staat is de hazenstand gemiddeld weer tot het niveau van vóór de opening van de jacht terug te brengen, is het handhaven van jacht inderdaad niet gerechtvaardigd. Anderzijds moet men zich echter ook afvragen of het beëindigen van de jacht de achteruitgang van de hazenstand zou stoppen. Met andere woorden: of de dichtheidsafhankelijkheid in de voortplanting en de sterfte bij uitsluiting van de jacht wel voldoende zou zijn om de geconstateerde achteruitgang te stoppen. Deze vraag is niet zonder meer positief te beantwoorden. De verlaging van de jachtdruk zoals die in de Noordoostpolder heeft plaatsgevonden (fig. 3), heeft daar niet geleid tot herstel van de hazenstand. Het is waarschijnlijk dat stoppen van de jacht de teruggang voor enige tijd zou vertragen of tot een beperkt herstel zou leiden, waarna de teruggang zich weer verder zou voortzetten. Wil men de teruggang van de hazenstand op lange termijn bestrijden, dan zal het zaak zijn de echte oorzaken weg te nemen. Die oorzaken op te sporen blijft een taak voor hen die belang hechten aan het voorkomen van hazen in het 'vrije veld'.

Summary

Long-term fluctuations in European hare populations are common, but the synchronous declining tendency in the size of shooting bags during the last decades in several mid- and western European countries, including The Netherlands, is striking. In general this phenomenon is suggested to be connected with aspects of modern agriculture, but quantitative evidence is scarce. Furthermore, it is unknown to what extent the decline is the result of a decreasing reproduction rate and/or increasing mortality rate.

Information about these parameters from The Netherlands was not available. Therefore, data were collected on litter size, production of young per adult female and the proportion of recruitment in shooting bags. Observations of nursing behaviour revealed that all members of a litter gather daily, the time of which is strictly related to sunset. This knowledge enabled us to collect information about the survival of young up to the end of the normal one month nursing period, which was 52% in the observed litters. The calculated number of 5.7 young weaned per adult female per year, compared with the average number of 3.4 young per adult female found in shooting bags, indicates a higher mortality rate in young than in adults during the time from weaning up to the shooting season. Unfortunately it was not possible to collect enough data to determine trends in these parameters.

The percentage of young found in bags in three different areas during a period varying from 5 to 10 years, was in one area positively correlated with the total number of hares shot. In the other two areas this percentage was negatively correlated with the number of adults shot. It is hypothesized that the relative importance of density dependent and density independent factors affecting the recruitment determines which kind of correlation will be found.

A density dependent mortality factor which is supposed to cause the negative correlation between the percentage of young and the density of adults in the winterpopulation is coccidiosis. Mechanised agriculture will be a density independent mortality factor of increasing importance in young. Little is known about the influence of modern agriculture on the physical condition of hares and consequently on the reproduction rate, through decreasing the diversity of herbs, and quantitative data regarding this are desirable.

Literatuur

Abildgard, F., Andersen, J. & Barndorff-Nielsen, O., 1972: The hare population (*Lepus europaeus* Pallas) of Illumø Island, Denmark. Dan. Rev. Game Biol., *6*, 5: 1-32.

Adamczewska-Andrzejewska, K. & Szaniawski, A., 1972: Relationship between the real increase and yield of hares in Poland. Acta theriol., *17*, 19: 259-265.

Anderegg, R., 1979: Über die Biologie des Feldhasen (*Lepus europaeus* Pallas). Feld Wald Wasser, *7*, 2: 6-14.

Andersen, J., 1952: Fluctuations in the field hare population in Denmark compared with certain climatic factors. Papers on Game Res., *8*: 41-43.

Andersen, J., 1957: Studies in Danish hare-populations. I. Population fluctuations. Dan. Rev. Game Biol., *3*, 2: 89-131.

Asferg, T., 1980: Vildtudbyttet 1977/78 og 1978/79. In: Dansk Vildtforskning 1980: 47-48. Fog, M. (Ed). Kalø-Rønde, Vildtbiol. St. medd. nr. 170.

Bouvier, G., Burgisser, H. & Schneider, P.A., 1954: Monographie des maladies du lièvre en Suisse. Lausanne, Serv. Vét. Cant. et Inst. Galli-Valerio, 68 pp.

Bresiński, W., 1976: Weather conditions vs. European hare population dynamics. In: Ecology and management of European hare populations: 105-114. Pielowski, Z. & Pucek, Z. (Eds). Warszawa, Pol. Hunt. Ass.

Broekhuizen, S., 1975: The position of the wild rabbit in the life system of the European hare. Papers to the XIIth Congr. Int. Union Game Biol., Lisbon. Stencil, 7 pp.

Broekhuizen, S. & Poelma, F.G., 1969: De natuurlijke doodsoorzaken bij hazen in 1968. De Ned. Jager, *74*, 8: 214-215.

Broekhuizen, S. & Poelma, F.G., 1970: Ziekten en parasieten bij Nederlandse hazen in 1969. De Ned. Jager, *75*, 10: 276-277.

Broekhuizen, S. & Kemmers, R., 1976: The stomach worm, *Graphidium strigosum* (Dujardin) Railliet & Henry, in the European hare, *Lepus europaeus* Pallas. In: Ecology and management of European hare populations: 157-171. Pielowski, Z. & Pucek, Z. (Eds.). Warszawa, Pol. Hunt. Ass.

Coles, C.L. (Ed.), 1981: Le lièvre brun d'Europe. Proc. Symp. Rome may 1980. Paris, Cons. Int. Chasse, 121 pp.

Davies, S.F.M., Joyner, L.P. & Kendall, S.B., 1963: Coccidiosis. Edinburgh, Oliver & Boyd, 264 pp.

Fichter, A., 1975: Radiotelemetrie: Feldtechnik und Anwendung bei Reh und Feldhase. Zool. Inst. Univ. Zürich, Diplomarbeit. 39 pp.

Flux, J.E.C., 1967: Reproduction and body weights of the hare *Lepus europaeus* Pallas, in New Zealand. N.Z. J. Sci., *10*: 357-401.

Friedemann Zedka, H., 1981: Österreichs Jagdstatistik 1980. Österr. Weidwerk, (10): 532-538.

Frylestam, B., 1979a: Structure, size, and dynamics of three European hare populations in Southern Sweden. Acta theriol., *24*, 33: 449-464.

Frylestam, B., 1979b: Reproduction of the European hare in Southern Sweden. Holarctic Ecology, *3*: 81-86.

Göransson, G. & Frylestam, B., 1981: Agriculture and Wildlife, a broadbased research project. Leaflet Dep. Animal Ecol. Univ. Lund (4pp).

Jezierski, W., 1965: Studies on the European hare. VII. Changes in some elements of the structure and size of population. Acta theriol., *10*, 2: 11-25.

Kerschagl, W., 1965: Wildkrankheiten. Wien, Österr. Jagd u. Fischerei-Verlag d. N.-O. Landesjagdverb. 328 pp.

Klingeren, B. van, Koeman, J.H. & Haaften, J.L. van, 1967: A study on the hare (*Lepus europaeus*) in relation to the use of pesticides in a polder in The Netherlands. Rapports,Les, du VII^{e} congrès; Union Int. Biol. Gibier, Beograd, sept. 1965. Beograd, l' Union org. chass. Yougoslavie; 309-316.

Kötsche, W. & Gottschalk, C., 1972: Krankheiten der Kaninchen und Hasen. Jena, Fischer Verlag, 294 pp.

Kutzer, E. & Frey, H., 1977: Der Feldhase in Österreich. C: Die Jagdstrecken in den Jahren seit 1949. Österr. Weidwerk, *8*: 420-423.

Kutzer, E., Thiemann, G., Grünberg, W. & Frey, H., 1976: Beiträge zu einer Feldhasenstudie. I. 'Gesundenuntersuchung' an erlegten Feldhasen aus österreichischen Revieren. Z. f. Jagdwiss., *22*, 1: 50-61.

Leeuwenberg, F., 1981: Jachtstatistieken in Nederland. Den Haag, Min. v. Landb. en Visserij, 3 pp.

Merz, H., 1973: Die Gruppierungstendenz beim Feldhasen (*Lepus europaeus* Pallas) in Abhängigkeit der Nachtzeit in Juli/August 1973. Zool. Inst. Univ. Zürich, semesterarbeit. 16 pp.

Merz, H., 1976: Nächtliche Standplatzwahl individuell gekenzeichneter Feldhasen (*Lepus europaeus* Pallas) innerhalb ihrer Aktionsräume. Zool. Inst. Univ. Zürich, Diplomarbeit. 39 pp.

Middleton, A.D., 1936: Periodic fluctuations in British game populations. I.C.I. Game Res. adv. leafl. nr. 6: 23 pp.

Möller, D., 1967: Der nutzbare Zuwachs der Hasen in Abhängigkeit von regionalen Klimaunterschieden. Arch. Forstwes., *16*, 6-9: 927-930.

Möller, D., 1975: Zum Altersaufbau der Hasenpopulation in der Deutschen Demokratischen Republik. Beitr. Jagd- u. Wildforschung, *9*: 315-325.

Nováková, E. & Hanzl, R., 1966: Influence des conditions meterologiques de l' hiver et du printemps sur l' état physique des lièvres en automne. Forestier Suisse, *2*: 116-126.

Passberger, E., 1981: Vor und nach der Flurbereinigung. Die Pirsch,*33*, 18: 1262-1267.

Petrov, P., 1976: Über die Faktoren die den realen Zuwachs des Hasen bestimmen. In: Ecology and management of European hare populations: 115-118. Pielowski, Z. & Pucek, Z. (Eds). Warszawa, Pol. Hunt. Ass.

Petrov, P. & Dragoev, P., 1962: Untersuchung mancher Besonderheiten über die Vermehrung des Feldhasen (*Lepus europaeus* Pallas) in Bulgarien. Bull. For. Inst. Sofia, *10*: 143-168.

Petrusewicz, K., 1970: Dynamics and production of the hare population in Poland. Acta theriol., *15*, 26: 413-445.

Pfister, H.P. & Rimathé, R., 1979: Die Schweizerische Hasenforschung. Feld Wald Wasser, *7*, 2: 3-5.

Pielowski, Z., 1968: Die Jahresbilanz einer Hasenpopulation in Polen. Tag. Ber. Dt. Akad. Landwirt. Wiss. Berlin, 104: 129-137.

Pielowski, Z., 1971. Length of life of the hare. Acta theriol., *26*, 6: 89-94.

Pielowski, Z., 1976: Number of young born and dynamics of the European hare population. In: Ecology and management of European hare populations: 75-78. Pielowski, Z. & Pucek, Z. (Eds). Warszawa, Pol. Hunt. Ass.

Pielowski, Z. & Pucek, Z. (Eds), 1976: Ecology and management of European hare populations. Warszawa, Pol. Hunt. Ass.: 236 pp.

Pielowski, Z. & Raczyński, J., 1976: Ecological conditions and rational management of hare populations. In: Ecology and management of European hare populations: 269-286. Pielowski, Z. & Pucek, Z. (Eds). Warszawa, Pol. Hunt. Ass.

Puppe, K., 1966: Untersuchungen über die Variationsbreite des nutzbaren Zuwachses des Hasen in Abhängigkeit von regionalen Klimaunterschiede. Beitr. Jagd- und Wildforsch., *5*: 109-117.

Rieck, W., 1955: Feldhase und Wildkaninchen. In: Jagd und Hege in aller Welt: 180-184. Deutsch. Jagdschutzverb. (Ed). Düsseldorf, Kölzig.

Rieck, W., 1956:Untersuchungen über die Vermehrung des Feldhasen. Z. Jagdwiss., *2*, 1: 49-90.

Rieck, W., 1962: Analyse von Feldhasenstrecken nach dem Gewicht der Augenlinse. Trans. 5th Congr. Intern. Union Game Biol., Bologna 1961. Supp. Ricerche Zool. appl. Caccia *4*, 1: 21-29.

Rimathé, R., 1977: Zur saisonalen Abundanzdynamik des Feldhasen (*Lepus europaeus* Pallas) im Schweizerischen Mittelland. Diss. Zürich, 126 pp.

Spittler, H., 1976: Witterungsfaktoren als Grundlage für Vorhersagen über die Entwicklung des Hasenbesatzes. In: Ecology and management of European hare populations: 115-118. Pielowski, Z. & Pucek, Z. (Eds). Warszawa, Pol. Hunt. Ass.

Spittler, H., 1981: Zur Situation des Feldhasen in der Bundesrepublik Deutschland. In: Le lièvre brun d'Europe: 31-36. Coles, C.L. (Ed). Paris, Cons. Int. Chasse.

Strandgard, H. & Asferg, T., 1980: The Danish bag record II. Dan. Rev. Game Biol. *11*, 5: 112 pp.

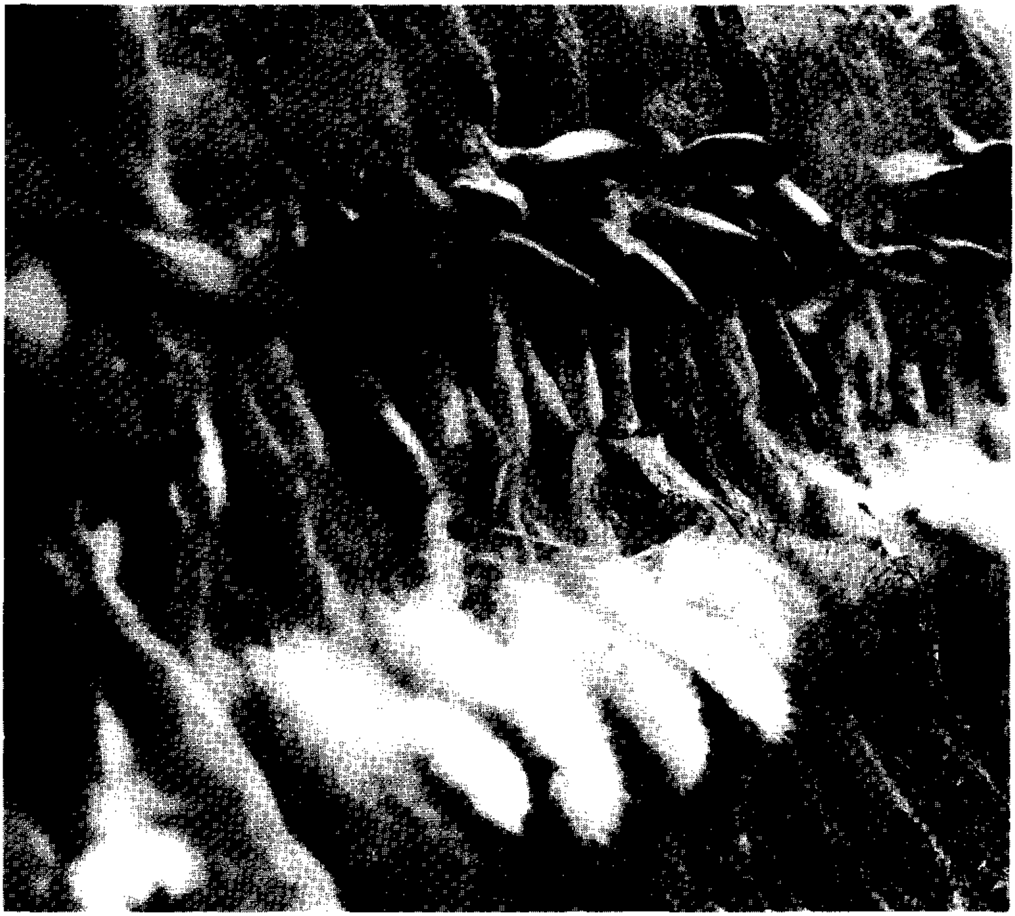
Tapper, S.C. & Barnes, R.F.W., 1981: Changes in the numbers of hares shot in Britain since 1900. In: Le lièvre brun d'Europe: 11-19. Coles, C.L. (Ed). Paris, Cons. Int. Chasse.

Tapper, S. & Parsons, N., 1979: The status of the Brown hare in Britain. In: Annual Review of the Game Conservancy for 1978: 67-75.

Art. II

Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands

By S. Broekhuizen and F. Maaskamp



Nauwkeurige leeftijdsbepaling is belangrijk. Bij hazen is het probleem van die bepaling nog steeds niet geheel bevredigend opgelost.....

Foto: Joost van der Ven

Sonderdruck aus Z. f. Säugetierkunde Bd. 44 (1979) H. 3. S. 162—175
VERLAG PAUL PAREY · HAMBURG 1 · SPITALERSTRASSE 12

Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands

By S. Broekhuizen and F. Maaskamp

Research Institute for Nature Management, Arnhem, The Netherlands

Receipt of Ms. 31. 10. 1978

Abstract

Material of known age was collected in the field to obtain references in order to age Dutch hares *(Lepus europaeus* Pallas) by means of body weight, eye lens weight, length of the hind foot, stages of ossification of the cartilage in the ulna and the radius, and growth

U.S. Copyright Clearance Center Code Statement: 0044-3468/79/4403-0162 $ 2.50/0
Z. Säugetierkunde 44 (1979) 162—175

ISSN 0044—3468/ASTM-Coden: ZSAEA 7

lines in the periosteal bone of the lower jaw. In the few hares where we examined the latter criterion, the lines gave an overestimation of age, because accessory lines in the structure of the bone could not be clearly distinguished from annual growth lines. The other criteria provided rough estimates of age for increasing periods of life in the following order: length of hind foot (up to 3 months), body weight (4 months), epiphyseal cartilage (7 months) and eye lens weight (1 year).

There is no criterion available for precise ageing Dutch hares.

Introduction

The student of the population ecology of an animal species is inevitably confronted with processes dependent on age. Therefore, accurate ageing is important. In hares the problem of ageing has not yet been solved satisfactorily, although several attempts have been made to determine usable ageing criteria. The most important of these are: body weight, eye lens weight, length of the hind foot, stages of ossification of the epiphyseal cartilage in the long bones, and the annual growth lines in the periosteal bone of the lower jaw. Because incisors and molars have open roots, and growth from the base wears down at the top throughout a hare's life age determination by incremental structures is not possible.

We collected material from Dutch hares for age reference and compared this with data from other countries to study conformity. In addition, we considered to what extent the various ageing criteria are applicable to the different categories of hares studied: live hares which could not be injured, hares shot which could only be slightly damaged, and hares found dead in the field at different stages of decomposition.

Beside the criteria mentioned, others have also been considered in literature, such as the length of the ears (Tiemeier and Plenert 1964), the ossification of the skull and the pelvis (Bujalska et al. 1965), the length of the jaws and the teeth, and the width of the oral cavity (Kleymann and Schneider 1974). The applicability of these criteria is apparently small, and we do not discuss them in this paper.

Review of ageing criteria from the literature

Body weight

Although body weight is easy to measure, even in live hares, its use as criterion for ageing is limited because the period of rapid growth in hares is short. Moreover, this growth is influenced by the animal's condition and it may vary with the geographical situation. Hence, it can be expected that body weight will vary in hares of the same age.

Because young hares are very rarely recaptured in the field, most growth curves have been based on weighing of hares in captivity (a. o. Hediger 1948; Reynolds and Stinson 1959; Pilarska 1969; Broekhuizen 1971; Spagnesi 1972; Pepin 1974). The unnatural conditions of captivity, however, influence growth. For instance, curves of Pilarska (1969), Broekhuizen (1971) and Spagnesi (1972) showed a very restricted growth for the first one-and-a-half months of life of the leverets, whilst the body weights of fully grown captive hares appeared to be low as compared to the weights of wild hares. Only Pielowski (1971) presented a growth curve based on data from hares living under field conditions in a large enclosure.

The question arose as to whether the growth curve composed by Pielowski (1971) could be used for ageing wild hares in Holland. In an earlier paper Pielowski (1969) showed that in some years during winter the average weight of hares shot in the eastern part of Poland was 1 kg higher than that of hares from Poznań, a western province of that country. In the latter province the weight of hares more than one year old was on average higher than 4 kg. These weights proved to be notably higher than comparable ones from Holland. This raised the question whether the body weight of young leverets in Holland was also significantly lower than in western Poland.

Eye lens weight

The advantage of the eye lens weight as a criterion for ageing (compared with the weights of the body or any other organ), is due to the fact that it is tied off from an epithelium. New lens fibers are continuously being proliferated by the growth and elongation of the epithelial cells at the lens equator (Lord 1959). Because there is no mechanical wear, the lens increases in size during the whole lifetime, although the rate of growth of the lens decreases notably after body growth has stopped. Friend (1967c) reported that this was already indicated by the English scientist Smith in 1883, but it was only after nearly three-quarters of a century that Lord (1959) used the weight of the eye lens for ageing cottontail rabbits, and by this introduced the method into game biology. After that, lens weight has been used for ageing in a great number of mammals, Lagomorpha included. Its significance as a criterion for ageing is further strengthened by the finding of Friend and Severinghaus (1967) that, although the growth of the lens is influenced by the food of the mother during the prenatal phase, food conditions do not have an effect during the postnatal phase of life.

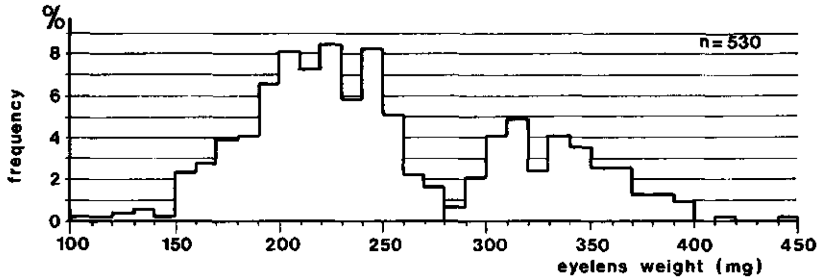


Fig. 1. Histogram of eye lens weights of hares from a hunting area at Schiphol (near Amsterdam), shot in the hunting season 1971 (15 Oct.—31. Dec.). The low frequency of the 280-290 mg class marks the autumnal pause between the production seasons of 1970 and 1971

The weight of the lens can be measured by various methods. The most preferable is the one in which it is formalin fixed and dried (Friend 1967a). By means of the dry weight, the relative age can be determined. For *Lepus europaeus* this was done by a. o. Rieck (1962), Bujalska et al. (1965), Walhovd (1966), Wandeler and Huber (1969) and Möller (1969). Dry weight of the lens is, however, influenced by decomposition (Montgomery 1963; Rongstad (1966), by freezing (Montgomery 1963; Pelton 1970; Broekhuizen 1971), by the length of the formalin fixation and the concentration of the formalin (Friend 1967a; Broekhuizen 1971), and by the method of drying (Möller 1969; Cabón-Raczińska and Racziński 1972).

Rieck (1962) showed that, because in Europe there is hardly any reproduction in wild hares from the second half of September up to the end of December, it is quite possible to differentiate between first-year-hares and older ones from frequency diagrams of eye lens weights of hares collected in a short period. An illustration of such frequency diagram is shown in fig. 1.

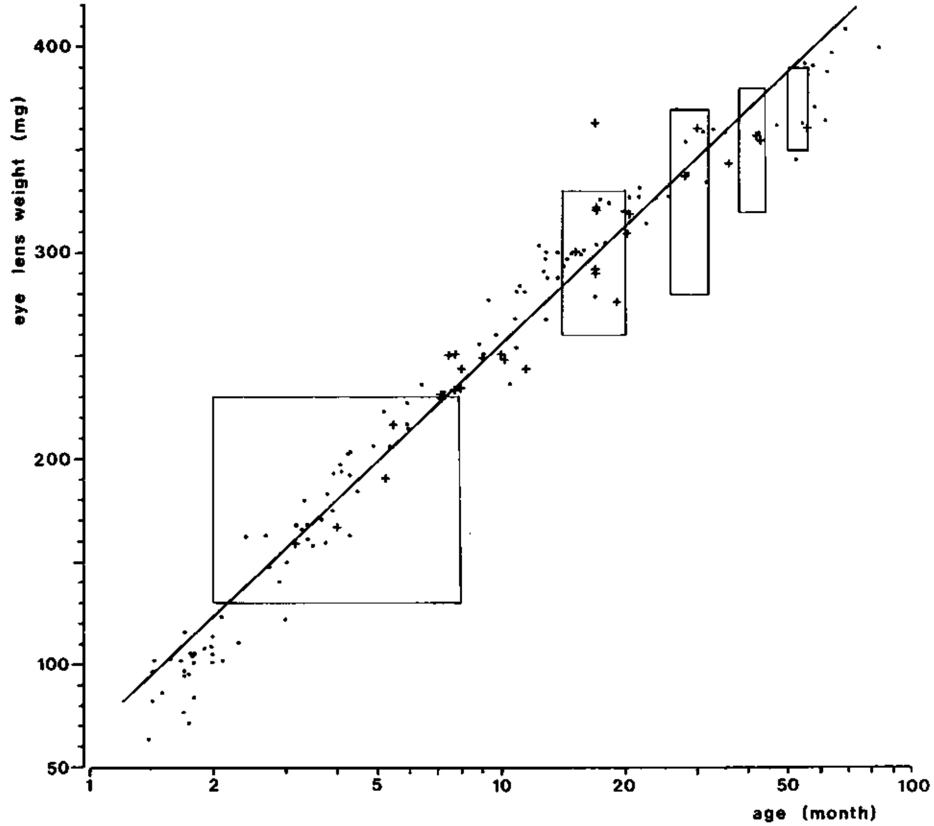


Fig. 2. Relationship between age and eye lens weight in European hares. Rectangles: estimated ranges of lens weights of Danish hares from Illumö, after ANDERSEN and JENSEN (1972). Dots: hares born in captivity in France, collected by PEPIN (1974). Line: regression of lens weight on age based on PEPIN's data. Crosses: Dutch hares living under field conditions. Age plotted on a log scale

For ageing individual hares, a reference curve of lens growth has to be available. This should be based on hares the age of which is precisely known. A draft for such a curve was published earlier (BROEKHUIZEN 1971), and more references have been collected since. ANDERSEN and JENSEN (1972) collected eye lenses from 90 hares from the small Danish island Illumö, where the year of birth of the hares was known. Assuming that these hares were born between April and September, the relationship between eye lens weight and age can be estimated roughly (fig. 2).

PEPIN (1974) determined the eye lens weights of 35 hares born in captivity, and he found the following regression of weight (y) on age:

$$y = 88.5 \ln (\text{age in days}) - 246$$

Later Pepin collected data on 36 more hares of known age, including weights of hares older than 3 years. We added these figures to those of earlier date and, after exclusion of the leverets younger than 42 days, this resulted in the relation

$$y = 83.3 \ln (\text{age in days}) - 222.2$$

For the first two years of life, this regression fits well with the distribution of the eye lens weights collected by ANDERSEN and JENSEN (1972), as shown in fig. 2. After the second year, however, both ANDERSON and JENSEN's data and PEPIN's data deviate from the linear regression which illustrates that the relation is in fact not linear. Also, the eye lens weights of PEPIN's leverets younger than two months are under the regression line.

Although fig. 2 shows that the data of ANDERSEN and JENSEN correspond well with those collected by PEPIN, comparison is complicated by the fact that the Danish hares were wild, whilst the French hares were in captivity in a different climate. Moreover, the lenses were treated differently. They were all fixed in formalin 10 %, but PEPIN dried his material for two days at 100 °C, whilst ANDERSEN and JENSEN dried their hare lenses at 90 °C for four days. Because MÖLLER (1969) as well as CABOŃ-RACZIŃSKA and RACZIŃSKI (1972) showed that the weight was hardly influenced by variable drying times longer than 24 hours, the difference in drying time is of less importance than the difference between the temperatures.

To establish the references curve of lens growth in Dutch hares and for better assessment of the effects of captivity and lens treatment we collected some more data.

Length of the hind foot

The hind food of hares is very hairy and sinewy without much muscle tissue, and is therefore often left by predators and scavengers. The hind feet can desiccate, especially in summer time, which means that this part of predation victims can be found after a long time.

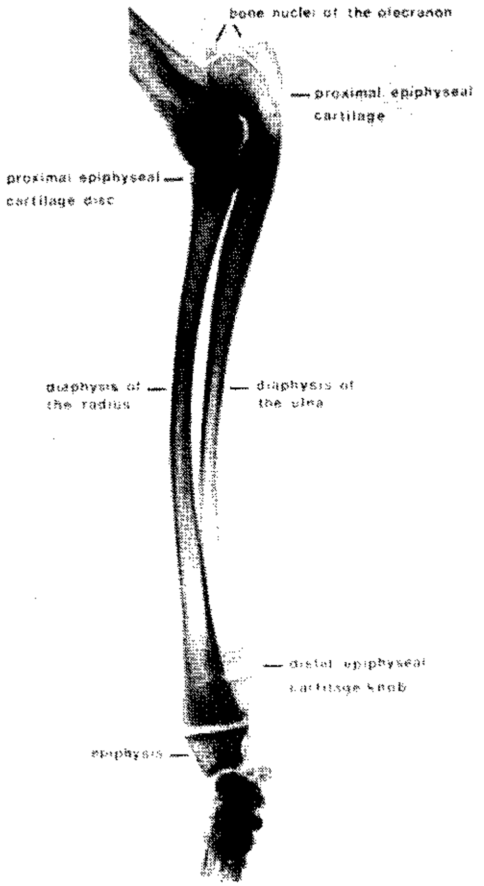


Fig. 3. X-ray photograph of the left ulna and radius of a hare in the 3rd stage of ossification. Lateral view

Ossification of the epiphyseal cartilage of the ulna and the radius

The length growth of the long bones is located in epiphyseal cartilage discs between the middle piece (diaphysis) and the end pieces (epiphyses), as shown for the ulna and the radius in fig. 3. When the length growth has stopped, the epiphyseal discs ossificate. After that, the division between the diaphysis and the epiphysis is sometimes visible as an epiphyseal line or it disappears completely.

In young hares the cartilage discs between the diaphysis and the distal epiphysis of the ulna and the radius from a protruding knob. The distal epiphyseal knob of the ulna, which is nearly 1 cm above the wrist joint, is particularly pronounced in young hares and can easily be felt through the skin. STROH (1931) pointed out the

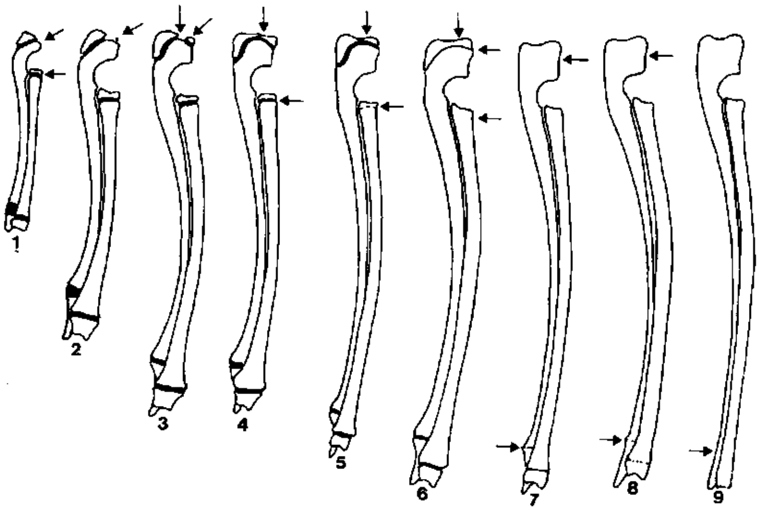


Fig. 4. Stages of ossification of the ulna and the radius of *Lepus europaeus*. Arrows indicate distinguishing marks; the arrows at the bottom of the stages 7, 8 and 9 show the fading out of the distal epiphyseal knob (character of STROH). Thick black lines indicate epiphyseal cartilage

possibility of discriminating between young and fully grown hares by means of this criterion, and that is why it is usually called "STROH'sches Zeichen" in German literature. Several authors have studied the disappearence of this knob. STROH and later also BOBACK (1957) stated this to occur between 10 and 12 months. ANDERSEN (1958) and WALHOVD (1966), and later also PIELOWSKI concluded that the thickening was not palpable through the skin after 6 months of age.

Trying to contribute to this question, we traced by monthly X-raying the ossification of all the epiphyseal cartilage discs of the ulna and the radius in hares reared in captivity (BROEKHUIZEN 1971). Nine different stages of ossification were described, which are shown in fig. 4. These stages can also be identified in cleaned bones. From this preliminary study it appeared that the ossification in young hares born in captivity and nursed by their mothers proceeded faster than in young hares reared by hand. We collected some more data on the question whether the ossification in young hares nursed by the doe in captivity develops at the same rate as in young wild hares, and at which age the distal epiphyseal knob disappears in the latter case.

Annual layers in the periosteal zone of the lower jaw

As a result of seasonal changes in the rate of deposition of secondary bone by the periosteum, adhesion lines divide this appositional bone into layers secreted during periods of variable growth rate. When diminished growth is mainly restricted to one season, for example the winter, the age in years of the animal can be simply determined by counting the number of adhesion lines.

The deposition of periosteal bone does not occur in all bones and, if present, the thickness and the possibility of counting the adhesion lines will vary greatly from place to place. In Lagomorpha several authors found the lower jaw to be very usable for distinguishing the adhesion lines. By counting these lines, BERNSTEYN and KLEVEZAL (1965) were able to determine the age of two Asian pika species *(Ochotona rutila* and O. *microtis)* and MILLAR and ZWICKEL (1972) used this criterion for ageing the American pika *O. princeps*. Ohtaishi et al. (1976) determined the age of two Japanese *Lepus* species *(L. timidus ainu* and *L. bracyurus etigo)* by means of the periosteal growth lines in the lower jaw. They found that besides microtome sections, ground sections were also usable after decalcifying and staining the polished surface. Frylestam and Von Schantz (1977) showed that ageing by means of the periosteal growth lines of the lower jaw is also possible in *Lepus europaeus*.

A great advantage of counting annual layers in the periosteal bone is that it provides a method of determining absolute age, and we tried to establish whether this method could also be used to age Dutch hares.

Material and methods

Body weight

To test the applicability of the growth curve of Pielowski (1971) to Dutch data is not simple. Apart from the rareness of the recaptures of young hares and the possibility that their condition influences the probability of recapture, it is questionable whether the weights of young hares, whose condition is too poor to survive to adulthood, can be used for a growth curve. At the condition of a hare of unknown age cannot be quantified, it seemed best to compare the maximum weights of young wild hares of known age in Holland with the maximum growth rate found by Pielowski (1971) in 30 young hares from his enclosure.

We determined the body weight of 14 wild hares up to 9 months old, from which the age was well known and which were likely in a good condition when recaptured. They were all found in the valley of the river IJssel near Zutphen (52.06 N; 06.13 E).

Eye lens weight

Most of the material we collected came from hares which were captured, marked and released in the first weeks of their life. Their age at first capture was estimated by means of the body weight. Some of these hares were shot later on, and their lenses could be stored in 10 cc formalin 10%. After three weeks fixation the lenses were cleaned on filter paper, dried at 80 °C for 6 days and then weighed, according to the method of Rieck (1962) and Walhovd (1966). After weighing, the material was dried again for 6 days at 100 °C, for comparison with Pepin's data.

Beside the lenses of wild hares, we collected some lenses from hares of known age kept in captivity.

Length of the hind foot

As we did not age predation victims until towards the end of the study, few data about the length of hind feet of hares of known age have been collected. We estimated the age of leverets by means of the body weight up to about their first month, and by means of the stage of ossification of the ulna and the radius when older. In such hares, the length of the hind foot was measured as the distance between the foremost nail point and the end of the heel bone.

Ossification of the epiphyseal cartilage of the ulna and the radius

Data were collected from young hares which had been caught, marked, released and then recaptured in the field. For marking with ear tags, leverets must be at least several days old. When the age was not exactly known, this was estimated by means of the growth curve of the body weight. The age of the marked young hares was between a few days and six weeks. Several of the young were recovered as victims of grass mowers, traffic or shooting.

Annual layers in the periosteal zone of the lower jaw

We had only four fresh skulls of Dutch wild hares, known to be more than one year old, at our disposal. Through the region of the first molar, transverse sections of the lower jaw were prepared by microtome as well as by grinding.

Results

Body weight

In fig. 5A the maximum growth curve is drawn through the highest body weights of the young hares of known age. For comparison, the maximum growth rate found by Pielowski (1971) is also presented. In fig. 5B the frequency distribution of the weights of adult hares is given. These hares were all shot on drives during the shooting seasons 1967—1977 throughout Holland. They were considered adult when the distal epiphyseal knob of the ulna could not be felt through the skin.

Fig. 5A shows that the maximum weights of young hares in Holland are lower than the maximum weights reported by Pielowski (1971). This indicates that during the first four months the body weight of Dutch hares increases less fast than in hares from western Poland.

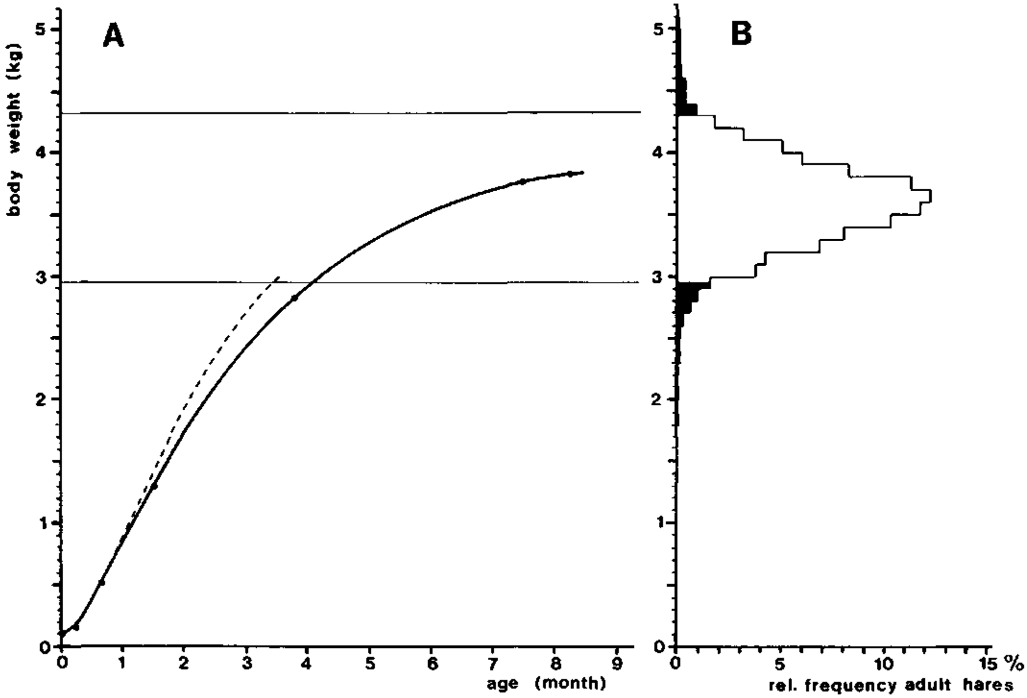


Fig. 5. A = maximum growth curve in young Dutch hares (solid line) and in young Polish hares (broken line); B = frequency distribution of body weights of Dutch hares over 8 months old, shot during hunting seasons (n = 5333). (See text)

Using the maximum growth curve for ageing Dutch hares, only their minimum age can be determined. Fig. 5 shows that the curve can only be used up to the age of four months, because in hares of five months old the highest body weights are already within the 95 % limits of the weights of adult hares (the white part of the histogram in fig. 5B), provided that the weights of the adults are normally distributed.

Eye lens weight

Fig. 2 shows the eye lens weights, obtained from lenses dried at 100 °C. On average the weight of the lens after drying at 80 °C proved to be 4 % higher than after drying at 100 °C. Fig. 2 shows that the eye lens weights of wild Dutch hares agree fairly well with the weights collected by PEPIN from hares in captivity. The same holds for the data of ANDERSEN and JENSEN (1972), although their drying at 90° C made them perhaps 2 % heavier. Differences in climate and living conditions of wild and captive hares seem to be unimportant with regard to the great individual variation. Therefore, it is allowed to join data from Dutch wild hares and the data from hares reared in captivity, as done in fig. 6. In agreement with PEPIN's data a log linear regression does not represent the real course of growth; therefore, we fitted the curve in fig. 6 by eye.

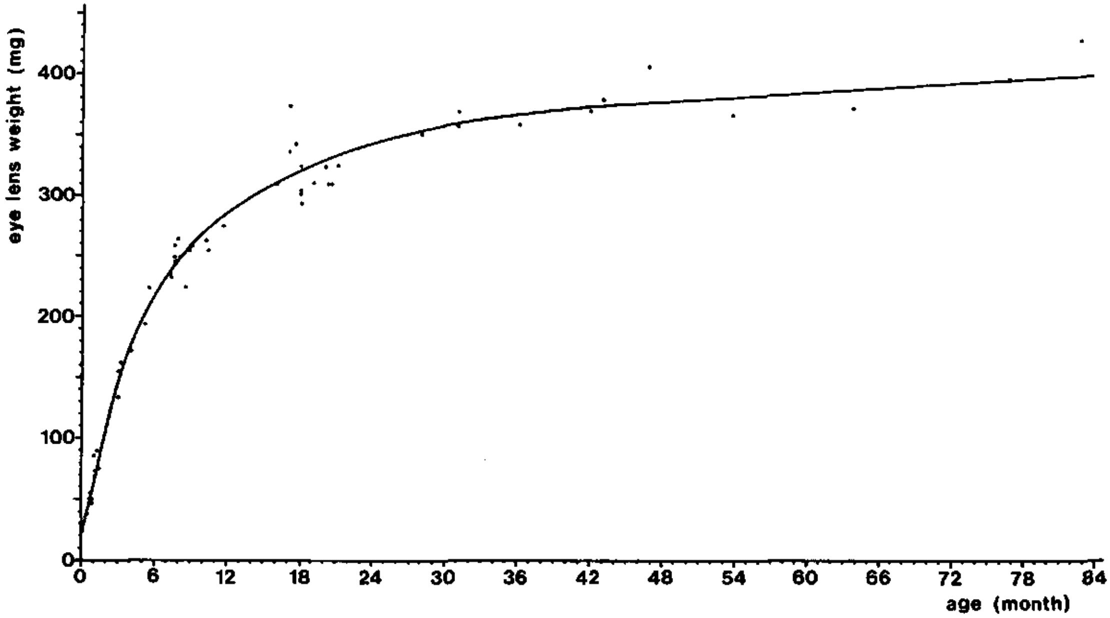


Fig. 6. Reference curve for ageing by means of the weight of the eye lens, fixed in formalin 10 % and dried at 80 °C. The curve, which is fitted by eye, is based on hares of known age, both from the field and from captivity

Figs. 2 and 6 show that after the first year of life the age of individual hares cannot be determined accurately by means of the eye lens weight. However, to distinguish the first year hares from the older ones the eye lens weight is quite well usable, as shown in fig. 1.

Length of the hind foot

The relationship between the length of the hind foot and the age is shown in fig. 7. From this figure it becomes clear that leverets can only be distinguished from adults (adult means here: eye lens weight heavier than 280 mg, stage of ossification number 9) when they are younger than two months old. At the age of three months, there is already a considerable overlap with adult hares. When the length of the hind foot is shorter than 12 cm, the hare is probably less than 8 months old; when

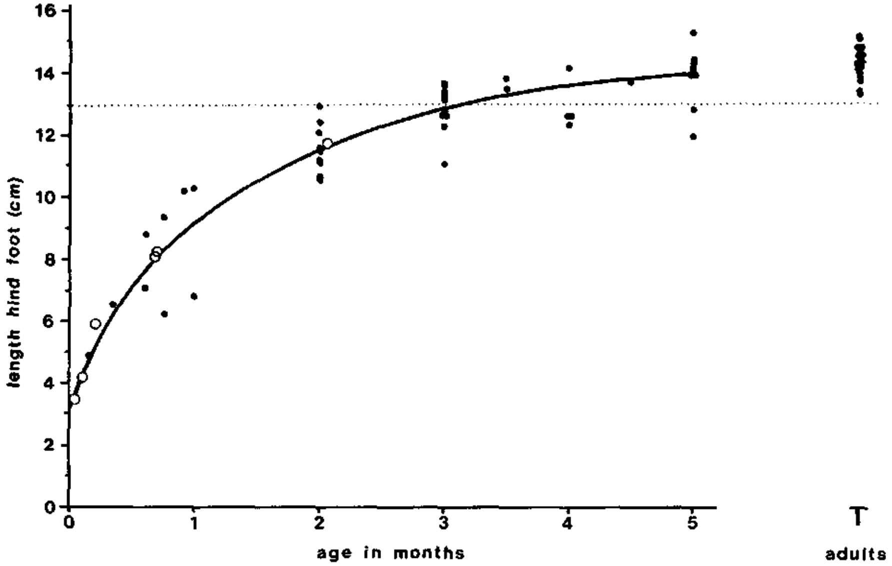


Fig. 7. Relationship between age and the length of the hind foot. Circles: hares of known age. Dots: hares the age of which has been estimated by means of their lens weights (up to 1.5 months) or by the stage of ossification of the ulna and the radius (older than 1.5 months)

the hind foot is shorter than 10.5 cm it is most likely that the hare is less than one month old.

Ossification of the epiphyseal cartilage of the ulna and the radius

The relationship between the age in wild hares and their stage of ossification of the ulna and the radius is shown in fig. 8. For comparison, stages of ossification of four young born in captivity are also given. Fig. 8 shows that the rate of ossification in wild hares agrees with that of hares born in captivity and nursed by their mother. The first three stages are passed through in two months. At the end of the third month of life, stage 4 and sometimes stage 5 are reached. Fig. 8 shows that the stage of complete ossification (9) is reached after 7 to 9 months. This agrees with the conclusions of ANDERSEN (1958), WALHOVD (1966) and PIELOWSKI (1975).

Just as with the eye lens weight, also in the rate of ossification a notable amount of variation occurs. Because both criteria are often used as alternatives, it is useful to know their relationship. This is shown in fig. 9 for hares of unknown age. It appears that by using both criteria, a difference of 2 to 3 months is possible between estimation by means of the eye lens growth, and estimation by means of the stage of ossification of the cartilage in the ulna and the radius.

Annual layers in the periosteal zone of the lower jaw

All authors who used this method, reported that reliable countings can only be made in some narrow zones of the jaw, that adhesion lines can be double and that there are sometimes accessory lines, resulting in more lines than the correct age in years. It is necessary to distinguish and then exclude the "false" accessory lines.

In the microtome sections as well as in ground sections of the lower jaw, we found more periosteal lines than could be expected according to the age of the hares.

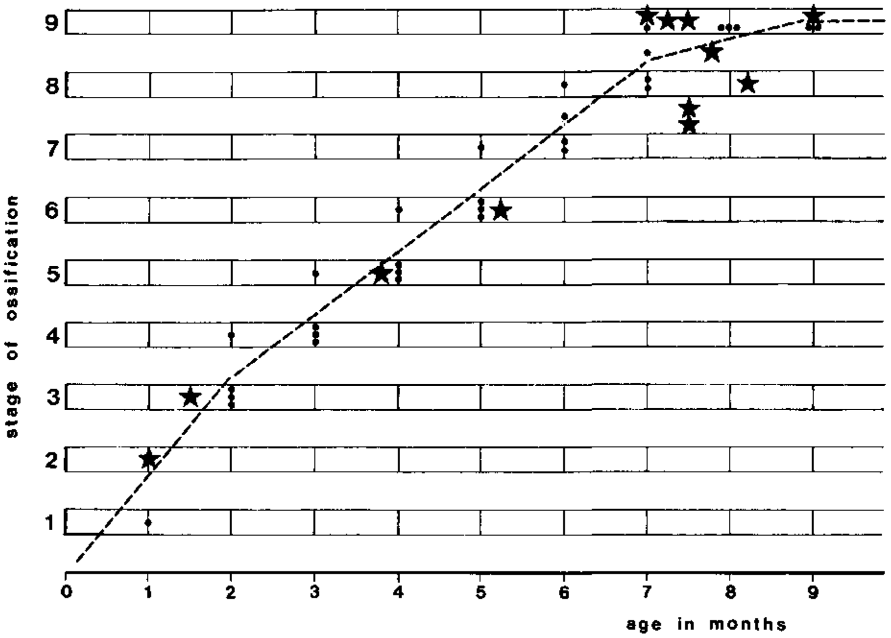


Fig. 8. Stages of ossification in four hares born in captivity (dots) and of twelve hares of roughly known ages living in the field

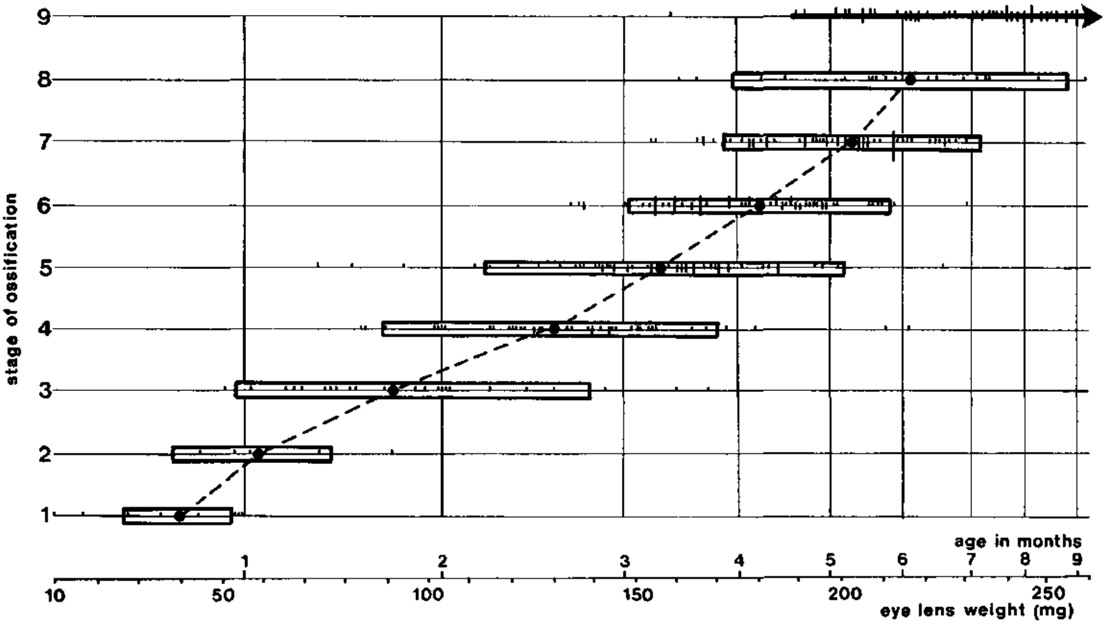


Fig. 9. Ranges of eye lens weights (dried at 80 °C) at the nine stages of ossification shown in fig. 4. Outlined are the 90 % intervals, belonging to a supposed normal distribution of the eye lens weights of hares with stages 1—8. The broken line connects the means of the lens weight distributions at these stages. Stage 9 is the final stage, which remains for the rest of life, as indicated by the arrow. Age scale based on lens growth curve

We were unable to distinguish reliably between the annual and the accessory growth lines, probably due to the scarcity of material of known age and the lack of experience. But it seems also possible that the adhesion lines from the winter seasons are less pronounced in Dutch hares, due to the mild atlantic winter climate without much snow during the last seven years. More material has to be studied.

Discussion

Apart from the periosteal lines, none of the criteria studied is useful for accurate determining the age of hares. Body weight is highly dependent on the condition of the hare, and only provides determination of minimum age, unless the hare is supposed to be in optimal condition. In that case minimum age can be estimated for the first 4 months.

The eye lens weight increases during the whole lifetime, but at the age of 6 months and older, the individual variation is so great that errors of up to one month and more can be made. In hares older than 6 months the individual variation increases rapidly. Because there is no reproduction from October till January, it is possible to distinguish yearlings from older animals in samples collected in a short interval. The eye lens weight can only be used if the lens is fresh. Therefore, this criterion is most suitable for ageing hares which have been shot and which are not to be mutilated.

The length of the hind foot is only suitable for ageing hares which are not more than two months old. This method is less exact than the preceding one, but it is valuable in cases where predators and scavengers have left this most sinewy part of the corpus.

The ossification of the epiphyseal cartilage of the ulna and the radius provides a rough age determination up to 7 months. After some practice, stages 6, 7 and 8 can be recognized by palpation through the skin. This criterion constitutes a supplement to ageing by means of the body weight in live hares and it is also usable in skeletons.

It is uncertain whether adhesion lines in the periosteal bone of the lower jaw of hares living under the mild winter conditions of Holland are sufficiently pronounced to distinguish them from accessory lines. A detailed study of the layers in the periosteal bone might provide a more reliable criterion to determine the different year classes.

Zusammenfassung

Altersbestimmung bei Feldhasen (Lepus europaeus Pallas) in den Niederlanden

Feldhasen mit bekanntem Alter wurden in Holland aus freier Wildbahn gesammelt und zu Altersbestimmungen herangezogen. Körpergewichte, Augenlinsengewichte, Hinterpfotenlängen, Entwicklungsgrad der Verknöcherungen von Radius und Ulna sowie Zuwachslinien im periostalen Gewebe des Unterkiefers dienten als Unterscheidungsmerkmale. Das letztgenannte Merkmal konnte nur bei wenigen Tieren herangezogen werden. Es ergab sich eine Überschätzung des Alters, weil zusätzliche Strukturen im Unterkiefer nicht deutlich von Jahreszuwachslinien unterschieden werden konnten. Die übrigen Merkmale ließen nur grob Rückschlüsse auf das Alter der Tiere zu. An den Hinterpfotenlängen konnte das Alter bis zu 3 Monaten, an den Körpergewichten bis zu 4 Monaten, am epiphysealen Knorpel bis zu 7 Monaten und an den Augenlinsengewichten bis zu 1 Jahr abgeschätzt werden. Für genauere Altersdatierungen bei holländischen Hasen fehlt bis heute eine eindeutige Methode.

Literature

Andersen, J. (1958): Some studies on hare populations. Trans. 3rd Congr. Intern. Union Game Biol., Danish Rev. Game Biol. **3**, 70—71.

Andersen, J.; Jensen, D. (1972): Studies on the European hare XXVIII: The weight of the eye lens in European hares of known age. Acta Theriol. **17**, 87—92.

Bernsteyn, A. D.; Klevezal, G. A. (1965): Age determination of red- and longeared pika. Zool. zhurnal Moscow **44**, 787—789.

Boback, W. A. (1957): Altersmerkmale und Abschußplanung beim Hasen. Forst und Jagd **7**, 17—19.

Broekhuizen, S. (1971): Age determination and age composition of hare populations. Union Intern. Biol. de Gibier X^e Congrès, Paris, 477—489.

Bujalska, G.; Caboń-Raczyńska, K.; Raczyński, J. (1965): Studies on the European hare VI: Comparison of different criteria of age. Acta Theriol. **10**, 1—10.

Caboń-Raczyńska, K.; Raczyński J. (1972): Studies on the European hare XXVII: Methods for determination of age in the European hare. Acta Theriol. **17**, 75—86.

Friend, M. (1967a): Some observations regarding eye-lens weight as a criterion of age in animals. N. Y. Fish and Game J. **14**, 91—121.

— (1976b): Relationship between eye-lens weight and variations in diet. N.Y. Fish and Game J. **14**, 122—151.

— (1967c): A review of research concerning eye-lens weight as a criterion of age in animals. N.Y. Fish and Game J. **14**, 152—165.

Friend, M.; Severinghaus, C. W. (1967): Influence of nutrition of eye-lens weight in deer. N.Y. Fish and Game J. **14**, 166—175.

Frylestam, B.; Schantz, T. von (1977): Age determination of European hares based on periosteal growth lines. Mammal rev. **7**, 151—154.

Hediger, H. (1948): Die Zucht des Feldhasen *(Lepus europaeus* Pallas) in Gefangenschaft. Physiol. Comp. et Oecol. **1**, 46—62.

Klevezal, G. A.; Kleinenberg, S. E. (1969): Age determination of mammals by layered structure in teeth and bone. Fish. Res. Board. Canada, transl. ser. 1 nr. 1024.

Kleymann, M.; Schneider, E. (1974): Zur Altersbestimmung beim Feldhasen *(Lepus europaeus* Pallas). Z. Jagdwiss. **20**, 209—212.

Lord, R. D. (1959): The lens as an indicator of age in Cottontail Rabbits. J. Wildl. Mgmt. **23**, 358—360.

Millar, J. S.; Zwickel, F. C. (1972): Determination of age, age structure, and mortality of the pika, *Ochotona princeps* (Richardson). Can. J. Zool. **50**, 229—232.

Möller, D. (1969): Augenlinsengewicht und Stroh'sches Zeichen als Altersweiser beim Feldhasen. Unsere Jagd. **19**, 36—37.

Montgomery, G. G. (1963): Freezing, decomposition, and raccoon lens weight. J. Wildl. Mgmt. **27**, 481—483.

Ohtaishi, N.; Hachiya, M.; Shibata, Y. (1976): Age determination of the hare from annual layers in the mandibular bone. Acta Theriol. **21**, 168—171.

Pelton, M. R. (1970): Effects of freezing on weights of cottontail lenses. J. Wildl. Mgmt. **34**, 205—207.

Pepin, D. (1974): Mise au point de techniques pour l'étude de populations de lièvres. Bull. de l'Office Nat. de la Chasse **2**, 77—119.

Pielowski, Z. (1969): Sex ratio and weight of hares in Poland. Acta Theriol. **14**, 119—131.

— (1971): The individual growth curve of the hare. Acta Theriol. **16**, 79—88.

— (1975): Charakterystyka ekologiczna populacji zajaca *Lepus europaeus* Pallas, 1778. Roczniki Akademii Rolniczej w Poznaniu, Zeszyt **65**.

Pilarska, J. (1969): Individual growth curve and food consumption by European hare *(Lepus europaeus* Pallas 1778) in laboratory conditions. Bull. Acad. Pol. Sci. Cl. II, **17**, 299—305.

Reynolds, J. K.; Stinson, R. H. (1959): Reproduction in the European hare in southern Ontario. Can. J. Zool. **37**, 627—631.

Rieck, W. (1962): Analyse von Feldhasenstrecken nach dem Gewicht der Augenlinse. Trans. 5th Congr. Intern. Union. Game Biol., Bologna 1961, 21—29.

— (1967): Wann verschwindet das Stroh'sche Zeichen beim Junghasen? Der Deutsche Jäger **85**, 308.

Rongstad, O. J. (1966): A cottontail rabbit lens-growth curve from southern Wisconsin. J. Wildl. Mgmt. **30**, 114—121.

Spagnesi, M. (1972): Brevi osservazioni sull'allevamento e sull'accrescimento dei giovani di Lepre europea *(Lepus europaeus* Pallas) nati in cattività. Ricerche di biologia della selvaggina **53**, Bologna.

STROH, G. (1931): Zwei sichere Altersmerkmale beim Hasen. Berliner Tierärztl. Wschr. 47, 180—181.

TIEMEIER, O. W.; PLENERT, M. L. (1964): A comparison of three methods for determining the age of black-tailed jack-rabbits. J. Mammalogy **45**, 409—416.

WALHOVD, H. (1966): Reliability of age criteria for Danish hares (*Lepus europaeus* Pallas). Danish Rev. Game Biol. 4, 106—128.

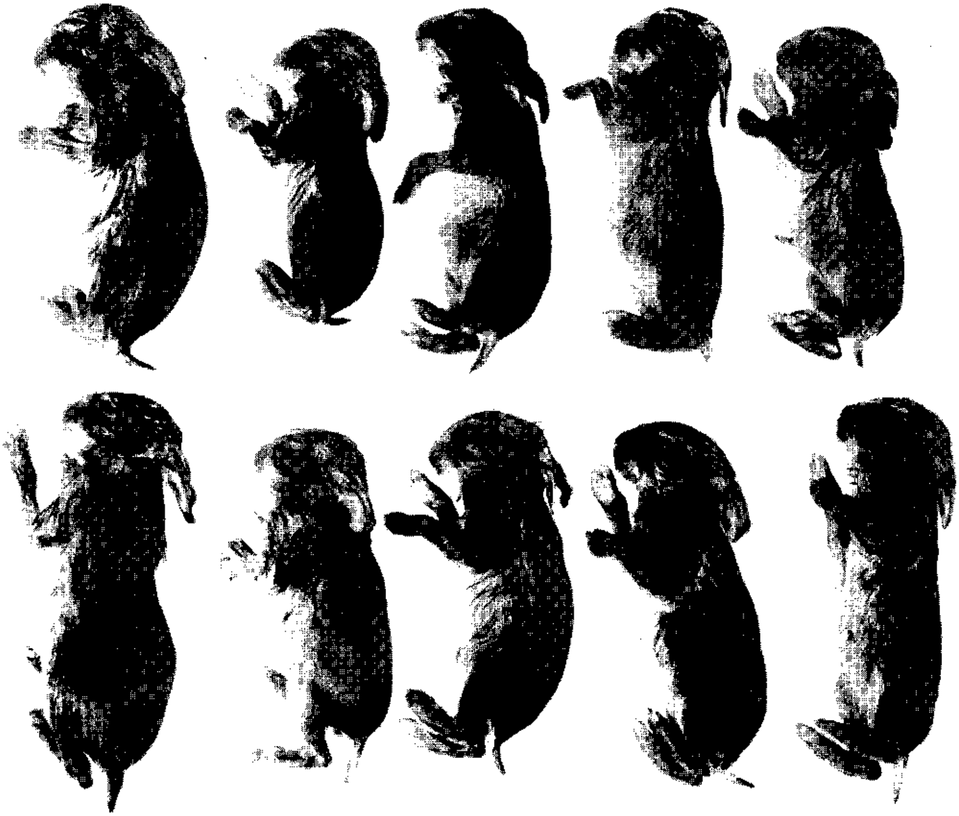
WANDELER, I.; HUBER, W. (1969): Zum Altersaufbau der bernischen Feldhasenbestände im Jahre 1967. Rev. Suisse de Zool. 76, 680—686.

Authors' address: SIM BROEKHUIZEN and FRANS MAASKAMP, Research Institute for Nature Management (R.I.N.), Kemperbergerweg 67, NL-6816 RM Arnhem, The Netherlands

Art. III

Growth of embryos of the European hare (*Lepus europaeus* Pallas)

By S. Broekhuizen and Lise Martinet



Ofschoon het lichaamsgewicht niet een erg nauwkeurig kenmerk is, is dat tot nu toe het enig beschikbare voor de leeftijdsbepaling bij embryo's.

Foto: Roel van Beek

Sonderdruck aus Z. f. Säugetierkunde Bd. 44 (1979) H. 3. S. 175—179
VERLAG PAUL PAREY · HAMBURG 1 · SPITALERSTRASSE 12

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Growth of embryos of the European hare (*Lepus europaeus* Pallas)

By S. BROEKHUIZEN and LISE MARTINET

Research Institute for Nature Management, Arnhem, The Netherlands, and
Station de Physiologie Animale, I.N.R.A., Jouy-en-Josas, France

Receipt of Ms. 31. 10. 1978

For ageing embryos of the European hare, body length and body weight could be simple criteria. In literature, the only data available for the weight of embryos of known age are given by FRAGUGLIONE (1962). At the "Station de Physiologie Animale" in Jouy-en-Josas hares reproduce in captivity. Data about the body weight of embryos were collected from does of which the data of conception was known. These data, as well as those from FRAGUGLIONE already mentioned, are given in table 1 and fig. 1. Embryos were weighted without placenta and membranes after wiping off on blotting paper. The body weights vary considerably in embryos of the same age. Due to this variation and the restricted material it is not to conclude whether embryos from small litters grow faster compared to embryos from large litters. Using the curve from fig. 1 as a reference for age determination, which is fitted by eye through the dots, a large margin of error has to be taken into account. The variation in weight is also reflected in the birth weights represented in literature and summarized in table 2, and is partly due to the fact that the period of gestation varies between 37 and 44 days (MARTINET et al. 1970).

Although body weight is not a very exact criterion, it is at present the only one which is available. Using this, with due reservations, the curve of fig. 1 can be taken as a reference for the average growth of the body weight of hare embryos. The data of FRAGUGLIONE have not been taken into account, because the divergence from the weights of the young French embryos is too large.

U.S. Copyright Clearance Center Code Statement: 0044-3468/79/4403-0175 $ 2.50/0
Z. Säugetierkunde 44 (1979) 175—179

ISSN 0044—3468/ASTM-Coden: ZSAEA 7

Table 1

Body weights (g) in embryos of known age

Each weight represents the average of one litter, except those from Fraguglione (1962)

age (days)	litter size			data of Fraguglione	characteristics
	1	2	3+4		
10				10	
14		0.14			
13-16		1.2	1.6		
16				25	
16-19	2.5				
25	5.8; 9.9	6.7; 15			
26	10				
25-28	18.8; 21	22.1	17.7		embryo hairless up to the 28th day
28	15		17.7; 19.5	40	pigmentation of the skin
30	32	31			
30-33		30.4			dark skin
32	57; 58; 61; 71	68	48		
34	62	29; 42; 50			hairy
35	60; 60; 101	50		65	eyes closed
37			50		
38	37; 75	57; 65	65; 66		eyes mostly open
39	100	62; 95; 110	85		
42-47				130-140	

Table 2

Weight at birth of European hares

weight (g)		field / captivity	reference
mean	range		
± 130	100-165	field	Flux (1967)
130	100-170	captivity	Hediger (1948)
100-110	80-140	field	Kolosov et al. (1965) (cit. Pielowski) (1971)
113	40-180[1]	captivity	Martinet et al. (1970)
130		field (?)	Müller-Using (1954) Rieck (1953)
107	65-155	field	Pielowski (1971)
105	48-148	captivity	Spagnesi (1972)
150		field	Valentinčič (1956)
101 (n=14)	80-130	field	Broekhuizen (unpubl.)

[1] Weights under 75 g have to be counted as due to parturitions before term.

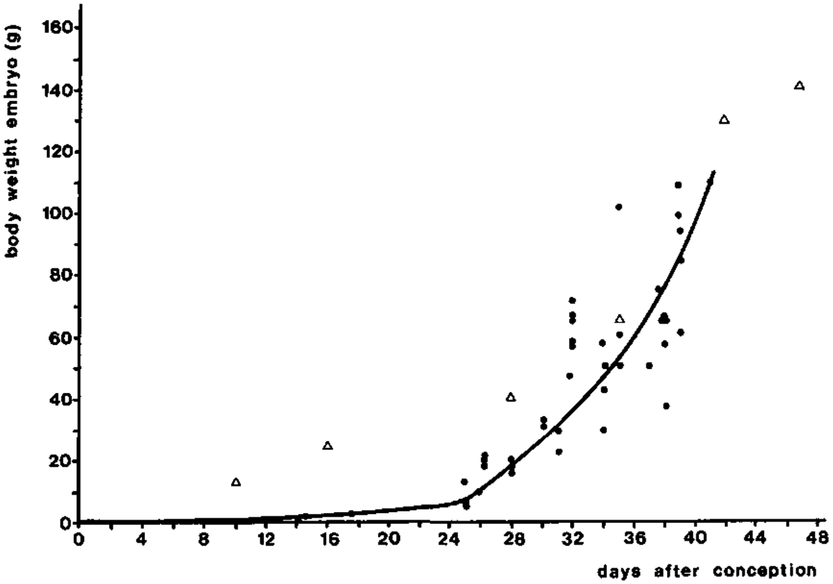


Fig. 1. Growth curve of the body weight in embryos of the European hare. Triangles: data from Fraguglione (1962)

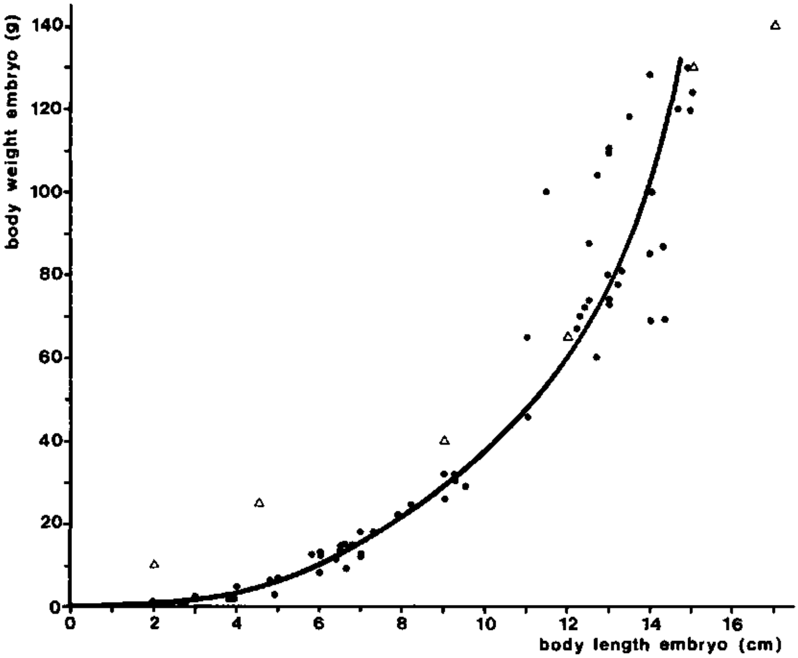


Fig. 2. Relation between body length and body weight in embryos of the European hare. Triangles: data from Fraguglione (1962)

As there are in literature only a few data about the length of embryos, also in the paper by FRAGUGLIONE (1962), the relationship was determined between the body weight and length, as found in embryos of hares in The Netherlands (fig. 2). The embryos were measured from the skull to the end of the body, without changing their posture. Here, the weights obtained did not include placenta and membranes either.

FRAGUGLIONE's data are also given in fig. 2, and it appears that in embryos up to 40 g the body length is much smaller, compared with the length of Dutch embryos of the same weight. We have no explanation for this difference.

On the basis of fig. 1 and 2, an average prenatal growth curve of the body length can be constructed, as given in fig. 3. FRAGUGLIONE's data about body length are added to this figure, as well as some data about embryos from Jouy-en-Josas. The spread of these data, the indirect evidence for the curve and also the shape of the curve do not encourage us to use them for a precise age determination.

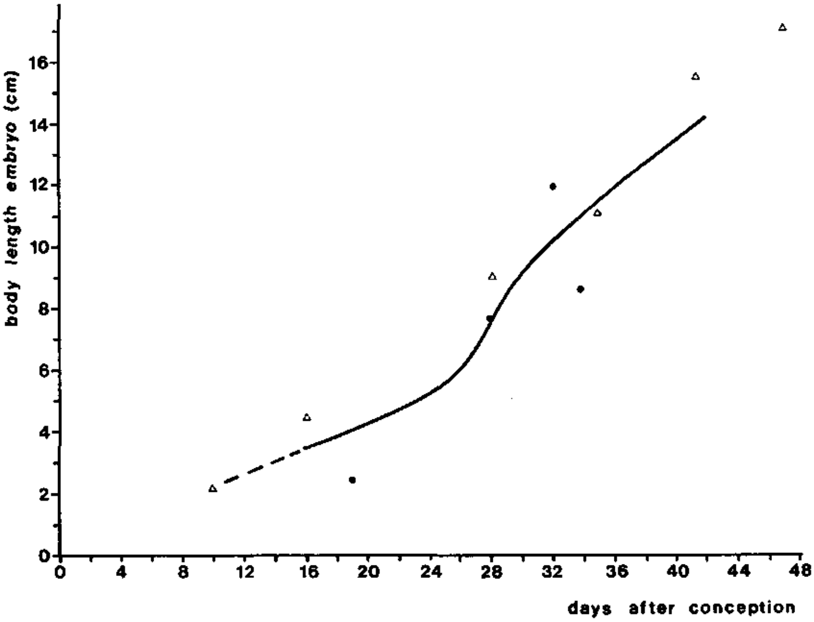


Fig. 3. Relation between body length and age in embryos of the European hare. Curve: constructed on the basis of Fig. 1 and 2. Triangles: data from FRAGUGLIONE (1962); dots: data from embryos from Jouy-en-Josas

The shape of the curves of fig. 1 and fig. 3 is not the same as corresponding curves for *Lepus americanus*, given by BOOKHOUT (1964). He found that the growth of the body weight as well as the body length proceed gradually, without abrupt changes. This suggests that the distinct acceleration in the increase of the body weight around the 24th day of prenatal life, as found in *Lepus europaeus*, may be the result of insufficient data.

Although more data are needed, the given growth curves may be used as a provisional reference for ageing.

References

BOOKHOUT, T. A. (1964): Prenatal development of snowshoe hares. J. Wildl. Mgmt. **28**, 338—345.

FLUX, J. E. C. (1967): Reproduction and body weight of the hare *Lepus europaeus* Pallas, in New Zealand. N.Z.J. Sci. **10**, 357—401.

FRAGUGLIONE, D. (1962): Le foetus du lièvre commun *(Lepus europ.* P.). Revue du Royal St. Hubert Club Belgique **2**, 35—37.

HEDIGER, H. (1948): Die Zucht des Feldhasen *(Lepus europaeus* Pallas) in Gefangenschaft. Physiol. Comp. et Oecol. **1**, 46—62.

KOLOSOV, A. M.; LAVROV, J. P.; NAUMOV, S. P. (1965): Biologia promylovih zverei SSSR. Moskova. Transl. 113 Bur. Anim. Pop., Oxford.

MARTINET, L.; LEGOUIS, J. J.; MORET, B. (1970): Quelques observations sur la reproduction du lièvre européen *(Lepus europaeus* Pallas) en captivité. Ann. Biol. anim. Bioch. Biophys. **10**, 195—202.

MÜLLER-USING, D. (1954): Diezels Niederjagd. Hamburg und Berlin: Paul Parey.

PIELOWSKI, Z. (1971): The individual growth curve of the hare. Acta theriol. **16**, 79—88.

RIECK, W. (1953): Der Feldhase. Merkblätter des Niederwildausschusses des D.J.V., 4.

SPAGNESI, M. (1972): Brevi osservazioni sull'allevamento e sull'accrescimento dei giovani di Lepre europea *(Lepus europaeus* Pallas) nati in cattività. Ricerche di biologia della selvaggina no. 53, Bologna.

VALENTINČIČ, S. I. (1956): Resultate zweijähriger Beobachtungen und Studien über den idealen Zuwachs beim Feldhasen auf der Insel „Biserni ostok". Z. Jagdwiss. **2**, 152—160.

Authors' addresses: SIM BROEKHUIZEN, Research Institute for Nature Management, Kemperbergerweg 67, NL-6816 RM Arnhem, The Netherlands; LISE MARTINET, Station de Physiologie Animale, Institut National de la Recherche Agronomique, F-8350 Jouy-en-Josas, France

Art. IV

Survival in Adult European Hares

Sim BROEKHUIZEN

Om hun levensverwachting te kunnen bepalen werden volwassen hazen gevangen en van oormerken voorzien.

Foto: Roel van Beek

ACTA THERIOLOGICA
Vol. 24, 34: 465—473, 1979

STUDIES ON THE EUROPEAN HARE. XXXVI

Survival in Adult European Hares

Sim BROEKHUIZEN

Broekhuizen S., 1979: Survival in adult European hares, Acta theriol., 24, 34: 465—473 [With 4 Tables & 1 Fig.].

The average annual survival rate of adult European hares (*Lepus europaeus* Pallas, 1778) in The Netherlands, determined as 0.34—0.38, was established by recoveries of hares which had been ear tagged in their adult phase, and by means of the ratio of first-year hares to older hares shot in December, assuming that survival in adult hares is independent of age. This rate was compared with data from literature. The survival rates from various European countries show a great variation. It is not clear whether hunting influences the average survival rates.

[Res. Inst. for Nat. Manage, Kemperbergerweg 67, 6816 RM Arnhem, The Netherlands].

I. INTRODUCTION

In relation to population dynamics of hares, it is important to know the survival rate of adult hares. Information about this is still scarce, most likely due to the fact that hares of different year classes cannot be easily distinguished in the field. Therefore, to determine the survival rate, hares were marked with ear tags, which is very labour intensive. In order to read these marks, the investigator either has to rely on hares being recaptured, or on the recovery of dead marked animals being reported. In practice, captures as well as recoveries are concentrated in the non-productive period, *i.e.* the end of autumn and the beginning of winter. In this period the conditions in the fields of the countryside are most suitable for catching hares and it is also the hunting period. This implies that the survival rate can only be determined for the whole reproductive season. Up to now it appears to be impossible to quantify the mortality in the course of the reproductive season.

We collected some data about the survival rate in Dutch hares from recoveries of tagged hares as well as by means of the ratio of first-year to older hares in the shooting bags during December. The results are compared with literature data from other European countries, which were obtained from different situations and by using different methods. These literature data will first be reviewed briefly.

II. REVIEW OF SURVIVAL DATA FROM LITERATURE

Information on the survival of adult hares has been obtained from a study of a population composed of hares of known age (Abildgård *et al.*, 1972), from the results of repeated recaptures of marked animals of known age (Pielowski, 1971 and 1975), from a study of the age composition of a random shooting (Frylestam & Von Schantz, 1977), and from reported recoveries by shooting of hares ear tagged as young (Rieck, 1955 and 1956).

1. Population of Known Age Composition

From the beginning of 1957 up to the end of 1970, more than 95% of the hare population of the Danish island Illumö was marked with numbered ear tags. Hence, unique data are available about the age composition of an entire population (Abildgård *et al.*, 1972). Since this investigation concerned an island situation, the influence of migration could be ignored, except perhaps one severe winter when the sea was frozen. It should be kept in mind that no predatory mammals occur on Illumö. There was no killing by hunting, but due to the capture operations 2—3% died. During the study it became obvious that after 1962, unmarked adult hares were exceptions. The maximum age was 7 years. As can be expected, the mortality in young hares appeared to be notably higher than in adults. The average annual mortality rate in the adult females and males was 45 and 38% respectively.

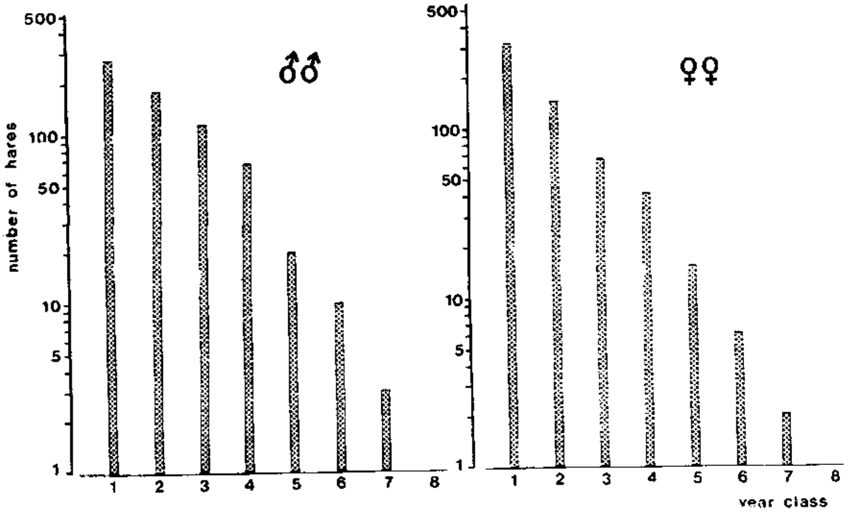


Fig. 1. Number of hares in the various year classes, present on the Danish isle Illumö in the first catches of November/December during the period 1962—1970 (after data from Abildgård *et al.*, 1972).

The distribution among the different year classes of the hares, examined during the first winter captures (November or December) of the years 1962—1970, is shown in Fig. 1, which was composed after data presented by Abildgård *et al.* (1972). The numbers are plotted on a log-scale. As the tops of the columns representing the numbers of females nearly fit to a straight line, the mortality rate in the females appears to be independent of age. In the males the annual mortality rate during their first three years is lower than in females. **Abildgård** *et al.* (1972) reported that particularly in years of high density and in the periods of decrease afterwards, the mortality in males was lower than in females.

2. Recaptures of Hares Tagged as Young

The survival of hares can be investigated by means of repeated recaptures of marked animals of known age. The age of hares can only be reliably estimated in the young; therefore, it is necessary to mark the leverets. The most extensive study using this method was carried out near Czempiń in the province of Poznań in Western Poland (Pielowski, 1971 and 1975). The young hares found in the field were ear tagged and released. During the winter about 30% of the population was caught, and exported, except the marked animals which were released again. In this way data were collected about the number of young surviving the different year classes. From these data I have constructed a life table (Table 1). The average annual mortality rate was calculated as $q_x = \Sigma d_x / \Sigma l_x$, and turned out to be 0.49 over the first 7 years.

Table 1

Life table for the hare population near Czempiń, based on data from Pielowski (1975).

Age (years)	l_x	d_x	q_x
0—1	1.000	0.500	0.500
1—2	0.500	0.278	0.556
2—3	0.222	0.086	0.387
3—4	0.136	0.062	0.456
4—5	0.074	0.024	0.324
5—6	0.050	0.015	0.300
6—7	0.035	0.011	0.314
>7	0.024	0.024	1.000
Total	2.041	1.000	
$\bar{q}$ (1—7)			0.489

l_x — proportion of animals that survived to the year class x; d_x — difference between two succeeding values of l_x; q_x — mortality rate of the year class x ($q_x = d_x/l_x$).

Since we consider the survival rate in adult hares, it is to be noted that in the life table the age class of 0—1 year is included. As capturing took place in winter time, one would expect most of the hares caught to be older than 4 months, since the majority of the young born in late summer and autumn die before the winter, due to parasitic infections such as coccidiosis and strongylosis. Assuming that the survival of young hares of five months and older does not differ from that of adults, all hares of five months and over have been considered as »adults«.

The oldest hare recaptured in the Czempiń area was at least 12.5 years old. However, the proportion of hares older than 7 years was small (2.4%). All hares older than 6 years proved to be females.

3. Age Composition of a Random Shooting

From hares killed at a shooting session, an impression can be gained of the age composition of the population. A disadvantage of this method is that it is hardly possible to be sure about the nonselectiveness of the shooting. By using the number of periosteal growth lines in the lower jaw as a criterion for age, Frylestam & Von Schantz (1977) determined the age composition of a sample of 39 hares shot from an area in South Sweden. The number of hares (*l*) belonging to the different year classes was determined; the differences between the l-values of succeeding year classes (*d*) indicate the annual mortality. Although the sample may be too small to be representative for the population, I constructed a »life table«, and from this the average annual mortality rate was calculated to be 0.49. It should be noted that also in this case the first-year-hares have been included as »adults«.

4. Recoveries from Shooting of Hares Tagged as Young

Recoveries of marked hares are mostly obtained from shot or dead animals. Data from the latter are so scarce, that they cannot be discussed separately.

Table 2

Life table based on recoveries from ear tagged hares, collected by Rieck (1955, 1956).

Age (years)	d	l	l_x	d_x	q_x
0—1	81	130	1.000	0.623	0.623
1—2	29	49	0.377	0.223	0.618
2—3	8	20	0.154	0.061	0.396
3—4	7	12	0.092	0.054	0.587
4—5	1	5	0.038	0.008	0.210
5—6		4	0.031	0.023	0.742
6—7	0	1	0.008	0.000	
7—8	1	1	0.008	0.008	1.000
Total	130	222	1.708	1.000	
q_x					0.585

Rieck (1955 and 1956) collected recoveries of shot hares and I assembled them in a life table (Table 2). The first-year-hares shot during the hunting seasons are again considered as »adults«.

Table 2 shows, like Table 1, no significant difference in mortality rate between first-year and second-year-hares. The mean annual mortality rate was 0.58, and the oldest hare recovered was 7 years of age.

Calculating the mean annual mortality rate, mortality was assumed to be independent of age. In contrast to the mortality among the adult females of Illumö (section II.1), there is no basis here for this assumption, because the numbers recovered at older ages are too small to demonstrate any significance between differences. Furthermore, the recoveries collected by Rieck were mainly from shot hares (91.5%). Since it is unlikely that such a high proportion of the population dies through hunting, the rate of recovery in shot hares must be much higher than in hares died by other causes. Since the calculation is only based on recoveries from shootings, it is important to know whether hunting is age-dependent, especially within the mature section of the population. Unfortunately no sufficient information is available about this. Rieck (1967) compared the bag of a drive from November with that of a succeeding drive over just the same area one month later. There was no significant difference between the proportion of first-year-hares from November (76%) and that from December (72%) ($\chi^2=2.03$; $P>0.05$); this implies that the chance of being shot on drives for first-year-hares and older ones is about the same. So it may be assumed that mortality caused by shooting is not dependent on age. An effect of senescence may be neglected.

III. RESULTS OF OWN INVESTIGATIONS IN THE NETHERLANDS

1. Recoveries from Shootings of Hares Tagged as Adult

For several years hares were caught and ear tagged in The Netherlands at the end of the shooting season and just afterwards. These hares were released partly in the same area and partly in other fields. Some of them were recovered, mainly because they were shot. To calculate the survival rate of these hares, we used only recoveries from animals which were estimated to be at least 5 months old, when they were caught. The estimation was done by the stage of ossification of the distal epiphyseal knob of the ulna (Broekhuizen & Maaskamp, 1979). Only the recoveries from shoots were used. Although it was not confirmed, it was assumed that the recovery rate was the same in the various fields. It was assumed also, that every year a similar proportion was shot and the survival rate of tagged hares of at least 5 months old was independent of age and calendar year. Taking all these

Table 3

Recoveries from Dutch ear tagged hares, marked at the age of 5 months or older. Recoveries from shootings only (n=418).

Year of marking	Number marked	Time between marking and recovering (years)									
		0—1	1—2	2—3	3—4	4—5	5—6	6—7	7—8	8—9	9—10
1968	1	1	0	0	0	0	0	0	0	0	0
1970	2	0	0	0	0	0	0	0	0		
1971	74	9	0	1	0	1	0	0			
1972	48	4	1	1	0	0	0				
1973	95	11	5	2	0	0					
1974	177	18	8	0	2						
1975	7	1	0	0							
1976	3	1	0								
1977	11	1									

assumptions into account, the survival rate was calculated by applying a model given by Cavé (1977)[1] (Table 3).

The survival rate was found to be 0.34 (S.D.: 0.10) and the recovery rate 0.163 (S.D.: 0.018). The differences between the observation and the expectation from Cavé's model may be due to chance ($\chi^2=3.23$; $\nu=5$; $P=0.34$), so there are no reasons to reject the assumptions of the model. Comparing the mortality rate in the first year with that of the succeeding years, there is no significant difference, so the assumption of mortality being independent of age in hares of 5 months and older can be maintained.

2. Recruitment in Stable Populations

When a population is stable in the long term, the average number of mature animals dying per year must be equal to the average number of yearlings joining the reproductive part of the population. In that situation the percentage of first-year-hares at the start of the reproductive season (recruitment) equals the annual mortality rate in the older hares, provided that in the latter mortality is age-independent. On those conditions the mortality rate in adult hares can be obtained from the recruitment.

Hunting statistics show that the level of the hare populations may fluctuate. Adamczewska-Andrzejewska & Szaniawski (1972), Pepin (1974) and Möller (1975) showed that also the proportion of first-year-hares can vary considerably, not only year by year but also between different areas in one year. Since in The Netherlands the reproductive season starts at the end of December (Broekhuizen, in prep.), the percentage of first-year-hares shot in December can be used as a measure of the recruitment. However, this percentage has to be obtained from data collected during several years from several areas, assuming that hunting does not affect the age composition of the population.

Investigation of the eye lens weight of 4801 hares collected every year in December from shooting bags during the years 1967—1975 in 24 different areas, showed that 62% of the hares were first-year animals. We defined hares as first-year when their eye lens fixed in formalin 10% and dried at 80°C, was less than 280 mg in weight (Broekhuizen & Maaskamp, 1979). At an average recruitment of 62%, therefore, the average survival rate in hares older than one year should be 0.38.

---

[1] I am greatly indebted to Dr A. J. Cavé for conducting the computation.

IV. DISCUSSION

The average survival rate in adult hares from The Netherlands as obtained by recoveries from hares ear tagged as adult (0.34), corresponds, notwithstanding the presuppositions, very well with that obtained from the mean recruitment just before the beginning of the reproductive season (0.38). Therefore, the survival rate in adult hares from The Netherlands is set at approximately 0.35.

Comparing this figure with the survival rate of males (0.62) and females (0.55) calculated by Abildgård *et al.* (1972) in the unexploited population from Illumö, and that (0.51) found by Pielowski (1975) in an unexploited part of a population near Czempiń, the survival rate we found in The Netherlands is remarkably low. The difference is unlikely only to be the result of the exploitation of the Dutch hares by hunting. During the period 1966—1970, Adamczewska-Andrzejewska & Szaniawski(1972) found 54% adults in shooting bags from the Polish province of Poznań (where Czempiń is also located). During the same period, they found 52% adult hares in their total material from 5 provinces. When these populations are supposed to be stable, the survival rates were respectively 0.54 and 0.52. This shows that survival in exploited populations may have the same high value as in unexploited populations, and it suggests that the exploitation is counterbalanced by compensatory mortality.

Table 4

Data from the literature about the percentage of hares older than one year, found in shooting bags.

Country	Years	Numbers examined	% ad.	Author
G.D.R., N part	1965—1972	6287	74	Möller, 1975
G.D.R., S.E. part	1965—1972	10976	65	„
G.D.R., S.W. part	1965—1972	16687	54	„
Poland, 5 provinces	1966—1970	24595	52	Adamczewska-Andrzejewska & Szaniawski, 1972
Poland, prov. Poznań	1966—1970	7762	54	„
The Netherlands	1967—1975	4801	38	Own data
Switzerland	1967, Oct.-Nov.	414	47	Wandeler & Huber, 1969
Denmark	1963, Dec.	146	35	Walhovd, 1966
France, Provins	1971—1972	435	26	Pepin, 1974
F.R.G., Biebesheim	1964, Nov.	798	24	Rieck, 1967
F.R.G., Biebesheim	1964, Dec.	402	28	„

In the period 1965—1972, Möller (1975) found in the south-west, south-east and northern parts of the G.D.R. 53, 65 and 74% respectively, adult hares in shooting bags. This also indicates survival rates which are not lower than found in Illumö and Czempiń. It is not reported whether hunting in Poland and the G.D.R. influenced the age composition. It is premature, therefore, to conclude that shooting does not affect the survival rate of adult hares. Sufficient information on the ecological conditions in the various areas is also lacking. Data about the percentage of adult hares in shooting bags obtained from short-term investigations in different European countries (Table 4), indicate that also lower survival rates in adult hares occur in exploited populations. Due to the different ecological conditions and the incidental character of these samples, it is not possible to evaluate the differences.

From the average survival rate in adult hares from The Netherlands, set at 0.35, the average expectation of further life can be calculated by the formula $(2—m)/2m$, where m is the annual mortality rate (Lack, 1954). So the expectation of further life found for a Dutch adult hare is about one year (1.04).

REFERENCES

1. Abildgard F., Andersen J. & Barndorff-Nielsen O., 1972: The hare population (*Lepus europaeus* Pallas) of Illumö island, Denmark: A report on the analysis of the data from 1957—1970. Dan. Rev. Game Biol., *6*, 5: 32p.
2. Adamczewska-Andrzejewska K. A. & Szaniawski A., 1972: Relationship between the real increase and the yield of hares in Poland. Acta theriol., *17*, 19: 259—265.
3. Broekhuizen S., in prep: Reproduction in the European hare (*Lepus europaeus* Pallas) in The Netherlands.
4. Broekhuizen S. & Maaskamp F., 1979: Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands. Z Säugetierkunde, 44: 162—175.
5. Cavé A. J., 1977: Pitfalls in the estimation of age-dependent survival rates of birds from ringing and recovery data. Die Vogelwarte, *29*, Sonderheft: 160—171.
6. Frylestam B. & von Schantz T., 1977: Age determination of European hares based on periosteal growth lines. Mammal Rev., 7, 3—4: 151—154.
7. Lack D., 1954: The natural regulation of animal numbers. Clarendon Press: 1—343. Oxford.
8. Möller D., 1975: Zum Altersaufbau der Hasenpopulationen in der Deutschen Demokratischen Republik. Beiträge Jagd- u. Wildforsch., *9*: 315—325.
9. Pepin D., 1974: Mise au point de techniques pour l'étude de populations de lièvres. Bull. de l'Office Nat. de la Chasse, *2*: 77—119.
10. Pielowski Z., 1971: Length of life of the hare. Acta theriol., *16*, 6: 89—94.
11. Pielowski Z., 1975: Charakterystyka ekologiczna populacji zająca *Lepus europaeus* Pallas. Diss. Roczniki Akademii Rolniczej w Poznaniu, Poznań: 33p.
12. Rieck W., 1955: Feldhase und Wildkaninchen. [In: »Jagd und Hege in aller Welt«]. Deutsch. Jagdschutzverband, Bonn: 180—184.

13. Rieck W., 1956: Untersuchungen über die Vermehrung des Feldhasen. Z. Jadgwiss., 2, 1: 49—90.
14. Rieck W., 1967: Ergebnisse der Untersuchung von Feldhasenstrecken. Union, Int. Biol. du Gibier, 7th Congr. Beograd-Ljubljana: 383—388.
15. Walhovd H., 1966: Reliability of age criteria for Danish hares (*Lepus europaeus* Pallas). Dan. Rev. Game Biol., 4, 3: 105—128.
16. Wandeler I. & Huber W., 1969: Zum Altersaufbau der bernischen Feldhasenbestände im Jahre 1967. Rev. Suisse Zool., 76, 3: 680—686.

Accepted, June 20, 1979.

Sim BROEKHUIZEN

PRZEŻYWALNOŚĆ DOROSŁYCH ZAJĘCY SZARAKÓW

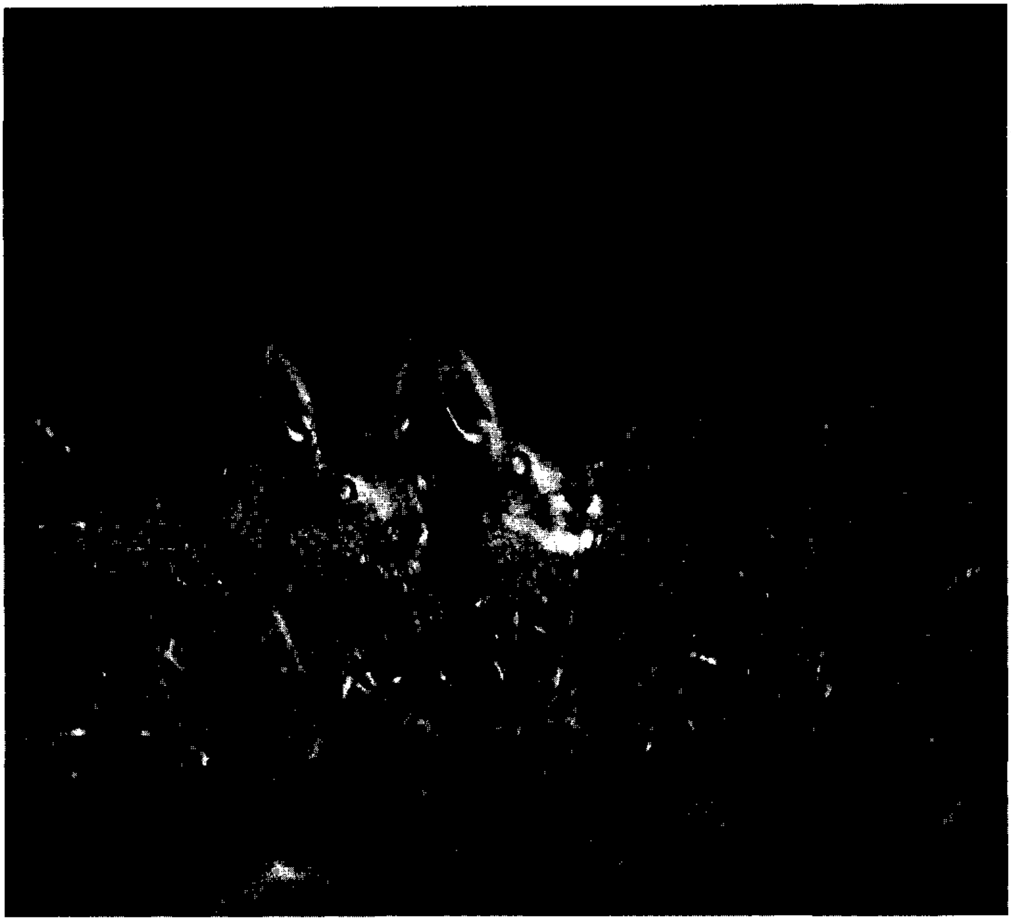
Streszczenie

Średnią roczną przeżywalność dorosłych zajęcy szaraków (*Lepus europaeus* Pallas, 1778) określono w Holandii na 0,34—0,38. Podstawą do wyliczenia było znakowanie (Tabela 3) oraz analiza stosunku ilościowego osobników tegorocznych do starszych strzelanych w grudniu — przy założeniu, że przeżywalność dorosłych jest niezależna od wieku. Uzyskane wyniki porównano z danymi literaturowymi, które mówią o dużym zróżnicowaniu przeżywalności w różnych krajach Europy (Tabele 1, 2, 4, Ryc. 1). Nie jest jasne czy fakt polowania na danym terenie wpływa istotnie na średnie wskaźniki przeżywalności.

Art. V

Behaviour of does and leverets of the European hare (*Lepus europaeus*) whilst nursing

SIM BROEKHUIZEN AND FRANS MAASKAMP



Jonge haasjes keren ongeveer drie kwartier na zonsondergang terug naar hun plaats van geboorte en wachten daar op de komst van hun moeder.

Foto: Frans Maaskamp

Ongeveer één uur na zonsondergang komt de moerhaas naar de plaats waar ze haar jongen wierp om te zogen. Daar accepteert ze dan elk aanwezig jong.

Het zogen duurt maar enkele minuten. De moerhaas zoogt zittend, met haar voorlopers een beetje gespreid.

Vaak gaan de jongen gedurende de laatste minuut van het zogen op de rug liggen en lijkt het of de moer hun urine oplikt (foto van t.v.-monitorbeeld).

Het einde van het zogen wordt bepaald door het wegspringen van de moerhaas. Op de foto heeft één jong zich alweer omgedraaid, één ligt nog op de rug.

Reprinted from *J. Zool., Lond.* (1980) **191**, 487–501

Behaviour of does and leverets of the European hare (*Lepus europaeus*) whilst nursing

SIM BROEKHUIZEN AND FRANS MAASKAMP
Research Institute for Nature Management, Arnhem, The Netherlands

(*Accepted 11 December 1979*)

(With 6 figures in the text)

After birth in one particular place, the leverets of a litter dispersed after a few days. In the evening, the leverets were observed gathering at, or near, their birth place to await nursing. There the doe would arrive later, about one hour after sunset, to nurse the young gathered there. Individual recognition between leverets and their doe seemed of no importance, and meeting was dependent on time and place. The young were nursed for only a few minutes and their urine, excreted during nursing, was licked up by the doe, which finished nursing by jumping away from the young. The leverets dispersed again and kept apart from each other until they gathered again the next evening. Usually leverets are nursed for four weeks, but longer nursing periods were found in the last litters of the breeding season. The nursing behaviour is probably adapted to prevent discovery of leverets by predators.

Contents

Introduction

Information about the behaviour of doe-hares, *Lepus europaeus* Pallas, and leverets at birth and nursing is scarce and contradictory. The pre-partus behaviour of does has never been studied, and consequently there is no information about factors determining the locality of the place of birth. Old English literature (Topsell, 1607, cited by Evans & Thomson, 1972; Millais, 1907, cited by Koenen, 1956) mentioned that doe-hares give birth to young of one litter in different places. More recently, it has been suggested that after birth the young are actively dispersed by the doe herself (IJsseling & Scheygrond, 1960; Tegner, 1969).

0022–5460/80/080487+16 $02.00/0

On the other hand, numerous cases are known of litters found in the field with several young together. Moreover, there are two descriptions of the birth of a complete litter at one particular point (Brassica, 1961; de Jong, 1969).

We have made a number of observations to solve this problem with the aim of giving a full description of the behaviour of does and leverets at nursing. This paper is an extension of the preliminary observations reported by Broekhuizen & Maaskamp, 1976.

Material and methods

Nursing was observed from 47 litters in the field. Two of these litters were located in the North-eastpolder (52°40′N; 05°40′E), one on grass and one on arable land. The other 45 litters were situated near the village of Brummen (52°05′N; 06°09′E): 44 on grass or arable land in the IJssel River valley and one in a beech forest.

Observations were made with 8 × 56 or 11 × 80 binoculars. After twilight 55 W 12 V spotlights were used, powered by motor-accumulators. Most observations were made from cars, sometimes from a caravan. It appeared that neither adult hares nor leverets were disturbed by a white spotlight if the car stood still and the spotlights were rotated slowly. When hares were very nearby, the central beam of the spotlight was directed slightly to the side of the animals being observed. The white reflection of the leverets' eyes, in contrast with the more red or pink reflection of the eyes of the adult hares, made it easy to recognize and to follow the young, although sometimes white reflecting eyes of rabbits were confusing.

During the observations it became clear that the leverets were nursed shortly after sunset. Therefore, most of the observations were started at about sunset and terminated after nursing was finished. This was called an observation period. Most litters were only observed during some of these periods. In May and June 1974 one litter was observed continuously day and night for three weeks, and after sunset till sunrise during the rest of the nursing period. In addition, in April 1976, one litter and the doe hare were observed continuously for 48 hours.

The number of litters observed and the number of observation periods spent watching them are given in Fig. 1. The spread of the observations over the year is given in Table I.

TABLE I

Distribution of the observation periods over the year

Month	Year, number of litters under observation each month, and number of observation periods per litter ( )	Total number of observation periods
February	1976: 3 (7; 3; 2)	12
March	1976: 10 (8; 6; 5; 5; 5; 3; 2; 2; 1; 1)	38
April	1976: 13 (10; 10; 5; 5; 4; 4; 4; 2; 2; 2; 1; 1; 1)	51
May	1974: 1 (4)	4
	1975: 1 (3)	3
	1976: 12 (6; 4; 4; 4; 2; 2; 2; 1; 1; 1; 1; 1)	29
June	1974: 3 (26; 3; 1)	30
	1975: 1 (1)	1
	1977: 1 (1)	1
July	1975: 6 (17; 8; 5; 4; 2; 1)	37
	1977: 1 (3)	3
August	1975: 6 (15; 12; 11; 5; 3; 2)	48
September	1975: 5 (24; 13; 7; 3; 1)	48
October	1975: 5 (12; 11; 11; 8; 2)	44
November	1975: 1 (26)	26
	Total	375

Some young could be caught and marked with an ear-tag. Aluminium bird wing-tags were used for leverets up to about two weeks; the older ones were marked with plastic ear-tags from Dalton-type rotor. The tags were plastered with reflecting tape (Scotch lite), which enabled easy and individual recognition of the leverets.

The age of the leverets, when caught, was established from their body weight and the length of the hind foot (Broekhuizen & Maaskamp, 1979). The age of leverets which were not caught was estimated from their size, but these estimations are inaccurate.

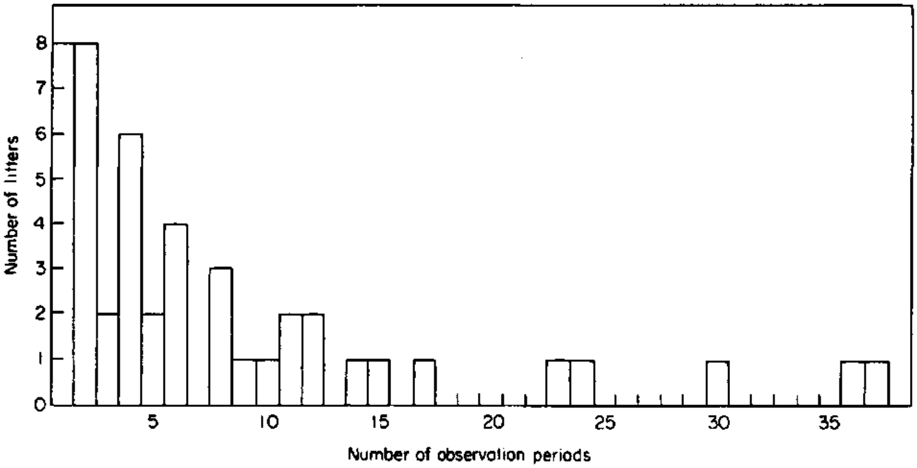


FIG. 1. Frequency of the number of litters observed during different observation periods. It is shown that most litters were observed for a short number of periods.

Results

Dispersion of young

During our field observations we did not observe any leverets being born, though five times we found leverets on their first day of life, which we could see from their wet, sticky fur. The numbers of such young ones varied, and amounted to 1, 2, 3, 4 and 4, respectively. In Holland the number of embryos found in pregnant females varies from 1 to 10, but litters of five and more are exceptions (Broekhuizen & de Wit, 1972). This suggests that at least some of the females give birth to complete litters in one place. However, finding day old single young may indicate that some females behave in another way.

Single young leverets may result from different causes:

1. They constitute litters of one;
2. The doe gives birth to the complete litter in one place, but she carries the young to different places shortly after birth;
3. As 2, but the young leave their birth place by themselves shortly after birth;
4. The doe gives birth to the young of one litter in different places.

As to point 1, litters of one are not interesting from the present point of view. Their occurrence cannot be excluded but they will be left out of consideration.

As to point 2, during our long and intensive observations we never saw a doe carrying away one of her young. Dispersion of young by the doe hare is, therefore, considered to be very unlikely.

As to point 3, active dispersion of the young has been observed several times. This may be illustrated by the following case histories, from which we tried to quantify the dispersion in relation to the age of the leverets.

Case history A. May 1976 a litter of four newly born young (the fur not yet dry) was found in a pasture. This litter was checked in the evening immediately after nursing, when they were still together. The next afternoon the leverets had spread over distances varying from a half to one metre from the place of birth, and on the third evening we found two leverets 3 and 8 m respectively from the birth place. This strongly suggests that the leverets may disperse actively at a very young age.

Case history B. May 1974 a litter of four leverets, still together, was found in a hay field during mowing. An area of 2 m^2 surrounding the litter was not mowed. Pickets, 10 m apart, were placed in four directions from the litter to facilitate the estimation of dispersion distance. One leveret disappeared during the first night and another a week later. At the end of the fifth week one of the remaining leverets was caught and fitted with a radio-collar. We could trace this leveret for 10 days more, until it was killed by a predator in its seventh week and information stopped. The litter was kept under continuous observation as described in the chapter on materials and methods.

It turned out that the young were nursed by the doe every night about one hour after sunset. After nursing the doe disappeared into the dark and the young then left the high grass and dispersed amongst the surrounding mown vegetation. The distance over which they explored the field increased on successive nights, but during the first 10 days of life they always returned later in the night to the unmown area, where they probably were born.

Every night the mean maximum distance between the young and the unmown area was estimated by means of the pickets. These distances are presented in Table II, together with data on dispersion of a litter of *L. americanus* obtained from Rongstad & Tester (1971). It is shown that during the first 10 days of life the young explored the field after nursing over increasing distances. At the 11th day the young reached the edges of the mown field where the vegetation was much higher, providing good cover for the leverets. From this time on, the young did not return to the nursing area in the same night, but spent the whole next day in the high vegetation, returning to the nursing area after sunset. It is shown in Table II that the distances over which the young dispersed still increased as they grew older to about 400 m in their sixth week. It is also shown that *L. americanus* leverets behaved in a similar way.

The behaviour of the leverets during the first 10 days of life differs from that reported in case history A, where the young were found dispersed during the day from the day after their birth. Our observations about young gathering before nursing (see next section) indicate strongly that the leverets normally return to the place of birth shortly before the next nursing. Therefore, we tend to consider the return to the nursing place in the same night, as described in case history B, as an artefact resulting from the removal of cover around the place of birth. We assume that the increasing distances over which the mown field was explored in successive nights about equal the dispersion distances under conditions of cover surrounding the nursing place.

As to point 4, all our observations support point 3, and consequently we consider the possibility of does giving birth to young of one litter on different places as to be very unlikely.

Gathering of leverets and their doe

In the previous section it was shown that leverets of one litter spend the day some distance from the birth place, normally separated and isolated from each other. When the behaviour of leverets found singly in the field was studied from a hide, they always became active in the evening and went to another place where they waited for the doe to nurse them. It was observed 123 times that some leverets came up to the same place from different directions to wait close together for nursing. The equal sizes of the leverets and their constant numbers on successive evenings made it very likely that they belonged to the same litter.

TABLE II

Dispersion of a litter of ***Lepus europaeus*** *during the first months of life, compared with data from a litter of two young of* ***L. americanus****, obtained from Rongstad & Tester (1971)*

Day of life	*L. europaeus* Maximum distance to the place of birth (m)	*L. americanus* Separation between young by day (m)
1	<1	0
2	1	
3	1·5	
4–5	3	
6	4	
7	8	
8	10	18
9	>20	
10–11	80	18
13	80	30
Week of life	**Approximate maximum distance to the place of birth by day (m)**	**Approximate maximum distance to the place of birth at all times (m)**
2	80–100	70
3	80–100	150
4	120	160
5	230	180
6–7	400	140
8–9	unknown	300
10–11	unknown	560

One or more young from seven gathering places could be ear-marked. Such young always gathered and waited at the same place, showing that each litter had its own fixed place to wait for nursing.

During the study seven times very young leverets were found together during the day. We assumed that such young were still at their birth place. Observations showed that after these young had dispersed, they gathered in the evening at the place where they were found, i.e. the probable place of birth. This suggests that the location of the place to wait for nursing is determined by the place of birth.

In many cases we noticed the young when they were already close to the gathering place. The time of arrival of the leverets on the gathering place could frequently be determined (Fig. 2). The average was 45 min after sunset. Arrivals varied from 10 to 70 min after sunset; this was primarily due to between litter variation, since within the litter variation is very small (see p. 493).

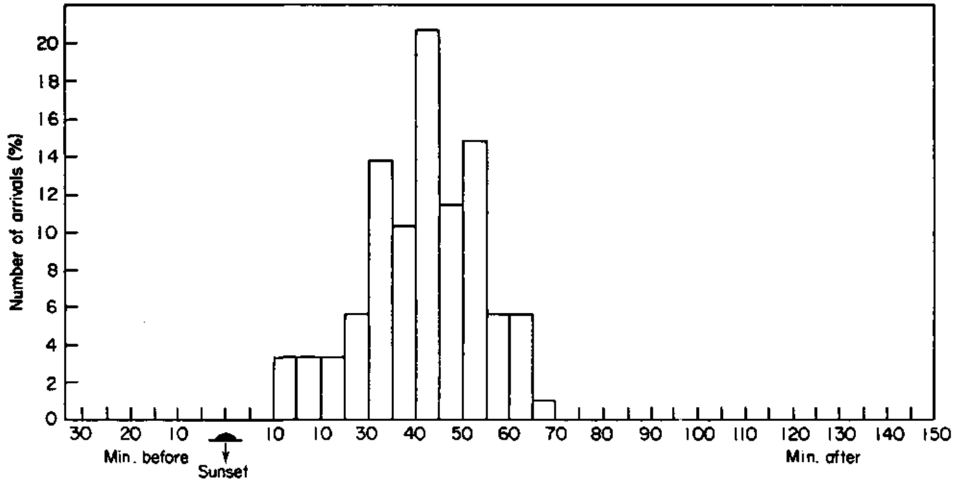


FIG. 2. The time of arrival of the young on the gathering place in relation to sunset. $N=87$.

After the young had waited for some time, a doe hare normally came up to nurse them. It could be proved by studying two radio-collared does that they joined the young at the same place on successive evenings, and probably this was the normal pattern.

When the doe comes up to the gathering place, the young behave differently. When they are still very young, they normally wait at the gathering place, but the older leverets sometimes go to meet the doe and try to suckle straight away. Some does return to the original gathering place for nursing, followed by their young, but others, however, nurse the young at some distance from the original gathering place, and because a doe arrives from the same direction on successive evenings, nursing gradually shifts in that direction (Table III).

In one out of 21 litters with two or more leverets the young were not nursed together if they had not all gathered when the doe arrived. This may be related to the exceptionally early arrival of this doe on the nursing place. In the other litters the doe nursed all her young simultaneously. Having nursed her young once, the doe refused all resuckling attempts.

It has been observed that the young of different litters when born less than 40 m apart, may mix together when gathering for nursing. If they are still mixed when the doe arrives, they are all accepted and nursed. This suggests that there are no special family ties between a mother and her children, but that nursing occurs because a lactating doe meets some eager baby-hares at a predetermined place in the field.

Frequency and time of nursing

In May and June 1974 a litter was observed continuously for three weeks. From then until nursing had ended, the litter was observed continuously each night from sunset until two hours after sunrise. During this period the young were never observed to be nursed during day time, and only once each night about one hour after sunset (Broekhuizen & Maaskamp, 1976).

TABLE III

Mean distance between birth place and nursing places of a litter observed in May and June 1974, related to the leverets' age

Weeks after birth	Mean distance between birth place and nursing places (m)
1	0·5
2	2
3	10·5
4	21·4
5	33·5

These data could be supplemented with observations from another litter on 15–16 April 1976 by noting the behaviour of a radio-collared doe and her young. Two nursings were seen, both about 80 min after sunset. The rest of the time the doe was out of sight of the young.

More data were obtained from observations started at sunset from litters which had been found during the day. In all cases nursing was observed about one hour after sunset.

From these observations it can be concluded that young hares are nursed once every 24 hours.

Immediately after arrival of the doe nursing is started. Starting times have been measured frequently; they appear to be highly correlated with sunset (Fig. 3). On average nursing started 63 min after sunset. All nursings more than 90 min after sunset appeared to be caused by interference from predators or man.

Figure 3 includes one literature reference (Bos, 1967): the remarkably early nursing on 21 March. This observation was done by the naked eye in daylight. We observed one nursing at a similar time of the day (22 May) from a litter which was seen to be nursed at normal times on other evenings, indicating that the time of nursing is not completely fixed.

Variation in the start of nursing

The observed variation in the start of nursing raises the question of what stimulates the doe and the leverets to go to the gathering place. Two aspects of variation have to be distinguished: differences between litters and variation from day to day within litters. Both aspects are illustrated in Fig. 4, in which the starting times of nursing for three litters observed simultaneously are shown. Two does nursed in the same pasture whilst the third nursed about 800 m away, also in a pasture. During the period given on the abscissa in Fig. 4, the last doe nursed on average 42 min after sunset. The other does started nursing later: on average 7 and 23 min, respectively. As the light regimes were the same for all three, it is likely that the does had different individual threshold values for the stimulus activating them to go to the nursing place.

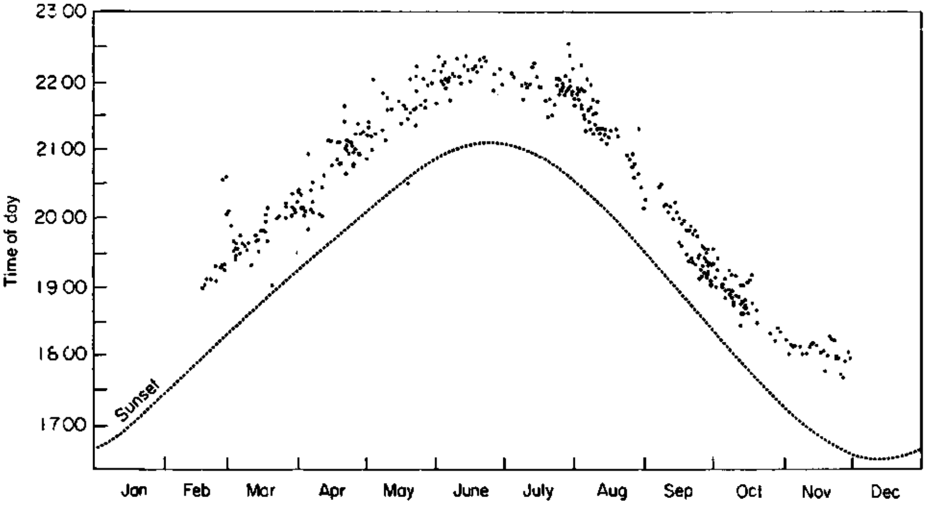


FIG. 3. Start of nursing. The dotted line indicates time of sunset; each point gives the start of an observed nursing.

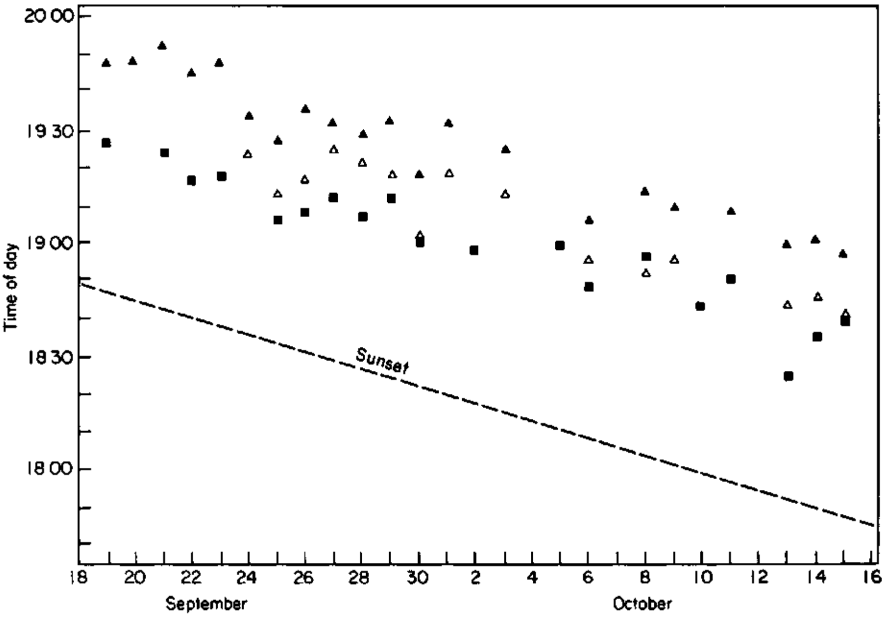


FIG. 4. The starting time of nursing for three different litters. The two litters indicated by triangles were nursed on the same pasture; the litter indicated by squares was nursed about 800 m away from the others.

Unfortunately we were usually unable to determine the time of arrival of the young at the nursing places. The few data we collected from the litters presented in Fig. 4 are summarized in Table IV and indicate that young arriving early probably have does which do the same.

Day-to-day variation in nursing time may have different causes. Firstly hares are often delayed on their way to the nursing place by interference either from other hares, from predators or from man. Secondly, differences in light intensity may be important. Table V gives data on the variation in nursing time on successive evenings related to cloud-cover. A change from bright sky to heavy cloud usually brings the time of nursing forward, while the opposite change may result in the young being nursed later. Less marked changes in cloudiness did not cause a clear change in nursing time.

Although light intensity seems to be important to the nursing time, it is improbable that light intensity is the direct stimulus for the doe and the leverets to go to the nursing place. We always needed a spotlight in spring and autumn, whilst in June and July the arrival of the leverets could be observed without a spotlight, and in bright weather sometimes even the nursing.

TABLE IV

Differences between arrival times (min) of the young of the litters presented in Fig. 4

Date (1975)	Open triangle compared with square	Closed triangle compared with square	Closed triangle compared with open triangle
21 September		+17	
23 September		+30	
24 September			+5
28 September	+5		
3 October			+2
8 October	+2	+3	+1
14 October			+5

TABLE V

Changes of nursing time on two successive evenings in relation to the parallel changes of cloud cover

Change of cloud cover (%)	N	Changes of the time of nursing Advancement >5 min	Change <5 min	Retardation >5 min
+100	14	79%	21%	0%
+50	15	33%	60%	7%
Equal	63	22%	56%	22%
−50	14	14%	43%	43%
−100	11	9%	18%	73%

Cloud cover was determined as fully overcast (100%), half overcast (50%) or nil. *N* is number of observations.

Length of the nursing period

The nursing period can be divided into two phases: one in which milk is indispensable to the young and one in which milk is supplementary and green food is most important. There is no abrupt change from the first to the second phase. In captivity, as well as in the field, leverets were observed nibbling green food from the age of four days onwards, but in the beginning this is probably not ingested. Using a T.V.-circuit, we observed proper feeding on green food in two leverets, born in captivity, from their 12th day. The leverets we observed continuously for three weeks in the field (see p. 490) showed proper grazing when they were 13 days old, and from their 17th day they ate grass regularly. This confirms data of Hediger (1948), Rieck (1953) and Pielowski (1971), who found milk supplementary for leverets aged 17, 17 and 15–18 days, respectively. So it seems justified to put the change to the second nursing phase at an average age of 17 days.

Field observations on the length of the total nursing period are summarized in Table VI. Age determination of the litters was difficult, because we did not want to disturb the leverets' behaviour by catching them. The age criteria used are also given in Table VI.

TABLE VI

Length of nursing period of some hare litters under field conditions, arranged in order of birth date

Age when found (estimated)	Criterion for estimation	Birth date	Nursing period
2 days	Body size, young together	28 March	23 days
1 day	Fur still wet	27 May	33 days
1 week	Body weight 190–280 g	14 July	32 days
2 weeks	Body size	23 August	57 days
2 weeks	Body size	9 September	42 days
2 weeks	Body size	28 September	>67 days

The Table shows a large variation in the length of the total nursing period. Martinet *et al.* (1970), working with captive hares, found a nursing period of about one month to be normal. This confirms our data from the middle of the breeding season. The shortest period, 23 days, was observed in a litter where the doe often arrived at the nursing place before the young were gathered. After the 23rd day the young gathered on the nursing place for another two evenings, but the doe did not show up. This suggests that the nursing period is terminated by the doe, not by the young. This was confirmed by later observations.

Table VI shows that some litters are nursed for much longer than one month. The litters concerned were probably the last of the doe's breeding season, as the observations were all from September or later. This suggests that does nurse longer when they do not become pregnant. So when lactating females are killed during the shooting season, which starts in The Netherlands on the 15th of October, this does not necessarily mean that the leverets left behind are dependent on nursing.

Prolonged nursing periods in the last litters of the season were also reported for *Lepus americanus* (Rongstad & Tester, 1971), the European rabbit (Lockley, 1973) and the swamp rabbit (Sorensen *et al.*, 1972), and this may be characteristic for all Lagomorpha.

Length of a nursing bout

Data on the length of a nursing bout are summarized in Fig. 5. The Figure shows that nursing becomes shorter with the increasing age of the leverets. In general, undisturbed nursing takes less than 6 min; only one out of 241 bouts was more than that. Nursing is more variable during the leverets' first week of life; in the 3rd and 4th week the length becomes more or less constant at 2–3 min.

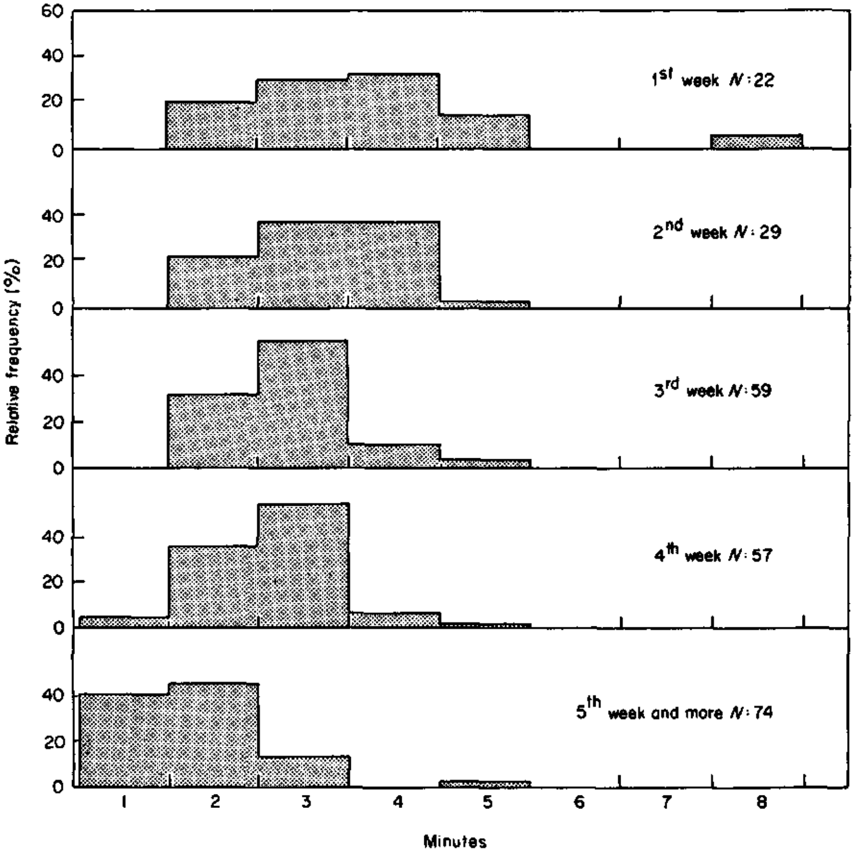


FIG. 5. Histograms of the length of the nursing bout per evening in relation to the age of the leverets. Nursing bouts shorter than 0·5 min have been included in the lowest time class. *N* is the number of nursing bouts measured.

After the 4th week the length of the nursing bout decreased sharply. In most litters this period of short nursing lasted only a few days and then the doe did not show up any more. Nursing after five weeks, observed during autumn, was even shorter and lasted only about half a minute after the 6th week (2 litters).

Urine licking

During nursing the doe always sits in an upright posture with her forelegs straddled, enabling her to watch around while the young suckle. We never observed a doe lying on her side during nursing like other mammals do.

Many times it was observed that the young turn on their back during the last minute of the nursing bout. Mostly the young turn spontaneously, sometimes after the doe bends her head forward. Then the doe licks the genital region of the young in succession. It is highly probable that the leverets produce urine during this ceremony, which is then ingested by the mother. Although the licking behaviour could be recorded in the field on video-tape, we could not prove that the doe really licks urine, but the rhythmic movements of her tongue make this very likely.

The behaviour was observed during the whole nursing period. In one, probably non-pregnant doe observed in autumn, licking stopped after her young was about one month old, although nursing was continued for at least one and a half months more. Therefore, licking urine seems to be a characteristic element of the doe's nursing behaviour up to and including the fourth week of the nursing period.

Discussion

Our observations showed that leverets can disperse from their place of birth at a very early age. For practical reasons we had to make our observations in fields with low vegetation, and it may be that the very early dispersion we observed is related to the lack of cover or to disturbance. We were informed by farmers about day time findings of leverets up to two weeks old close together in undisturbed fields with good cover, suggesting that the availability of good cover may reduce the dispersion tendency of the young.

When dispersed at day time, subsequent gathering of the leverets seems to be determined by two factors: the tendency to go to the place of birth about three quarters of an hour after sunset, and the tendency to join other leverets during that time. Individual recognition between leverets is unlikely to play a part, at least not during the first few weeks.

The leverets and the doe do not recognize each other, for we repeatedly observed leverets trying to suckle hares other than their mother, if these passed by the nursing place while the leverets had gathered there. When the doe was accompanied by other hares, the leverets seemed to be confused and found the doe by trial and error.

Our observations suggest that the doe hare is only willing to nurse near the birth place, although she becomes more tolerant about nursing her leverets at some distance when they come to meet her as they get older. During the first weeks of the nursing period she seems to be prepared to accept any young that stay near the place of birth. We got the impression that individual recognition in does and leverets grows when the latter become older, especially at the time that the young start to eat green food. However, we could not confirm this.

Nursing once a day is also reported for *Lepus americanus* (Rongstad & Tester, 1971) and *L. timidus* (Dyballa, 1978), and seems to be typical for *Lepus*-species living in the field. Sorensen *et al.* (1972) found the same in the swamp rabbit (*Sylvilagus aquaticus*), where the leverets are nursed in front of the nest. Lockley (1973) found in a colony of wild rabbits (*Oryctolagus cuniculus*) that low ranking does, having their young in special breeding stops, also nursed once a day. Dominant does, with their young in a warren, were found to nurse twice a day. We observed leverets of European hares being nursed more frequently when kept with the doe in cages. This might suggest that nursing once a day is an adaptive behaviour to reduce the risk of predation in those cases where doe and leverets live separately and have to gather in the open air for nursing.

The gathering of the young was found to occur about three quarters of an hour after sunset throughout the seasons. This implies that gathering and subsequent nursing do not take place at the same light intensity, since this varies considerably for an hour after sunset over the seasons (Fig. 6). Daan & Aschoff (1975) have shown that in South Germany (48°N) various diurnal birds and mammals terminate their activity primarily in relation to sunset, not light intensity. If this also holds for diurnal predators in The Netherlands (52°N), it might be that the time of nursing in hares has been evolved in relation to the end of the activity period of predators hunting visually.

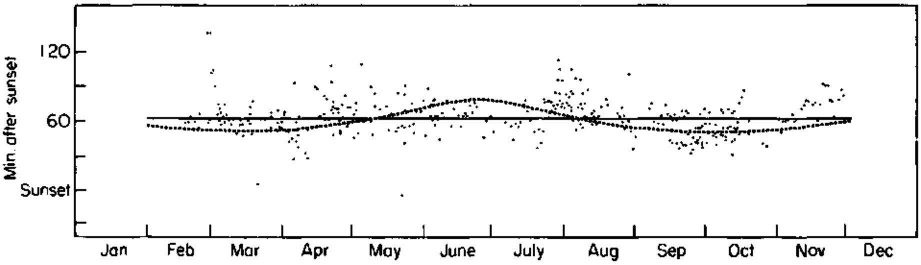


FIG. 6. Distribution of the start of nursing in relation to sunset. The solid line gives the mean time of nursing. The broken line gives the moment that the sun has sunk 8 degrees below the horizon. This line indicates the shift of a definite measure of light intensity with respect to sunset.

Nursing behaviour in *L. americanus*, as described by Rongstad & Tester (1971), and in *L. timidus*, as described by Dyballa (1978) appears to be very similar to the nursing behaviour in *L. europaeus*. This also holds for the remarkable shortness, only a few minutes, of the nursing bouts. As similar short nursing bouts are also found in wild rabbits (Boback, 1970), this may be characteristic for all Lagomorpha species. Both hares and rabbits have highly concentrated milk with 11–24% fat and 11–20% protein (Broekhuizen & Maaskamp, 1979). This, and the coherent shortness of the nursing bouts, may be other adaptations to reduce predation.

The licking up of the leverets' urine may be considered in the same light. Towards the end of a nursing bout the stomach will be expanded and the abdominal organs hard pressed. Therefore, the leverets will tend to urinate at that moment, but this would mark the nursing place if the urine was not ingested by the mother.

Summary

Young hares were found to be nursed only once per 24 hours, at or near the place where they were born, about one hour after sunset. During the leverets' first week of life, the length of the nursing bouts varies from 2 to 8 min. The bouts shorten during the second and third week to 2–3 min. A nursing bout ends by the doe's jumping away from her leverets.

After being nursed, the young move away separately in different directions over the

field, and remain concealed until it is time to return to the nursing place shortly after the next sunset. The distance over which the leverets disperse increases with age.

The doe arrives at the nursing place about one quarter of an hour later than the young, and nursing starts immediately. After nursing the doe leaves, and normally does not contact the young until the next evening.

When gathering for nursing, young of different litters born up to 30–40 m apart, may join together with the result that some leverets arrive at the wrong nursing place. When the doe comes up, she does not refuse, but nurses them together with her own young. This suggests that individual recognition between the young and their doe is of no importance. This suggestion is supported by the fact that young waiting at a nursing place try to suckle all hares coming past.

During the first few days of a nursing period all leverets are nursed at or very near to the place of birth. Later, when the young get older, they go to meet the doe when she first appears, and this may result in a gradual shift of the nursing place away from the place of birth into the more or less constant direction from which the doe arrives. In other cases the doe refuses to nurse when the young come to meet her, and then nursing is tied to the place of birth for a much longer period.

The normal length of a nursing period is about one month. During the first 17 days of this period milk is indispensable. In the last part of the breeding season, September and October, the nursing periods sometimes extend to more than a month. The nursing bouts then shorten to less than 1 min.

It was often seen that the leverets turn on their back during the last minute of a nursing bout. Then the doe makes a series of rhythmic licking movements with her tongue in the genital region of the young. It is assumed that this behaviour of the doe has the function of ingesting the leverets' urine.

It is suggested that several aspects of nursing behaviour, such as the synchronous gathering of the young, the shortness of the nursing bouts, the time of nursing, the licking of the leverets' urine by the doe, and the dispersion of the young, are adaptations to reduce the risk of being found by predators during the leverets' first weeks of life.

REFERENCES

Boback, A. W. (1970). *Das Wildkaninchen.* Wittenberg Lutherstadt: Ziemsen Verlag.

Bos, C. (1967). De lente zet goed in. *Ned. Jager* **72:** 247.

Brassica (1961). Hazen huisdieren. *Ned. Jager* **66:** 398–399.

Broekhuizen, S. & Maaskamp, F. (1976). Behaviour and maternal relations of young European hares during the nursing period. In *Ecology and management of European hare populations*: 59–67. Pielowski, Z. & Pucek, Z. (Eds). Warszawa: Pol. Hunt. Ass.

Broekhuizen, S. & Maaskamp, F. (1979). Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands. *Z. Säugetierk.* **44:** 162–175.

Broekhuizen, S. & de Wit, J. (1972). De worpgrootte bij hazen in Nederland en een extreem geval daarvan. *Ned. Jager* **77:** 552–553.

Daan, S. & Aschoff, J. (1975). Circadian rhythms of locomotor activity in captive birds and mammals: Their variation with season and latitude. *Oecologia (Berl.)* **18:** 269–316.

Dyballa, P. (1978). Schneehäsin beim Säugen. *Wild und Hund* **81:** 265.

Evans, G. E. & Thomson, D. (1972). *The leaping hare.* London: Faber & Faber.

Hediger, H. (1948). Die Zucht des Feldhasen (*Lepus europaeus* Pallas) in Gefangenschaft. *Physiol. comp. Oecol.* **1:** 46–62.

IJsseling, M. A. & Scheygrond, A. (1960). *De zoogdieren van Nederland.* Zutphen: Thieme.

Jong, H. de (1969). Hazengeboorte. *Ned. Jager* **74:** 560.

Koenen, F. (1956). *Der Feldhase.* Wittenberg Lutherstadt: Ziemsen Verlag.

Lockley, R. M. (1973). *The private life of the rabbit.* London: Transworld Publishers.

Martinet, L., Legouis, J. J. & Moret, B. (1970). Quelques observations sur la reproduction du lièvre européen (*Lepus europaeus* Pallas) en captivité. *Annls Biol. anim. Bioch. Biophys.* **10:** 195–202.

Pielowski, Z. (1971). The individual growth curve of the hare. *Acta theriol.* **16:** 79–88.

Rieck, W. (1953). Der Feldhase. *Merkbl. Niederwild. D.J.V.* No. 4.

Rongstad, O. J. & Tester, J. R. (1971). Behaviour and maternal relations of young snowshoe hares. *J. Wildl. Mgmt* **35:** 338–346.

Sorensen, M. F., Roger, J. P. & Baskett, T. S. (1972). Parental behaviour in swamp rabbits. *J. Mamm.* **53:** 840–849.

Tegner, H. (1969). *Wild hares.* London: John Baker.

Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Art. VI

Annual production of young in European hares (*Lepus europaeus*) in the Netherlands

SIM BROEKHUIZEN AND FRANS MAASKAMP

Het bleek noodzakelijk gegevens te verzamelen over het aantal jongen dat een moerhaas voortbrengt.

Foto: Sim Broekhuizen

Reprinted from *J. Zool., Lond.* (1981) **193,** 499–516

Annual production of young in European hares (*Lepus europaeus*) in the Netherlands

SIM BROEKHUIZEN AND FRANS MAASKAMP
Research Institute for Nature Management, Arnhem, the Netherlands

(*Accepted 13 May 1980*)

(With 3 plates and 6 figures in the text)

In the Netherlands, hares have a period of sexual inactivity in autumn. Even though a reactivation of spermatogenesis was found from the second half of November onwards, first conceptions did not occur until the last week of December. Throughout January, the proportion of pregnant females increased to 80% in February in healthy adults, but only to 8% in diseased ones. Due to the spread in the start of the breeding season caused by variations in health and age, no synchronization in birth was found. Consequently, in order to be able to determine the annual production of young, the gradual change in pregnancy rate and mean litter size over the year had to be taken into account. Taking mean monthly values for healthy adult females, an average annual production of nearly 11 young was found. Compared with other European countries, annual production in the Netherlands is relatively high which is probably due to a comparatively long breeding season.

Contents

Introduction

While studying the population ecology of the European hare (*Lepus europaeus* Pallas) in the Netherlands, it became necessary to have some data about the production of young per female hare. Because no data from the Netherlands were available, and because data from the literature concerning production in other countries vary remarkably as the summarized data in Table I show, we had to collect the relevant data ourselves.

Due to the fact that data collected by counting hares and their young in the field are very inaccurate with respect to the question involved here, we tried to determine the annual production of young per female in an indirect way, by considering the pregnancy rate over

0022-5460/81/040499+18 $02.00/0

the season, the number of embryos found in pregnant females, the duration of the gestation period, the time necessary for the doe to become pregnant again, and pre-natal mortality. In calculating the annual production, the mortality rate of females during the reproduction season was left out of consideration.

Two cases of extra-uterine pregnancy are described in detail, because the literature on this abnormality is contradictory.

TABLE I

Annual production of young per adult female in various parts of the world

Author	Country	Number of young
Kosolov (1941)	U.S.S.R. (Moscow province a.o.)	7
Raczyński (1964)	Poland (Poznań province)	7·8
Scarlatescu *et al.* (1962)	Rumania	8
Valentinčič (1956)	Yugoslavia (Biserni otok)	8·7
Frylestam (1979)	Sweden (southern part)	6·8–8·9
Pielowski (1976)	Poland (Poznań province)	6·5–9·0
Reynolds & Stinson (1959)	Canada (southern Ontario)	9·0
Flux (1967)	New Zealand	9·8
Kosolov (1941)	U.S.S.R. (pre-Caucasus region)	10
Rieck (1956)	Federal Republic of Germany	up to 11
Möller (1976)	German Democratic Republic	2·3–11
Petrov & Dragoev (1962)	Bulgaria	up to 12

Materials and methods

In the Netherlands, hares are officially protected from the 1 January to 15 October. This regulation, which ensures an undisturbed breeding season, hampered the collecting of data on reproduction. However, registered sportsmen are sometimes licensed to shoot hares outside the hunting season. From 1967 to 1973 a questionnaire was sent to these licence holders, asking for information about the number and size of embryos if present in the shot female hares and about the presence of a distal epiphyseal knob in the ulna and the radius in order to determine the age of the hare.

In addition to the questionnaire we also collected data from our own examinations of diseased female hares found dead in the field, which had either been shot or been victims of predators, traffic or agricultural activities. Hares shot outside the hunting season were obtained from two sources: from June 1968 to June 1970 some hares were shot monthly by registered gamekeepers in the province of Drenthe, and on 19 January 1971 we had the opportunity to examine hares from Schiphol (Amsterdam airport) which had to be shot to restrict crop damage.

Because it is likely that the production of young depends on the health and age of the mother, and because it can be assumed that some of the victims had died by inertness due to their poor condition, we decided to note the cause of death, the occurrence of bacterial infections and the amount of parasitic infestation, while the age was determined by the stage of ossification of the epiphyseal cartilage in the ulna and the radius, or by the weight of the eye lens as described in a previous paper (Broekhuizen & Maaskamp, 1979). Hares were considered healthy if there were no signs of bacterial infections, if they had only slight or moderate parasitic infestations, and if they had no bodily defects. Hares without a palpable distal epiphyseal cartilage knob on the ulna or whose eye lens weight exceeded 240 mg were considered to be eight months or older and called adult. The females were examined for the presence of corpora lutea graviditatis, embryos, placental scars and lactating lacteal glands. Table II gives the distribution of the adult hares examined per month, and Fig. 1 shows the areas from which healthy adult females were collected from February to October.

We collected 107 pregnant, adult and healthy does which together with the data from the questionnaires, made a total of 220 pregnancies. We also received many diseased hares from sportsmen and gamekeepers which were used to illustrate the influence of health on reproduction.

TABLE II

Numbers of adult female hares examined per month

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Healthy hares													
Drenthe	4	4	6	6	6	6	8	7	4	8	5	5	69
Schiphol	50										9	36	95
Elsewhere	6	3	9	6	3	4	5	2	5	5	10	13	71
Total	60	7	15	12	9	10	13	9	9	13	24	54	235
Diseased hares													
Drenthe	0	3	2	0	2	2	3	2	1	5	2	2	24
Elsewhere	18	21	21	19	6	4	5	3	7	4	9	20	137
Total	18	24	23	19	8	6	8	5	8	9	11	22	161

Results

Age of sexual maturity in healthy females

As the calculation of the mean production of young per female depends on whether all females are taken into account or only the healthy and sexually mature ones, we restricted the calculation to the latter. Consequently, we had to establish the age of sexual maturity.

Establishing sexual maturity is complicated by the fact that in hares reproduction activity is interrupted in the autumn. Therefore, inactivity need not only be the result of sexual immaturity, but also of the seasonal interruption. To eliminate individual variation in length of this seasonal interruption, only data from females in good health collected from February to August inclusive were used. Their age was determined by examining the stage of ossification of the epiphyseal cartilage in the foreleg, because undamaged eye lenses were not always available. From females with completely ossified cartilage, those with undamaged eye lenses of 300 mg and more were selected in order to obtain a group of at least one year old.

The presence of corpora lutea was used to determine whether or not the females were reproductive. The results are summarized in Table III, which shows that sexual maturity can be reached at the age of 4 months, but that most females become sexually mature at the age of 6 or 7 months. Nearly 83% of females of 8 months and older were shown to be sexually mature, and nearly 88% of the females over one year old were pregnant. From the data in Table III we decided to consider all females of 8 months and older to be sexually mature. In this paper they are called "adults", and are characterized by the absence of the distal epiphyseal knob in the ulna and radius.

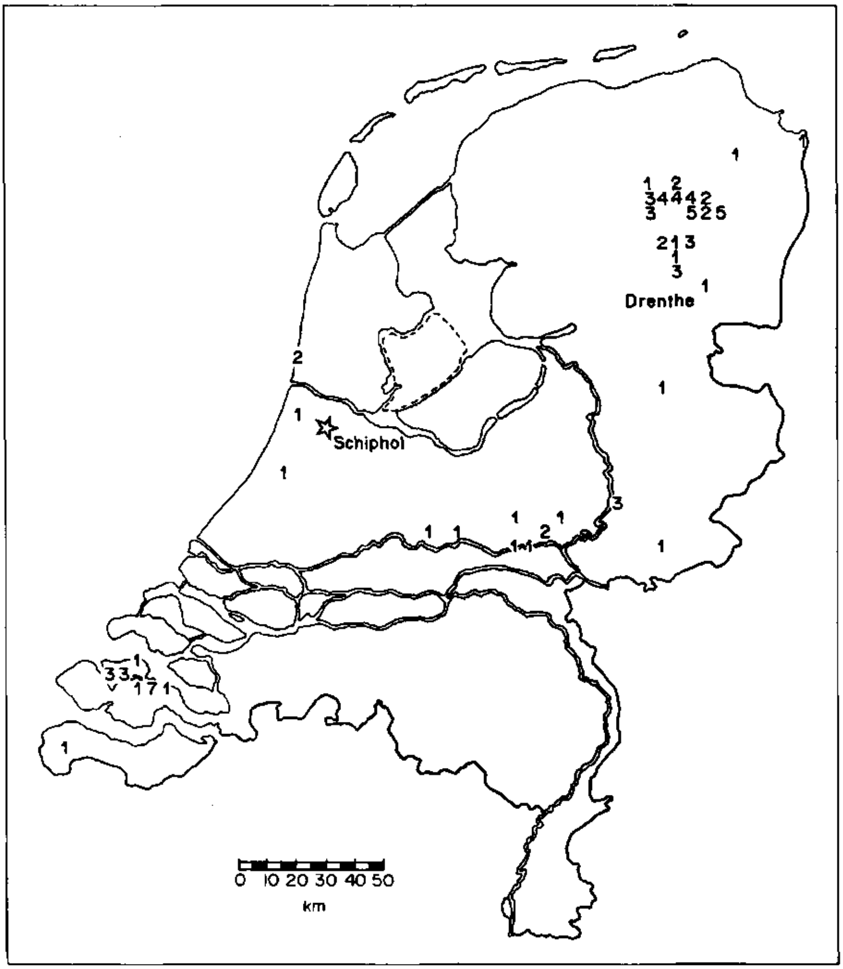


FIG. 1. Areas from which healthy adult females were collected from February to October. The numbers indicate the numbers of females investigated.

TABLE III

Pregnancy in healthy female hares from February up to and including August, in relation to their age

Age in months	Number examined	% pregnant
2	16	0
3	16	0
4	17	6
5	8	50
6–7	9	67
8 and more	87	83
> 12	34	88

Pregnancy rate and reproduction season

From both the healthy and diseased adult females mentioned in Table II, the pregnancy rate per month was established by examining the uteri for embryos (Fig. 2). In the first category, pregnancy starts during January and ends during September. From February to the end of August the majority of females were pregnant: on average 80%. Of the females which were not pregnant during that period, 50% were lactating, so overall 90% were involved in breeding. In the diseased females, only 21% were pregnant and 17% lactating during that period, so only 38% were breeding. This clearly illustrates the influence of health on the pregnancy rate.

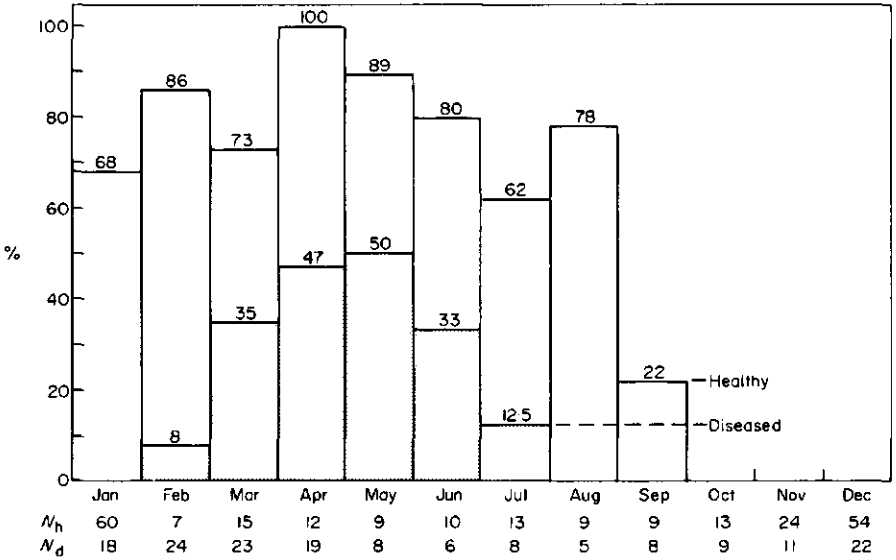


FIG. 2. Monthly percentages of adult hares pregnant. N_h and N_d indicate the numbers of healthy and diseased hares investigated.

On 19 January 1971 we were able to study the start of the reproduction season in more detail from 43 adult and 17 sub-adult (5–8 months old) healthy females shot at Schiphol. From these hares, of which the presence of corpora lutea and embryos, and also the body weight could be determined, the majority of the adults had been impregnated and had embryos, but in the sub-adults these percentages were lower (Table IV). This indicates that differences in age also contribute to the variation in the start of the breeding season.

Out of the seven adult females which did not possess corpora lutea on 19 January 1971, four proved to have low body weights (Fig. 3). As during the first two weeks of pregnancy the embryos hardly contribute to the female's total weight (Broekhuizen & Martinet, 1979), the fact that the physical condition affects the start of the female's breeding season is illustrated once more.

The largest embryo found on 19 January 1971 was 50 mm long and was estimated to be about three weeks old (Broekhuizen & Martinet, 1979). This indicates that the breeding season started in the last week of December 1970. However, because on 19 January 1971 the majority of the sub-adult females was not yet pregnant, the moment of conception for the first litter of 1971 may vary by at least one month, and the start of the reproduction season is not well synchronized.

TABLE IV

Percentages of female hares with corpora lutea graviditatis and with visible embryos, shot at Schiphol in 1971

	Date	Number investigated	% with corpora lutea	% with embryos
Adults	19 January	43	84	79
	1 November	6	0	0
	20 December	18	0	0
	31 December	4	50	0
Sub-adults	19 January	17	29	12
	1 November	16	0	0
	20 December	13	0	0
	31 December	7	14	0

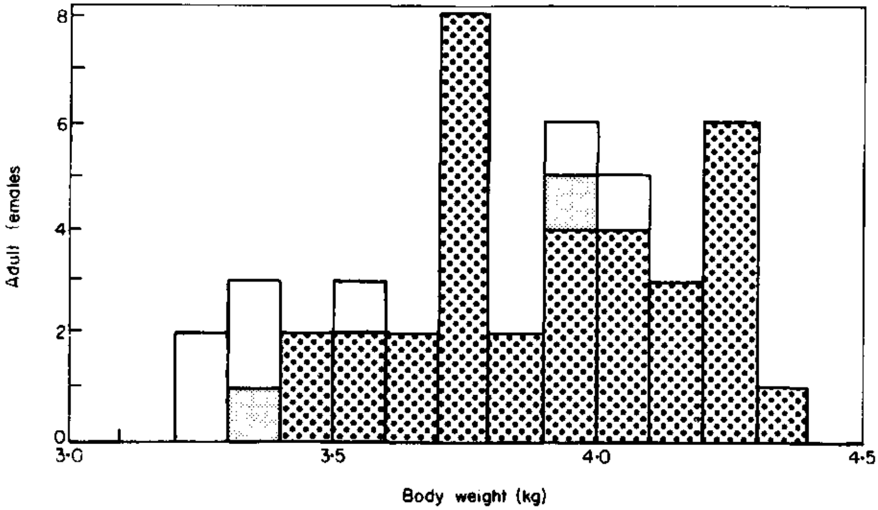


FIG. 3. The distribution of the body weights of female hares from Schiphol, shot on 19 January 1971. Unshaded: without corpora lutea; lightly shaded: with corpora lutea; heavily shaded: with corpora lutea and visible embryos.

In November and December 1971 we collected more data about the presence of corpora lutea and visible embryos in shot females from Schiphol. These data are also summarized in Table IV, and show that in adult as well as in sub-adult females breeding started between 21 and 31 December. Since visible embryos were not yet present on 31 December, though corpora lutea did occur, the first conceptions must have taken place just before, i.e. in the last week of December, as in 1970.

Because ovulation in hares is induced by coitus, it can be assumed that the start of the female's reproduction season and the variation in first conception are dependent on the development of spermatogenesis. To check this possibility, we collected data about the presence of spermatozoa in the cauda epididymidis of males shot in 1971 and 1972 at Schiphol. Like the females, the males were divided into adults and sub-adults by the ossification of the epiphyseal cartilage in the foreleg. Figure 4 shows the percentages of adult and sub-adult males with spermatozoa in the cauda epididymidis in relation to date. It can be concluded that in adult males spermatogenesis is reactivated from the end of November. By the middle of December spermatozoa were found in the majority of the adult males and in about half of the sub-adults. Möller (1976) showed that in the German Democratic Republic males are willing to copulate from the beginning of December; we obtained similar results in the Netherlands. Moreover, dominant males are ready to copulate with more than one female (F. Oomen-Kalsbeek, unpubl. report). Therefore, it is unlikely that asynchronous impregnation of females is due to insufficient numbers of reproductive males and this means that the start of the breeding season is determined by the development of the females.

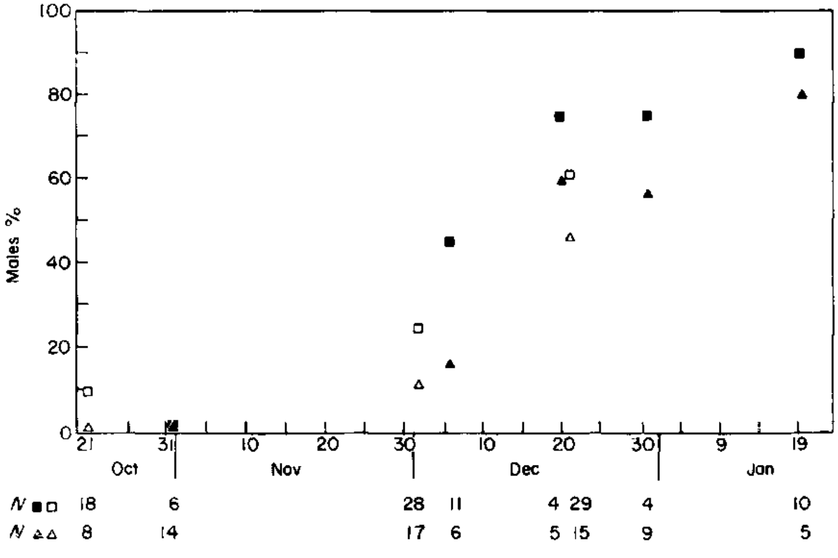


FIG. 4. Percentages of males with spermatozoa in the cauda epididymidis among shot hares at Schiphol. ■ ▲, 1971; □ △, 1972; ■ □, adults; ▲ △, sub-adults.

Litter size and its monthly variation

The number of embryos per pregnant female varied from one to three for January and the autumn, and from one to five for April and May. Litters with more than five young seem to be exceptional in the Netherlands. The literature also provides only few data about larger litters: Jacob (1956) found nine embryos and Tropilo (1963) found seven. A very exceptional find was reported by Broekhuizen & de Wit (1972), concerning a doe killed by a dog, with 10 nearly full-grown young. The photo of these foetuses (Plate 1) shows that the occurrence of a little white crown in the head fur is an unreliable mark for distinguishing between young from litters with only one, and litters with more young, as is sometimes suggested by hunters.

Figure 5 shows the mean number of embryos per pregnant adult female in the different months, taken from the questionnaires and from our own observations. The figures from the questionnaires tend to be higher than our observations, especially early in the year, but this may be due to the tendency that one is more inclined to mention findings of larger litters. The figure shows that the mean number of embryos per pregnant adult increases from January onwards and reaches a maximum in May, after which the number seems to

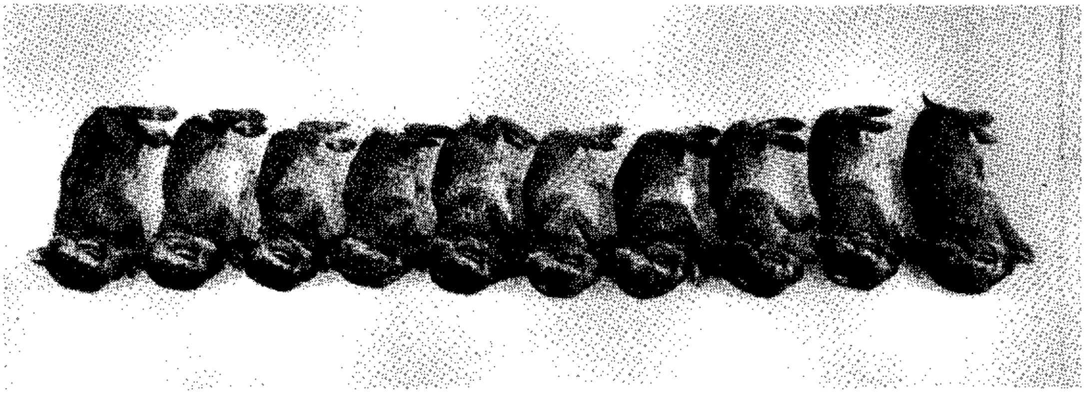


PLATE I. Litter of 10 nearly fully developed foetuses from a female hare killed by a dog. Notice the absence of the white hairs on the head of some of the young, indicating that this is an unreliable mark for determining litter size (see text).

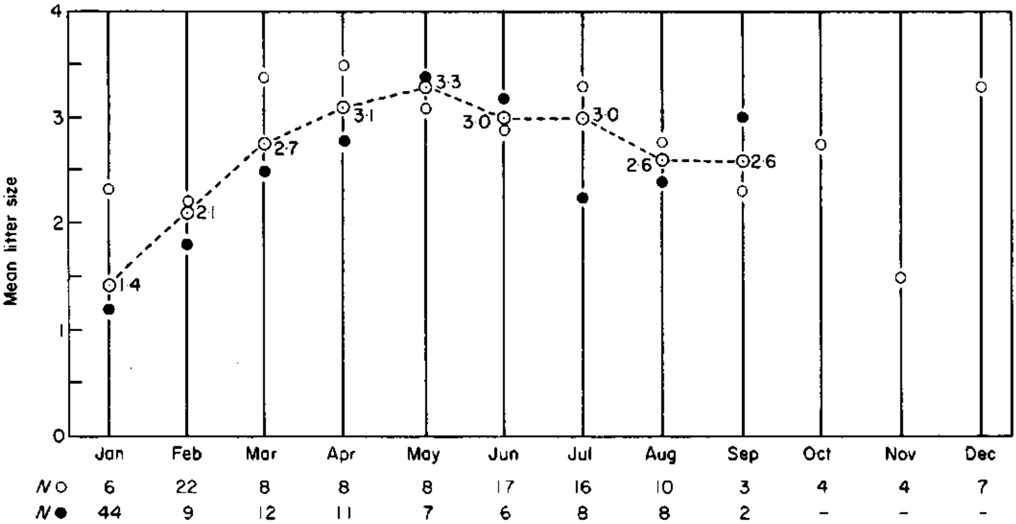


FIG. 5. Mean number of embryos per pregnant adult, showing the variation in litter size over the breeding season. ○, inquiry; ●, own data; -○-, average.

drop slightly. For the months October, November and December only data from the questionnaires were available, as we had not found pregnancies from our own observations.

The mean annual litter size can be calculated as the quotient of:

(1) the sum of the products of the mean monthly litter size (data from Fig. 5) and the corresponding pregnancy-proportion (data from Fig. 2), called "monthly contributions" (Table V), and
(2) the sum of the monthly pregnancy-proportions.

The values are summarized in Table V and the mean annual litter size proved to be 2·68.

TABLE V

Annual litter size among healthy adult females

Month	Mean litter size (data from Fig. 5)	Pregnancy proportion (data from Fig. 2)	Monthly contribution
January	1·4	0·68	0·952
February	2·1	0·86	1·806
March	2·7	0·73	1·971
April	3·1	1·00	3·100
May	3·3	0·89	2·937
June	3·0	0·80	2·400
July	3·0	0·62	1·860
August	2·6	0·78	2·028
September	2·6	0·22	0·572
October	—	0	—
November	—	0	—
December	—	0	—
Total		6·58	17·626

Mean annual litter size = 17·626/6·58 = 2·68

Gestation and conception

According to literature before 1940, the gestation period varied between 30 and 65 days. After 1940 it became evident from observations on hares in captivity that the gestation period lasts approximately six weeks: Notini (1941) found in Sweden a mean period of 43 to 44 days, Bieger (1941) found 42 days in Germany, as did Hediger (1948) in Switzerland. More recently Martinet, Legouis & Moret (1970) mentioned mean gestation periods of 41 and 40 days respectively in breeding stocks near Paris and in the south of France. The causes of the differences between the data are not known, but the gestation period might be affected by climate.

We have no observations about the length of the gestation period in the Netherlands. According to the literature, this is assumed to be 42 days. How soon after giving birth females in the field conceive again, is not known. Because, during the height of the reproduction season, from February to the end of May, an average of 87% of the healthy females are pregnant (Fig. 2), it is likely that there is a delay of several days between birth and the next conception, due to reduced willingness on the part of the females to copulate after giving birth. So the average time between two successive births in the field will be 42/0·87 = 48 days, or about 1·6 months at least.

When studying hares in captivity, Hediger (1948) observed copulations a few days before the litter, which resulted in conception. Hediger's report led to an animated discussion in the literature on the phenomenon of "superfetation" and its underlying principles. Stieve (1952) assessed maturation of ova during pregnancy, which indicates that the uterus horns may function autonomously. He also established that matured foetuses prevent the penetration of spermatozoa into the uterus horn. Nevertheless, Martinet, Legouis & Moret (1970) found conception of newly ovulated ova in females where both uterus horns contained large foetuses. In the opinion of Martinet & Raynaud (1973), therefore, ova from induced ovulations were fertilized by spermatozoa from the preceding copulation. In an experiment they showed conception in a pregnant female after copulation with a vasectomized male, and the idea advanced by Horáček & Uher (1965), that superfetation is the result of non-synchronous implantation of ova of the same ovulation period, can be rejected. Flux (1967) found three cases of superfetation in females with embryos of 100–120 g. Because the descriptions of superfetation refer almost always to females with mature foetuses, he suggested that, in hares, corpora lutea graviditatis may cease functioning a few days before parturition. However, Flux (1967) stated that superfetation, defined as the simultaneous occurrence of distinctly developed embryos of different ages, is rare in wild hares, and he did not observe any superfetation in 428 examined pregnant females. Raczyński (1964) also found no superfetation in 70 pregnant females in the wild. In our material, we found no embryos at clearly distinct phases of development, so it seems justified to neglect the phenomonen of superfetation in calculating the production of young. It is erroneous to assume superfetation from the presence of embryos heavier than 8 g in lactating females, as done by Möller (1971). He estimated that the lactation period lasted no longer than 15 days, confirming data of Hediger (1948) and Notini (1941), which would imply that embryos weighing more than 8 g started development before lactation started, i.e. before the birth of the preceding litter. Our observations (Broekhuizen & Maaskamp, 1980; Maaskamp, 1978) on nursing showed that in general the lactation period lasts about one month. Therefore, the occurrence of embryos weighing up to 30 g in lactating females does not necessarily indicate superfetation.

Mean annual production of young

With the data on monthly pregnancy rate, litter size and minimum birth interval, it is possible to calculate the monthly production of young per healthy adult female:

$$\frac{\%\ \text{Pregnant females} \times \text{Mean litter size}}{\text{Time between two successive births in months} \times 100}$$

From Table VI the total annual production per female can be calculated to be nearly 11.

Pre-natal mortality

The determination of the litter size by counting embryos could be influenced by pre-natal mortality, which can occur either before or after implantation of the ova. In the literature, evidence about pre-natal mortality is mainly obtained from the difference between the number of corpora lutea and the number of normal embryos observed. Because we may have missed very young implantations during the examination of the uterus, we restricted our data to females in which at least one embryo was found. Although the pre-natal development of embryos in the animals examined had reached different stages when the animals were killed, the data cover only a part of the total pregnancy period and are only indicative of the total rate of pre-natal mortality.

The proportion of pre-natal mortality obtained from the differences between the numbers of corpora lutea and embryos observed in healthy and diseased females is given in Table VII. The Table shows a significantly higher proportion of pre-natal loss in diseased females than in healthy ones ($\chi^2 = 8{\cdot}2$; $P < 0{\cdot}01$). Nevertheless, we found a 6% pre-natal loss even in healthy females, and because in these females no resorbed embryos were found, it is likely that most and perhaps all pre-natal losses in healthy females occurred before or shortly after implantation and pre-natal loss of older embryos can be neglected. So, our calculation of the production of young does not seem to be seriously influenced by pre-natal mortality.

TABLE VI

Production of young per healthy adult female per year

Month	% pregnant	Litter size	Time between successive births in months	Production of young
January	68	1·4	1·6	0·59
February	86	2·1	1·6	1·13
March	73	2·7	1·6	1·23
April	100	3·1	1·6	1·94
May	89	3·3	1·6	1·84
June	80	3·0	1·6	1·50
July	62	3·0	1·6	1·16
August	78	2·6	1·6	1·27
September	22	2·6	1·6	0·36
October	0	—	—	—
November	0	—	—	—
December	0	—	—	—
Total production per year				11·02

TABLE VII

Pre-natal mortality (due to loss of ova or resorption of embryos) in pregnant females with at least one embryo

	Total number of corpora lutea	Number of normal embryos	Percentage pre-natal loss
Healthy females	145	136	6
Diseased females	62	50	19

Extra-uterine pregnancy

Although we did not observe resorption from visible embryos, we received two females with mis-developed embryos, due to extra-uterine pregnancy. Plate II shows the interior of the abdominal cavity of one of these, with two encapsulated embryos, and Plate III shows five extra-uterine embryos from the other female. The unrolled embryo in this figure is malformed, as in all cases of extra-uterine pregnancy described (Benesch, 1940; Raich, 1953; Horáček & Uher, 1964; Rittenbach, 1965; Flux, 1967; Broekhuizen & de Wit, 1972; Evans & Griffith, 1972; Hager, 1973). According to the description of Hager, the umbilical cord was shrivelled or absent, and the eyes had fallen in. The capsules were detached in the abdominal cavity, and not connected to the female's abdominal wall by a thin tissue, as found by Horáček & Uher (1964). In one case Horáček & Uher concluded that the extra-uterine embryo had remained in the abdominal cavity for at least four months.

The embryos shown in Plate III were found in a hare shot on 28 December. No corpora lutea were present in the ovaries. The two embryos shown in Plate II were found on 19 March in a wild female which had died of pneumonia. We detected two corpora lutea in each of the ovaries, while three distinct placental scars were present in the uterus, indicating that the female had been pregnant though already bearing the two encapsulated embryos in her abdominal cavity. Also, the finding of the extra-uterine pregnancy in December indicates that the foetuses had been in the abdominal cavity for a long time.

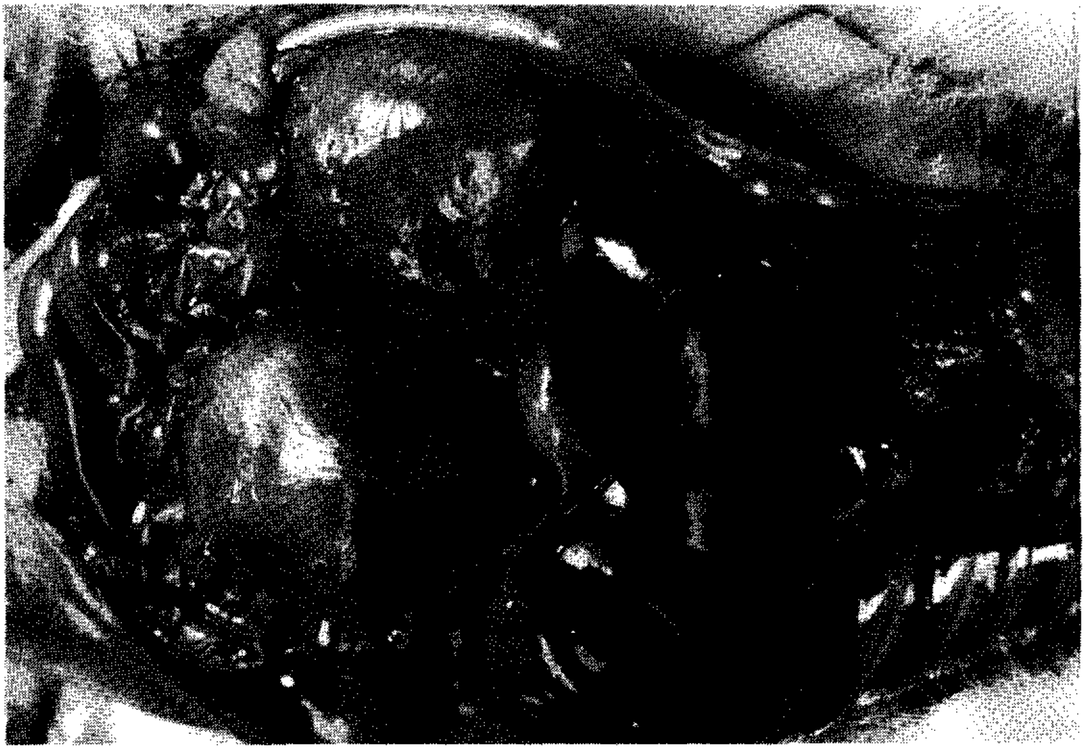


PLATE II. Opened abdominal cavity of a female hare with two encapsulations of extra-uterine foetuses.

The term "extra-uterine pregnancy" suggests development of embryos inside the abdominal cavity. In the opinion of Horáček & Uher (1964) however, it is much more likely that the foetuses get into the abdominal cavity at the end of their embryonic development and mummify. This view is shared by von Braunschweig (1973), who stated that the embryos get into the abdominal cavity during parturition by tearing the wall of the uterus. The fissure might heal later on, whilst the young mummify without harming the doe.

As extra-uterine pregnancy occurs very infrequently and does not prevent further reproduction of the female, the influence of this phenomenon on the mean annual production of young per female can be ignored.

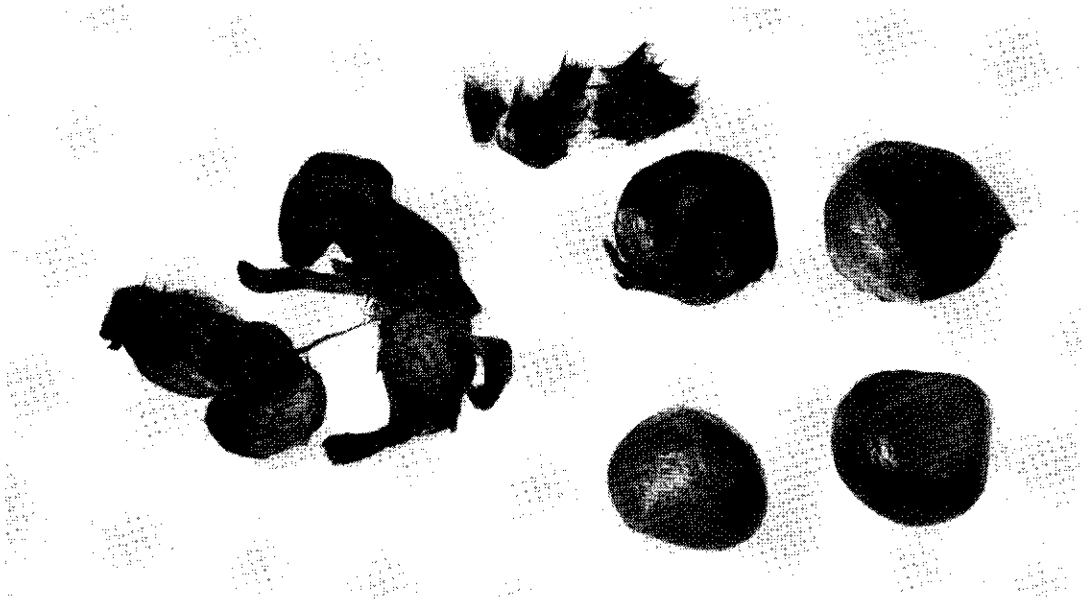


PLATE III. Five extra-uterine foetuses from the abdominal cavity of a female hare. Bottom-right: two encapsulated foetuses. Top-right: two foetuses from which the capsules have been completely and partly removed. Left: an unrolled foetus from which the loose felt-like hairs (top-middle), normally found between foetus and capsule, have been removed.

Discussion

From our data we concluded that in the Netherlands sexual maturity in female hares is reached between four and eight months of age. This confirms the literature, in which it is generally accepted that female hares are sexually mature at the age of seven or eight months (Rieck, 1956; Raczyński, 1964; Brüll, 1970), but pregnancy occasionally occurs between four and five months of age (Bruns, 1955; Pepin, 1976). Due to this variation and the fact that physical condition also affects fecundity, the moment of first conception may vary by at least one month between individuals. Synchronization in the start of the breeding and in the birth of the first litters, as found by Valentinčič (1956) in Yugoslavia, does not occur in the Netherlands and consequently the percentage of pregnancy will gradually change over the breeding season. For simplicity we determined the percentage of pregnancy for periods of one month, although this is rather inaccurate when the gestation period lasts about six weeks.

The annual production of young per female hare in the Netherlands of nearly eleven, as calculated from our limited material, seems to be one of the highest among the European data (Table I). As our data only refer to adult and healthy females, it is likely that the high figure for annual production partly results from this restriction. Unfortunately, it is difficult to estimate the proportion of a population which is in a sub-optimal condition.

Another aspect that complicates the comparison with the literature data is the calculation of the annual production by multiplying the mean litter size and the mean number of litters per year, as done by most authors. This leads to an underestimation of the annual production, as the pregnancy rate is maximal when the litter size also reaches its maximum. Often corrections to the uneven distribution of the data over the year have not been applied, and sometimes it is not indicated whether data only apply to healthy adult females or not. Notwithstanding these objections, Flux (1967) compiled literature data to study the suggestion of Barrett-Hamilton (1912) that the mean litter size decreases with an increasing number of litters per female per year. Flux correlated the mean litter size to the mean annual temperature. Like Barrett-Hamilton, Flux assumed that the length of the breeding season, and by that the number of litters, is mainly determined by the climate. In this connection it should be mentioned that in New Zealand Flux (1967) found that the start of the reproduction season in females, normally around the shortest day, could be earlier or later according to higher or lower temperature than normal in the preceding months, although the relative day length is considered to be the proximate factor for the start of the reproduction season (Flux, 1965; Martinet, 1976). Hewson & Taylor (1975) found a correlation between the length of the breeding season in Scotland and the temperatures during the last four months of the year.

The correlation between the mean litter size and the mean annual temperature, as found by Flux (1967), is given in Fig. 6. It should be noted that Flux corrected the original values of the mean litter size given by Raczyński (1964) and Reynolds & Stinson (1959), 2·3 and 1·9 for Poland and southern Ontario respectively, to 2·8 to compensate for the uneven distribution of the data over the year. In the meantime more literature became available. Pielowski (1976) found a mean litter of 2·3 in Poland, which equals the uncorrected data of Raczyński. However, Pielowski obtained his data from litters in the field that were up to five days old. Countings of embryos are likely to exceed this figure, because some litters disperse two days after birth and it is then difficult to locate all the young. In Scotland, Hewson & Taylor (1975) confirmed Flux's findings. In the German Democratic Republic Möller (1971) found a mean litter size of 2·8 for two "normal" years, which, after correction for uneven distribution of litter size and pregnancy rate over the year, provided a mean annual litter size of 2·73. Lincoln (1974) gave figures on the pregnancy percentage and the mean litter size per month for females older than five months, from which the annual litter size in Norfolk can be calculated as 2·58. Frylestam (1979) examined the litter size in three areas in the south of Sweden for three years. From his data a mean annual litter size of 2·44 could be calculated. Finally Petrov & Dragoev (1962) give a mean annual litter size of 2·5 for Bulgaria.

The addition of the above mentioned data to Fig. 6 strengthens the correlation between annual litter size and mean annual temperature, and supports the hypothesis of Barrett-Hamilton. Although the mean annual litter size in the Netherlands is relatively high, the data fit rather well to the correlation found by Flux, as Fig. 6 shows. From this correlation it can be concluded that the relatively high annual production of young per female found in the Netherlands is mainly the result of a long reproduction season.

Due to the limited data available, no information could be obtained about annual variation in ovulation, conception, litter size, pregnancy rate and pre-natal loss. Because it is likely that these aspects contribute to population fluctuations, more investigations are desirable.

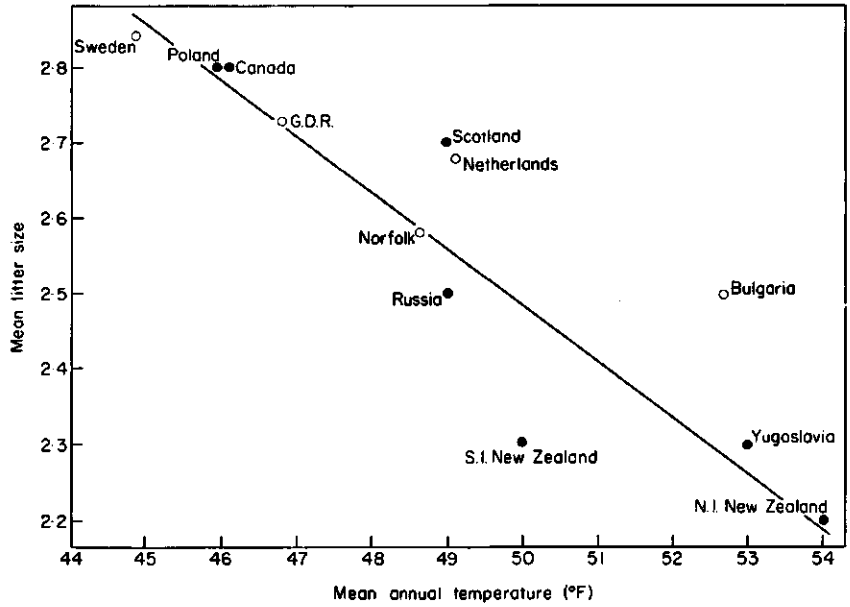


FIG. 6. Relation between the mean annual temperature and the mean litter size in different countries. Dots and regression line are from Flux (1967). For the circles, see the text. The temperature in the German Democratic Republic (mean value from Rostoc, Berlin, Leipzig and Magdeburg), Bulgaria (mean value from Sofia, Plovdiv and Burgas), Norfolk and Malmö are taken from Thran & Broekhuizen (1965).

Summary

Due to their adaptive colouration and their concealing behaviour, it is difficult to find young hares in the field. Consequently, it is also difficult to determine the production of young in a direct way from countings in the field. For this reason, in this study the production was based on the number of embryos found in pregnant females.

Sexual maturity was found in some females of four months old, but from the age of eight months all can be assumed to be sexually mature. Although the activation of the spermatogenesis and the reproduction activity in males is related to age, it was found that the majority of the males have spermatozoa during the second half of December, when the first conceptions occur.

Pregnancy in females was found to be related to health and age. Because populations could not be sampled in a random way, the measurement of the production of young was restricted to apparently healthy females of eight months and older. The females showed

an asynchronous start of reproduction after the autumnal period of sexual inactivity, mainly due to differences in age. The moment of first conception may vary by at least one month.

As a consequence of the asynchronous reproduction, the annual production of young had to be calculated from the mean litter size per month, the proportion of pregnant females per month, and the time between two successive births, by the equation:

$$\text{Annual production} = \sum_{\text{Jan}}^{\text{Dec}} \frac{\%\ \text{Pregnant females} \times \text{Mean litter size}}{\text{Time between two successive births in months} \times 100}$$

The mean litter size per month varies throughout the breeding season, and was found to be highest in April and May. The mean rate of pregnancy per month was also found to vary throughout the year, with its maximum in April and May, while it is negligible from October to December.

Since the mean gestation period in hares is about 41–42 days, and assuming that in the field doe hares have a few days of reduced willingness to copulate after parturition, the time between two successive births was taken to be 1·6 months. From the collected data (Table VI), the mean annual production of young per healthy adult female was calculated to be nearly eleven.

Superfetation, known from hares in captivity, was not observed in our material and will not influence the production of young. Extra-uterine pregnancy was occasionally found. Since it does not always prevent a normal pregnancy, its impact on the production of young can also be neglected. Pre-natal mortality, due to the loss of ova or resorption of small embryos, measured as the difference between the number of corpora lutea and the number of embryos, was found to be about 6% in healthy females with at least one visible implantation. This value is low compared to the literature. Resorption of large embryos was not observed in healthy females.

In comparison with other European countries, the calculated annual production of young per doe hare is relatively high in the Netherlands (Tables I and VI). This is not due to a relatively high mean annual litter size, because its value (2·68, Table V) fully agrees with the relation between the mean annual temperature and the litter size, established by Flux (Fig. 6). Therefore, the high annual production in the Netherlands must be explained by a relatively high proportion of pregnancy throughout the year.

REFERENCES

Barrett-Hamilton, G. E. H. (1912). *A history of British mammals.* London: Gurney & Jackson.

Benesch, F. (1940). Zur Abdominalgravidität bei Feldhasen. *Wiener tierärztl. Monatschr.* **27**: 155–159.

Bieger, W. (1941). *Handbuch der deutschen Jagd.* **1**: Berlin: Parey.

Braunschweig, A. von (1973). Interessanter Befund an einer Feldhäsin: Antwort des Instituts für Wildforschung und Jagdkunde der Universität Gottingen. *Pirsch* **25**: 107–108.

Broekhuizen, S. & Maaskamp, F. (1979). Age determination in the European hare (*Lepus europaeus* Pallas) in the Netherlands. *Z. Säugetierk.* **44**: 162–175.

Broekhuizen, S. & Maaskamp, F. (1980). Behaviour of does and leverets of the European hare (*Lepus europaeus*) whilst nursing. *J. Zool., Lond.* **191**: 487–501.

Broekhuizen, S. & Martinet, L. (1979). Growth of embryos of the European hare (*Lepus europaeus* Pallas). *Z. Säugetierk.* **44**: 175–179.

Broekhuizen, S. & Wit, J. de (1972). Een geval van buitenbaarmoederlijke zwangerschap bij een haas (*Lepus europaeus*). *Ned. Jager* 77: 619.

Brüll, H. (1970). Histologische Beiträge zur Geschlechtsreife des Feldhasen (*Lepus europaeus* Pallas). *Finn. Game Res.* **30**: 329–332.

Bruns, H. (1955). Hasenbesatz und Hasenstrecke. *Anblick* **10**: 6.

Evans, J. & Griffith, R. E. (1972). Reproductive anomalies in Black-tailed jackrabbits. *J. Mammal.* **53**: 192–194.

Flux, J. E. C. (1965). Timing of the breeding season in the hare, *Lepus europaeus* Pallas, and the rabbit, *Oryctolagus cuniculus* (L.). *Mammalia* **29**: 557–562.

Flux, J. E. C. (1967). Reproduction and body weights of the hare *Lepus europaeus* Pallas, in New Zealand. *N.Z. Jl Sci.* **10**: 357–401.

Frylestam, B. (1979). Reproduction of the European hare in Southern Sweden. In *Population ecology of the European hare in Southern Sweden:* 1–16. Frylestam, B. Thesis Univ. Lund.

Hager, E. (1973). Interessanter Befund an einer Feldhäsin. *Pirsch* **25**: 107.

Hediger, H. (1948). Die Zucht des Feldhasen (*Lepus europaeus* Pallas) in Gefangenschaft. *Physiol. comp. Oecol.* **1**: 46–62.

Hewson, R. & Taylor, M. (1975). Embryo counts and length of breeding season in European hares in Scotland from 1960–1972. *Acta theriol.* **20**: 247–254.

Horáček, V. & Uher, J. (1964). On fetuses found in the abdominal cavity of the hare, *Lepus europaeus* Pallas. *Zool. listy* **13**: 249–254.

Horáček, V. & Uher, J. (1965). Zur Kenntnis der Geschlechtszyklus und der Superfötation bei dem Feldhasen *Lepus europaeus* Pall. *Zool. listy* **14**: 107–116.

Jacob, A. (1956). Häsin mit 9 Junghasen. *Deutsche Jäger* **73**: 458.

Kosolov, A. M. (1941). [Reproductive biology in the common hare (*Lepus europaeus* Pall.).] *Zool. Zh.* **20**: 154–171 (In Russian. Transl. 113 Bureau Animal Popul. Oxford Univ.).

Lincoln, G. A. (1974). Reproduction and "March madness" in the Brown hare, *Lepus europaeus*. *J. Zool., Lond.* **174**: 1–14.

Maaskamp, F. (1978). Nachtleben der Junghasen durchleuchtet. *Jäger* **96**: 32–33.

Martinet, L. (1976). Seasonal reproductive cycles in the European hare, *Lepus europaeus*, raised in captivity. Role of photoperiodicity. In *Ecology and management of European hare populations:* 55–58. Pielowski, Z. & Pucek, Z. (Eds). Warszawa: Pol. Hunt. Ass.

Martinet, L., Legouis, J. J. & Moret, B. (1970). Quelques observations sur la reproduction du lièvre européen (*Lepus europaeus* Pallas) en captivité. *Annls Biol. anim. Bioch. Biophys.* **10**: 195–202.

Martinet, L. & Raynaud, F. (1973). Survie prolongée des spermatozoides dans l'utérus de la hase: explication de la superfoetation. *Inserm.* **26**: 295–308.

Möller, D. (1971). Beitrag zur Reproduktion des Feldhasen (*Lepus europaeus* Pall.) in der Deutschen Demokratischen Republik. *TagBer. dt. Akad. LandWiss. Berl.* No. 113: 191–202.

Möller, D. (1976). Die Fertilität der Feldhasenpopulationen. In *Ecology and management of European hare populations:* 69–74. Pielowski, Z. & Pucek, Z. (Eds). Warszawa: Pol. Hunt. Ass.

Notini, G. (1941). Om harens biologi. *Svenska Jägerförbundet Medd.* No. 4.

Pepin, D. (1976). *Phase finale de cycle de reproduction du lièvre,* ***Lepus europaeus.*** Intern. report. Jouy-en-Josas: Lab. de la Faune sauvage et de Cynégétique, I.N.R.A.

Petrov, P. & Dragoev, P. (1962). Untersuchung mancher Besonderheiten über die Vermehrung des Feldhasen (*Lepus europaeus* Pall.) in Bulgarien. *Izv. Centr. nauč.-izsled. inst. gorata* **10**: 143–168.

Pielowski, Z. (1976). Number of young born and dynamics of the European hare populations. In *Ecology and management of European hare populations:* 75–78. Pielowski, Z. & Pucek, Z. (Eds). Warszawa: Pol. Hunt. Ass.

Raczyński, J. (1964). Studies on the European hare. V: Reproduction. *Acta theriol.* **9**: 305–352.

Raich, J. (1953). Zwei Falle von Bauchhölenträchtigkeit beim Feldhasen. *Ost. Arbeitskreis Wildtierforsch.* No. 7–8: 62.

Reynolds, J. K. & Stinson, R. H. (1959). Reproduction in the European hare in southern Ontario. *Can. J. Zool.* **37**: 627–631.

Rieck, W. (1956). Untersuchungen über die Vermehrung des Feldhasen. *Z. Jagdwiss.* **2**: 49–90.

Rittenbach, P. (1965). Bauchhölenträchtigkeit beim Feldhasen. *Unsere Jagd* **15**: 161–162.

Scarlatescu, G., Almasan, H. & Nestorov, V. (1962). Contributii la problema cunoasterii cresterii in efectiv a iepurilor in conditiile tarii noastre. *Revta Padur.* **77**: 365–367.

Stieve, H. (1952). Zur Fortpflanzungsbiologie des europäischen Feldhasen (*Lepus europaeus* Pallas). *Zool. Anz.* **148:** 101–114.

Thran, P. & Broekhuizen, S. (1965). *Agro-climatic atlas of Europe* I. Wageningen: Pudoc; Amsterdam: Elsevier.

Tropilo, J. (1963). 7 plodow u zajeczycy. *Low. Polski* **2:** 14.

Valentinčič, S. I. (1956). Resultate zweijähriger Beobachtungen und Studien über den idealen Zuwachs beim Feldhasen auf der Insel "Biserni otok". *Z. Jagdwiss.* **2:** 152–160.

Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Art. VII

Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in The Netherlands

By S. Broekhuizen and F. Maaskamp

Anders dan bij territoriale dieren worden plaatsvaste hazen zowel overdag als 's nachts in groepjes waargenomen.

Foto: Françoise Oomen-Kalsbeek

Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in The Netherlands

By S. Broekhuizen and F. Maaskamp

Research Institute for Nature Management, Arnhem, The Netherlands

Receipt of Ms. 10. 6. 1981

Abstract

To examine aspects of dispersion in hares, data about movements and home range were collected from recoveries of tagged individuals as well as from radio-tracked animals. Most hares moved less than 500 m from the capture place, even the sucklings, and the mean home range size observed was 29 ha, showing a sedentary way of life. Displaced hares mostly could establish themselves near the place of release, and a low degree of agonistic behaviour to an introduced tame conspecific was observed.

Home ranges overlapped considerably, and at night clustering was observed. While in the twilight hares grazing gregariously showed less attentive interruptions compared with hares grazing solitarily, anti-predation behaviour was thought a function of clustering.

As from literature is known that under circumstances with poor food supply, such as in desert and in areas with deep snow cover, hares become more territorial during the reproduction season and more migratory in the winter, the results suggest that in our study areas food was not in short supply, presumably due to a high hunting pressure in autumn.

Introduction

Although in South-East Europe, after periods with heavy snow, groups of hundreds of roaming hares have been observed (Angermann 1973), roaming over large distances seems the exception in this species. Data collected by Andersen (1951), Rieck (1953, 1955), Szederjei (1959), Douglas (1970) and Pielowski (1972) showed that about 80 percent of tagged animals released on their capture place, were recovered within a distance of 3 km, and less than 10 percent were found more than 5 km away. Rieck (1953) calculated from his recoveries of tagged hares that the home range rarely exceeded 500 ha. Pielowski (1972) recovered tagged individuals in areas of about 350 ha, while he concluded from observations of the movements of hares being pursued, that hares are familiar with an area

U.S. Copyright Clearance Center Code Statement: 0044-3468/82/4701-0022 $ 02.50/0
Z. Säugetierkunde 47 (1982) 22–32

ISSN 0044-3468 / InterCode: ZSAEA 7

of about the same size. However, he also pointed out that a distinction should be made between the larger area covered by the hare's movements during its life time, and the several clearly defined areas, far smaller in size and occupied temporarily and periodically, situated within the boundaries of that total home range. By repeatedly shifting its area of activity, a hare would be kept informed of the situation within the total home range. The area in which PIELOWSKI observed a hare during one day was on average 20 ha.

MERZ (1976), following hares during a three month period of radio-tracking, and SCHNEIDER (1978), who collected data over periods of 0.5 to 1.5 years by direct observation, found total areas of activity of about the same size as the areas of daily activity observed by PIELOWSKI (1972). Their data clearly point to a non-migratory way of life, from which one might expect territoriality. Indeed, RIMATHÉ (1977) and SCHNEIDER (1978) found indications that the movements observed in subadults were not only due to an urge to explore, but were also caused by intolerant behaviour from adults, possibly their own parents. On the other hand, DOUGLAS (1970) and SZEDERJEI (1959) found that most of the leverets were able to establish themselves in the area they were born in, and even within the home range of the parents. Also contrary to territorial animals, resident hares are often observed in groups, by day as well as at night. Although several authors showed an influence of field conditions on the distribution of hares (a. o. BRÜLL 1973; FIECHTER 1975; FRYLESTAM 1976; JEZIERSKI 1968; MERZ 1976; PIELOWSKI 1966; RIMATHÉ 1977), MERZ (1973, 1976) observed clustering at night which he could not explain by a preference for certain vegetation, but in his opinion could have a social function. The same was suggested by PIELOWSKI (1966) and JEZIERSKI (1968) dealing with clustering in the daytime.

Since literature about spacing out and social clustering does not conform, we collected additional data about the size and changeability of the home range, the movements of adult and juvenile hares, the behaviour after introduction to unknown area and about clustering and its possible function.

Material and methods

Capturing, tagging and recoveries

Size and changeability of the home range were examined from recoveries of tagged individuals, as well as by direct observation in the field. For both methods animals had to be captured. Leverets, unless they were found by accident, were located by searching meadows about three quarters of an hour after sunset, using a binocular provided with a spotlight. At that time the leverets left their hiding places in order to gather for nursing (BROEKHUIZEN and MAASKAMP 1980). Attempts were made to capture the leverets by using a hoopnet after they had been nursed and the doe had withdrawn. In total 99 leverets were tagged with a numbered aluminium chicken wingmark. Beside the number, the name and phonenumber of the institute were also punched on the tag, to facilitate the notification of recovery. Leverets were aged by means of body weight and length of the hind foot (BROEKHUIZEN and MAASKAMP 1979). After tagging they were released on the same spot where they were captured.

Adult hares were captured by chasing them into vertically placed long nets. No drugs were treated for handling. Nearly five percent of the animals captured were lost through shock and accidents. Apart from the wing tag in the ear already mentioned, a numbered plastic tag of the "Dalton-rototag" type was connected to the other ear. During the years 1968–1978 637 adult hares were captured and tagged at ten different locations, 132 of which were released at the spot they were captured, and 505 were released on fields 10 to 90 km away from their capture place. Capturing took place in the second half of December and the first half of January, just at the beginning of the reproduction season.

Hares were considered as adult, when they were aged as six months or older from the stage of ossification of the distal epiphyseal cartilage knob of their ulna (BROEKHUIZEN and MAASKAMP 1979). Recoveries from our own field work were neglected, in view of the biased chance of notification.

Measuring of the home range by direct observation

Home ranges of 13 hares (8 females and 5 males) were determined by radio-tracking. Technical data on radio-transmitters, their connection to the animal and the receiving units used were described earlier

(BROEKHUIZEN et al. 1979). For these hares the ear tags and the radio-collar were plastered with reflecting "Scotchlite" tape, to facilitate observation at night using the spotlight.

Since it was almost impossible to track hares during the whole night, it was done either from dusk till midnight or from midnight till morning. Generally one hare was tracked intensively. We attempted to locate it by triangulating the radio or by spotlight view every quarter of an hour. The location of other radio-collared hares in the vicinity was determined at the beginning and at the end of the observations, and in the time in between as far as possible.

Home range was defined according to BURT (1943): "that area which is traversed by the animal (male) in all its activities as gathering food, resting, mating, caring for young. It excludes occasional sallies outside that area and shall be calculated for a specific period of time". The size of the home range was determined according to the minimum observation area method of ODUM and KÜNZLER (1955), connecting the outermost observations to the smallest convex figure in which all the other observations are located.

The periods in which the home ranges of the various hares were determined, are given in table 1. The hares numbered as 1–6 and 10–13 lived in the area "Cortenoever" about 4 km south of Zutphen, a town in the valley of the river Yssel (52.06 N; 06.13 E). This area was mainly used for dairy. The hares 7–9 lived in the "Noordoostpolder" (52.45 N; 05.13 E), mainly used for arable farming.

Behaviour after introduction in unknown areas

Besides the recoveries of hares that had been moved, the behaviour after introduction in an unknown area was also studied from a female hare raised in captivity, which was released in September, at the end of the reproduction season, in the area "Cortenoever". The animal was radio-collared for swift locating, and since it was familiar with human presence and activity, it could easily be observed from a car. Special attention was given as to whether the introduction induced agonistic behaviour in the established hares which finally resulted in the introduced hare being chased away.

During the first three days after introduction, the animal was observed continuously, and afterwards from 5.00–10.00 p.m. In the 14th night after introduction, the introduced hare was predated by a polecat.

Determination of clustering

As clustering can also be the result of nonuniformity of the habitat, we studied the distribution of hares on very uniform, cultivated meadows. During May and June 1977, ten meadows in the area "Cortenoever" were observed twelve times between 6.00 p.m. and 7.00 a.m. This was done from a car, using binoculars with a spotlight. The meadows, the location of which is indicated in fig. 2, were selected for their appropriately low vegetation. In these meadows several points were marked with reflection-tape to facilitate the location of the hares observed. The spots on which they were first observed, were marked on a map. The distances between the marked hares observed per meadow area were compared with random distributions of the same number of hares on the same area.

Influence of clustering on alertness

The influence of clustering on the alertness of the hares was quantified by measuring the frequency of attentive interruptions during grazing, i.e. when hares stopped grazing to look around briefly. Observations were made between two hours before and one hour after sunset, and between one hour before and two hours after sunrise, from a car and without using a spotlight so as to prevent any disturbance of the hares' behaviour. Protocols were recorded on tape, for being worked out afterwards. Grazing bouts shorter than four minutes were not taken into account.

The observations were made on the same meadows used for studying clustering, as far as the grass was short enough to observe grazing and attentive behaviour in detail. The observations were restricted to hares located 50–100 m from the road, to enable making detailed observations without influence by road-traffic.

Results

Size and changeability of the home range

The size of the home ranges of the 13 radio-tracked hares during the total periods of observation are shown in table 1. The mean size was found to be 29 ha. The relation between the length of the observation period and the size of the home range turned out to be insignificant ($r = 0.29$; $n = 13$; $p. = 0.05$), and the individual differences are distinct.

Table 1

Observation periods and home ranges of 13 radio-collared hares

C = Cortenoever, N = Noordoostpolder

hare	sex	area	observation period	period of intensive observations	number of observation-nights		home range (ha)
					'intensive'	'incidental'	
1	♀	C	31 July'73 - 30 Aug.'73	1 Aug.'73 - 30 Aug.'73	15	17	25.5
2	♂	C	31 July'73 - 4 Oct.'73 19 Jan.'74 - 15 Feb.'74	1 Aug.'73 - 4 Oct.'73 19 Jan.'74 - 15 Feb.'74	31 13	15	59.5
3	♂	C	25 Aug.'73 - 8 Feb.'74	25 Aug.'73 - 20 Sep.'73	16	43	12
4	♀	C	25 Aug.'73 - 4 Dec.'73	25 Aug.'73 - 27 Nov.'73	45	20	16
5	♂	C	18 Oct.'73 - 6 Dec.'74	18 Oct.'73 - 6 Dec.'73	25	21	13.5
6	♀	C	19 Jan.'74 - 15 Feb.'74	19 Jan.'74 - 15 Feb.'74	13	2	7.5
7	♀	N	15 Jan.'75 - 7 Feb.'75	20 Jan.'75 - 5 Feb.'75	4	9	13.5
8	♂	N	15 Jan.'75 - 3 Apr.'75	20 Jan.'75 - 21 Mar.'75	19	12	30
9	♂	N	15 Jan.'75 - 16 May '75	20 Jan.'75 - 15 May '75	27	9	72
10	♀	C	15 July'75 - 31 Oct.'75	22 July'75 - 10 Aug.'75	16	23	23
11	♀	C	24 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	10	14	57
12	♀	C	14 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	10	15	13
13	♀	C	14 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	11	14	30
							Mean: 29

The cumulative increase of the home ranges of the hares numbered 1–6 in table 1 is shown in fig. 1^A, while for the same animals fig. 1^B shows the area size which would be used till the end of the observations. For reasons of comparison, for both graphs only data obtained from nights during which the animals were tracked intensively were used. The figures show an increase of the total home range due to utilisation of areas not previously in use, and a decrease of the area which was observed to be used after that. This indicates shifts of the activity area which involves abandoning parts of the area. Such shifts may be gradual as well as abrupt. Not only new areas are involved, but also areas occupied earlier can be taken in use again.

Home ranges of hares tracked simultaneously sometimes showed an extensive overlap, as is illustrated in fig. 2 for hares studied near "Cortenoever". Hares with overlapping home ranges were repeatedly observed close together, also when they were of the same sex.

Movements in adults and young

Fig. 3 shows the distances between the places of release and recovery of individually tagged hares, in relation to the time involved. The location of the place of recovery was not always exactly known, especially when the hare was shot during a drive. Of the hares recovered within one kilometer from the place of release, those for which it was certain that the distance was less than 500 m, are indicated separately.

From 132 adult hares released on the spot where they had been captured, 24 (18 %) were recovered (fig. 3^A), of which 58 % were shot and 4 % killed by traffic. Nearly all the recoveries concerned animals which moved less than 1 km from their place of release, and for 58 % that distance was certainly less than 500 m. From the data it can be concluded that movement does not increase with age.

From 99 leverets, estimated at 5 weeks old maximum age and supposedly still being nursed, 23 were recovered (fig. 3^B), of which 56 % were shot. No traffic victims were reported. Nearly all the movements found were less then 1 km, and for two third certainly less than 500 m.

The data indicate that also in young hares movement does not increase when they grow older. Movement of the young does not seem to differ from adults.

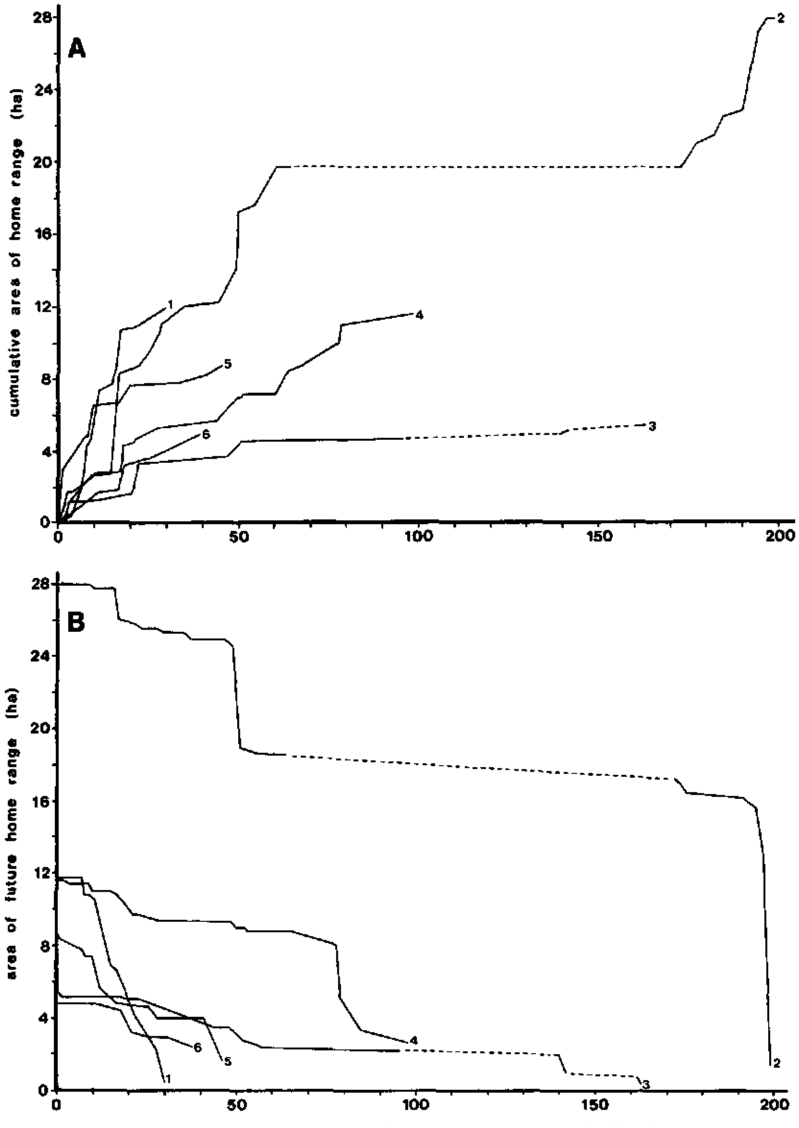


Fig. 1. Areas of realized (A) and future (B) home range in the course of the observation periods of the radio-tracked hares 1–6 from table 1, based on data from nights of intensive observation

Movements among introduced hares

From 505 introduced adult hares, 90 (18 %) were recovered (fig. 3^{C}), of which 70 % were shot and 19 % killed by traffic. Only 54 % of the recovered animals moved over more than 1 km and 9 % over more than 3 km. The data indicate that movement does not increase with time, so it is likely that the added movements in introduced hares mainly occurred just after releasing. The relatively high percentage of traffic victims also indicated movement before the animals were settled.

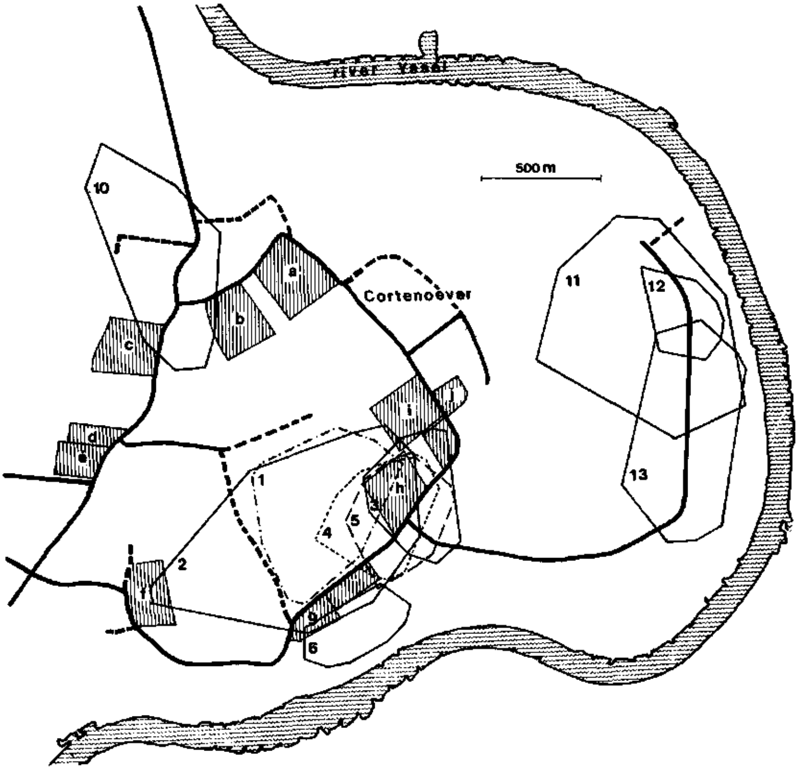


Fig. 2. Home ranges of radio-tracked hares in the area "Cortenoever", numbered as in table 1. The pastures from which clustering data were collected (table 3) are shaded

In fig. 4, the bearings indicate the direction and distance of migration related to the direction of the place of origin. A tendency of migration into the direction of the place of origin cannot be observed.

Interactions between an introduced and indigenous hares

Table 2 summarizes the observations of encounters between a released hare raised in captivity and indigenous hares during a fortnight just after releasing. Apart from this, we observed the hares 13 times passing by within 7 m of each other, without any obvious interaction.

From table 2, no distinct difference in behaviour between the introduced hare and the indigenous ones can be concluded. No chasing away of the introduced hare occurred, and the hare stayed in the area in which it was released.

Clustering

The comparison between observed distributions of hares on the meadows in the "Cortenoever" area and simulated random distributions is summarized in table 3. Out of 81 observations the observed distances were smaller than the simulated ones on 59 occasions, and they were larger 22 times. Since the difference is significant (sign test on observations and Monte Carlo simulations: $T = 37$; $n = 81$; $p < 0.01$) it may be concluded that hares at

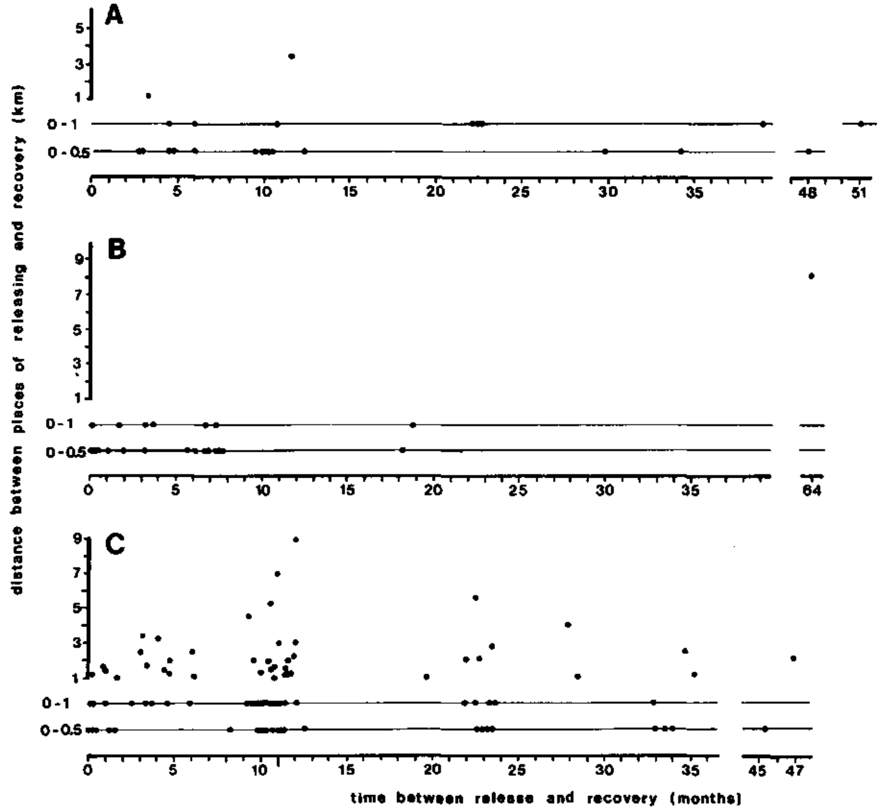


Fig. 3. Distances between the places of release and recovery of tagged hares, related to the time passed between release and recovery. A: tagged as adult, B: leverets tagged in their suckling phase, C: tagged as adult and released in a strange area

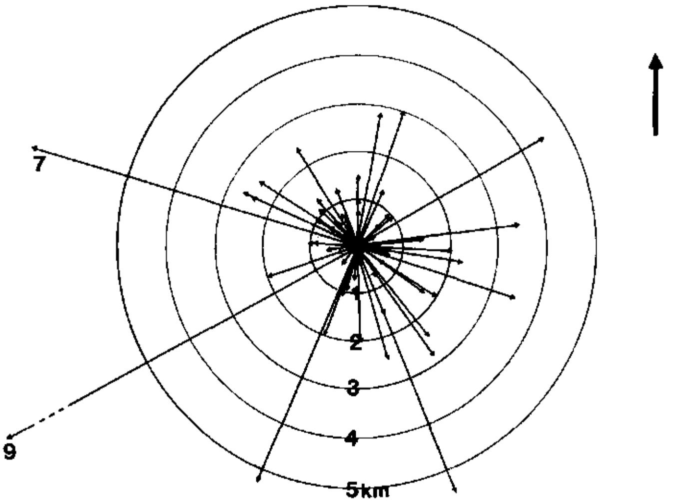


Fig. 4. Distance between release points (centre) and place of recovery (point of arrow) in displaced hares, with the bearings of migration related to the direction of the place of origin (arrow right)

Table 2

Behaviour in 19 encounters between a female hare released from captivity and conspecifics living in the wild

behaviour	hare released from captivity	'wild' hares
contact sought	9	10
sniffing at the conspecific	2	4
following each other	8	10
encircling the other one without approaching	6	3
leaping	0	2
aggressive behaviour (boxing, kicking, biting)	3	3
breaking off the meeting by going away	7	10
breaking off the meeting by flight	1	1

Table 3

Observed distribution of hares on pastures near Cortenoever (Fig. 4), compared with simulated random distributions

field	number of observations	total number of hares	mean sum of distances to the nearest neighbour per observation		numbers of positive (f) and negative (g) difference between (d) and (e)	
(a)	(b)	(c)	simulated (d)	observed (e)	(f)	(g)
a	12	94	485.8	246.4	10	2
b	6	15	290.5	208.9	4	2
c	4	17	305.3	241.5	3	1
d	8	30	277.2	160.9	7	1
e	6	21	290.7	194.9	4	2
f	7	29	289.0	299.3	5	2
g	7	25	393.9	200.8	6	1
h	11	54	246.2	214.0	5	6
i	11	73	376.4	264.1	7	4
j	9	50	221.3	156.9	8	1
Total	81				59	22

night are more clustered than could be expected from a random distribution. During the observations, no indications were obtained that clustering was bound to a particular condition or usage of the meadows, such as height of the grass or the presence of cattle. Only within 10 m from the road relatively few hares were observed.

Frequency of attentive interruptions during grazing

For describing the distance between two grazing hares, three categories were distinguished, viz. 0–7 m: hares grazing gregariously; 8–30 m: hares grazing in open clusters; more than 30 m: hares grazing solitarily. The observed frequencies of attentive interruptions within these categories are shown in fig. 5. A distribution is made between observations made around sunset and those made around sunrise. From the figure it can be concluded that solitarily grazing hares showed a higher frequency of attentive interruption than grazing hares in open clusters, whilst in the latter category the frequency exceeded that of hares grazing gregariously. Also at dawn the solitarily grazing hares showed the highest frequency of looking up. Differences between hares grazing in open clusters and those grazing gregariously were not observed, due to increased alert behaviour in the gregarious hares. It is likely that this increase is connected with a higher rate of sexual interactions in the morning, as found by F. OOMEN-KALSBEEK and K. NOORDAM (unpubl. data).

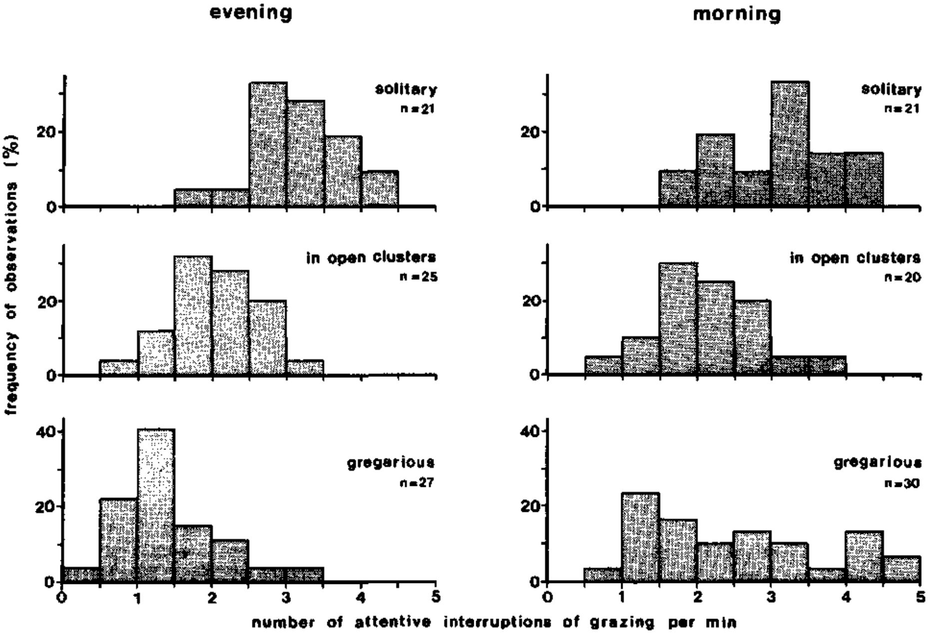


Fig. 5. Distribution of the number of attentive interruption of grazing per min in hares grazing solitarily, in open clusters and gregariously. *Left:* observations from two hours before till one hour after sunset; *right:* observations from one hour before till two hours after sunrise

Discussion

The collected data clearly indicate that in The Netherlands hares are very sedentary, even though their home range is not a fixed area. Occasionally the activity area is shifted. This, however, does not result in a continuous extension of the total home range, which is in agreement with the idea of PIELOWSKI (1972), that the home range "contains several clearly defined areas, far smaller in size and occupied periodically, situated within the boundaries of the whole home range". However, the size of the home ranges we observed was on average about ten times smaller than that mentioned by PIELOWSKI (29 ha versus 300 ha), and more in agreement with the home ranges observed by MERZ (1976) and SCHNEIDER (1978).

From fig. 1^A it is likely that, where the observation periods varied from a few weeks to several months, the home ranges had not reached their ultimate size in all cases. Nevertheless we found no significant correlation between the total home range size and the length of the observation period, indicating that in most of the home ranges a large part of the ultimate size had been covered within a few weeks. This is in agreement with the recoveries of tagged hares, which also show that over longer periods and in other areas, most hares do not move more than 500 m and migration over more than 1 km is exceptional. This also holds for juveniles and sub-adults. Observations on dispersion of leverets after being nursed show that their radius of action can be several hundreds of meters at the end of the suckling phase (BROEKHUIZEN and MAASKAMP 1980). This indicates that the ultimate home range can already be reached during the suckling phase, and that generally juvenile hares do not need to migrate to become residents.

Home ranges of neighbouring hares, also when they are of the same sex, can greatly overlap (fig. 2). This, and the low degree of agonistic behaviour, even towards newly introduced hares, indicates a high degree of tolerance within the home range area. Therefore, the greater tendency to leave the place of release in introduced hares (fig. 3) is unlikely to be caused by antagonistic behaviour of indigenous conspecifics, or by 'homing', as was found in some introduced hares by JEZIERKSI (1968) (fig. 4). As the greater moving distances in the former mainly occurred immediately after release, they are more likely to be a response to being caught and transported, or, as PIELOWSKI (1972) expressed it, to be caused by shock.

The distribution of hares on meadows in the "Cortenoever" area showed an underdispersed clustered pattern. This may reduce the risk of predation, because it enables the perception of signals from conspecifics during twighlight and in the dark, when spotting of potential predators is most difficult. The function of the clustering behaviour was not studied, but the lower frequency of attentive interruptions during grazing in the presence of conspecifics indicates a decreased need for attention.

The combination of a non-migratory way of life, a low degree of intolerance, and a tendency to cluster does not always occur in hares. ANGERMANN (1973) mentioned roaming groups of hares in South-East Europe during periods of heavy snowfall outside the reproduction period. LINDLÖF (1978) observed aggressive dominance ranks in hares feeding from a hay stack when snow cover was deep. In *Lepus americanus* it was shown that when food was short, juveniles were expelled by adults and that immigrating adults more successfully settled than juveniles when the food supply was artificially increased (WINDBERG and KEITH 1976). These studies all indicate that the food supply determines behaviour and spatial distribution.

The behaviour and spatial distribution of the hares we studied suggest that food shortage was not involved. This may hold for most of The Netherlands, because nearly all hare populations are hunted. Consequently, before winter starts and before the reproduction season a substantial part of the populations will be eliminated. Besides, in The Netherlands long periods with thick snow cover were exceptional in the last decade. Hence, the food supply is unlikely to be the limiting factor in population regulation.

Acknowledgements

We are greatly indebted to the following students for their assistance: FRANÇOISE OOMEN-KALSBEEK, KARIN NOORDAM, TON KNIJFF, JAAP VAN EGMOND, AUKE PETTEN, RUUD CRUL and WIM VAN KRAAIJ. They all contributed to our knowledge of home range use in hares.

Zusammenfassung

Ortsveränderungen, Aktionsräume und Gruppierungen beim Feldhasen (Lepus europaeus Pallas) in den Niederlanden

Zur Untersuchung verschiedener Aspekte der Verbreitung des Feldhasen wurden Ortsveränderungs- und Lebensraumdaten gesammelt an Hand von Rückmeldungen markierter Individuen sowie durch Verfolgung der Bewegung von Hasen, die mit Sendern versehen waren.

Die meisten Hasen, auch Säuglinge, wanderten weniger als 500 m vom Markierungsplatz. Die mittlere beobachtete Lebensraumgröße war 29 ha. Dies deutet auf eine gewisse Standortstreue der Tiere hin.

Versetzte Hasen siedelten sich meistens in der Nähe der Aussetzungsstelle an. Nur selten wurde aggressives Verhalten ortsansässiger Hasen diesen ausgesetzten Tieren gegenüber beobachtet.

Die Lebensräume verschiedener Individuen überschneiden sich bedeutend. Nachts wurden Gruppierungen beobachtet. Da während der Dämmerung gesellig äsende Hasen weniger Aufmerksamkeitsunterbrechungen zeigten als allein äsende Tiere, wird vermutet, daß diese Vergesellschaftung teilweise als Feindvermeidungsverhalten anzusehen ist.

In der Literatur wird beschrieben, daß in Gebieten mit schlechten Nahrungsverhältnissen – wie in der Wüste oder in schneereichen Gebieten – Hasen während der Fortpflanzungszeit territorial sind und im Winter mehr wanderlustig werden. Die Ergebnisse dieser Untersuchung zeigen hingegen eine bleibende Standortstreue der Tiere. Diese läßt vermuten, daß in den von uns untersuchten Gebieten kein Futtermangel auftritt. Möglicherweise spielt dabei der hohe Jagddruck im Herbst eine Rolle.

References

Andersen, J. (1951): Hvor meget vandrer haren? (On the movements of marked European hares *[Lepus europaeus]* in Denmark). Vildbiol. St. Kalö. medd. 5.

Angermann, R. (1973): De Haasachtigen. In: Het Leven der Dieren. Ed. by Grzimek, B. Utrecht: Het Spectrum, 486–540.

Broekhuizen, S. (1971): Gemerkte haas 70 km verder teruggemeldt. De Ned. Jager **76**, 23, 824.

— (1979): Survival in adult European hares. Acta theriol. **24**, 34, 465–473.

Broekhuizen, S.; van 't Hoff, C. A.; Jansen, M. B.; Niewold, F. J. J. (1980): Application of radio tracking in wildlife research in The Netherlands. In: A handbook on biotelemetry and radio tracking. Ed. by C. J. Amlaner and D. W. MacDonald. Oxford: Pergamon Press, 65–84.

Broekhuizen, S.; Maaskamp, F. (1976): Behavior and maternal relations of young European hares during the nursing period. In: Ecology and management of European hare populations. Ed. by Z. Pielowski and Z. Pucek. Warszawa: Pol. Hunt. Ass., 59–67.

Broekhuizen, S.; Maaskamp, F. (1979): Age determination in the European hare (*Lepus europaeus* Pallas) in The Netherlands. Z. Säugetierkunde **44**, 3, 162–175.

— (1980): Behaviour of does and leverets of the European hare *(Lepus europaeus)* whilst nursing. J. Zool. (London) **191**, 487–501.

— (1981): Annual production of young in European hares in the Netherlands. J. Zool. (London) **193**, 499–516.

Brüll, U. (1973): Wildfutterpflanzengesellschaften und Futterwert der von Feldhasen (*Lepus europaeus* Pallas) genutzten Pflanzen. Diss. Hamburg, 162 p.

Burt, W. H. (1943): Territoriality and home range concepts as applied to mammals. J. Mammalogy **24**, 346–352.

Douglas, M. J. W. (1970): Movements of hares *Lepus europaeus* Pallas, in high country in New Zealand. N. Z. Jl. Sci. **13**, 287–305.

Fiechter, A. (1975): Radiotelemetrie: Feldtechnik und Anwendung bei Reh und Feldhase. Zool. Inst. Univ. Zürich, Diplomarbeit. 39 pp.

Frylestam, B. (1976): Effects of cattle-grazing and harvesting of hay on density and distribution of an European hare population. In: Ecology and management of European hare population. Ed. by Z. Pielowski and Z. Pucek. Warszawa: Pol. Hunt. Ass. 199–203.

Jezierski, W. (1967): Four cases of "home instinct" in the European hare. Acta theriol. **12**, 173–175.

— (1968): Some ecological aspects of introduction of the European hare. Acta theriol. **13**, 1–30.

Koenen, F. (1956): Der Feldhase. Wittenberg-Lutherstadt: Ziemsen Verlag.

Lindlöf, B. (1978): Aggressive dominance rank in relation to feeding by European hare. Viltrevy **10**, 145–158.

Merz, H. (1973): Die Gruppierungstendenz beim Feldhasen (*Lepus europaeus* Pallas) in Abhängigkeit der Nachtzeit im Juli/August 1973. Zool. Inst. Univ. Zürich, Semesterarbeit. 16 pp.

— (1976): Nächtliche Standplatzwahl individuell gekennzeichneter Feldhasen (*Lepus europaeus* Pallas) innerhalb ihrer Aktionsräume. Zool. Inst. Univ. Zürich, Diplomarbeit. 39 pp.

Odum, E. P.; Künzler, E. J. (1955): Measurement of territory and home range in birds. The Auk **72**, 128–137.

Pielowski, Z. (1966): Forschungen über den Feldhasen. XII. Die Raumstruktur der Population. Acta theriol. **11**, 449–484.

— (1972): Home range and degree of residence of the European hare. Acta theriol. **17**, 93–103.

Rieck, W. (1953): Der Feldhase. Merkblätter des Niederwildausschusses des DJV 4. München: Mayer Verlag.

— (1955): Feldhasen und Wildkaninchen. In: Jagd und Hege in aller Welt. Ed. by Deutscher Jagdschutzverband. Düsseldorf: Kölzig Verlag, 180–184.

Rimathé, R. (1977): Zur saisonalen Abundanzdynamik des Feldhasen (*Lepus europaeus* Pallas) im Schweizerischen Mittelland. Diss. Zürich, 126 pp.

Schneider, E. (1978): Der Feldhase. München: BLV Verlag.

Szederjei, A. (1959): Beobachtungen über den Feldhasen in Ungarn. Z. Jagdwiss. **5**, 81–94.

Windberg, L. A.; Keith, L. B. (1976): Experimental analyses of dispersal in Snowshoe hare populations. Can. J. Zool. **12**, 2061–2081.

Authors' address: Sim Broekhuizen and Frans Maaskamp, Research Institute for Nature Management (R.I.N.), Kemperbergerweg 67, NL-6816 RM Arnhem, The Netherlands