BREEDING ECOLOGY OF MEADOW BIRDS (CHARADRIIFORMES);

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

RIJKSUNIVERSITEIT GRONINGEN

BREEDING ECOLOGY OF MEADOW BIRDS (CHARADRIIFORMES);

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Proefschrift

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ALBERT JAKOB BEINTEMA

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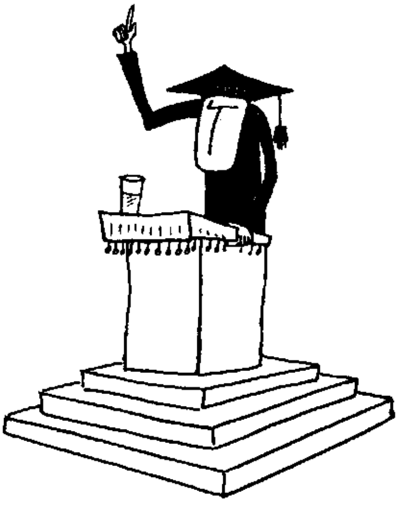

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VOORWOORD

Conducteur heb ik nooit willen worden. Mijn eerste ambitie was dokter worden. Geen gewone, maar één met messen. Vóór het einde van de lagere school stond echter al vast dat biologie mijn vak zou zijn. Zelfs alle leraren die getracht hebben mij het verschil tussen gekartelde en gezaagde bladranden bij te brengen hebben mij daar niet van af weten te houden. Ook stond vast dat er maar één plaats was waar je fatsoenlijk biologie kon studeren: Groningen. Belangstelling voor de natuur heb ik van thuis meegekregen, maar de ecologische bril om de wereld door te zien komt uit Groningen. En als ik een bioloog ecologische onzin hoor uitkramen is nog steeds mijn eerste gedachte: 'jij komt niet uit Groningen'. Het is voornamelijk professor Baerends geweest die de Groninger zoölogenopleiding de goede naam bezorgd heeft, die door de huidige docenten zo met zorg in stand gehouden wordt. De colleges Algemene Zoölogie van professor Baerends golden als de enige die je echt niet kon of zelfs maar zou willen missen, al moet ik bekennen dat ik ze toch geregeld heb moeten laten schieten omdat ze onaanvaardbaar vroeg in de ochtend aanvingen.

Weidevogels hebben eigenlijk nooit zozeer mijn belangstelling gehad. Zeevogels zouden mijn toekomst zijn. Vandaar dat ik naast de dieroecologie bijvakken deed in de oceanografie bij professor Postma op het Nederlands Instituut voor Onderzoek der Zee en in de zoögeografie van zeevogels bij professor Voous in Amsterdam. Om vast in de sfeer te komen van verre ontdekkingsreizen naar zeevogeleilanden stuurde Baerends mij een jaar naar Schiermonnikoog met de verrukkelijk vage opdracht 'ga maar eens naar bergeenden kijken', met als aanbevolen litteratuur 'The Mountain Gorilla' van George Schaller. Het idee om echte zeevogels van nabij te bestuderen op het afgelegen Tristan da Cunha is in de planfase blijven steken. Wel heb ik het genoegen gehad oog in oog te staan met de berggorilla's uit Schallers boek.

De bergeenden in mijn curriculum maakten dat in aanmerking kwam voor een baan op het Rijksinstituut voor Natuurbeheer (RIN) om onderzoek te doen aan waterwild (dat heette toen nog zo). Vermeldenswaard is dat de sollicitatiecommissie, onder aanvoering van Jan Rooth, mij thuis bezocht. Jan heeft zich daar voornamelijk beziggehouden met het leeg trekken van mijn boekenkast, omdat dat naar zijn zeggen de beste manier was om te kijken hoe iemand is. Waterwild. Ik moest maar eens naar nonnetjes gaan kijken, want daar was niet zoveel van bekend. Verder vond Jan dat iemand die 's-winters naar wintergasten kijkt best in de broedtijd broedvogels kan bestuderen. Dus ik moest ook maar eens wat aan tureluurs gaan doen. Het gevolg daarvan was dat ik in het technisch overleg dat het RIN toen nog geregeld had met het Staatsbosbeheer, onmiddellijk werd aangesproken als weidevogeldeskundige. Er bleek een enorme behoefte te bestaan aan informatie over weidevogels en weidevogelbeheer. Er bleef maar één weg over om te bewandelen: proberen weidevogeldeskundige te worden. Het echte waterwild (en de nonnetjes) moesten daarbij onvermijdelijk naar de achtergrond verhuizen.

Onderzoek doe je niet alleen. Dit is de plaats om iedereen waarmee ik in de loop der jaren heb samengewerkt te bedanken. Collega's op het RIN, studenten, stagiaires, gewetensbezwaarden, medewerkers bij andere diensten en niet te vergeten vrijwilligers. In de laatste categorie verdienen vooral de ringers vermelding, die jarenlang duizenden snavelmaatjes van weidevogelkuikens hebben verzameld. Na enige aarzeling heb ik besloten hier geen namen op te sommen. Niet alleen zijn het er heel veel, maar ook is niet altijd scherp te onderscheiden wie nu wel of niet heeft bijgedragen tot dat deel van het weidevogelonderzoek dat in dit proefschift is gebundeld. Ook verwijs ik naar de 'acknowledgements' bij ieder van de afzonderlijke hoofdstukken.

In veel voor- of dankwoorden kan men lezen hoezeer partner en gezin geleden hebben onder de totstandkoming van het proefschrift. In mijn geval is dat niet zo. Ik zou ook niet willen beweren dat de totstandkoming van dit proefschrift geleden heeft onder partner en gezin. Eerder is het zo dat partner, gezin en de totstandkoming van dit proefschrift in gelijke mate geleden hebben onder mijn overige RIN-activiteiten, die mij vaak toch nog op verre en vreemde plaatsen deden belanden, variërend van Timboektoe tot Kaap Hoorn. Als ik Dineke, Kike en Nienke ergens voor moet bedanken is het wel de enthousiaste en positieve manier waarop ze mijn omzwervingen altijd benaderen.

Tenslotte een woord van dank aan mijn promotor, die het aangedurfd heeft de supervisie over mijn onderzoek op zich te nemen. Zijn commentaar op manuscripten was soms niet mals, maar leidde zonder uitzondering tot kwaliteitsverbetering. Ik heb grote bewondering voor de manier waarop hij altijd weer kans ziet kleine brokjes onderzoeksresultaten in te passen in De Grote Lijn. Wie Rudi kent weet hoe moeilijk het soms kan zijn om hem te spreken te krijgen. Maar het moet gezegd worden dat hij in de kritieke fase bewonderenswaardig vaak bereikbaar was en meestal ook deed wat hij beloofde te doen.

En laat ik niet vergeten de vogels te noemen. Want zonder vogels was er geen onderzoek aan vogels. En dat zou het leven toch een stuk onaangenamer maken. Dus laten we er met z'n allen voor zorgen dat vogels blijven. Ik hoop dat ik met mijn werk hiertoe een beetje heb mogen bijdragen.

Albert Beintema

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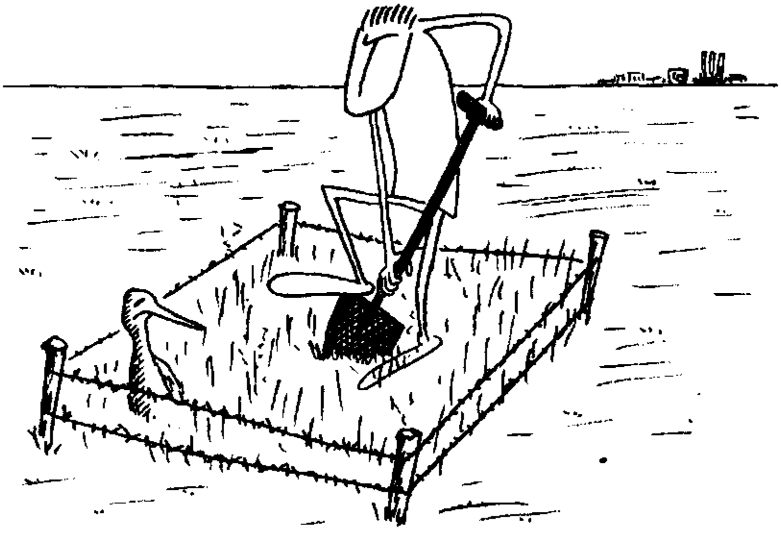

WEIDEVOGELS IN NEDERLAND; BEHEER EN BESCHERMING

INLEIDING EN SAMENVATTING
Introduction and summary

ABSTRACT This chapter gives an introduction to the typical Dutch phenomenon of the 'meadow bird' community. 'Meadow birds' are those birds characteristically breeding in Dutch agricultural grasslands. Fourteen bird species are classified as being genuine meadow birds, but in this thesis I further confine the term to the wader species of this assemblage: Oystercatcher *Haematopus ostralegus*, Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus*, Ruff *Philomachus pugnax*, and Common Snipe *Gallinago gallinago*. My meadow-bird research at the Research Institute for Nature Management includes several aspects which are not dealt with in this thesis, such as migration and winter distribution, and many of the practical aspects of nature management, aiming at conservation of this threatened community. The eight chapters specifically deal with breeding ecology, and follow the sequence of events during the breeding season. Chapter 1 gives a general overview of the meadow-bird problem in The Netherlands, chapter 2 deals with factors affecting the timing of breeding, chapter 3 deals with nest success up to hatching. Chapters 4 to 8 are all devoted to the chick stage, as this is the stage which still holds most mysteries. Chapters 4 and 5 give details about growth and the thermoregulatory aspects affecting time budgets of chicks. Chapter 6 deals with feeding ecology of chicks. Chapter 7 presents a method to estimate the relative body condition of chicks encountered in the field, and chapter 8, finally, gives estimates of chick survival up to fledging, based on the results of an extensive ringing programme.

ONTSTAAN VAN DE WEIDEVOGELGEMEENSCHAP

Het verschijnsel weidevogel

Een 'weidevogel' is een typisch Nederlands begrip. Het gevolg daarvan is dat andere Europese talen er geen woord voor kennen. Toch is in de laatste tien jaar de weidevogelproblematiek ook een rol gaan spelen in de natuurbescherming in onze buurlanden. Door contact met het Nederlandse weidevogelonderzoek zijn in Groot-Brittannië en Duitsland de begrippen 'meadow bird' en 'Wiesenvogel' bezig in bepaalde kringen ingeburgerd te geraken.

Onder weidevogels kunnen in principe alle vogelsoorten verstaan worden die in agrarisch grasland (weiland en hooiland) broeden. Evolutionair gezien zijn agrarische graslanden een recent verschijnsel. Dat betekent dat geen enkele weidevogelsoort er van oorsprong voorkomt, maar dat ze ooit vanuit natuurlijke (open) biotopen dit grasland bezet hebben (Voous 1965). Uiteraard zijn ze ook nog steeds in natuurlijke biotopen te vinden. De mate waarin agrarisch grasland als belangrijk broedbiotoop een rol is gaan spelen, verschilt van soort tot soort. In het algemeen onderscheiden we in Nederland 14 soorten weidevogels (Verstrael 1987): Wilde Eend (*Anas platyrhynchos*), Zomertaling (*Anas querquedula*), Slobeend (*Anas clypeata*), Kuifeend (*Aythya fuligula*), Scholekster (*Haematopus ostralegus*), Kievit (*Vanellus vanellus*), Grutto (*Limosa limosa*), Tureluur (*Tringa totanus*), Wulp (*Numenius arquata*), Kemphaan (*Philomachus pugnax*), Watersnip (*Gallinago gallinago*), Veldleeuwerik (*Alauda arvensis*), Graspieper (*Anthus pratensis*) en Gele Kwikstaart (*Motacilla flava*). Deze soorten kunnen in grote delen van Nederland in grasland aangetroffen worden en worden daarom wel aangeduid als 'primaire weidevogels'. Daarnaast zijn er nog eens 14 soorten 'secundaire weidevogels', die slechts lokaal in grasland voorkomen of die minder specifiek aan grasland gebonden zijn. De kern van de weidevogelgemeenschap wordt gevormd door een zestal steltlopers: Scholekster, Kievit, Grutto, Tureluur, Kemphaan en Watersnip. In dit proefschrift heb ik mij in hoofdzaak tot deze zes soorten beperkt, waarbij Kievit, Grutto en Tureluur dé meeste aandacht hebben gekregen.

In internationaal opzicht neemt Nederland een belangrijke positie in als broedgebied voor weidevogels. In extreme mate is dat het geval voor de Grutto, waarvan we aannemen dat ca 80% van de Europese populatie binnen onze landsgrenzen broedt. Maar ook voor de andere soorten geldt dat Nederland een aanzienlijk groter deel van de populatie herbergt dan men op grond van de oppervlakte van ons land zou mogen verwachten (Van Dijk 1983, Van Dijk et al. 1989).

Opkomst en ondergang van de weidevogels

Weidevogels zijn thans cultuurvolgers. Van oorsprong zullen er in Nederland maar op beperkte schaal levensmogelijkheden voor weidevogels zijn geweest. Toen de mens in toenemende mate gronden begon te ontginnen ten behoeve van de landbouw, ontstond steeds meer potentieel broedbiotoop voor vogels van open gebieden. Vooral in de graslanden heeft een geleidelijke toename van de voedselrijkdom door bemesting en intensivering van het gebruik deze gebieden in eerste instantie steeds geschikter gemaakt. Tegelijkertijd zijn ook de negatieve neveneffecten van het grondgebruik steeds meer een rol gaan spelen: men is geleidelijk aan steeds vroeger gras gaan oogsten en door toenemende bemesting zijn de veedichtheden sterk toegenomen. Dit betekent vooral een vermindering van de kans op broedsucces, door toenemend risico eieren of kuikens te verliezen (vernieling door machines en vertrapping door vee). Tussen deze twee tegengestelde krachten speelt zich het weidevogelverschijnsel af. Ook op de voedselvoorziening heeft toenemende bemesting twee tegengestelde invloeden. Aan de ene kant neemt de biomassa aan ondergrondse fauna (regenwormen) sterk toe, waardoor de volwassen vogels zich in principe in hogere dichtheden kunnen vestigen. Aan de andere kant vinden veranderingen plaats in het aanbod van de bovengrondse fauna (arthropoden), waardoor de gemiddelde prooigrootte voor kuikens afneemt en het dus moeilijker wordt om per tijdseenheid voldoende voedsel op te nemen.

Op de intensiveringsschaal kan men zich dus een ondergrens voorstellen van een minimaal vereiste hoeveelheid beheersintensiteit om het weidevogelverschijnsel tot bloei te laten komen en een bovengrens van een maximaal toelaatbare beheersintensiteit, waarboven het fout gaat. Onder fout gaan wordt dan verstaan: te weinig nakomelingen voortbrengen om de natuurlijke mortaliteit onder de volwassen vogels te compenseren. Het begrip 'beheersintensiteit' is hier in zeer algemene zin gebruikt en behelst alle factoren als ontwatering, bemesting, inscharingsdichtheid, maaidata, maaifrequentie, enzo-

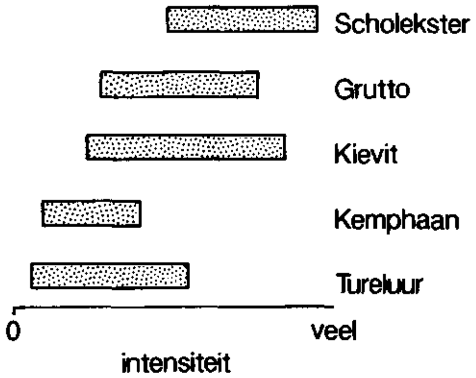

Fig. 1. Voorkeur en tolerantie van weidevogels ten aanzien van beheersintensiteit. Voor iedere soort is het traject aangegeven dat valt binnen de minimaal vereiste en maximaal toelaatbare beheersintensiteit. Voor de beheersintensiteit is een arbritraire schaal gekozen.

voort. Ondergrens en bovengrens van de 'geschiktheid voor weidevogels' verschillen per vogelsoort, afhankelijk van populatiedynamische eigenschappen. Dit is de basis voor de in het Nederlandse weidevogelbeheer veel gehoorde begrippen 'kritische weidevogel' en 'niet-kritische weidevogel'. Het tolerantiebereik van de zes genoemde steltlopersoorten voor beheersintensiteit is schematisch weergegeven in figuur 1.

Bij de factoren die Nederland zo geschikt hebben gemaakt als weidevogelland, speelt de waterhuishouding een centrale rol. Bij slechte ontwatering ontwikkelt de vegetatie zich langzaam en kunnen vee en machines pas laat de wei in, in verband met de geringe mechanische draagkracht van natte bodems. Zodoende kan een voor de vogels gunstige combinatie ontstaan van grote voedselrijkdom en het pas laat optreden van beheersactiviteiten. Deze combinatie is in Europa betrekkelijk zeldzaam en komt juist in Nederland veelvuldig voor. De lage ligging van veel gebieden heeft een goede ontwatering lange tijd ernstig belemmerd, waarbij ook grondsoort en klimaat en rol spelen. De beste weidevogelgebieden vinden we op combinaties van klei en veen (voedselrijkdom plus geringe mechanische draagkracht). Verdroging in het voorjaar wordt in belangrijke mate vertraagd door regenval.

ONTWIKKELING VAN HET WEIDEVOGELONDERZOEK

Voordat er op het Rijksinstituut voor Natuurbeheer sprake was van weidevogelonderzoek in algemene zin, werd begonnen met het bestuderen van de Tureluur (Beintema & Timmerman 1976). Uitgangspunt was dat weidevogelbeheer in toenemende mate problemen opriep en dat al een redelijke hoeveelheid kennis beschikbaar was over de Kievit (Klomp 1951, 1954, Kraak et al. 1940) en de Grutto (Van Balen 1959, Haverschmidt 1963, Mulder 1972). Al heel spoedig bleek dat vanuit de natuurbeherende instanties, met name het Staatsbosbeheer, dringende behoefte bestond aan meer kennis over weidevogels in het algemeen. Daarom werd begonnen met een meerjarig onderzoek in Friesland, waarbij getracht werd door middel van inventarisaties en correlatief onderzoek inzicht te krijgen in de factoren die het voorkomen van weidevogels bepalen (Beintema & Van den Bergh 1976, 1977, 1979, Holwerda 1980, De Weijer 1976). Daarbij werd steeds duidelijker dat langs de correlatieve weg wel aanwijzingen gevonden konden worden, maar nooit de werkelijke mechanismen die aan de waargenomen verschijnselen ten grondslag liggen. Daarom werd na een aantal jaren gekozen voor een analytische aanpak, waarbij getracht werd door middel van detailstudies de bouwstenen aan te dragen die uiteindelijk een goed gefundeerd weidevogelbeheer mogelijk zouden moeten maken. Deze wijziging in aanpak vormt in feite de grondslag voor dit proefschrift.

In een volgende fase werd getracht de kennis over weidevogels in modelvorm samen te brengen (Beintema & Müskens 1981a, Beintema 1986a, Spaak 1988, Kramer & Spaak 1990). Daarbij staat de toepassingsgerichtheid (het voorspellen van effecten van inrichtings- en beheersmaatregelen) centraal. Hieraan wordt in dit proefschrift echter slechts op zeer beperkte schaal aandacht besteed (hoofdstuk 3).

Het onderzoek aan kuikens heeft raakvlakken met de dierfysiologie. Het onderwerp thermoregulatie (Visser 1983, Visser & Beintema 1987, Visser et al. 1989) is door Visser uitgebouwd tot een apart promotieonderzoek.

INHOUD VAN DIT PROEFSCHRIFT

Overzicht van de hoofdstukken

Hoofstuk 1 kan gezien worden als een algemeen inleidend hoofdstuk. Hierin wordt de Nederlandse weidevogelgemeenschap geïntroduceerd, waarbij een vergelijking wordt gemaakt met een natuurlijk 'weidevogel'-systeem, zoals we dat nog aantreffen in de Noordamerikaanse prairie. Daarna wordt de Nederlandse weidevogelproblematiek (kritische en niet-kritische soorten, bedreigingen, natuurbescherming, beheer) geschetst. In de volgende hoofdstukken wordt min of meer de gang van zaken tijdens het broedseizoen chronologisch gevolgd. Hoofdstuk 2 behandelt factoren die het vestigingstijdstip van de volwassen vogels bepalen en de veranderingen in de loop van deze eeuw die in deze vestiging hebben plaatsgevonden als gevolg van veranderingen in het graslandbeheer. In hoofdstuk 3 volgt de nestfase, waarbij aandacht wordt besteed aan de factoren die het uitkomstsucces negatief kunnen beïnvloeden, zowel de natuurlijke (predatie) als de agrarische (vertrapping door vee, verlies door machines). De hoofdstukken 4 t/m 8 hebben alle betrekking op de kuikenfase. De kuikenfase krijgt naar verhouding veel aandacht, omdat dat de periode is waarover het minste inzicht bestond (in het beheer wordt vaak niet verder gekeken dan het uitkomen van de eieren). Ook heeft de kuikenfase de meest complexe problemen te bieden. Hoofdstuk 4 en 5 behandelen de groei van kuikens en hun tijdsbesteding in afhankelijkheid van de weersgesteldheid en de mate waarin kuikens daarop met hun thermoregulatie kunnen reageren. Hoofdstuk 6 gaat in op het voedselgedrag en de voedselkeuze van de kuikens. Hoofdstuk 7 biedt een methode om van een willekeurig in het veld gevangen kuiken iets te zeggen over zijn relatieve lichaamsconditie. Hoofdstuk 8 sluit tenslotte de kuikenfase af met schattingen van het totale opgroeisucces, gebaseerd op ringwerk. Studies over trek en overwintering zijn buiten het kader van dit proefschrift gelaten.

Hoofdstuk 1. Polders in Nederland: een traditioneel weidevogelbiotoop

A.J. Beintema

Graslanden zijn overal ter wereld aan verandering onderhevig. Aan de ene kant verdwijnen natuurlijke graslanden door ontginning, aan de andere kant worden graslanden gecreëerd, waar bossen en moerassen plaats moeten maken voor weidegrond. In Europa zijn oorspronkelijke graslanden (steppen, poesta's) op enkele snippers na verdwenen. Men vindt er nog steeds Kieviten en Grutto's, maar deze soorten zijn tegenwoordig grotendeels afhankelijk van cultuurland. Sommige vogelsoorten van open gebieden, zoals de Kievit, hebben zich goed kunnen aanpassen aan het broeden in cultuurland. Andere, zoals de Goudplevier, konden dat niet.

Het is interessant de Nederlandse weidevogelgemeenschap te vergelijken met een natuurlijk graslandsysteem, zoals we dat nog tot op zekere hoogte in Noord-Amerika aantreffen. Hier hebben de meeste soorten zich slecht kunnen aanpassen, als de prairie werd gecultiveerd. Een uitzondering vormt de Killdeerplevier *Charadrius vociferus*, die zelfs op grindwegen en platte daken is gaan broeden. Er is een grote mate van overeenkomst tussen de avifauna's van de Noordamerikaanse natuurlijke prairie en de Nederlandse cultuursteppe. In het Nederlandse grasland behoren vier eendesoorten tot de regelmatige broedvogels, in de prairie zijn dat er zes (in beide gevallen is daar één talingsoort en één duikeend bij; de overige zijn grote zwemeenden). In Nederlands grasland vinden we één rallesoort en twee soorten hoenders, in de prairie treffen we één ral en drie hoenders aan. In Nederland kunnen acht steltopersoorten in grasland broeden, in de prairie zijn dat er negen. Aan typisch graslandbewonende zangvogels vinden we in Nederland tenslotte zeven soorten en in Noord-Amerika tien. Slechts drie soorten komen zowel in de Noordamerikaanse prairie als in de Nederlandse weilanden voor: de Wilde eend, de Slobeend en de Watersnip. Over het algemeen is de prairie dus iets soortenrijker. De gelijkenis gaat niet op voor de zoogdieren, die nieuw gecreëerde gebieden veel moeilijker kunnen koloniseren en daardoor in Nederland in veel geringer soortenaantal voorkomen. Dit weerspiegelt zich ook in de variatie aan predatoren.

Hoofdstuk 2. Vervroeging van het broedseizoen van weidevogels

A.J. Beintema, R.J. Beintema-Hietbrink & G.J.D.M. Müskens

Uit ringdata van weidevogelkuikens kan historische informatie verkregen worden over de broedseizoenen. Er is een verschil tussen ringdata en geboortedata, omdat niet alle kuikens op dezelfde leeftijd geringd worden. In het begin van het seizoen zullen vooral kleine kuikens gevangen worden, op het eind vooral grote. Toch kan ervan uitgegaan worden dat een verschuiving in de geboortedata weerspiegeld zal worden in een soortgelijke verschuiving in de ringdata.

In Nederland worden sinds 1911 vogels geringd. Uit de gegevens (ringgegevens en terugmeldingen) van de Nederlandse Ringcentrale valt af te leiden dat voor Kievit, Grutto, Tureluur en Kemphaan geldt dat zij hun broedseizoen in de loop van de twintigste eeuw met ongeveer twee weken hebben vervroegd. Het duidelijkst komt dit naar voren bij de Kievit en de Grutto. Het patroon bij de Scholekster vertoont enige onduidelijkheden en van de Watersnip zijn te weinig gegevens voorhanden om conclusies te trekken.

De verschuiving van broedeizoenen kan niet verklaard worden door wijzigingen in de wetgeving ten aanzien van het eierrapen. Ook kunnen er onvoldoende wijzigingen in het klimaat worden aangetoond om een dergelijke verschuiving aannemelijk te maken. De verklaring moet gezocht worden in veranderingen in het agrarisch gebruik van grasland. Door een geleidelijk toenemende bemesting en verbeterde ontwatering is de grasgroei steeds vroeger tot ontwikkeling gekomen. Daarmee samenhangend zijn ook de oogsthandelingen vervroegd (inscharen van vee, maaien). De snelheid waarmee de grasoogst vervroegd is, komt goed overeen met de snelheid waarmee de broedseizoenen van de weidevogels zijn verschoven. Het is aannemelijk dat verbeterde ontwatering en toenemende bemesting niet alleen een vervroeging van de grasgroei hebben veroorzaakt, maar ook een vervroeging in de ontwikkeling van het bodemleven, waardoor de weidevogels eerder in staat zijn voldoende eiwitten op te nemen om eieren aan te maken (Högstedt 1974).

De vraag of het vroeger uitkomen van de eieren ook repercussies heeft voor de kuikens komt aan de orde in de hoofdstukken 4 en 8.

Hoofdstuk 3. Broedsucces van weidevogels

A.J. Beintema & G.J.D.M. Müskens

In de loop van de jaren kon een groot aantal gegevens verkregen worden over lotgevallen van weidevogelnesten. Uitkomstsucces van weidevogelnesten werd bepaald met de methode van Mayfield (1961, 1975), waarbij de overleving van nesten wordt uitgedrukt als een dagelijkse overlevingskans. Aan de hand van deze kans kan het uiteindelijk broedsucces geschat worden. Het voordeel van deze methode is dat men niet afhankelijk is van het bebroedingsstadium op het moment dat een nest voor het eerst wordt aangetroffen. Ook kunnen afzonderlijke overlevingskansen bepaald worden voor verschillende verliesoorzaken. De belangrijkste verliesoorzaken zijn predatie en vertrapping door vee.

Dagelijkse overlevingskansen ten aanzien van predatie konden bepaald worden voor 17 vogelsoorten. Soorten die hun nest verstoppen in hoog gras, lijden minder verlies door predatie dan soorten met open nesten. Vooral prederende vogels die vanuit de lucht op zichtwaarnemingen moeten vertrouwen, zullen de verborgen nesten minder goed kunnen vinden. Voor alle soorten geldt dat de nesten tijdens de leg zwaardere verliezen te verduren hebben dan tijdens het broeden. Hier speelt een rol dat onvolledige legsels vaker onbeschermd achtergelaten worden. De predatiedruk is niet gelijkelijk over het seizoen verdeeld. Vroeg in het voorjaar is de predatiedruk het hoogst, maar ook aan het eind van het seizoen neemt de predatie weer toe. Voor Scholekster, Kievit, Grutto en Tureluur geldt dat de perioden met de minste predatie samenvallen. Dit kan deels een gevolg zijn van het feit dat vogelpredatoren dan zelf jongen hebben en daardoor, hoewel ze meer voedsel nodig hebben, een minder grote actieradius hebben. Er kan echter ook sprake zijn van 'swamping', waarbij bij gelijkblijvende absolute predatiedruk de overlevingskans voor elk individueel nest verhoogd wordt door het grote totale aanbod aan nesten. De predatiedruk verschilt van jaar tot jaar. Vooral in jaren volgend op de periodieke ineenstorting van veldmuizenpopulaties is de predatie op nesten zwaar. In dit opzicht zullen de kleine zoogdieren (Wezel, Hermelijn) een belangrijke rol spelen.

Vertrapping door vee is ook uitgedrukt als dagelijkse overlevingskans, maar dan in een gestandaardiseerde vorm, waarbij het 'vertrappingsgetal' de kans geeft dat een nest één dag beweiding overleeft bij een veedichtheid van één dier per hectare. Bij hogere veedichtheden komt het aantal dieren per hectare daar als exponent boven te staan. Hieraan ligt de veronderstelling ten grondslag dat vee zich willekeurig verplaatst. Deze veronderstelling is in principe niet juist, maar de waarnemingen wijzen uit dat het uitgaan van een standaardvertrappingsgetal een voldoende nauwkeurige benadering geeft. Bij gelijke inscharingsdichtheid geeft jongvee de hoogste vertrappingsverliezen. Melkvee vertrapt ongeveer de helft minder en schapen nog veel minder. Bij gelijke beweidingsdruk (uitgedrukt in grootvee-eenheden per ha) wordt door jongvee ongeveer viermaal zoveel vertrapt als door melkvee. Het effect van begrazing door schapen komt dan tussen dat van jongvee en melkvee in te liggen. De vogels kunnen weinig tegen vertrapping ondernemen. Alleen zeer agressieve Scholeksters en Kieviten zijn een enkele maal in staat de koers van een grazend dier te laten wijzigen.

Met behulp van de dagelijkse overlevingskans van nesten ten aanzien van predatie in combinatie met standaardvertrappingsgetallen is het mogelijk voor ieder beweidingsregime de uiteindelijk kans op uitkomstsucces te berekenen. Daartoe is een simulatiemodel ontwikkeld, waarin ook maaidata (overlevingskans nul) kunnen worden opgenomen en waarin rekening wordt gehouden met het optreden van vervolglegsels als de vogels hun nest vroegtijdig verloren hebben. Door gebruik te maken van graslandgebruikskalenders kunnen met dit model de effecten van verschillende beheersregimes vergeleken worden.

Hoofdstuk 4. Groei van weidevogelkuikens

A.J. Beintema & G.H. Visser

Groei van kuikens werd gemeten in gevangenschap en in het veld. In het veld werd gebruik gemaakt van terugvangsten van kuikens die op hun geboortedag in het nest geringd waren. Voor een aantal groeiparameters worden groeicurven gepresenteerd, voor Kievit, Grutto en Tureluur. Om deze onderling te kunnen vergelijken, werd voor al deze curven de Gompertz groeicoëfficiënt berekend. Gemiddeld groeien kuikens in gevangenschap sneller dan in het veld. Dit is vooral het geval bij de Kievit. In het veld blijkt de groei vaak enige vertraging op te lopen. Dit is het gevolg van het feit dat de onderzochte soorten nestvlieders zijn, waarbij de kuikens zelf hun voedsel moeten verzamelen, terwijl ze nog niet in staat zijn hun lichaamstemperatuur op peil te houden. Bij koud of nat weer moeten de kuikens veelvuldig door de ouders opgewarmd worden. Er kan dan te weinig tijd overblijven om voldoende voedsel op te nemen. Hierop wordt uitvoeriger ingegaan in hoofdstuk 5. Groeivertraging treedt bij de Kievit tot latere leeftijd op dan bij de Grutto, omdat Kieviten er langer over doen om een effectieve temperatuurregulatie te ontwikkelen. Voor kleine kuikens kan aangenaam foerageerweer gedefinieerd worden als droog weer tussen zonsopgang en zonsondergang bij een temperatuur van 15°C of hoger. Bij de meeste weidevogelsoorten valt het begin van het geboorteseizoen ongeveer in de tijd dat het aantal 'aangename uren' per dag plotseling sterk toeneemt. Alleen bij de Kievit is sprake van een vroege periode waarin waarschijnlijk veel kuikens door koud weer in de problemen raken. Dit kan mede een gevolg zijn van de kunstmatig in de hand gewerkte broedseizoenvervroeging (hoofdstuk 2).

De groeicoëfficiënten van de weidevogelsoorten worden vergeleken met die van andere steltlopers. Plevieren (Charadriidae) blijken over het algemeen iets langzamer te groeien dan strandloperachtigen (Scolopacidae). Verschillen in groeisnelheid kunnen verband houden met verschillen in opgroeistrategie onder verschillende klimatologische omstandigheden. Daarbij kunnen ook zoögeografische aspecten een rol spelen.

Ten behoeve van de praktijk worden nomogrammen gepresenteerd, die gebruikt kunnen worden om van in het veld gevangen weidevogelkuikens aan de hand van de snavellengte de leeftijd te schatten.

Hoofdstuk 5. De invloed van weer op tijdsbesteding en ontwikkeling van weidevogelkuikens

A.J. Beintema & G.H. Visser

Kleine kuikens van nestvlieders moeten zelf hun voedsel bijeenzoeken, maar ze zijn niet in staat hun lichaamstemperatuur op peil te houden. Tijdens het voedselzoeken koelen ze af, zodat ze op gezette tijden door een van de ouders opgewarmd moeten worden. De tijdsindeling van een kuiken bestaat dan ook in hoofdzaak uit een afwisseling van perioden waarin ze vrij rondlopen om voedsel te zoeken en perioden waarin zij onder de veren van een ouder verblijven. De lengte van foerageer- en opwarmperioden varieert met de buitentemperatuur. Hoe kouder het is, hoe korter de foerageerperioden en hoe langer de opwarmperioden zijn. Boven een bepaalde drempeltemperatuur behoeft het kuiken in het geheel geen externe verwarming. Neerslag leidt tot een extra verkorting van de foerageerperioden en een verhoging van de drempeltemperatuur. Het deel van de tijd dat een kuiken aan voedselzoeken kan besteden neemt toe met de leeftijd, omdat het kuiken dan meer eigen warmte kan produceren. Daardoor worden de foerageerperioden langer, de opwarmperioden korter en de drempeltemperatuur waarboven geen verwarming meer nodig is wordt lager. Als gevolg daarvan is bij Gruttokuikens al na een dag of negen geen opwarmen meer tijdens de daglichtperiode waar te nemen. Kievitkuikens ontwikkelen zich aanzienlijk langzamer en worden tot een leeftijd van ca drie weken nog geregeld door een ouder opgewarmd. De ontwikkeling van Tureluurkuikens is vrijwel identiek aan die van Gruttokuikens. Onder slechte weersomstandigheden kan het voorkomen dat een kuiken zo weinig tijd overhoudt om voedsel te zoeken dat groeivertraging optreedt. Bij aanhoudend slecht weer kan zo verhoogde sterfte optreden. Kuikens komen dan niet om van de kou, maar verhongeren. Kievitkuikens lopen door hun tragere ontwikkeling langer risico's wat het weer betreft dan Grutto- en Tureluurkuikens.

Uit de gegevens is een rekenmodel afgeleid waarmee de beschikbare foerageertijd voor een kuiken berekend kan worden, uitgaande van de leeftijd van het kuiken en de weersomstandigheden (temperatuur en neerslag).

Hoofdstuk 6. Voedselecologie van weidevogelkuikens

A.J. Beintema, J.B. Thissen, D. Tensen & G.H. Visser

De kuikens van nestvlieders verzamelen hun eigen voedsel. Ze zijn daarom aangewezen op bovengrondse fauna, die op de bodem of in de vegetatie leeft. Alleen Scholeksterkuikens worden door hun ouders gevoerd en kunnen zodoende de rijke ondergrondse fauna benutten, die buiten het bereik van de korte snavels van de andere kuikens leeft.

Aan de hand van faecesanalyses werd het dieet bestudeerd van kuikens van Kievit, Grutto, Tureluur, Kemphaan en Scholekster. Faeces werden verzameld tijdens het ringen van kuikens. Bij kuikens in gevangenschap, die afgepaste hoeveelheden van goed herkenbare insekten kregen, werd vastgesteld dat het voedsel maar een paar uur in het darmkanaal blijft. Dat betekent dat in het veld verzamelde faecesmonsters in de regel een beeld geven van de voedselkeuze van een kuiken binnen het aanbod in de directe omgeving van de vangplaats.

Kievitkuikens verzamelen in hoofdzaak ongewervelden die op of vlak boven de bodem leven. Het dieet bevat veel loopkevers. Daarnaast graven zij in halfverteerde koeievlaaien naar mestkevers en larven van wapenvliegen. Gruttokuikens zijn veel actiever in hun gedrag en jagen op insekten die zich hogerop in de vegetatie bevinden. Hun dieet bevat dan ook meer vliegende insekten. De kuikens van Tureluur en Kemphaan nemen een tussenpositie in. Scholeksterkuikens worden door hun ouders gevoerd met emelten en regenwormen.

Om een indruk te krijgen van het voedselaanbod voor kuikens, werd de graslandfauna bemonsterd. Tot eind mei neemt het aantal arthropoden in het grasland sterk toe. In juni kan weer een daling optreden. De samenstelling van het dieet wordt niet alleen door de voedselkeuze bepaald, maar ook door het aanbod. Veranderingen in het dieet in de loop van het seizoen en verschillen (binnen één vogelsoort) tussen gebieden en biotopen kunnen in hoofdzaak verklaard worden door verschillen in voedselaanbod. De verschillen tussen de dieten van weidevogelsoorten worden bepaald door gedrag (Kievit versus Grutto), het al of niet door de ouders gevoerd worden (Scholekster versus andere soorten) en de plek van voorkomen: de Kemphaan vertoont het meest gevarieerde dieet, maar dit wordt waarschijnlijk in hoofdzaak bepaald door het terreintype waar deze soort nog aangetroffen kan worden.

Hoewel het insektenaanbod niet voor juni begint te dalen, is bij de kuikens al vanaf half mei verminderde groei te constateren. Een hypothese is dat de kuikens om energetische redenen niet in staat zijn geheel op insekten op te groeien, maar dat ze noodgedwongen voor het vliegvlug worden moeten omschakelen op grotere, energierijkere prooien: regenwormen. Later in het seizoen zou deze omschakeling steeds moeilijker worden, naarmate de wormen zich in de uitdrogende grond steeds dieper terugtrekken. Dit probleem kan zich vooral in droge voorjaren voordoen. Het effect zal versterkt worden door ontwatering en verbeterde drainage.

Ook de bemestingsgraad van het grasland speelt een rol. Deze is van invloed op de gemiddelde prooigrootte. Bij een hogere bemestingsgraad worden de prooien kleiner en zal een omschakeling op regenwormen eerder noodzakelijk zijn.

Hoofdstuk 7. Een conditie-index voor weidevogelkuikens

A.J. Beintema

Groei van weidevogelkuikens wordt in belangrijke mate bepaald door de mogelijkheden om aan voldoende voedsel te komen. Als onvoldoende voedsel opgenomen kan worden, treedt groeivertraging op. Snavellengte en lichaamsgewicht reageren verschillend op groeivertraging en op herstel daarna. Daardoor is het mogelijk uit de verhouding tussen snavellengte en gewicht een conditie-index af te leiden. Conditie-index $CI = OW/EW$, waarbij OW het waargenomen gewicht en EW het verwachte gewicht is behorende bij de waargenomen snavellengte. Gestandaardiseerde verwachte gewichten voor iedere snavellengte worden gepresenteerd voor Kievit, Grutto, Tureluur en Scholekster. Jaarlijkse fluctuaties in gemiddelde CI zijn gecorreleerd met de totale regenval over de maand mei. Omdat jaarlijkse fluctuaties in de overlevingskans van kievitkuikens eveneens gecorreleerd zijn met regenval in mei (hoofdstuk 8), is het aannemelijk dat CI van invloed is op deze overlevingskans.

Hoofdstuk 8. Overleving tijdens de kuikenfase

A.J. Beintema

Van 1976 t/m 1985 is van enige tienduizenden kuikens van Kievit, Grutto, Tureluur en Scholekster de leeftijd bepaald op het moment dat zij door een ringer werden gevangen. Aan dit project werd meegewerkt door een groot aantal vrijwilligers (ringers). De leeftijd werd geschat aan de hand van de snavellengte. Uit de geschatte leeftijden werden alle geboortedata teruggerekend. De verdeling van de geboortedata over het seizoen verschilt vooral bij de Kievit sterk tussen Friesland en de rest van Nederland. Het rapen van kievitseieren leidt tot synchronisatie in het uitkomen van de eieren. Deze synchronisatie wordt nog versterkt door nazorgactiviteiten, waardoor veel kievitnesten uitkomen en er dus weinig vervolglegsels laat in het seizoen optreden. Ondanks de vertraagde start komt zodoende de mediane uitkomstdatum in Friesland gemiddeld een dag eerder te liggen dan in de rest van Nederland. In mindere mate is een soortgelijke synchronisatie bij de andere soorten te zien. Met het toenemen van de leeftijd neemt de kans toe om na het vliegvlug worden teruggemeld te worden. Uit leeftijdspecifieke terugmeldingpercentages kon een schatting gemaakt worden van de dagelijkse kans op overleving van de kuikens en van de totale opgroeikans. Bij de Kievit is het opgroeisucces over een heel seizoen gecorreleerd met de totale regenval in de maand mei. Vroege kuikens en late kuikens blijken over het algemeen slechter te overleven dan kuikens die in het midden van het seizoen geboren worden. De kuikens die in het tweede kwart van de geboortedataverdeling vallen (tussen de 25ste en de 50ste percentiel), lijken de beste kansen te hebben om te overleven. Vooral voor de eerste helft van het seizoen geldt dat de opgroeikansen in natte voorjaren beter zijn dan in droge.

OVER DE GRENZEN

De weidevogelproblematiek stopt niet bij onze landsgrenzen, aangezien we te maken hebben met trekvogels die een belangrijk deel van hun jaarcyclus buiten Nederland doorbrengen. Ook studies naar trek en overwintering van weidevogels zijn in belangrijke mate gestuurd door vragen die van buitenaf op het Rijksinstituut voor Natuurbeheer zijn afgekomen. Dit geldt onder meer voor studies naar de trekgewoonten van de Zomertaling en de Watersnip, naar aanleiding van vragen vanuit de toenmalige Directie Faunabeheer, die verband hielden met voorstellen tot wijzigingen van de Jachtwet (Beintema & Müskens 1978, 1981b, 1983).

Uit internationaal oogpunt is de Grutto onze belangrijkste weidevogelsoort. Grutto's trekken naar West-Afrika, evenals een aantal andere belangrijke karakteristieke Nederlandse broedvogels. Dit is aanleiding geweest voor het Wereld Natuur Fonds om in 1982 de actie 'Spaar de Trekvogels' te starten, waarbij de Grutto een van de doelsoorten was. In dat kader is een hele reeks onderzoekingen van start gegaan, te beginnen met een analyse van de beschikbare ringgegevens (Beintema & Drost 1986), uitmondend in een serie expedities naar de overwinteringsgebieden in West-Afrika en doortrekgebieden in Noord-Afrika en Zuid-Europa, in samenwerking met instituten uit Duitsland, Frankrijk en Italië (Altenburg & Van der Kamp 1985, Altenburg et al. 1985, 1986, Beintema 1986b, 1988b, 1989, Beintema et al. 1987).

Op grond van de overeenkomstige problematiek in West-Afrika hebben de gruttostudies op hun beurt geleid tot een uitvoerige analyse van de beschikbare ringgegevens van de Kemphaan (Van Dinteren 1989).

WEIDEVOGELBEHEER IN NEDERLAND

Weidevogelbeheer in Nederland kent verschillende vormen. Vroeger waren weidevogels gewoon een nevenprodukt van normale agrarische bedrijfsvoering, maar in de laatste decennia hebben de vogels de modernisering in de landbouw niet meer kunnen bijhouden, zodat in toenemende mate een kloof is ontstaan tussen de belangen van de boeren en de weidevogels (Beintema 1983d, 1988a). In de plantenwereld hebben we hetzelfde verschijnsel gezien: blauwgraslanden en andere orchideeënrijke graslanden waren vroeger ook gewoon een nevenprodukt van het boerenbedrijf, maar met toenemende bemesting, vooral na de introductie van kunstmest, zijn dit soort graslanden met uitzondering van enkele reservaatjes uit Nederland verdwenen.

De oudste, en aanvankelijk meest logische vorm van weidevogelbeheer was het instellen van reservaten. Het beheer van weidevogelreservaten is in principe niet moeilijk en komt in feite neer op het imiteren van ouderwetse vormen van agrarisch beheer, met een combinatie van slechte ontwatering, een laag bemestingsniveau, lage inscharingsdichtheden van vee en late maaidata (Beintema 1975, 1983a, 1983b). In de jaren zeventig kwam voor het eerst naar voren dat intensivering van het weidebedrijf op zo'n grote schaal zou plaatsvinden dat achteruitgang van weidevogels nooit alleen met reservaten tegengegaan zou kunnen worden. Er werd gezocht naar mogelijkheden ook buiten reservaten regelingen te treffen. Er ontstond zelfs een stroming die zich geheel tegen het instellen van reservaten kantte en propageerde dat instandhouding van weidevogels alleen mogelijk zou zijn door op landelijke schaal grenzen te stellen aan de mate van intensivering. Het instellen van reservaten zou een dergelijke ontwikkeling in de weg staan. De waarheid ligt uiteraard in het midden. Voor de meest kritische soorten blijven reservaten noodzaak, daarbuiten zullen zij weinig kansen hebben. Voor de minder kritische, algemene soorten zullen de reservaten altijd onvoldoende opvangmogelijkheden bieden en zullen regelingen buiten reservaten een oplossing moeten bieden. Een betere onderbouwing van de verschillen tussen 'kritische' en 'niet-kritische' weidevogelsoorten heeft bijgedragen tot dit inzicht (Beintema 1983c, 1984).

Weidevogelbeheer buiten reservaten vindt thans in hoofdzaak plaats in het kader van de Relatienota. Om aanwijzing van geschikte gebieden mogelijk te maken waren landelijke karteringen van weidevogelgebieden noodzakelijk. Het eerste landelijke beeld werd gegeven op de zogenaamde 'Bolwerkkaarten'. Los van de discussies over voor en tegen van milieukarteringen, die zich vooral in de jaren zeventig afspeelden (Meelis & Ter Keurs 1976), hebben deze kaarten hun verdienste gehad als basis voor het latere Relatienotabeleid. Soortgelijke kaarten hebben we in een opeenvolging van Nota's Ruimtelijke Ordening en Structuurschema's Landelijk Gebied bij herhaling teruggezien, waarbij opvalt dat het areaal aan aangeduid weidevogelgebied voortdurend is gekrompen. Dit heeft niet zozeer te maken met een werkelijke vermindering van de gebieden waar weidevogels voorkomen (Beintema 1979), als wel met dalend optimisme over (landbouw)economische haalbaarheid. In uiterste vorm zien we dat in het Natuurbeleidsplan, waar de voor weidevogels van belang zijnde graslanden, voor zover ze buiten de Relatienotagebieden vallen, opeens nagenoeg geheel van de kaart geveegd zijn.

Heeft het weidevogelbeheer in Nederland een toekomst? De hierboven geschetste ontwikkeling geeft weinig reden tot optimisme. Toch zijn er ook positieve ontwikkelingen. Aanvankelijk was er vanuit de natuurbescherming grote scepsis ten opzichte van het effect van de Relatienota. Inmiddels blijkt dat in regio's waar op grote schaal beheersovereenkomsten gesloten zijn, sprake is van stabilisering of zelfs herstel van weidevogelpopulaties. Er is niet alleen sprake van een betere acceptatie van het instrument Relatienota in natuurbeschermingskringen, maar omgekeerd geldt ook dat in landbouwkringen de betekenis van het instrument Reservaat beter op waarde wordt geschat, nu wordt ingezien dat Relatienotabeheer en reservaatbeheer elkaar aanvullen (Beintema & Rijk 1988, 1989). Ook vanuit de landbouw is aanvankelijk zeer sceptisch tegen de Relatienota aangekeken. Inmiddels is de eerste contractperiode op veel plaatsen al verstreken, waarbij blijkt dat de overgrote meerderheid van de deelnemende boeren de overeenkomst wenst te verlengen.

De verwachting is dat de weidevogelpopulaties in Nederland op veel plaatsen nog een verdere achteruitgang te zien zullen geven en dat we de kritische soorten in de toekomst alleen in reservaten kunnen zien. Toch is er, uitgaande van de situatie in de broedgebieden, een basis om te geloven dat stabiele weidevogelpopulaties in Nederland (zij het dan op een lager niveau) gehandhaafd kunnen worden. De situatie van 'onze weidevogels' in hun overwinteringsgebieden zal echter in de toekomst meer aandacht vragen.

SAMENWERKINGSVERBANDEN

De eerste fase van het weidevogelonderzoek heeft zich afgespeeld in samenwerking met de Landinrichtingsdienst (toen Cultuurtechnische Dienst) in de provincie Friesland. Het broedsuccesonderzoek is in belangrijke mate gestimuleerd door de Directie Beheer Landbouwgronden, die in verband met het opstellen van regels voor beheersovereenkomsten in het kader van de Relatienota vooral behoefte had aan gegevens over vertrapping door vee (Beintema et al. 1982). Een deel van het weidevogelonderzoek, dat in het kader van het COAL-onderzoek (Coördinatie Onderzoek Aangepaste Landbouw) in Waterland is uitgevoerd en waarin vooral de Directie Beheer Landbouwgronden een grote rol heeft gespeeld, valt buiten het kader van dit proefschrift (Beintema et al. 1983, Buker et al. 1984, De Boer 1990). Onder auspiciën van de Nederlandse Raad voor Landbouwkundig Onderzoek (NRLO) is in 1981 de Contactcommissie Weidevogelonderzoek in het leven geroepen, waarin diverse instituten en instellingen (uit het Ministerie van Landbouw, Universiteiten, provinciale instellingen en particulier) die zich met weidevogelonderzoek bezighouden, hun activiteiten op elkaar hebben afgestemd en informatie hebben uitgewisseld. De activiteiten van deze commissie hebben geleid tot het uitbrengen van een naslagwerk dat een volledig overzicht geeft van al het in Nederland uitgevoerde weidevogelonderzoek tot en met 1985 (Verstrael 1987). Naast deze geformaliseerde verbanden is op bilaterale basis samengewerkt met diverse universitaire en andere onderwijsinstellingen (Van Dinteren 1989, Van Paassen 1980, 1981, Tensen 1984, Veldman 1982, Visser 1983, De Weijer 1976, Van der Werf 1974, Van der Zande 1974).

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Chapter 1

Man-made polders in the Netherlands: a traditional habitat for shorebirds.

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Man-made Polders in the Netherlands: a Traditional Habitat for Shorebirds

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Abstract.—The typical traditional Dutch grassland polder is a flat, open space, cut into squares by a maze of ditches and canals. It has a high water table and sometimes even winter inundations, hence no trees or buildings, which are found along the edges. Owing to a rare combination of soil, climate, hydrology, and management, these moist but fertile artificial prairies hold high densities (up to over 100 pairs/km^2) of six species of shorebirds, known as 'meadow birds.' This situation is now being changed with improved drainage, increased fertilization, earlier mowing, and higher cattle densities. Meadow-bird reserves can be recreated by imitating traditional methods and by keeping high water tables using dams and sluices. Meadow-bird management can be encouraged, for example, by financial compensation to private farmers for late mowing. Technically, we know how our meadow-bird populations can be preserved and managed; keeping them is mostly a political and financial matter. Despite some examples of very successful meadow reserves, Dutch meadow-bird populations are steadily declining.

Key words.—Agriculture, Netherlands, marshes, meadow, shorebirds, wetland.

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Grasslands are constantly changing all over the world. On the one hand grasslands are converted into arable fields by plowing or into deserts by overgrazing them. On the other hand, new grasslands are created by draining moors and marshes or by clearing wooded areas in favor of grazing cattle. Consequently, grassland avifaunas change. Destruction of prairies in the northern United States resulted in a dramatic reduction in numbers of the Marbled Godwit (*Limosa fedoa*) and the Upland Sandpiper (*Bartramia longicauda*) (Ryan 1982, Kirsch and Higgins 1976).

In Europe, destruction of most natural grasslands started too long ago to estimate ornithological consequences. The relics of European steppes and puztas still hold populations of e.g. Lapwings (*Vanellus vanellus*) and Black-tailed Godwits (*Limosa limosa*), but nowadays these species are more generally found in other habitats. Following deforestation and agricultural developments, they have considerably expanded their ranges in Europe in historic times (Glutz et al. 1975, 1977), and they are still doing so in Finland (Hilden 1983).

Not all shorebirds take so easily to the human steppe. In sharp contrast to the ubiquitous Lapwing, its close relative the Golden Plover (*Pluvialis apricaria*) has practically disappeared from the Central European moorlands as a probable result of habitat destruction. (It is still common on northern tundras). But even in this species, surprises are possible. In Western Germany, moorlands are being exploited by peat-digging companies. Until recently, this has caused a steep decline in Golden Plover numbers. Peat bogs to be exploited are first drained, then the top layer with all vegetation is removed. The bog is left bare for one or two years before the actual digging starts, and during this time a very thin vegetation is formed, mainly of common sorrel (*Rumex acetosella*). In recent years Golden Plovers have increasingly taken to nesting on these barren fields (Glutz et al. 1975, O.A.G. Münster pers. comm).

A similar, totally unexpected accommodation has been found in the Dotterel (*Charadrius morinellus*), a bird of tundra and high moorlands often thought to be even more delicate in its habitat choice than the Golden Plover. In the early sixties, Dotterels were found nesting below sea level in newly reclaimed polders in The Netherlands (Marra 1965, Sollie 1961), on bare soil, with only a sparse vegetation emerging from crops like beetroot and peas (Teixera 1979).

Although in North American prairie regions most shorebirds have shown little accommodation to human influence, there are some exceptions. The Killdeer (*Charadrius vociferus*) not only nests in all sorts of agricultural fields but has even taken to rooftop breeding (Demaree 1975, Wass 1974). After a period of decline, the Upland Sandpiper is now showing the first signs of accommodation to agriculture, as it is increasingly found nesting in alfalfa fields in the northeastern U.S. (Kirsch and Higgins 1976). The Marbled Godwit is still very much a bird of natural prairie in the western part of its range, but in the eastern part (Minnesota, Manitoba) it is commonly seen in intensively grazed and fertilized grasslands, in situations very much resembling the occurrence of the Black-tailed Godwit in western Europe. Small numbers of Marbled Godwits have even started to nest in stubble fields (Higgins 1975, Ryan 1982).

In recent years rooftop breeding has become a new fashion in The Netherlands in the Oystercatcher (*Haematopus ostralegus*) (Teixeira 1979) and the Little Ringed Plover (*Charadrius dubius*) (Anonymous 1983).

STUDY AREAS

Accommodation of shorebirds nesting in artificial agricultural grasslands is well developed in The Netherlands (Beintema 1975, 1983c, Glutz et al. 1975, 1977). Especially in the western and northern provinces large areas of grassland polders occur that are used for dairy farming. A Dutch polder is not always a reclaimed part of the sea or a lake. Many grassland polders have been formed by a gradual process of cultivation of marshy habitats, resulting in an area surrounded by a dike to keep excess water out and cut up by a maze of ditches and canals to drain fields and regulate waterflow towards a sluice or pumping device (windmills).

Some grassland polders in the western part of The Netherlands originate from peatbogs, which were drained in the Middle Ages by a system of ditches, to grow buckwheat crops. The bogs were relatively high above sea level, so excess water could simply flow off. Drainage led to a continuous settling of the soil. Then drainage systems repeatedly had to be adapted, until, over the ages, a level was reached beyond which no further drainage was possible with available techniques. Buckwheat growing ceased, and the only further use of the wetland was grazing (Van Braam et al. 1970).

In the northern part of the country, and around the former Zuiderzee, polders were formed by simply preventing areas from flooding by unusual high tides through building a protective dike around already existing land. A special combination of soil types is sometimes found where old peat deposits, formed in the past during regression periods of the sea, have been covered with a layer of clay during more recent transgressions. In contrast to peat grasslands, grasslands on clay are very fertile. They attract high densities of farmers, cattle, earthworms, insects, voles, and birds. On such grasslands, especially of the waterlogged type with peat underneath, intensive management during the nesting season is almost impossible, owing to the weakness of the soil. Even on more solid soil types, wet springs, not uncommon in the humid Dutch climate, have the same effect on management. Such temporary restrictions on access for cattle and machines give the birds time to safely hatch and raise families in an area of high biological productivity. In this respect The Netherlands are rather unique. These conditions are only very locally found elsewhere in Europe.

All types of grassland polders share some characteristics related to a traditional struggle against excess water. They have a high water table, which (at least before modern pumping stations were available) may even rise above the surface in winter, making them true wetlands. Wet conditions limit the occurrence of trees and buildings; these are mostly confined to major dikes, natural locations with higher ground (often dilluvial sand hills rising a few metres above peat or clay) or to artificial dwelling mounds. As a result, the traditional, old fashioned polder landscape is open; and the land is divided into small plots by a maze of ditches and canals. Furthermore, during the wet seasons the land is relatively inaccessible, thus leaving it undisturbed for birds.

RESULTS AND DISCUSSION

Meadow-bird Community

In the wet Dutch grasslands a community of birds has developed, collectively known as meadow birds in The Netherlands. Of course, the same species also nest in other countries, but in no other European country have meadow bird communities developed so well as in The Netherlands. Although the grasslands are man-made, they harbor relatively high proportions of European populations of several grassland-dwelling species. The most extreme example is the Black-tailed Godwit; about 90% of the European population nests within the northwestern part of tiny Netherlands (Van Dijk 1983, Mulder 1972). The Dutch meadow-bird community shows a remarkable similarity in species composition to the avifauna of North American prairies, as can be seen from Table 1. This similarity is most striking in the numbers and types of species of duck and shorebirds.

Affinities do not extend to raptors. As Dutch meadows lack the wealth in rodents of the American prairies, raptors are relatively scarce. The only abundant rodent is the field vole (*Microtus arvensis*), on which numerous Kestrels (*Falco tinnunculus*) prey during the nesting season. Also, all larger mammalian grazers and predators are totally absent. The only grazer larger than a vole is the hare (*Lepus europaeus*), and the only common mammalian predators are

Table 1. Comparison of bird use of Dutch meadows and North American prairies.

	The Netherlands	North America
Duck		
Mallard (*Anas platyrhynchos*)	x	x
Northern Shoveler (*Anas clypeata*)	x	x
Northern Pintail (*Anas acuta*)		x
Gadwall (*Anas strepera*)		x
Blue-winged Teal (*Anas discors*)		x
Redhead (*Aythya americana*)		x
Garganey (*Anas querquedula*)	x	
Tufted Duck (*Aythya fuligula*)	x	
Rails and Gallinaceaous Birds		
Yellow Rail (*Coturnicops noveboracensis*)		x
Corncrake (*Crex crex*)	x	
Gray Partridge (*Perdix perdix*)	x	
Quail (*Coturnix coturnix*)	x	
Northern bobwhite (*Colinus virginianus*)		x
Sharp-tailed Grouse (*Tympanuchus phasianellus*)		x
Greater Prairie Chicken (*Tympanuchus cupido*)		x
Shorebirds		
Lapwing (*Vanellus vanellus*)	x	
Oystercatcher (*Haematopus ostralegus*)	x	
Black-tailed Godwit (*Limosa limosa*)	x	
Curlew (*Numenius arquata*)	x	
Redshank (*Tringa totanus*)	x	
Ruff (*Philomachus pugnax*)	x	
Common Snipe (*Gallinago gallinago*)	x	x
Avocet (*Recurvirostra avosetta*)	x	
Killdeer (*Charadrius vociferus*)		x
Mountain Plover (*Charadrius montanus*)		x
Marbled Godwit (*Limosa fedoa*)		x
Long-billed Curlew (*Numenius americanus*)		x
Willet (*Catoptrophorus semipalmatus*)		x
Upland Sandpiper (*Bartramia longicauda*)		x
American Avocet (*Recurvirostra americana*)		x
Wilson's Phalarope (*Phalaropus tricolor*)		x
Songbirds		
Eurasian Skylark (*Alauda arvensis*)	x	
Meadow Pipit (*Anthus pratensis*)	x	
Yellow Wagtail (*Motacilla flava*)	x	
Whinchat *Saxicola rubetra*)	x	
Stonechat (*Saxicola torquata*)	x	
Corn Bunting (*Emberiza calandra*)	x	
Reed Bunting (*Emberiza schoeniclus*)	x	
Horned Lark (*Eremophila alpestris*)		x
Sprague's Pipit (*Anthus spraguei*)		x
Western Meadowlark (*Sturnella neglecta*)		x
Bobolink (*Dolichonyx oryzivorus*)		x
Lark Bunting (*Calamospiza melanocorys*)		x
Clay-coloured Sparrow (*Spizella pallida*)		x
Savannah Sparrow (*Passerculus sandwichensis*)		x
Grasshopper Sparrow *Ammodramus savannarum*)		x
Baird's Sparrow (*Ammodramus bairdii*)		
Chestnut-collared Longspur (*Calcarius ornatus*)		x
McCown's Longspur (*Calcarius mccownii*)		x

small mustelids, which prey on voles, and to a lesser extent on meadow-birds' nests. Predation on birds' nests is heavier than normal in years following a periodic collapse of vole populations (Beintema and Müskens in prep).

Both the Dutch and the American list of shorebirds represent a steep gradient in the amount of water required in the habitat, with Snipe and Phalarope at the wet end and the very different Oystercatcher and Mountain Plover at the dry end.

The central part in the meadow-bird community is formed by a group of six shorebird species: the Oystercatcher, the Lapwing, the Black-tailed Godwit, the

Redshank, the Ruff, and the Snipe. These six species receive most attention in research and in conservation measures, and their noisy presence in high densities is one of the most characteristic features of Dutch meadow-bird land. Often the term 'meadow bird' is reserved for these shorebirds only. Some information on the Dutch populations of these six species is given in Table 2.

Limiting Factors

Meadow-bird community development is a dynamic process. Changes constantly take place, as the grassland management is changing constantly. The change in management most in evidence is the increase in the intensity of farming, through increased fertilization and water control. Farmers always have tried to increase the production of their land, and they probably always will continue to do so. This leads to an increase in biomass on all levels, ranging from soil fauna to cattle (Beintema et al. 1985). Thus, one might expect that this development might lead to a similar, increasing density of adapted shorebirds, and this certainly is what must have happened in the past.

From recent developments, we know that the heavier species have shown the most recent increases. The order in which the six shorebird meadow birds are ranked, according to body weight, is: Snipe, Redshank, Ruff, Lapwing, Godwit, Oystercatcher. Godwits have shown a marked increase in the 1950s (Haverschmidt 1963). Oystercatchers have spread from the coast into the meadow habitat during the last decades (Hulscher 1972), and they are still increasing. A seventh addition to the list is the even heavier Curlew, which has started to increase in intensively used agricultural grasslands as late as the late 1970s (Van den Bergh 1986). This suggests that the smaller birds (left part of the ranked list) have come into the meadow-bird state much longer ago, leading to the hypothesis that explosive meadow-bird development ('meadowbirdification') occurs after a certain threshold of density of edible biomass (worms) has been passed and that the level of this threshold is related to body weight, especially through the requirements of the adult female in the period of egg production (Beintema 1983a).

Table 2. Numbers of breeding pairs (X 1000) of six shorebirds in The Netherlands and four other regions.[1]

	Region				
	NL	BF	CE	NE	GI
Oystercatcher	70	1	13	60	300
Lapwing	170	60	100	350	500
Bl.t. Godwit	100	0.8	10	1	0.1
Redshank	27	0.5	15	90	45
Ruff	1.3	0.01	0.7	170	0.01
Snipe	5.6	0.5	7	300	100
total	374	63	146	971	945
size of area[2]	1	14.2	17.2	28.2	7.7

[1] Regions simplified after Van Dijk (1983): NL = Netherlands, BF = Belgium + France, CE = Central Europe = West Germany + East Germany + Czechoslovakia + Switzerland + Austria + Hungary, NE = Northern Europe = Denmark + Norway + Sweden + Finland, GI = Great Britain + Ireland.

[2] Given as multiples of the size of The Netherlands.

Meadow-bird community development can take place when grasslands on suitable soil are kept moist throughout the nesting season, a condition rarely met with in Europe outside the Dutch polderland. The importance of wet conditions is twofold: first, when the soil dries out too much, the birds have difficulties in finding sufficient food, as the soil fauna retreats. When this is the case (e.g. in an exceptional dry spring), no new clutches are started, and birds which lose their nest to a predator fail to produce a replacement clutch, which they otherwise easily do (Beintema and Müskens in prep). The second, very important effect of wet conditions is a retardation of vegetation development and a late accessibility to the terrain for cattle and heavy machines. This leaves the birds time to safely raise families in this very fertile habitat.

Meadow-bird populations cannot indiscriminately grow with increasing biological production of their habitat, because agricultural intensification also implies an increase of the impact of management itself on nesting success. Two major causes of nest loss are destruction by agricultural machinery (notably mowing), and trampling by cattle. Dutch cattle densities are expressed as number of animals per hectare, and not as number of hectares per animal as in the U.S.A. Overall cattle densities in

Dutch dairy farms nowadays range between three and four animals/ha, but in a rotational grazing system actual densities may reach several dozens per hectare, during a couple of days. Under these circumstances, the probability of a nest surviving one day of grazing is close to zero (Beintema and Müskens in prep). Higher levels of fertilization not only result in higher cattle densities, but, combined with improved drainage, also in an earlier start of grazing (by two weeks over the last 50 years). Similarly, mowing dates have advanced by at least two weeks over the same period. This means that, although the birds have responded with a noticeable advance in laying dates (Beintema et al. 1985), they can no longer nest as quietly and safely as they used to do.

Nest losses are largely compensated by replacement clutches. Lapwings e.g. can be induced to start a new clutch eight times in succession in one nesting season (Klomp 1951, Beintema and Müskens in prep.). Normally, up to 40% of all nests are taken by predators, but as a result of replacement clutches, eventually about 90% of all pairs may achieve hatching success (Beintema and Müskens in prep). When losses due to mowing and trampling are added, one can reason that success can easily be diminished to a level at which the birds simply can no longer produce enough offspring to compensate for adult mortality (Beintema 1983a, Beintema and Müskens in prep). As soon as this is the case, reduction in numbers (and consequently densities) must follow. Theoretically, bird densities can reach their maxima when the intensity of agricultural management is just below the limit beyond which the productivity of the birds is no longer sufficient (Beintema 1983a). This critical limit is different for different bird species. When all parameters determining hatching success (taking replacement clutches into account) are known, one can estimate success under different management schemes by simulation (Beintema 1983a, Beintema and Müskens in prep).

When hatching success is compared to what is needed to compensate for adult mortality, one can compare the bird species' vulnerability to management. When the shorebirds mentioned before (Snipe excluded, as parameters are insufficiently known) are ranked according to decreasing vulnerability to management, the order Ruff — Redshank — Godwit — Lapwing — Oystercatcher is obtained (Beintema 1983a). For these five species one now can define a range of suitable agricultural intensity, between the minimum intensity needed (threshold), and the maximum intensity tolerated. On an arbitrary scale of agricultural intensity, this is illustrated in Figure 1. The order obtained also implies, that the Ruff will be the first one to disappear from the scene when management gets too rough. Indeed Ruff and Redshank have been decreasing in Dutch grasslands for many decades (Beintema 1975, 1983c), the Godwit (still increasing in the fifties) is presently decreasing (Mulder 1972, De Jong and Fabritius 1979); the Lapwing is relatively stable; and the Oystercatcher is still increasing (Hulscher 1972, Alleyn et al. 1971).

Meadow-bird Management

As a highly characteristic element in the Dutch avifauna and in the Dutch landscape, meadow birds have received much attention in research and conservation, especially since the negative influence of agricultural intensification became more evident during the last decades. The international importance of the Dutch populations (and, as a consequence, the international responsibility for them) has now widely been recognized, also by the Dutch Government.

Basically, meadow-bird management is quite simple. Providing that the basic habitat requirements are fulfilled, the only thing to be done is practicing dairy farming in the way Dutch farmers did it some fifty years ago. In fact this has been quite successfully effectuated in a number of strict reserves, specifically designed for meadow birds. From experiences of governmental and non-governmental nature conservancy organizations dealing with such reserves, some simple rules for meadow-bird management have been derived, including maintenance of high water tables, limits on the level of fertilization with preference for natural manure, a ban on mechanical activities (mowing!) between March 15th and June 15th, a limit on cattle densities, and a total ban on the use of pesticides (Beintema 1983b). Management can be performed by the organizations themselves, or the land can be given (under restrictions) to neighbouring farmers for a strongly reduced rent, or even for free.

Theoretically, there is no intensity level of ideal meadow-bird management, as different species respond differently (Fig. 1). From experience of organizations managing meadow-bird habitat, it is known that management aiming at maintenance of the Ruff (least intensive farming and strongest restrictions) gives the greatest variety in the meadow-bird community, even though other species do not reach their maximum densities (e.g. Van Orden et al. 1973). When Dutch grasslands are ranked according to densities of breeding Ruff, the top 10% holds high (not the highest!) densities of all other species. If the same areas are then ranked according to densities of breeding Lapwings, the top 10% holds only low densities of most other species, and no Ruff at all (Beintema 1975). Thus, the Ruff can be used as an indicator for the designation of areas to be managed as meadow-bird reserves.

Meadow-bird management is very expensive. Prices of Dutch grassland mostly range from about HFL 30,000-40,000 per ha (US $12,000-16,000 if 1 US$ = 2.5 HFL), and in some cases even many times more than that. The investments never will be compensated by agricultural production. As the economic gap between meadow-bird farming and modern dairy farming is continuously widening, the implementation of meadow-bird management is becoming increasingly difficult. As a compromise (inducing contradicting protests from both farmers and nature conservationists) the Dutch government has designed a plan, in which about 100,000 ha (5%) of the Dutch grassland can be managed for meadow birds, partly as strict reserves, but mostly (which is much less costly) through voluntary agreements with individual farmers, who then get paid for not doing the things they normally would do. There is a wide variety in the restrictions to be chosen. Accordingly financial compensations range from very little to HFL 1500 per hectare per annum, with an average of about HFL 750.

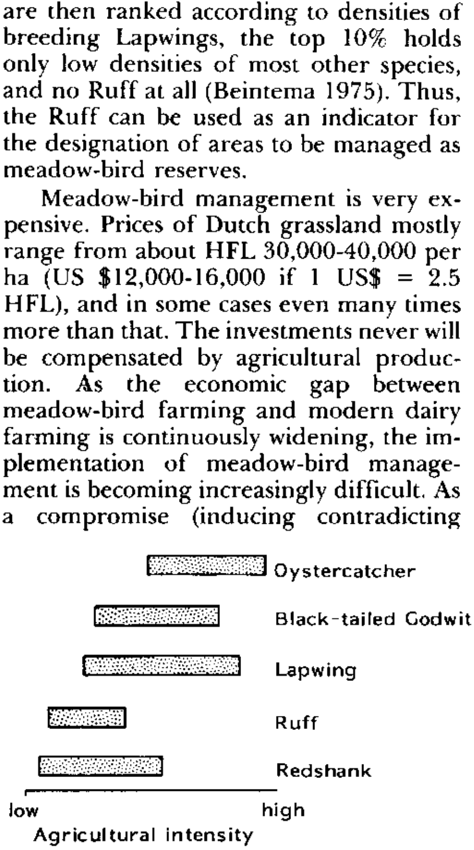

Figure 1. Hypothetical range of tolerance of meadow birds to agricultural intensity (pressure).

So far, only a small proportion of the area designated has come under effective management. There has been opposition from farmers refusing to take part in 'museum farming'. In some areas farmers claim that financial compensations are far from adequate, whereas nature conservationists complain that despite heavy investments the positive effect on the birds is virtually absent. However, in other places farmers find it a comfortable way of making profit from their land, and populations of the less vulnerable species (Lapwing, Godwit, Oystercatcher) are at least stable. For vulnerable species, like the Ruff, the system does not work. Dutch Ruffs will most likely only be found in reserves in the future.

In fact, meadow-bird management is no longer a technical or a biological problem. At present it is mostly a political and economical one. A helpful development could be that within the European Community, farmers (especially the Dutch ones) produce far too large quantities of dairy products, and since 1985 are being forced by regulations (and financial sanctions) to keep their production below certain levels. In practice, this may mean that further increase of cattle densities and other intensifications will no longer be profitable. It is hoped that these, and other developments will help bring solutions to save the unique qualities of the Dutch Prairie in the near future.

ACKNOWLEDGEMENTS

My work at the Research Institute for Nature Management has only been possible with the assistance of a great many helpers in the field during many years, such as assistants, students, and amateur ornithologists.

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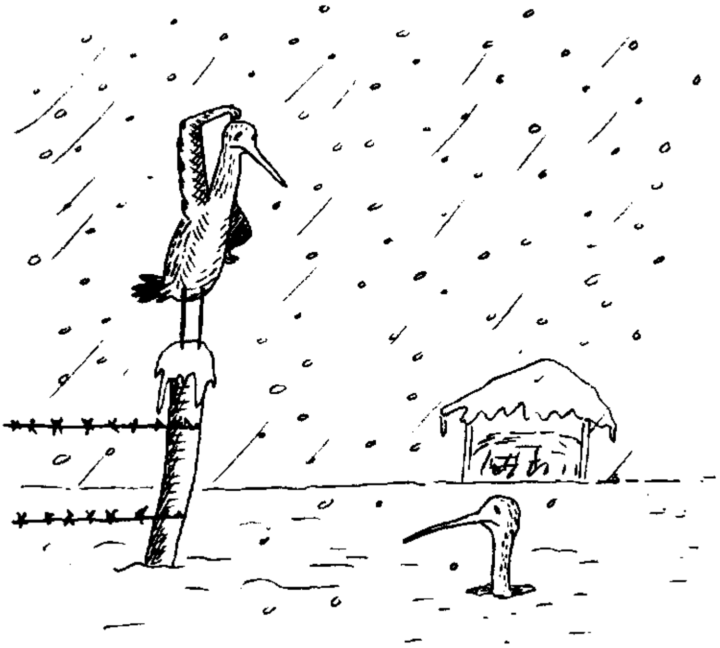
Chapter 2

A shift in the timing of breeding in meadow birds.

A.J. Beintema, R.J. Beintema-Hietbrink & G.J.D.M. Müskens



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A SHIFT IN THE TIMING OF BREEDING IN MEADOW BIRDS

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CONTENTS

1. INTRODUCTION

This paper deals with a recent shift in the timing of breeding in a group of wader species, and some of the possible causes. The species considered, collectively known as "meadow birds" in The Netherlands, are the Oystercatcher *Haematopus ostralegus*, the Lapwing *Vanellus vanellus*, the Black-tailed Godwit *Limosa limosa*, the Redshank *Tringa totanus*, the Snipe *Gallinago gallinago*, and the Ruff *Philomachus pugnax*.

Birds which live in a seasonal environment, face the problem to fit their cycle as well as possible into this seasonality. One of the most obvious examples is the timing of breeding of birds in temperate and colder regions. Nearly all such birds have a rather short, more or less fixed breeding season in spring. It has been postulated that birds tend to synchronize the chick stage with periods of maximum food availability (Lack 1954, 1968), but this may be modified by other demands. For instance, for both Lapwing (Klomp 1951) and Black-tailed Godwit (Van Balen 1959) it is believed that the final limit to the breeding season is set by the onset of moult. Similarly, the start of the season may be modified by the availability of food for the egg-producing female. In a number of species one can artificially advance breeding by supplementary feeding of the female (Drent & Daan 1980). Such species tend just to breed as early as food availability allows (Perrins 1970).

Natural climatic changes, which may lead to entire changes of the habitat, eventually may cause changes in both timing of breeding and breeding distribution. Similar effects can be obtained as a result of man's activities. Man has shown to be able to alter habitats drastically, and in many other ways to influence survival of young birds. In this paper both natural and human influences, which may have an effect on the timing of breeding in meadow birds, will be investigated.

One human activity with an obvious effect on the timing of incubation, is the taking of Lapwing eggs for consumption, which is, with certain restrictions, still allowed in The Netherlands. Especially in the northern part of the country, egging is a national sport, with a long tradition (Brouwer 1954). Although egging only receives minor attention in this paper, it was the question about its influence on Lapwing populations in The Netherlands, posed to the Research Institute for Nature Management in 1974, which initiated this study.

2. METHODS

Direct data to be used in an analysis of historical developments in timing of breeding do not exist. A general picture of the timing of breeding can be obtained by analysing ringing dates of chicks, assuming that these dates are correlated with laying dates. Imboden (1974) used ringing dates of recovered Lapwings to describe and compare the breeding season for many European countries. Ringing data are also very useful to study historical developments, as chicks have been ringed by the thousands in The Netherlands for many decades already. Data from the ringing centre Vogeltrekstation are available from 1911 onwards.

A first analysis was based on the ringing dates of recovered birds, these data being easily available. Data of this kind were presented earlier for the Lapwing (Beintema 1977), but they appeared to be quantitatively insufficient for the earliest years, and for the less numerous species. Therefore, patterns were recalculated on the basis of all original ringing dates, for which all the files of the Vogeltrekstation had to be extracted.

Ringing dates do not exactly reflect laying dates, since the ringing season runs from the first hatching date to the last fledging date. Consequently, the ringing season is about a month longer than the laying (and hatching) season. However, this is no reason for not using the distribution of ringing dates as an indicator for timing, as long as we do not assume major trends in mortality patterns over the years, even though variations in chick mortality are very likely to occur. Also, variations in hatching success give rise to variations in ringing dates, even in situations with identical laying dates. Still, it has to be assumed that a general shift in the timing of breeding inevitably will lead to a general shift in the chick-ringing season, and that a major shift in ringing dates strongly suggests a shift in the timing of breeding.

In order to minimize bias from sources described above, data from successive years were lumped together. The choice of periods was based on three considerations:

1. There is an increase in available data from 1911 onwards, because of increasing ringing activities.
2. There is a shortage of data during and shortly after World War Two.
3. Changes in law, affecting the duration of the Lapwing-egging season became effective in 1937 and 1956 respectively. In 1937 the limit was set at April 19th; in 1956 this was, outside the province of Friesland further advanced to April 12th. In Friesland it remained at the 19th (at present, the limit is April 12th in Friesland, and April 5th in the rest of The Netherlands, but this became effective after this study was undertaken. Closing dates are still further debated).

These considerations led to the choice of the following periods: 1911—1919, 1920—1929, 1930—1936, 1937—1949, 1950—1955, 1956—1959, 1960—1964, 1965—1969, and 1970—1974. The Netherlands were divided into 13 regions: the 11 provinces (excluding Wadden Islands and IJsselmeerpolders), The Wadden Islands, and the IJsselmeerpolders. For each period, each region, and each species, the ringing dates of the chicks were tabulated. Mean and standard deviation of ringing dates were calculated, and to present a more detailed description of the distribution, five percentiles were calculated: 10%, 25%, 50% (median), 75% and 90%.

For recent periods the material for the commoner species became too large to be conveniently handled, so the amount of data used was reduced by skipping parts of the files at regular intervals, in such a way, that within-year distributions were not affected, and good coverage of all years was maintained. For Snipe and Ruff all available material was used. Before 1960, only data for the Lapwing were restricted. Reduction to 50% took place in Oystercatcher and Black-tailed Godwit from 1960 onwards. In recent periods the material of the Lapwing was still further reduced to 20% in the last period. In spite of possible sampling errors the pattern found for the Lapwing was essentially the same as the one calculated earlier from recoveries (Beintema 1977). It is very unlikely that further extension of the material, which is extremely time consuming, would lead to major changes.

The numbers of data used, and the numbers of chicks ringed, are shown in Table 1. Where the numbers of data used were not restricted, there remain differences between these numbers, and the numbers of birds ringed. A small proportion of the birds had always been ringed with aberrant ring sizes. Files with such ring sizes were not extracted.

3. RESULTS

In all species of meadow birds, chicks nowadays are ringed much earlier than in the past, suggesting that all meadow birds tend to breed earlier. This is illustrated in Fig. 1 (In the graphs only the percentiles are shown. Mean and standard deviations of ringing dates are given in Table 2.) Trends are remarkably similar in all regions, with two exceptions. For the Lapwing the data from Friesland, and for the Oystercatcher the data from Zeeland and the Wadden Islands

Table 1. Number of data used for each species and period. WZ = number of data used for Wadden Islands plus Zeeland, F = number of data for Friesland, N = total number of data for The Netherlands. R = total number ringed in The Netherlands. N-F means Netherlands minus Friesland, etc. Numbers ringed up to 1949 are given as one total, separate totals for years only being available from 1941 onward. Note: up to 1959 ringing totals include all age classes (in earlier periods usually not many adults were ringed), separate year totals for pulli and fullgrown birds only being available from 1957 onward; from 1960 onwards only total numbers of ringed pulli are given

[1] 1928—1937 only, [2] 1957—1959 9 pulli only

Period	Oystercatcher				Lapwing				Godwit		Redshank		Snipe		Ruff	
	WZ	N-WZ	N	R	F	N-F	N	R	N	R	N	R	N	R	N	R
1911—19	142	163	305	3426	20	835	855	12847	18	1223	181	1075	19[1]	32	64	381
20—29	581	202	783		15	845	860		77		106				1	
30—36	576	309	885		193	1210	1403		420		297				126	
37—49	463	707	1170		591	1650	2241		582		259				59	
50—55	326	530	856	975	498	891	1389	5512	451	549	173	205	0	21	58	216
56—59	353	326	679	1112	460	1191	1651	5354	566	664	252	375	4	282[2]	130	209
60—64	737	542	1297	2943	440	1528	1968	7457	1066	2362	559	810	16	16	174	216
65—69	895	1001	1896	3483	406	2936	3342	14014	2360	6618	660	1296	84	95	359	400
70—74	562	1283	1845	3842	413	4434	4847	19862	2587	6044	394	1140	77	89	294	330
Total	4635	5063	9698		3036	15520	18556		8127		2881		200		1265	

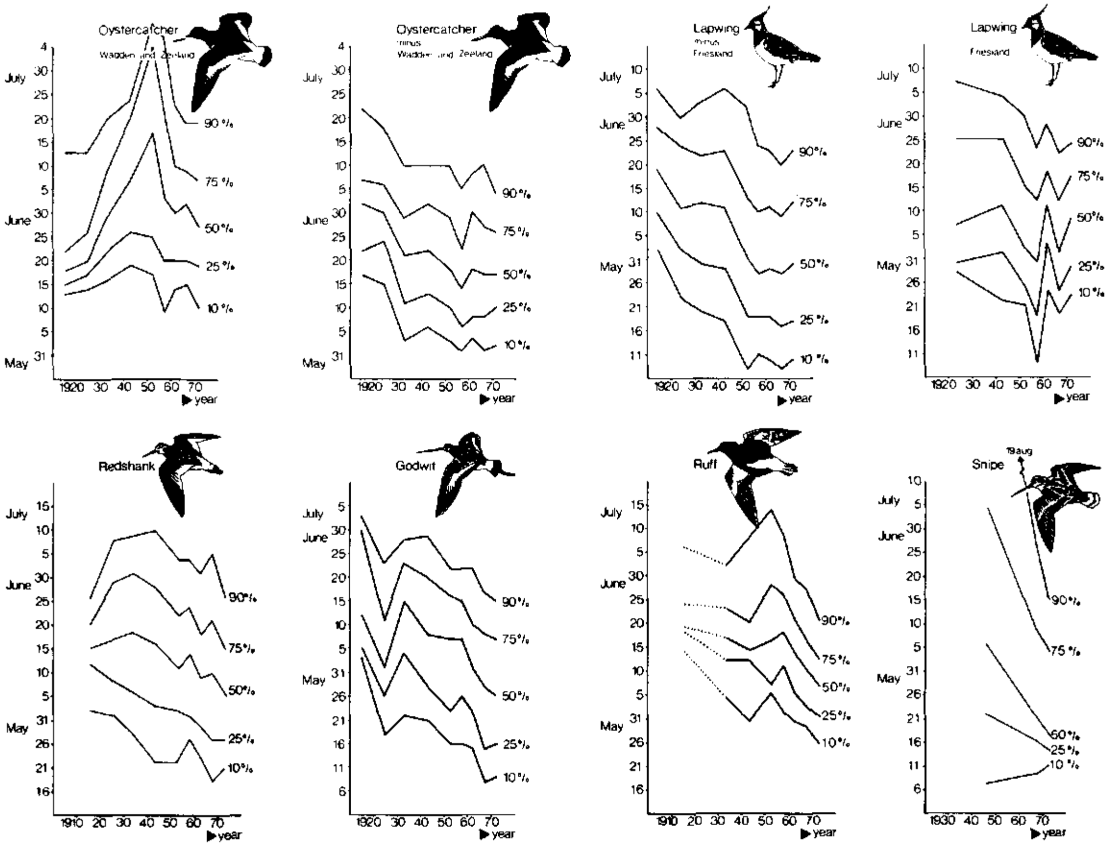

Fig. 1. Percentiles of distribution of ringing dates of chicks of meadow birds in The Netherlands, in 9 periods. For choice of periods see text, for mean and standard deviation see table 2.

differed strongly from the rest of the country. Therefore, these two categories are treated separately, whereas all other regional data are presented combined.

It has been shown earlier (Beintema 1977) that advanced breeding is not likely to be explained by changes in the limit of the egg-taking season, because Redshank, Ruff, and Oystercatcher breed too late in the season to be affected by changes in this limit within the first half of April. Moreover, it has been shown that for the Lapwing the different pattern for Friesland can be explained by the longer egging season, which prevents a further advance in laying (of eggs not taken), although the trend is still visible in the latter half of the season. As a result, Friesland has a markedly shorter chick season than the rest of The Netherlands.

The pattern for the Oystercatcher for the Wadden Islands and Zeeland is as yet hard to explain. Generally speaking, Oystercatchers breed later in these regions, for reasons discussed below, and the dates for the late Fourties and early Fifties are strongly deviating from any of the other patterns. Most of the data come from islands, where especially in early periods, hardly any bird ringer lived. Therefore, the Oystercatchers nesting on the islands might be the only category which was predominantly ringed on holidays. It should be noted that there are several years during and shortly after the Second World War, in which no Oystercatcher chicks at all were ringed until well in mid-summer. A lack of visits to the islands, for political or economic reasons may have caused the pattern observed. For Oystercatchers breeding at

Table 2. Mean ringing dates $\bar{d}$ and standard deviations s (days) for chicks of meadow birds in The Netherlands, for nine periods. (Numbers are given in Table 1.) N = Netherlands, WZ = Wadden Islands plus Zeeland, F = Friesland, N-F means Netherlands minus Friesland, etc.

Period	Oystercatcher				Lapwing				Godwit		Redshank		Ruff	
	WZ		N-WZ		F		N-F		N		N		N	
	$\bar{d}$	s	$\bar{d}$	s	$\bar{d}$	s	$\bar{d}$	s	$\bar{d}$	s	$\bar{d}$	s	$\bar{d}$	s
1911—1919	6/21	14	7/2	14	6/14	17	6/19	13	6/17	13	6/15	10	6/22	8
1920—1929	6/24	14	7/1	12			6/12	16	6/7	17	6/20	16	—	—
1930—1936	7/2	16	6/20	14			6/12	17	6/12	14	6/19	17	6/18	11
1937—1949	7/8	22	6/23	14	6/13	17	6/11	18	6/9	15	6/17	18	6/16	12
1950—1955	7/15	21	6/20	14	6/6	16	6/2	20	6/5	14	6/13	16	6/19	17
1956—1959	7/6	14	6/15	13	5/31	17	6/3	18	6/4	15	6/15	16	6/19	12
1960—1964	7/2	14	6/20	14	6/10	16	5/31	17	6/2	14	6/10	14	6/13	12
1965—1969	7/2	14	6/19	15	6/3	13	5/29	17	5/28	16	6/10	17	6/11	12
1970—1974	6/29	13	6/18	14	6/7	14	5/31	17	5/28	14	6/7	15	6/7	11

the seashore, destructive floods can also be of influence on chick production.

However, it is not the difference, but the similarity between most of the patterns which concerns us most. The phenomenon as a whole calls for an explanation of a general sort, which wil be investigated below.

There are two seemingly obvious, alternative explanations. In the first place, a general warming up of the western European climate for the last decades has been postulated. This could have caused an accelerated start of all processes in spring. Secondly, agricultural activities have been intensified considerably in The Netherlands, over the past decades. Improved drainage and the increasing amount of fertilizers applied lead to an accelerated growth of the grass in spring, and an increase in the production of biomass, including soil fauna. Lowering of the water table leads to a faster warming up of the soil in spring, and a better development of roots of the vegetation. This will already give rise to growth acceleration, but the main effect results from the application of fertilizers.

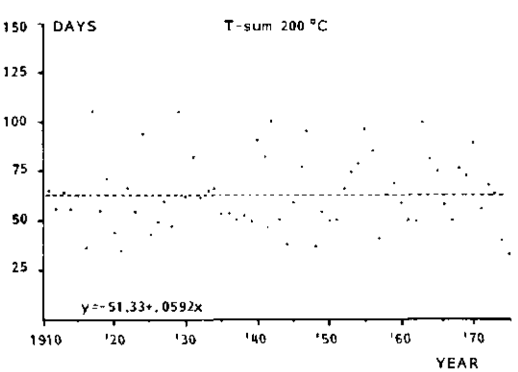

Fig. 2. Day on which T-sum 200 (explanation see text) is reached, in number of days from January 1st onwards, from 1911—1975 (data K.N.M.I. De Bilt). Correlation coefficient = .061; $\bar{y}$ = 63.6, SD = 18.1.

The climate hypothesis will be tested first. As a relevant parameter for the annual development of spring weather conditions the date on which Dutch farmers are advised to apply their first dressing of the season was chosen. This date corresponds with the estimated time when the vegetation accelerates its growth, and is a clear indication of the development of spring weather. The parameter used to estimate the day on which the grass reaches this stage in its physiology, is the temperature sum of 200 ° C (Jagtenberg 1966). T-sum 200 is calculated by adding all average day temperatures from the first of January onwards, discarding all values below zero. This T-sum 200 is reached between the end of February and the beginning of April, depending on the preceding winter conditions.

The day on which T-sum 200 is reached, is given in Fig. 2, from 1911 to 1975, for De Bilt, in the centre of The Netherlands. It can be seen, that whatever climatic changes may have taken place, there is no noticeable systematic shift in this date. Therefore, it seems most unlikely that a shift in timing of breeding in the order of magnitude of two weeks can be attributed to historical changes in spring weather conditions.

Testing the agricultural hypothesis, the amount of fertilizers used in The Netherlands was chosen as the most appropriate parameter.

Fig. 3 shows that there has been a tremendous increase in N-dressing, from the beginning of the century onwards, with the exception of the period 1940—45, when anorganic nitrogen was used for other purposes. It has been shown by various authors, that the mowing date is greatly depending on the N-gift, and that the same is true for the date on which cattle can be allowed to start grazing in the field. At the present level of N-application both mowing and grazing can start approximately two weeks earlier than in situations where no fertilizers are used (Van den Burg 1960, 1961, Jagtenberg 1968). From the combined data of Van den Burg and Jagtenberg the average shift in both mowing and first-grazing date in The Netherlands was estimated, as a function of the national level of N-application, as shown in Fig. 3. The estimated shifts are depicted in Fig. 4, together with the median ringing dates of chicks of the six species concerned. The data in Fig. 4 are not given as a correlation diagram, because it is not only interesting that there is a correlation: the most important feature is that the slopes of the graphs are remarkably similar.

The agricultural explanation is the only one which fits. It may also explain why Oystercatchers in Zeeland and the Wadden Islands breed later than those on the mainland. Firstly, Oystercatchers breeding at the seashore escape agricultural developments. Secondly, the islands have always lagged behind in their agricultural development, as compared to the mainland.

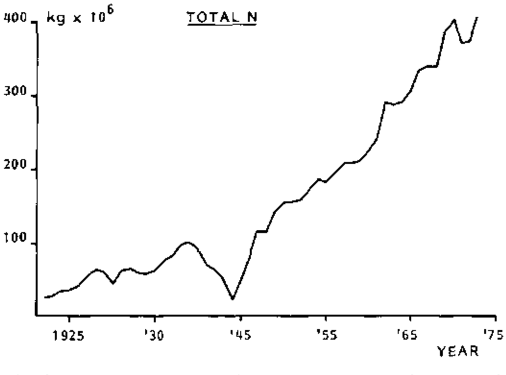

Fig. 3. Total amount of nitrogen applied as fertilizers in The Netherlands (all purposes). After Padmos 1966, Anonymus 1975.

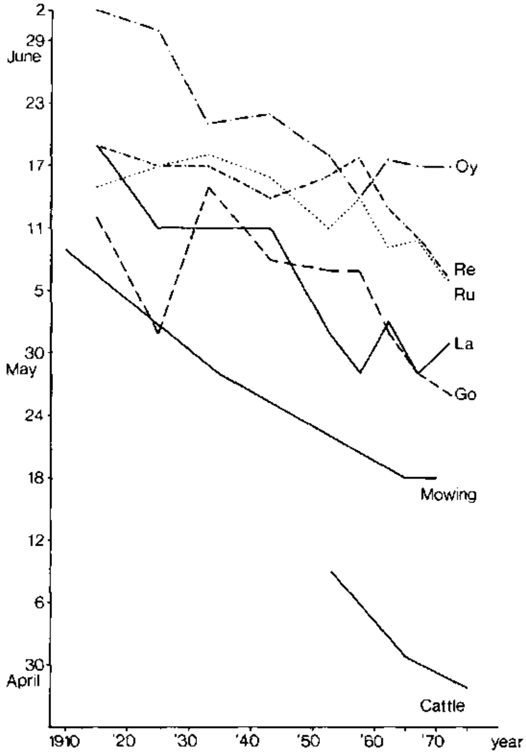

Fig. 4. Development of mean first mowing date and mean first grazing date for cattle (explanation see text) in The Netherlands together with the median ringing dates of chicks of Oystercatcher (Oy), Redshank (Re), Ruff (Ru), Lapwing (La) and Black-tailed Godwit (Go). Mowing and grazing data combined from Anonymus 1975, Van den Burg 1960, 1961, Jagtenberg 1968 and Padmos 1966. Median ringing dates from Fig. 1.

4. DISCUSSION

Two mechanisms could be involved if we assume that agricultural changes have caused the observed phenomenon. Firstly, if all birds breed just as early as they can manage, earlier development of a favourable food situation will lead to earlier egg-production (Perrins 1970). An indication is given by Högstedt (1974), who showed that the number of days elapsing between the date of arrival of the female Lapwing in the territory, and the laying date of the first egg, is strongly negatively correlated with the density of lumbricids in the territory, thus indicating that food supply (soil fertility) can influence the timing of breeding in this species.

The second mechanism which could be involved in the shift of breeding season, is selection through nesting success, assuming that timing of breeding is also genetically determined. There is an increase in agricultural activities, and correspondingly in nest-losses, with progressing time within one spring season (Beintema & Müskens 1981). This would favour early breeding, especially since agricultural activities have increased considerably over the years, due to intensifying of farming, and the effects of fertilizers. Van Noordwijk (1980) predicts that in the Great Tit selection of this kind can produce a shift in laying dates of about two weeks within only a few generations. Evidence for genetical changes may be found in the migration habits of the Black-tailed Godwit. This species not only shows a marked shift in its laying dates, but also in its time of arrival from its African winter quarters (Mulder 1972, Glutz von Blotzheim *et al.* 1977). When changes in Dutch grasslands are mainly caused by farmers, it is unlikely that conditions in these grasslands can be predicted while still in Africa, thus suggesting an internal change.

One interesting difference between the two postulated mechanisms should be noted. The first one operates in the egg production phase, so the shift may lead to unfavourable conditions in the chick stage. Increased chick mortality will of course counteract the mechanism, and put an end to the shift. The second mechanism operates on hatching success, and the shift may then lead to unfavourable conditions in the laying phase, for instance, when there is not yet sufficient cover of vegetation. Again, this may result in counteracting forces, *e.g.* through increased egg predation. Black-tailed Godwits have started breeding in very short grass already, and in recent years even in totally bare fields. Eventually, such a development could lead to a change in habitat choice.

It is as yet hard to assess to what extent early breeding will benefit the reproduction success, especially since both possible positive and negative effects are not quantitatively known, and may vary greatly from year to year. Early nests, without much cover, suffer more predation than later nests (Beintema & Müskens 1981). Also, early nests may lead to births in a still unfavourable season for the chicks. These may die of bad weather and lack of available insect food (note that this is an argument used by Frisian egg-takers in favour of egging).

On the other hand, an early start would give the birds a prolonged season, as there is no indication that the timing of moult, which terminates the breeding season (Klomp 1951, Van Balen 1959), has changed. This would enable the birds to produce more replacement clutches, in the case of repeated nest loss. All meadow birds show a remarkable capacity of producing repeat clutches. Thus, the same percentage of nest losses would give rise to a higher reproductive output. An early start would be particularly favourable as nest losses due to agricultural activities will increase with the progress of the season.

5. ACKNOWLEDGEMENTS

This analysis would not have been possible, in the first place, without all the work being done in the past by hundreds of enthusiastic bird ringers. We wish to thank B. J. Speek, during our studies manager of the Ringing Centre in Arnhem, and his staff, who made all material available for us, and offered us a great deal of help. We also wish to thank W. D. Bakkes, who did part of the dull and lengthy work on extracting files. Dr. R. H. Drent and Dr. J. Tinbergen gave useful comments on earlier drafts of this paper.

6. SUMMARY

Analysis of ringing dates of chicks of Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus*, Snipe *Gallinago gallinago*, Ruff *Philomachus pugnax*, and Oystercatcher *Haematopus ostralegus* show that in this century there has been a marked shift in the timing of breeding of these species in The Netherlands. Today, with some regional exceptions, all these species start breeding one or two weeks earlier than they used to do in the beginning of the century. Changes in egg-taking habits of man cannot be held responsible for this shift. General changes in the climate, such as a gradual warming up, appear to be insufficient to explain the changes observed. The shift fits rather well with shifts in agricultural activities. Both mowing and grazing start about two weeks earlier nowadays than at the beginning of the century, as a result of faster and enhanced growth of grass. The main causes are the increasing amounts of fertilizers used, and higher soil temperatures in spring, due to improved drainage. It is postulated that this not only affects the growth of the vegetation, but also the phenology of fauna, including birds. Changes may affect chick survival and habitat choice.

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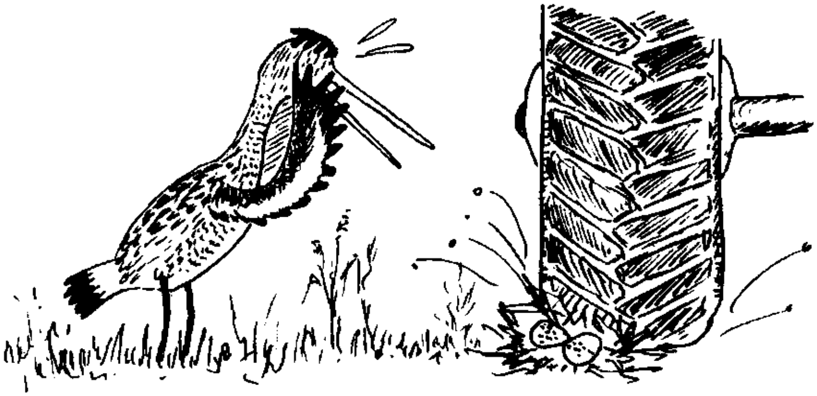
8. SAMENVATTING

Uit analyses van ringdata van kuikens van Kievit, Grutto, Tureluur, Watersnip, Kemphaan en Scholekster blijkt dat het broedseizoen van deze soorten in Nederland in deze eeuw aanmerkelijk vervroegd is. Afgezien van enige regionale uitzonderingen, broeden al deze soorten tegenwoordig een tot twee weken vroeger dan in het begin van deze eeuw. De verschuiving kan niet verklaard worden door wijzigingen in het eierraapseizoen. Ook het warmer worden van het klimaat in deze eeuw blijkt in het voorjaar onvoldoende te zijn om een zodanige verschuiving teweeg te brengen. Er is een goede overeenkomst met soortgelijke verschuivingen in de maaidatum en het weidestadium. Deze activiteiten vinden thans eveneens twee weken eerder plaats, als gevolg van vervroegde en versnelde grasgroei. Als voornaamste oorzaken worden de sterk gestegen kunstmestgift en de verhoogde bodemtemperatuur ten gevolge van ontwatering aangemerkt. Deze veranderingen zouden niet alleen de groei van de vegetatie beïnvloeden maar ook de ontwikkeling van de fauna, inclusief de weidevogels. De veranderingen kunnen van invloed zijn op de overlevingskansen van de kuikens. Ook kan de biotoopkeuze van de soorten een verandering ondergaan.

Chapter 3

Nesting success of birds breeding in Dutch agricultural grasslands.

A.J. Beintema & G.J.D.M. Müskens



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NESTING SUCCESS OF BIRDS BREEDING IN DUTCH AGRICULTURAL GRASSLANDS

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SUMMARY

(1) Daily survival rates of nests with respect to predation are referred to as *P*-values, trampling survival rates are expressed as 'standardized trampling values', estimated as daily survival rates at an exposure of one grazing animal ha^{-1}.

(2) *P*-values were lower during laying than during incubation. *P*-values in hidden-nesting species are higher than in open-nesting species. *P*-values are not constant, but are highest in the middle of the nesting season. *P*-values differ between regions and years, and are positively correlated with densities of voles, *Microtus* sp. In years following a collapse of vole populations, ground predators switch more to birds' nests.

(3) Standardized trampling values are independent of cattle densities and field size, hence the probability of surviving is a simple function of stock density and days exposure.

(4) A renesting model is presented, to estimate nesting success per pair, taking renesting into account, based on *P*-values and trampling values. The model enables the testing of the effects of different management schemes on nesting success.

INTRODUCTION

About two-thirds of the land area of the Netherlands consists of grasslands, mostly of a moist type. These grasslands, generally used for dairy farming, not only produce milk and butter, but also large quantities of birds, collectively known in the Netherlands as 'meadow birds'. The meadow-bird community is dominated by wader and duck species. The six main species are lapwing *Vanellus vanellus* (L.), black-tailed godwit *Limosa limosa* (L.), redshank *Tringa totanus* (L.), oystercatcher *Haematopus ostralegus* L., ruff *Philomachus pugnax* (L.), and snipe *Gallinago gallinago* (L.), the first four being the most numerous, with breeding populations in Holland of *c.* 110 000, 90 000, 60 000, and 20 000 pairs, respectively (van Dijk 1983). The international importance of the godwit population is particularly spectacular, as it represents 80–90% of all European black-tailed godwits.

The main factor that distinguishes Dutch meadows from other European ones is the high water table, which causes slow spring growth of the vegetation, and late accessibility for livestock and machines, in spite of fertile soils. This enables the birds to hatch their eggs safely in an area rich in food. This situation is rapidly changing with improved drainage and intensified management. However, the international importance of the Dutch meadow-bird areas is now widely recognized, and steps are being taken, privately and by the government, to preserve sufficient areas.

The practical manager of areas rich in meadow birds often notices that a large proportion of eggs fail to hatch, because of predation and agricultural activities, notably

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trampling by cattle and mowing. This paper analyses nest loss, and its significance in the population dynamics of meadow-bird species. The results may help in designing efficient management schemes, especially where compromises between the interests of birds and farmers are sought.

METHODS

Data collection

From 1974 to 1983, data have been collected on *c*. 18 000 nests of birds breeding in Dutch grasslands. Nests were found in the course of several research projects, partly at the Research Institute for Nature Management, and partly from other investigators.

Nests were located in three ways: (i) searching fields systematically, (ii) locating nests of flushed birds and (iii) watching birds returning to their nests after disturbance. Choice of method depended on bird population density, height of the vegetation, and whether incomplete clutches were to be included.

Nests were marked with sticks, which were put in a ditch and indicated direction, not distance. When the nest was close to a ditch, the stick was placed in the ditch at the far side (ditches were 6–20 m apart). As the data were from different sources, it was not possible to check for increased predation caused by marking. Workers agreed that, in artificial pastures, with dense patterns of ditches and many obstacles, sticks placed as described did not attract the special attention of predators.

Nests were not marked in grazed fields because, when a grazing cow encounters a stick, it becomes excited, trampling everything within a 10-m radius.

Nests were checked once or twice a week. During checks, nests were observed at some distance, in case predators should follow the trail. With few exceptions, nest losses were not increased on the day after a visit (Bart 1977; Willis 1973). In a few cases where a predator learned to follow the investigators, nests or fields were excluded from analysis.

The contents and outcome of each nest were noted. Recognizing trampling is easy but distinguishing between hatching and predation can be difficult. Typically, a hatched nest contains miniscule shell fragments from the first hole made by the chick. Predated nests may contain larger fragments or remains of spilt yolk. When all the eggs have been removed, the linings of the nest often look torn.

Calculation of nest survival; predation

It has long been recognized that studies in which nesting success is simply expressed as the percentage hatching from a sample of nests found may give seriously (mostly upwardly) biased results (Snow 1955; Mayfield 1961). The main bias comes from the obvious, but often overlooked, fact that nests lost before they could have been found are not included. Accordingly, Mayfield (1961, 1975) developed a useful method of measuring nesting success as daily survival rate, which he defined as the probability, P, that a nest present one day would survive to the next. It is estimated from the formula:

$$P = \frac{A}{A+B}$$

in which A = total number of 'nest days' (the sum of all daily totals of nests present during the observation period), and B = total number of nests lost. The day on which a nest is lost is not counted as a nest day. Nests were assumed to have been lost half way between the last two checks.

In its original form, Mayfield's method assumed constant survival rates through the nesting stage, and between individuals. Problems arise if this is not the case (Green 1977; Willis 1981), but these can be solved by grouping the data in short periods and subpopulations (Willis 1981). The problem then is the vast quantity of data needed for such subdivisions.

Daily survival rates, with regard to predation, were calculated with Mayfield's formula, and are referred to as '*P*-values'. The standard deviation, from which 95% confidence intervals were derived (Johnson 1979), is:

$$\text{S.D.} = \frac{B(-B)}{A^3}$$

Trampling by cattle

The calculation of survival rates with respect to trampling is more complex, since the cattle density and possibly the field size are also parameters. To tackle this, in earlier studies (Directie Beheer Landbouwgronden 1980; Beintema *et al.* 1982), complex likelihood functions were used, developed by J. Oude Voshaar and F. J. de Vries (personal communication). But eventually, survival rates were reduced to survival per animal per hectare per day, thus assuming that 10 days' grazing by one animal gives the same result as 1 day's grazing by ten animals. With this assumption (tested in the studies mentioned above, see also 'Trampling losses'), Mayfield's method can be adapted by first converting all data to standard densities of one grazing animal per hectare. The only problem is that statistical comparisons are not easily made, as the standard deviation given by Johnson (1979) is no longer valid (J. B. van Biezen, personal communication). Therefore, van Biezen developed an alternative estimator for trampling survival. Trampling intensity is estimated as:

$$I = \frac{C}{A}$$

in which C is the number of nests lost (due to trampling), and A is total exposure as the product of exposure days and stock density: a day with cattle density of 2 ha^{-1} is counted as 2 days, etc. Days on which observations were terminated were fully counted. Days on which a nest was lost (either by predation or trampling) were counted as 0·5 day (on days with cattle density of 2 ha^{-1} as 1 day, on days with density of 3 ha^{-1} as 1·5 days, etc.). The daily survival rate, standardized at a density of 1 ha^{-1}, is:

$$V = Exp(-I)$$

V is the 'standardized trampling value'; its standard deviation is:

$$\text{S.D.} = \frac{Exp(-I) \times \sqrt{C}}{A}$$

The derivation of these formulae is given in the Appendix.

RESULTS

Predation; differences between species

Daily survival rates with respect to predation (*P*-values) were calculated for seventeen species of grassland-dwelling birds, for the laying period and the incubation period separately (Table 1). Survival rates during laying were lower than in the incubation phase ($P<0\cdot05$). The difference was most significant in the lapwing, black-tailed godwit, oystercatcher, and redshank (no overlap in 95% confidence intervals), reflecting the number of observations available.

Bias may arise from partly predated, abandoned clutches, mistaken for nests in the laying phase. These are likely to be further removed by the predator. However, *P*-values during laying are lowest at the onset of the season, while the probability of occurrence of this error should increase when full clutches are getting more numerous, and incomplete ones scarcer.

Experienced workers were asked to classify the species according to the difficulty of finding their nests (Table 1). This resulted in an arbitrary scale, from 1 (easy) to 7 (difficult). Hidden nests suffered less predation during incubation than open ones ($P<0\cdot05$, Spearman rank correlation). In spite of conspicuous nesting, avocet and common tern showed high survival rates, probably a result of effective colonial anti-predator behaviour.

Seasonal variation in predation and density dependence

In the four most numerous wader species, *P*-values were calculated for different periods through the breeding season, for the incubation (Fig. 1a, 18 weeks) and laying phases (Fig. 1b, nine 2-week periods). The number of nest days per week reflected the seasonal distribution of the presence of nests.

TABLE 1. Daily survival rates (predation only) for grassland birds, during laying and incubation. *P* = *P*-value. Hiding score indicates how difficult nests are to find (arbitrary scale)

Species	Hiding score	Laying phase		Incubation	
		P	S.D.	*P*	S.D.
Lapwing *Vanellus vanellus* (L.)	3	0·928	0·0073	0·987	0·0007
Black-tailed godwit *Limosa limosa* (L.)	4	0·941	0·0060	0·989	0·0007
Redshank *Tringa totanus* (L.)	5	0·955	0·0084	0·993	0·0010
Ruff *Philomachus pugnax* l(L.)	6	—	—	0·999	0·0011
Snipe *Gallinago gallinago* (L.)	7	1·000	—	0·994	0·0043
Oystercatcher *Haematopus ostralegus* L.	1	0·950	0·0077	0·986	0·0010
Avocet *Recurvirostra avocetta* L.	1	0·958	0·0182	0·995	0·0018
Black-headed gull *Larus ridibundus* L.	2	0·953	0·0227	0·987	0·0030
Common tern *Sterna hirundo* L.	2	0·992	0·0078	0·996	0·0010
Mallard *Anas platyrhynchos* L.	4	0·963	0·0122	0·994	0·0016
Shoveler *Anas clypeata* L.	5	0·998	0·0022	0·996	0·0013
Garganey *Anas querqueula* L.	7	—	—	1·000	—
Tufted duck *Aythya fuligula* (L.)	6	1·000	—	1·000	—
Coot *Fulica atra* L.	2	0·992	0·0084	0·984	0·0040
Moorhen *Gallinula chloropus* (L.)	3	1·000	—	0·994	0·0062
Skylark *Alauda arvensis* L.	6	0·900	0·0949	0·987	0·0058
Meadow pipit *Anthus pratensis* (L.)	6	—	—	0·997	0·0029

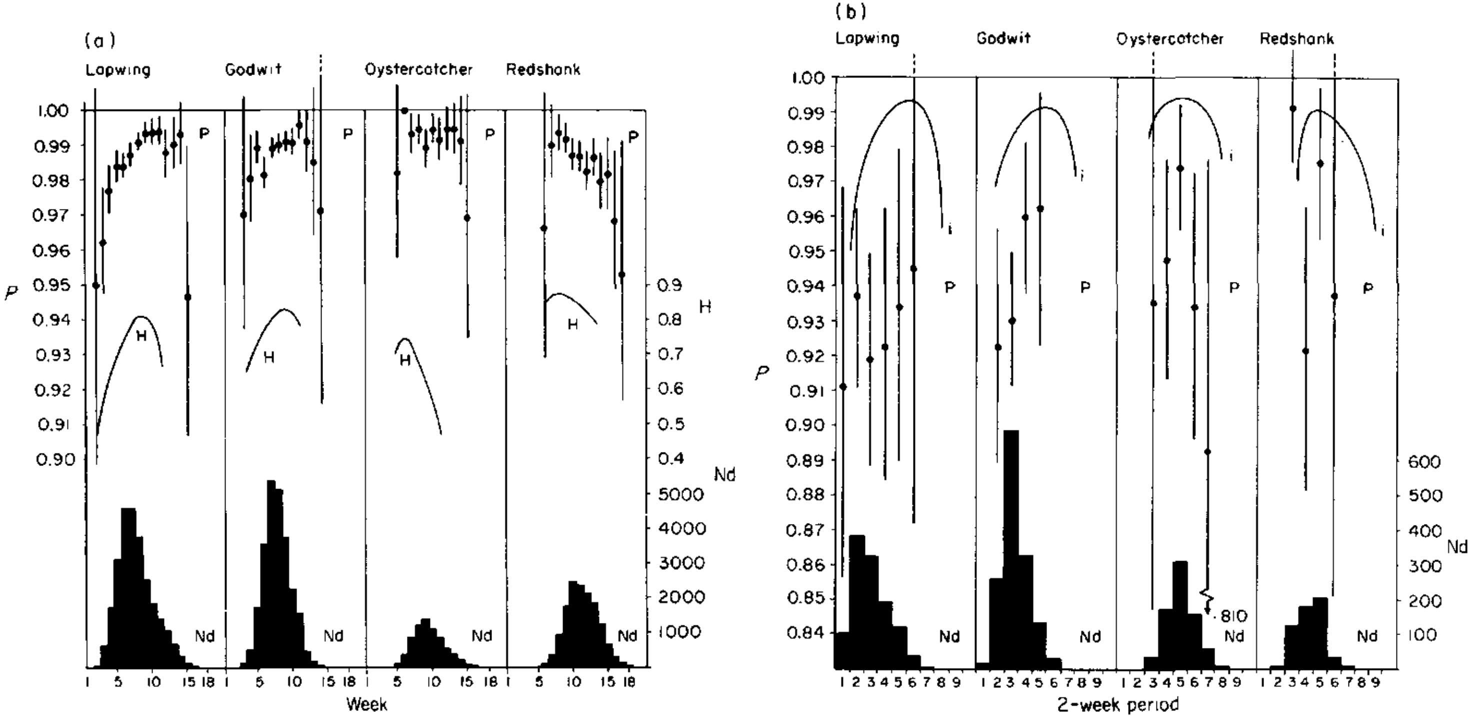

FIG. 1. Daily survival rates of nests and eggs (*P*-values; predation only) (a) during incubation per week and (b) during the laying phase per 2 weeks. Vertical lines indicate 95% confidence intervals. P = *P*-value. H = estimated survival over total incubation period (losses during laying not included). i = fitted lines for *P*-values during incubation. Nd = number of nestdays (a) per week or (b) per 2 weeks.

To illustrate the cumulative effect of P-values, Fig. 1a also gives the estimated hatching success H as a function of the date of the first day of incubation:

$$H = p_1 \times p_2 \times \ldots \times p_i$$

where p_1 is the P-value of the first incubation day and p_i is the P-value of the last incubation day, day i. When p is constant:

$$H = p^i$$

Figure 1 leads to the following observations:

(a) An increase in daily survival rate may be due to the least well-hidden nests being removed first (Miller & Johnson 1978), but the decrease later in the season cannot be explained by such selection, unless late nesters are of such poor quality (or inexperienced) that they do not effectively hide or guard their nests.

(b) An increase in cover with growing vegetation is an alternative explanation for the rapid increase of survival rates in the first weeks. Again, the decrease later in the season cannot be explained in this way.

(c) An inverse relationship may exist between the population density of a prey species, and the probability that an individual will be taken (swamping effect). This should give maximum survival rates during the peak of the season, when nest densities are highest. Species may add to each others' swamping effect; as in the early-nesting lapwing, maximum survival rates are reached later than the peak density (nest days), while in the late-nesting oystercatcher it is just the reverse.

(d) Another explanation for maximum survival rates being synchronized in all species, could be that survival depends on the predators themselves, e.g. because of a limited action radius in aerial predators (gulls and crows) during their own nesting season, or abundance of alternative food sources.

(e) Figure 1b does not allow much detailed analysis, but values in the laying phase follow a similar pattern but are smaller.

TABLE 2. Percentage variance accounted for in different regression models. $Y = P$-value per week during incubation (predation only). Models fitted: 1. X = number of nest days (N) per week of a single species, 2. $X = \log(N)$ of the same species, 3. multiple regression with $\log(N)$ of all four species. Contribution of species to 3, tested in 4–7, each with one species omitted from 3. Asterisks in 3 indicate difference from 2, asterisks in 4–7 indicate difference from 3 ($^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}001$)

Model	1	2	3	4	5	6	7
Species	N same species	Log(N) same species	Log(N) all species	Model 3 without lapwing	Model 3 without godwit	Model 3 without oyster-catcher	Model 3 without redshank
Lapwing	13·9	47·6	76·0*	—	63·8*	77·7	78·2
Godwit	12·7	46·2	54·8	53·1	—	59·5	57·0
Oystercatcher	28·7	50·7	69·4	73·1	72·6	—	71·7
Redshank	8·2	36·6	95·9**	94·7	72·2**	38·9**	—

Interspecific swamping was examined in more detail by multiple regression between weekly P-values (incubation) for each species and the logarithm of the number of nest days for the species in the same week. The results in Table 2 lead to the following observations.

(a) Godwit and oystercatcher do not benefit from swamping by lapwing or redshank.
(b) The lapwing (early nester) benefits from the godwit (early nester), and the redshank (late nester) benefits from the oystercatcher (late nester).
(c) The redshank–oystercatcher and lapwing–godwit relationships are not mutual, which may indicate that benefit is not based just on swamping, but perhaps on active defence by species that show the strongest antipredator behaviour (godwit and oystercatcher).

Differences between years and regions; the vole cycle

Overall seasonal P-values for different years and regions are given in Fig. 2. Similarities in patterns of variation in lapwing and godwit (for which we have most data) suggest that both species are affected in the same way.

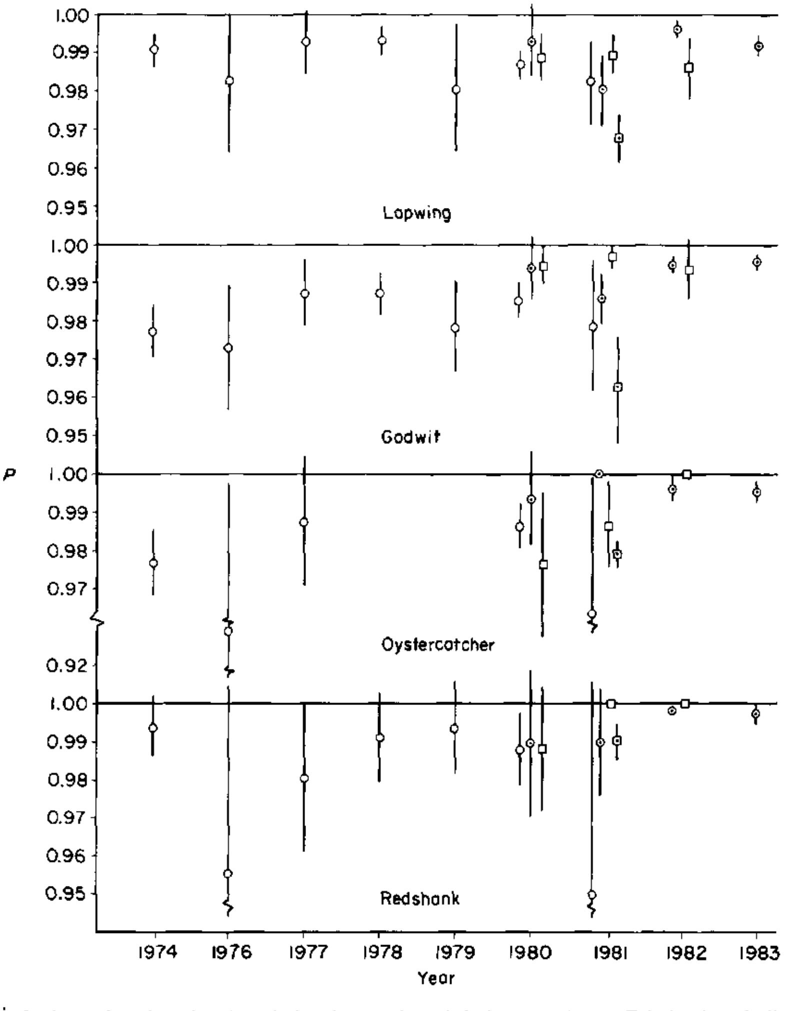

FIG. 2. Annual and regional variation in P-values (whole season). ○ = Friesland excluding Bandpolder, ⊙ = Noord-Holland, □ = Zuid-Holland, ⊡ = Bandpolder. Vertical lines indicate 95% confidence intervals.

Variations in predation pressure may be linked with numbers of field voles *Microtus arvalis* (Pallas), the preferred food of many predators that also eat wader eggs. In 1981, the authors noted that heavy predation of mustelids on redshank nests, in an area where nesting success had been high in the previous year, coincided with a collapse in vole populations. Similarly, Roselaar (1979) attempted to link annual variations in numbers of curlew sandpipers *Calidris ferruginea* (Pontoppidan) with lemming cycles in Siberia.

Data on regional vole densities were obtained from J. Buker, D. Jonkers, and J. de Jong (personal communication), and assigned to three density levels (March–June). Relationships between *P*-values (Fig. 2) and vole densities are given in Fig. 3. Especially in years when vole densities were low, predators appeared to switch from voles to birds. In fact, predation pressure on birds' nests (as a measure of the difficulty of obtaining voles) was not related to absolute vole densities, but to the amount and direction of change in these densities. Predator switching affected early nesters (lapwing and godwit) most.

Trampling losses

Trampling survival values were calculated for four types of husbandry commonly used in the Netherlands: (i) dairy cattle that graze during the day only, (ii) dairy cattle that stay in the field day and night, (iii) young cattle (day and night), (iv) sheep (day and night).

It has been suggested that animals graze more evenly over small fields, so that nests survive better in large fields. It has also been suggested that trampling per animal is heavier under high densities of cattle than under low. To test this, survival rates per animal per hectare per day, for the four types of livestock mentioned above, were calculated for each bird species, for two classes of cattle density and for three classes of field size (Fig. 4). Differences between classes were not significant (Spearman). One can therefore use one 'standardized trampling value' per type of livestock and per bird species

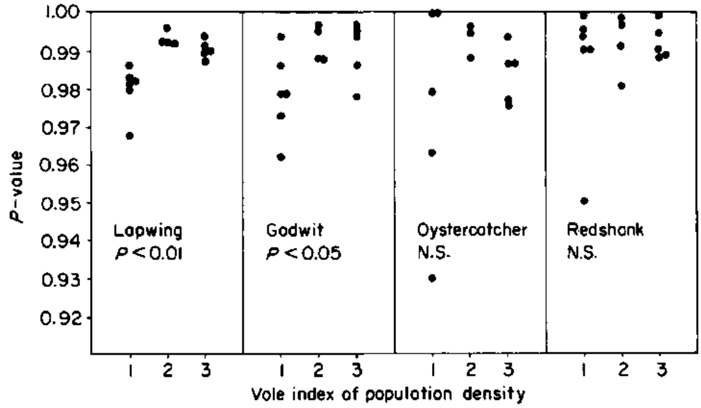

FIG. 3. Relationship between *P*-values (see Fig. 2) and regional vole densities after J. Buker, J. de Jong and D. Jonkers (personal communication) 3 = high density, 1 = low density after crash, 2 = intermediate cases.

	1974	1976	1977	1978	1979	1980	1981	1982	1983
Friesland	3	1	2	2	1	3	1		
Noord–Holland						3	1	2	2
Zuid–Holland						3	3	1	
Bandpolder							1		

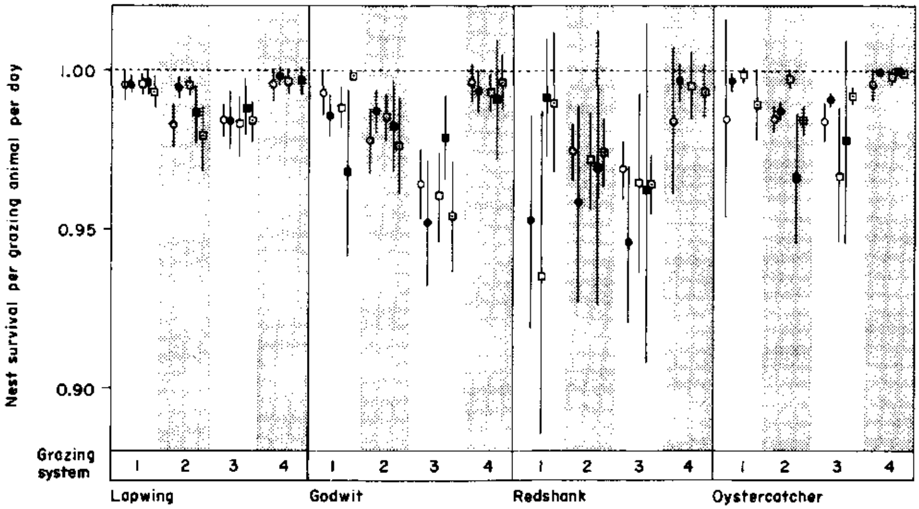

FIG. 4. Trampling values (daily survival rate per animal ha^{-1}) for different conditions under four grazing systems: 1 = dairy cattle during the day only; 2 = dairy cattle day and night; 3 = young cattle day and night; 4 = sheep day and night. ○ = 0–10 animals ha^{-1}, ● = > 10 animals ha^{-1}; □ = field 0–2·5 ha, ■ 2·5–5·0 ha, ⊡ = > 5 ha. Vertical lines indicate 95% confidence intervals.

(survival rate per animal per hectare per day). This is convenient, since, once these values are known, survival rates can be predicted for any complex grazing system. Standardized values are given in Table 3. Similar values were found for British cattle (R. Green, personal communication), and for beef cattle in extremely low densities in the U.S.A. with artificial nests (Koerth *et al.* 1983).

Young cattle were the worst tramplers, for most bird species, especially when trampling was compared with food consumption (Table 3). In terms of food consumption (or

TABLE 3. Basic trampling values and daily survival rates per grazing unit ha^{-1}. One grazing unit = 1 dairy cow = 2 yearlings = 10 sheep. Grazing systems: 1, dairy cattle during the day only; 2, dairy cattle day and night; 3, yearlings day and night; 4, sheep day and night

Species	Grazing system	Standardized trampling value	S.D.	Daily survival rate per grazing unit ha^{-1}
Lapwing	1	0·995	0·0013	0·995
	2	0·990	0·0017	0·990
	3	0·984	0·0024	0·968
	4	0·996	0·0015	0·970
Godwit	1	0·988	0·0027	0·988
	2	0·982	0·0031	0·982
	3	0·960	0·0050	0·922
	4	0·993	0·0026	0·932
Redshank	1	0·972	0·0097	0·972
	2	0·973	0·0045	0·973
	3	0·964	0·0045	0·929
	4	0·993	0·0034	0·932
Oystercatcher	1	0·996	0·0015	0·996
	2	0·986	0·0017	0·986
	3	0·991	0·0011	0·982
	4	0·999	0·0004	0·990

grazing pressure), one adult cow = three 'yearlings' = five sheep. Sheep have a reputation for damaging nests (they even eat eggs), but they did little harm per individual. It was their stocking density that did the damage.

Birds did little to defend their nests against grazers. They often flew off at the last minute, to avoid being stepped on. Only lapwing and oystercatcher actively tried to distract cattle. Table 3 suggests that oystercatchers had some success, especially with young cattle.

Interaction between predation and trampling

It has been suggested (Beintema *et al.* 1982) that losses due to predation are heavier in grazed than in ungrazed fields. This was tested for lapwing, black-tailed godwit, redshank and oystercatcher, for five periods, yielding twenty figures for grazed situations, and twenty for ungrazed ones. In the lapwing, two out of five comparisons gave a better survival in grazed fields, and in the godwit this was the case in four out of five. In oystercatcher and redshank, all ungrazed situations gave better survival values. Nineteen of the twenty matched pairs overlapped their 95% confidence intervals. One can therefore conveniently treat predation and trampling as independent influences.

Various additional losses

Trampling and predation were important causes of nest loss in Dutch pastures (Table 4), In addition, nests were destroyed by a variety of agricultural activities. In terms of daily survival rates, the probability of surviving mowing is zero. Survival rates for other activities, such as fertilizing, can be estimated from the percentage of the land touched by wheels.

Lapwings may abandon the nest when the vegetation becomes too tall. Godwits sometimes lost eggs in very tall, over-fertilized grass. They kept pulling at leaves to maintain the roof over the nest but, in this vegetation, leaves bent over too easily, and piled up on the bottom. Odd accidents occurred, such as nests being overrun by a hare, turned over by a surfacing mole, or fouled by explosion of a rotten egg.

Partial losses were most often due to infertile eggs. When one egg was damaged by cattle, the nest was abandoned. When a predator took one egg, it usually returned to collect the rest. Some chicks died in the shell. These chicks were often malformed. In the exceptionally wet spring of 1983, many godwit chicks died during hatching. Entire clutches were found dead, bills emerging from holes in the eggs.

When both clutch size and partial losses are taken into account, the average number of chicks hatching per successful nest is 3·21 for the lapwing, 3·56 for the godwit, 3·64 for the redshank, and 3·00 for the oystercatcher (Beintema & Müskens 1981). Harris (1969) found a decrease in clutch size in oystercatchers with season. Our data do not show such trends, for any of the species mentioned (Buker *et al.* 1984).

TABLE 4. Frequency of causes of nest loss (as % of total loss); P = predated, T = trampled, M = mechanically destroyed, A = abandoned, U = unknown

	P	T	M	A	U
Lapwing	44·0	22·7	7·1	7·4	18·9
Godwit	40·1	23·7	7·4	9·3	18·8
Redshank	26·3	51·6	10·1	8·4	3·6
Oystercatcher	42·1	33·5	8·9	9·1	6·5

Significance of nest loss and the impact of management

Ideas on the significance of nest loss may be subjective or even depend on vested interest. The Dutch province of Friesland has a long tradition of collecting lapwing eggs for consumption, a practise now restricted by law. People in favour of it may say that it is harmless because lapwings produce replacement clutches, but that predators should be exterminated. Others say that it is a threat to the lapwing, but that predators are harmless because lost clutches are replaced!

Replacement clutches play an important role in the productivity of meadow birds. Lapwings can be induced to lay eight clutches in succession. One cannot interpret nesting success studies, without taking into account replacement clutches. Quantitative information on replacement clutches is difficult to obtain. Information on replacement behaviour of lapwings is given by Klomp (1951), and of the black-tailed godwit by van Balen (1959).

To predict the impact of management on nesting success, a deterministic renesting model was developed (Beintema & Müskens 1981), in which theoretical nests were exposed to daily survival rates based upon P-values, modified by management. For each day, the fraction of nests surviving was set equal to the daily survival rate. Lost nests were, with certain restrictions, re-entered in the model on a later day. This model has been improved, and made stochastic. The fate of each nest is decided on each day by comparing the daily survival rate with a random number between 0 and 1, until the nest either hatches, or fails. Also, other parameters, such as the length of the laying period, incubation period, and replacement interval (number of days between loss and first egg of replacement clutch), are not fixed, but may be drawn from a distribution, each time they are needed for calculation. Distributions are based on field observations. Thus, repeated runs yield different outcomes, giving statistical information on the results. An outline of the model is given in Fig. 5. Parameters needed are:

(a) Properties of bird species: laying dates of first clutches, length of laying period, length of incubation period, length of replacement interval, probability of making a replacement clutch as a function of the date of nest loss, daily survival rates (P-values) throughout the season, for laying and incubating period separately (Figs 1 and 2), and species-specific standardized trampling values (Table 3).

(b) For each management unit (plot): dates of mowing and fertilizing, grazing dates, cattle densities, etc.

(c) Composite daily survival rates are obtained by multiplying P-values with agricultural daily survival rates derived from management schemes.

As a simple example of the use of the renesting model, Fig. 6a gives the relationship between cattle density and estimated nesting success (per pair) under permanent grazing; Fig. 6b gives the relationship between the first mowing date and nesting success (per pair), when activities after mowing inhibit any successful nesting or renesting. Parameters used were derived from earlier studies (Beintema & Müskens 1981), modified by the results presented in this paper.

DISCUSSION

Although predation took a heavy toll (roughly half of all nests were eaten), nesting success was high under natural circumstances, as a result of renesting (Fig. 6a, density 0). Therefore, predation cannot be considered as a major threat to the existence of meadow birds in the Netherlands.

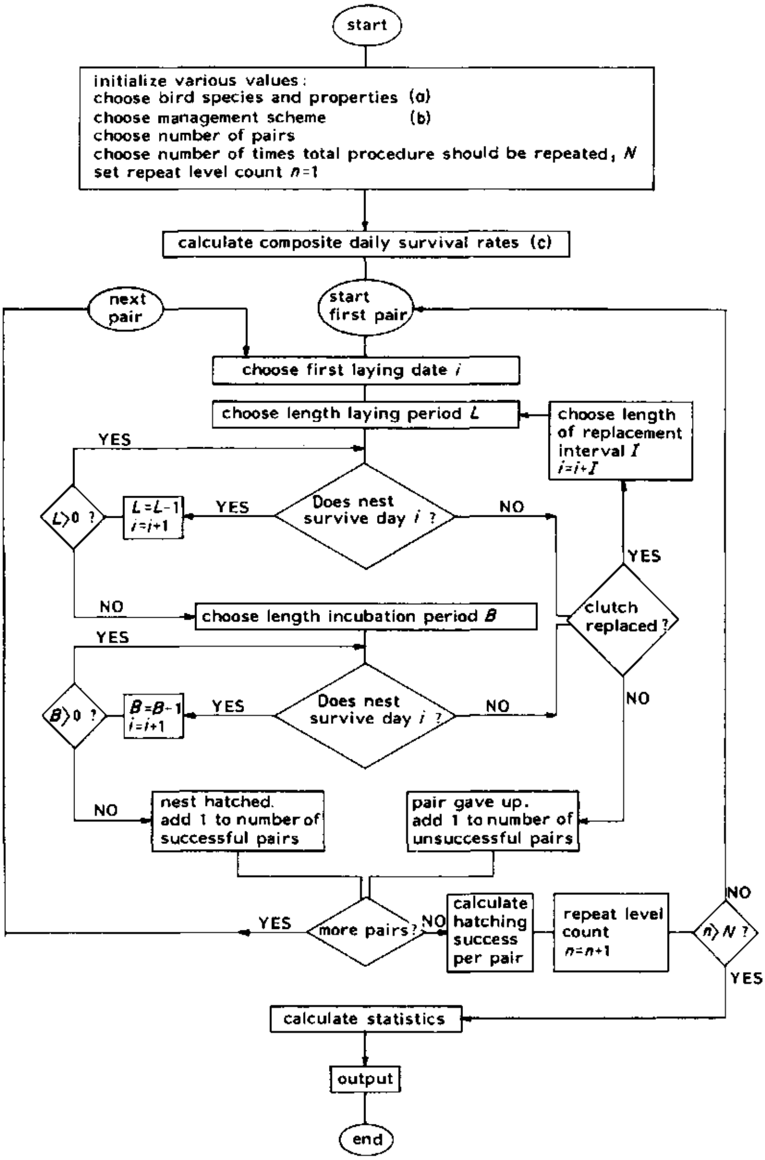

FIG. 5. Scheme of renesting model. Letters in parentheses refer to text.

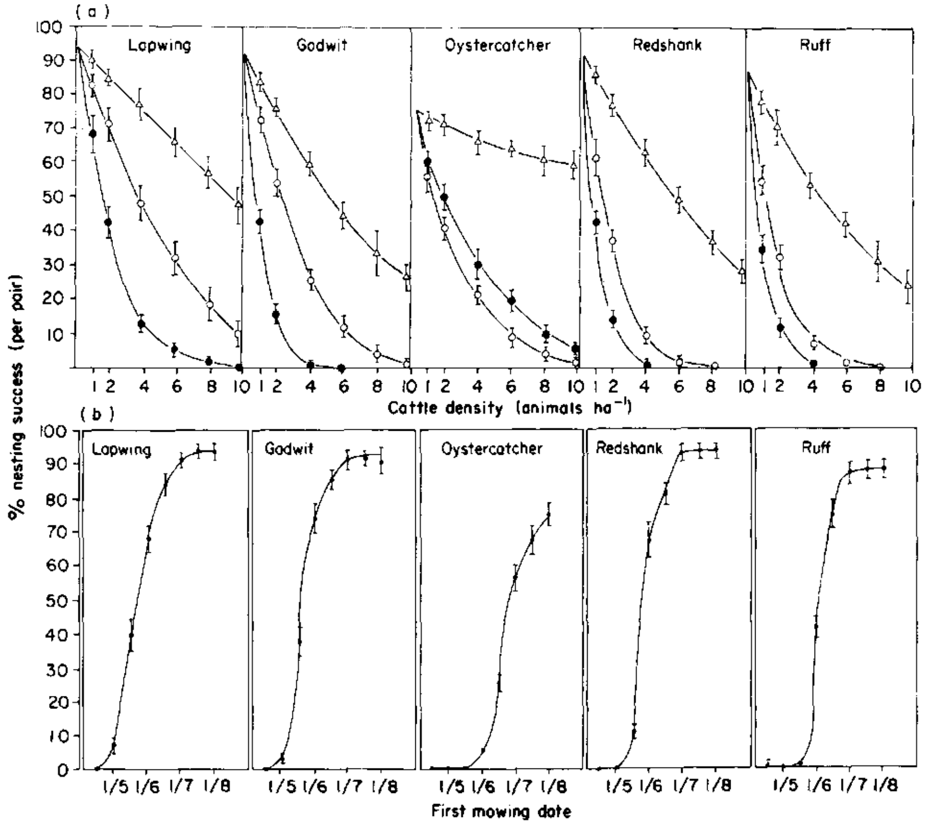

FIG. 6. Hatching success per pair according to renesting model in relation to (a) cattle density under permanent grazing and (b) in relation to first mowing date, when renesting after first mowing is inhibited. ○ = dairy cattle, ● = yearlings, △ = sheep, all grazing day and night. Vertical lines indicate 95% confidence intervals.

Under agricultural conditions, the impact of management rapidly exceeded the loss due to predation. In particular, the tremendous increase in cattle densities, following the increased fertilization (Beintema, Beintema-Hietbrink & Müskens 1985), had a severe effect on overall nesting success (Fig. 6b). Economically ideal management, as proposed by governmental agricultural agencies, has a devastating effect on nest survival (Beintema & Müskens 1981).

In the evaluation of the impact of nest losses, renesting plays a crucial role. Quantitative information on renesting is scanty, but it is known among farmers and egg collecters that during the first weeks of the breeding season *c.* 100% of all nests lost will be replaced. This has also been found by Klomp (1951) and van Balen (1959). Later in the season, the probability of renesting decreases, but more research is needed to quantify this; renesting may then be influenced by external factors other than time.

The use of a renesting model enables comparison of different management schemes with respect to their effect on nesting success. The outcome can be used as a relative measure for the pressure, or the intensity, of agricultural management (Beintema 1983).

There are two major points of criticism of the renesting model in its present form. First, replacement clutches are assumed to occur at the same location as the lost nest, and this is known not to be necessarily true. Second, the probability of replacement is related to season only, whereas in reality it may also be related to management, or the state of drainage. In the Lauwersmeer, Visser (1982) found that in dry situations the nesting season ended earlier than in moist situations, possibly because lost nests were not replaced. An explanation could be that the birds have problems in obtaining sufficient extra food for egg production when the soil fauna retreats to a greater depth.

Even predation pressure may depend on drainage, not only because dry terrain is more easily accessible to ground predators. In the Ganzengouw—an area that was very wet at the start of the nesting season, but which gradually dried out and where soil fauna was almost absent—Visser (1983) found an extremely high predation rate. Halfway through the season the area was practically deserted by the birds (mostly lapwings), indicating that no replacement clutches were produced. An explanation for the high predation rate could be that the birds had to travel far to feed, spending too much time away from the nest.

Finally, initial laying dates may depend on management; intensification of agriculture (improved drainage and fertilization) has induced an advance in laying dates of *c.* 2 weeks in all the species mentioned (Beintema, Beintema-Hietbrink & Müskens 1985). The model leaves freedom of choice of laying dates.

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APPENDIX

BY H. A. VAN BIEZEN

Estimation of probabilities of predation and trampling of nests and their standard deviations

(1) A 'nest day' is defined as 1 day of one nest during the observations. Thus, 3 days observation of two nests yields 6 nest days.

(2) The probability p that a day for one nest is a day of predation (= 1 minus the probability that this day is a day of survival in relation to predation) can be estimated by the formula

$$p = \frac{B}{A}$$

where A is the total number of observed nest days (nest days of nests where predation is observed, nest days of nests where trampling is observed, and nest days of nests where no predation or trampling has been observed) and B is the number of observed predations. It is important to include nest days of nests where no predation has been observed, because not including these days results in overestimation of the probability of predation.

(3) The formula for daily survival rate and its standard deviation given by Mayfield (1961, 1975) and Johnson (1979), based on the above, suggest that the days of predation follow a binomial distribution, A being the total number of samples and B being the number of 'successes', so that p is an estimator for the probability of a 'success' or of a nest day being a predation day.

(4) It is possible to estimate the probability of predation per day in another way, which is only interesting in the context of the more complex way in which the probability of trampling must be estimated: the 'intensity' of predation I can be estimated by the formula

$$I = \frac{B}{0{\cdot}5B + 0{\cdot}5C + D}$$

where C is the number of observed tramplings and D is the number of nest days without predation or trampling (so $A = B + C + D$). This estimator corrects for the fact that the moment of trampling or predation during the day is not known exactly. The mean time of most predation and trampling should be around the middle of the day, so in this estimator days of predation or trampling are counted as half days in the denominator. Note that there is a difference between the probability of predation per day and the 'intensity' of predation; however, this difference is small when both values are small. The probability of non-predation per day (the survival rate P in relation to predation) can be estimated by using the formula

$$P = Exp(-I)$$

So, the estimator for the probability of predation is $1 - Exp(-I)$.

(5) In an analogous way, it is possible to estimate the 'intensity' of trampling for cow density 1 by the formula

$$I = \frac{C}{0{\cdot}5b + 0{\cdot}5c + d}$$

where c is the sum of the products of the trampling days and the cow densities on those days, b is the sum of the products of predation days and the cow densities on those days and d is the analogous sum for the non-predation and non-trampling days. The probability of non-trampling per day for cow density 1 (the survival rate V in relation to trampling for cow density 1) can be estimated by using the formula

$$V = Exp(-I)$$

(6) The standard deviation of the estimator of the probability of non-trampling per day for cow density 1 can be estimated as

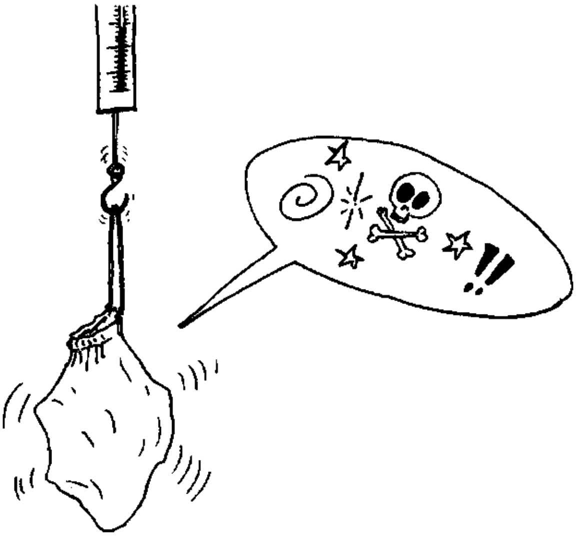
$$\text{S.D.} = \frac{Exp(-I)\sqrt{C}}{A}$$

This formula rests on the assumption that durations of trampling at a constant cow density have an exponential distribution as probability distribution. Further, this formula rests on a first-order Taylor series approximation and the supposition that, on average, the deviation from half-day duration for days of predation or trampling is negligible.

Chapter 4

Growth parameters in chicks of charadriiform birds.

A.J. Beintema & G.H. Visser



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GROWTH PARAMETERS IN CHICKS OF CHARADRIIFORM BIRDS

A.J. BEINTEMA[1] & G.H. VISSER[2]

ABSTRACT Growth curves are given, for the Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, and Redshank *Tringa totanus*. Gompertz' growth coefficients were calculated. Chicks in captivity generally grow faster than chicks in the field. In the field chicks often suffer from reduced growth, as a result of adverse weather conditions. In cold weather, so much time has to be devoted to keeping the chicks warm (brooded by a parent), that too little time remains to obtain sufficient food. Lapwing chicks are susceptible to reduced growth until a later age than Godwit chicks. In the species studied most chicks are born during a period when the number of dry hours above 15°C between sunrise and sunset, and hence the time available for foraging for small chicks, usually shows a sharp rise. Nomograms are presented for bill length, which can be used to estimate the age of wild chicks. In general, Scolopacidae grow faster than Charadriidae. In both families, the chicks grow faster than chicks of other precocial birds do. Differences in growth rates correspond with adaptations to different climatic conditions.

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INTRODUCTION

Growing chicks of nidifugeous charadriiform birds encounter many dangers. In order to minimize chick losses, different growth strategies are possible. In a cold climate, for example, a high growth rate helps to avoid losses due to exposure to bad weather. On the other hand, a high growth rate has its costs, in terms of energy intake. Another point of interest is the timing of the chick stage. An early start has the advantage of ensuring advanced development before the autumn migration takes place, but there is a greater risk of running into adverse weather conditions. In this paper we investigate these problems for three common Dutch species, the Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, and the Redshank *Tringa totanus*. Knowledge of growth parameters forms a basis for many ecological studies. In this respect, this paper serves a dual purpose: we present growth parameters, which can be used for age estimation of chicks in the field, but put these to a greater use by comparing them in a variety of related species.

METHODS

Growth in captivity

In order to determine which growth parameter could be most reliably measured and yield the best estimator of age, birds were raised in captivity. The following parameters were measured daily: body weight, total bill length, 'Nalospi' (bill tip to nostril, the word being derived from the German term 'Naseloch bis Spitze'), wing length, tarsus length, and length of middle toe. Chicks were kept in cages which included a small heated compartment, so that they could choose their ambient temperature. They were fed (ad libitum) on commercial chicken food, supplemented with dried shrimp and occasionally live insects. After having reached the fledging age, the birds were ringed and released.

Growth in the field

During an extensive chick-ringing programme between 1976 and 1985, a special effort was made to recapture chicks of a known age. Many volunteer ringers (this material will be dealt with elsewhere) participated in this programme. As families with chicks wander considerably, the probability of relocating ringed chicks rapidly decreases with the time since the last capture. The number of chicks available for catching also rapidly decreases with age, as a consequence of chick mortality (Beintema & Drost 1986). Thus, most recaptures of chicks of known age are of relatively young chicks, and occur over relatively short periods of time. To enhance the probability of recapturing of chicks of known age, as many chicks as possible were ringed in the nest on the day of hatching. This part of the ringing programme was closely linked to studies on nesting results, in which large numbers of nests were located and monitored in several study areas (Beintema & Müskens 1987). Bill length and body weight were measured in caught chicks. During observations on the development of thermoregulation in chicks, growth data was also obtained for seven, six and two broods of Lapwing, Black-tailed Godwit, and Redshank respectively (Beintema & Visser 1989).

Curve fitting and estimation of parameters

Growth was described using the growth model of Gompertz (Ricklefs 1967, 1968). The Gompertz equation is

$$W = A * e^{-e^{-Kt}}$$

where W is body weight, A is asymptotic weight, K is the growth coefficient, and t is the age, relative to the inflection point of the S-shaped curve. Curve fitting and estimation of growth parameters were done by computer with the versatile growth model developed by Schnute (1981). An important difference with the widely used graphic method of Ricklefs (1967), is that the Schnute model also estimates the asymptote, instead of using a predefined, fixed one.

RESULTS

Growth in captivity

Fig. 1 summarizes the growth parameters in Lapwing, Black-tailed Godwit, and Redshank. From the viewpoint of mass gain, the Godwit appears to have the fastest growth, the Lapwing the slowest. In all three species the feet are strongly developed at hatching (both the tarsus and middle toe already have their inflection points halfway during the embryonal stage) and hardly grow any further after two weeks. The wings, on the other hand, do not start to develop until after several days, especially in the Lapwing (c. 10 days). Thus, in the first week of the chick stage the wings cannot be used for age estimation and in the last weeks measurements of the feet cannot be used as such. Bill length and body weight show the most constant growth throughout the chick stage. In wader biometrics bill length in front of the nostrils ('Nalospi') is sometimes used instead of total length, as it can be measured more accurately. This may be true, but in certain birds, especially the Lapwing, the absolute growth of this part of the bill is only very small (1 mm in four days). Weight depends more on the feeding conditions of the chicks than the other growth parameters do. In the first days, chicks often lose weight. This leaves bill length as the only reliable growth estimator. In the relatively long-billed Godwit and Redshank, the bill still shows practically linear growth at fledging. In the Lapwing, bill length becomes less reliable as an age estimator after c. 25 days, as growth slows down. Wing length then becomes a better one. However, for the sake of uniformity, we decided to introduce total bill length as a universal age estimator for future fieldwork.

Growth in the field

Growth of the bill and body weight derived from retraps of wild chicks, are given in Fig. 2 for the Lapwing, Godwit, and Redshank. The curves for bill length are identical to those of the birds in captivity, except that the variation is larger. However the curves for body weight do differ. In contrast to captive chicks, Lapwing chicks in the field do not start to gain weight until after three days. Only very few manage to even approach the gain of the captive ones. In the field, the K-value is almost reduced to half. In the Redshank, wild chicks grow as fast as captive ones. In the Godwit, wild chicks grow a little slower, but many maintain the same growth as the captive ones. In all species, the young are fully fled-

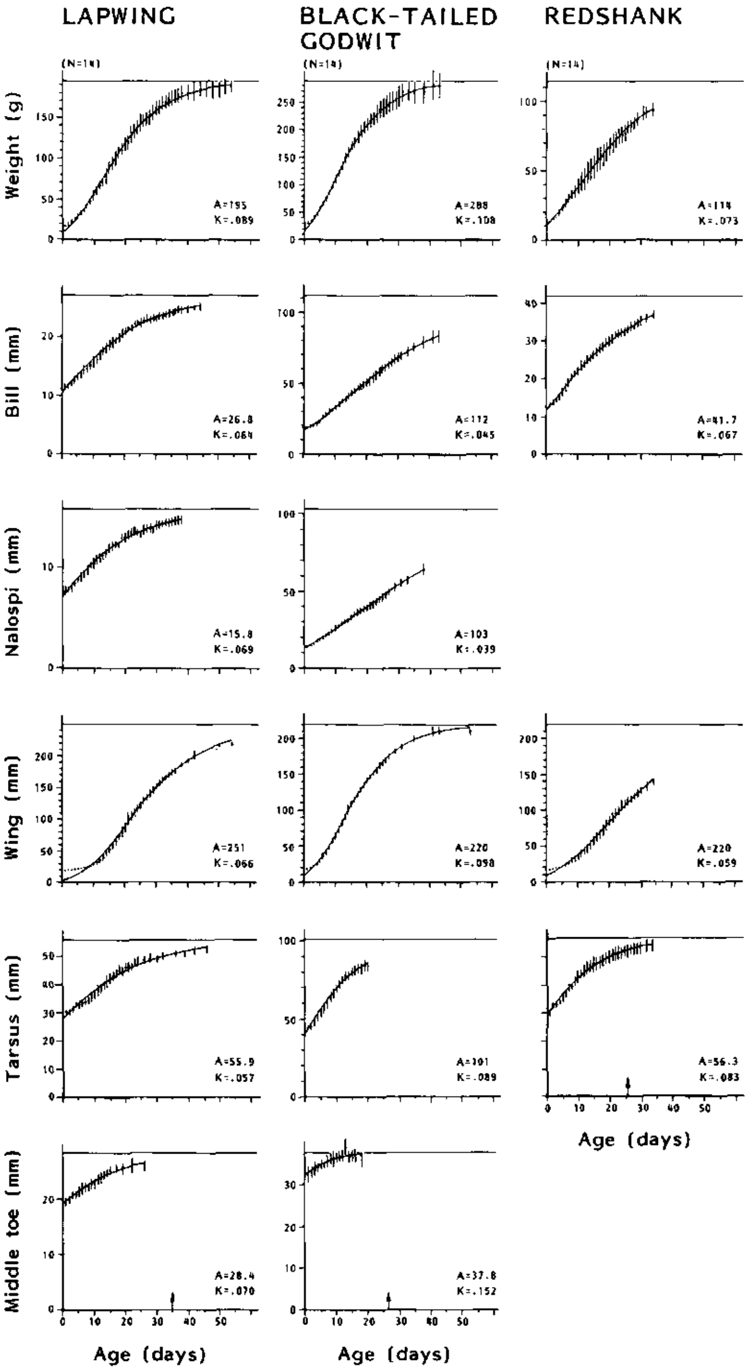

Fig. 1. Growth of captive chicks of the Lapwing, Black-tailed Godwit, and Redshank. All graphs show the asymptotic value (A) at the same scale. Vertical lines show the standard deviation. Lines are fitted according to the Gompertz' equation (Ricklefs 1968). K = Gompertz' growth coefficient. An arrow indicates the age of fledging.

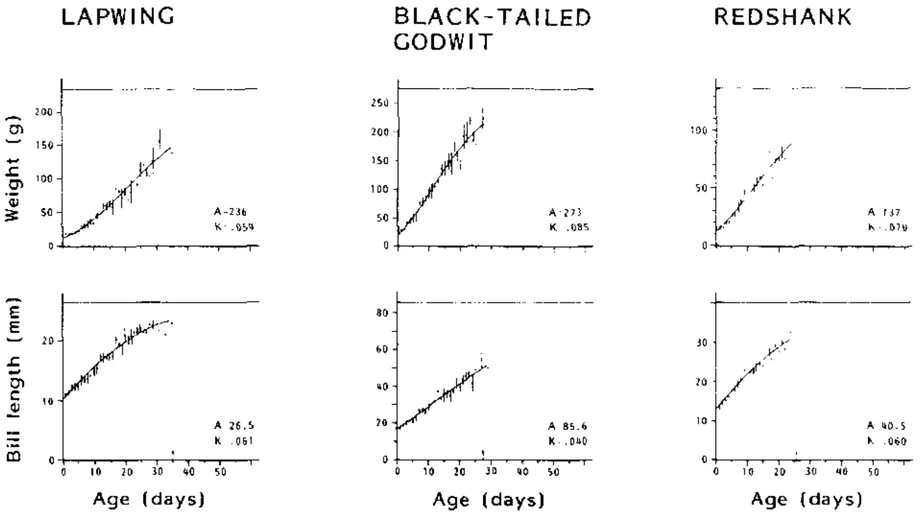

Fig. 2. Growth curves based on retraps of wild chicks of the Lapwing, Black-tailed Godwit, and Redshank. Legend as Fig. 1.

ged at weight levels of 65 - 70% of the asymptotic value. Some statistics from the field data (at birth and fledging) are given in Table 1.

Table 1. Bill lengths (mm) and weights (g) of three wader species at birth and at fledging. BB = bill length at birth, BF = bill length at fledging, WB is weight at birth, WF is weight at fledging, average given with standard deviation, range given between minimum and maximum values observed, *N* = number of observations.

		average	range	*N*
Lapwing	BB	10.6±0.7	8.0-14.0	1769
	BF	22.4±21.20	20.0-25.0	53
	WB	17.5±1.9	10-23	1152
	WF	158.9±14.7	115-185	36
B.t.Godwit	BB	17.2±0.9	12.3-20.5	1847
	BF	49.98±4.48	38.0-60.6	67
	WB	28.6±2.6	19-38	1431
	WF	192.0±25.4	140-250	46
Redshank	BB	12.7±0.6	10.7-14.5	646
	BF	32.32±1.54	28.3-36.1	34
	WB	15.6±1.6	10-24	488
	WF	87.4±8.0	70-99	31

The effect of weather on growth rate

When chicks find insufficient time to forage, this may result in reduced growth. Time available for foraging depends on the weather, since below a certain temperature, a chick needs to be brooded by a parent at intervals, to maintain its body temperature (Beintema & Visser 1989). In prolonged adverse weather conditions many Lapwing chicks die of starvation. To investigate the effect of weather on growth, the time available for foraging was calculated from the weather recordings, and the daily weight gain of chicks was calculated from the capture-recapture material. Time available for foraging can be described as the number of dry hours, above a predefined threshold temperature between sunrise and sunset. A threshold of 15°C was chosen, because this temperature gave most discriminative power between the colder and the warmer days, and between age classes of chicks. At this temperature, small chicks still need brooding, while the larger ones do not (cf Fig. 2 in Beintema & Visser 1989).

Those chicks with an interval of less than five days were selected from the recaptures. 254 recaptures were used for the Lapwing, while 110 were used for the Black-tailed Godwit. The material was insufficient for the Redshank. The average daily

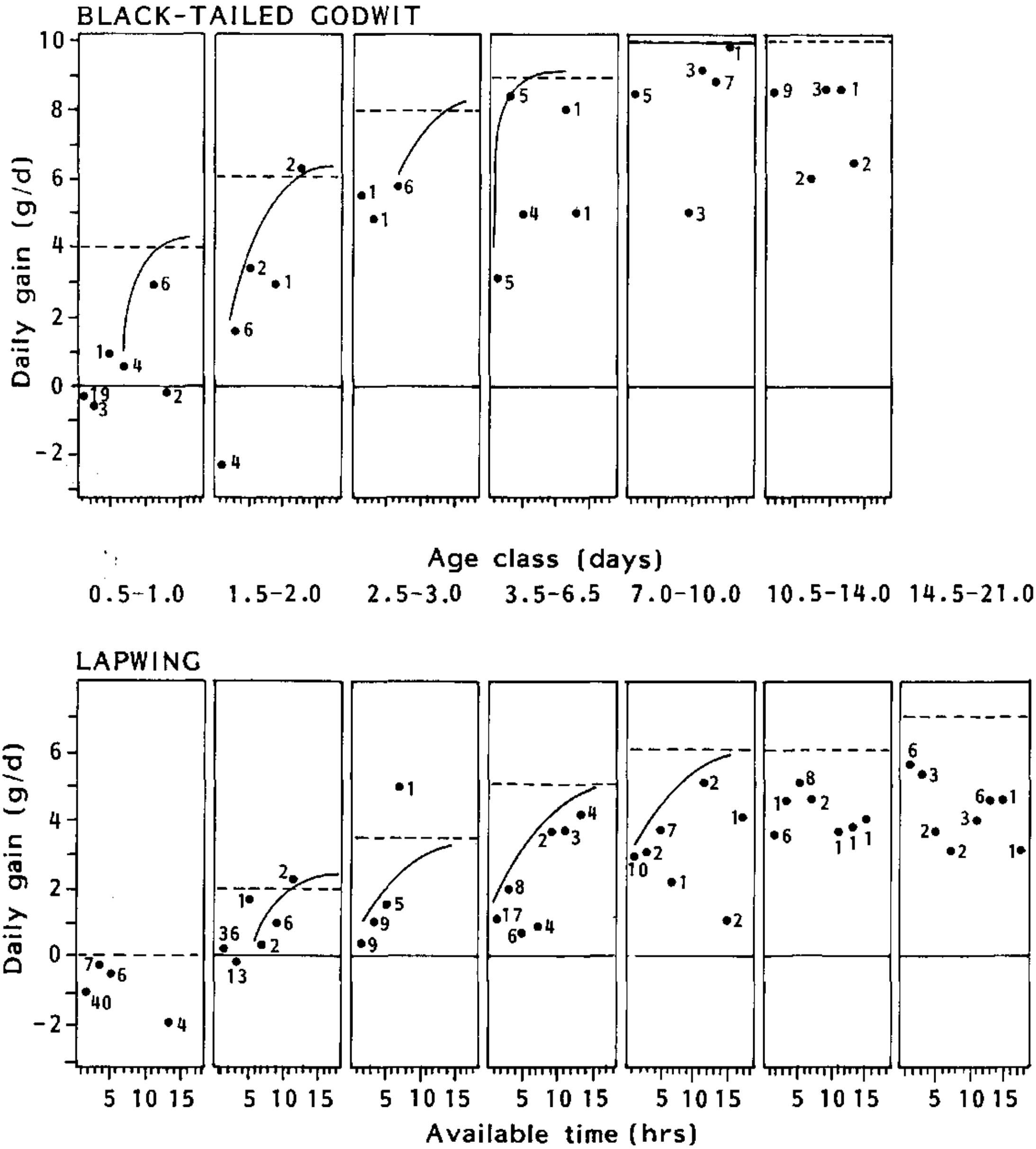

Fig. 3. Average daily weight gain in chicks of different age classes, in relation to the number of dry hours above 15°C, between sunrise and sunset. Curved lines roughly indicate the maximum growth achieved, dotted lines show growth in captivity.

weight gain, and the average number of hours 'available' time per day were calculated for each interval. Weight gain was plotted (Fig. 3) against time, in classes of two hours, for different age classes separately. A positive relationship between daily weight gain and the number of dry hours above 15 °C, can be seen in at least the first two age classes of the Black-tailed Godwit, and in at least the first four age classes of the Lapwing. Fig.3 can be tentatively summarized in Fig. 4. Fig. 4a gives a rough indica-

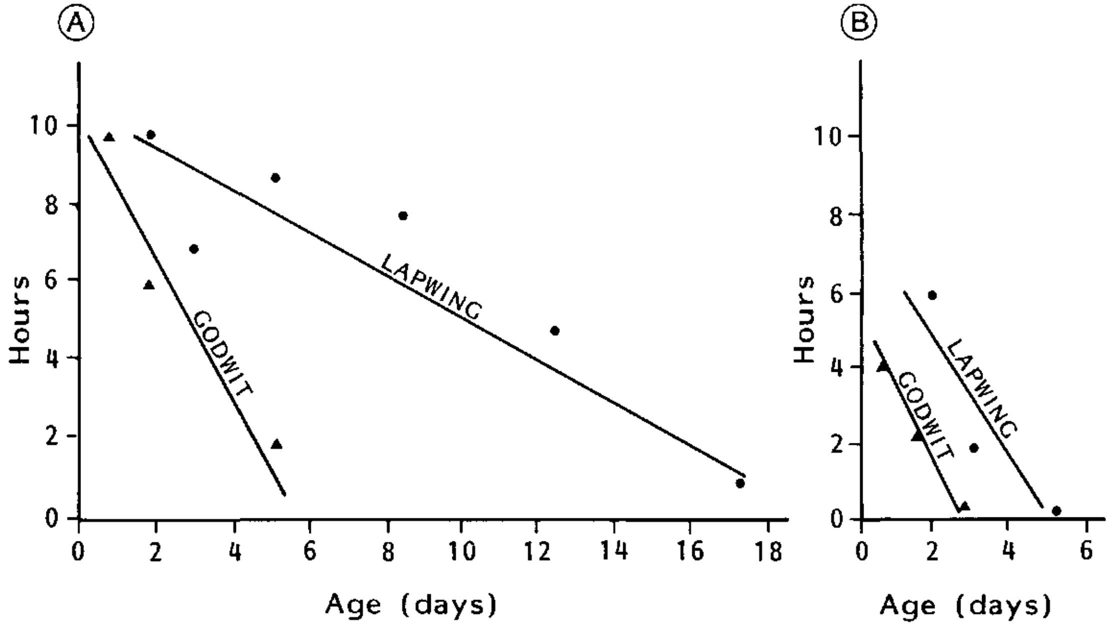

Fig. 4. Number of dry hours above 15°C needed for growth, for chicks of the Lapwing and Black-tailed Godwit, plotted in relation to age.

tion of the number of dry hours above 15°C needed for 'sufficient growth' - approaching growth rates in captivity - for different age classes. Fig. 4b gives the time needed to maintain 'zero growth': when less time is available, chicks lose weight and starve. Lapwing chicks remain vulnerable to bad weather much longer than Godwit chicks. This can partly be explained by a difference in growth rate between the two species. However more importantly, thermal independence develops much faster in the Black-tailed Godwit than in the Lapwing (Beintema & Visser 1989).

Nomograms for age estimation

Growth curves as presented in figs. 1, 2, and 3 cannot be used for age estimation as such, because of differences in the abundance of chicks in different age classes (as a result of mortality, chicks become less abundant with age). As an example: suppose that 50% of the chicks of age class 1 have a bill length of 11 mm, while 25% have a bill of 12 mm, and 25% a bill of 10 mm. Suppose that in age class 2 the distribution is: 25% 11 mm, 50% 12 mm, and 25% 13 mm. If age class 1 is more than twice as abundant as age class 2, then a randomly taken chick with a bill of 12 mm is more likely to belong to class 1 than to the expected class 2. In fact, of c. 27,000 Lapwing chicks caught and measured by 50 ringers between 1976 and 1985, almost 50% were two days of age or less (unpublished data). The recapture data has been regrouped in Fig. 5, to show age as a function of bill length. Curves have been fitted by eye. These are the curves that should be used for age estimation of chicks captured in the field.

DISCUSSION

Shape of growth curves

Wild chicks have a slower start than captive ones. The difference between Figs. 1 and 2 in this respect may partly be explained by the observed reduced growth under adverse conditions. But there is another complication in composite growth curves derived from many retraps: they include values of individuals that have died before fledging. This is especially true in the first week, when chick morta-

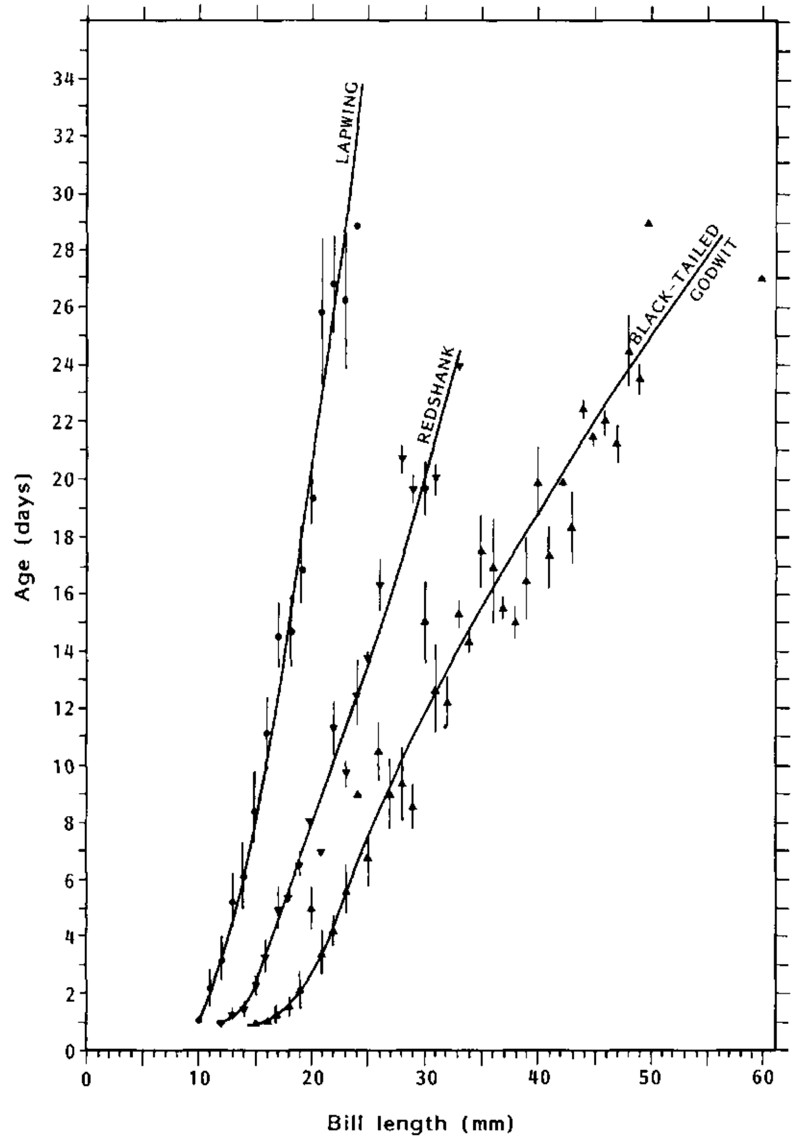

Fig. 5. Nomograms of bill lengths for age estimation. Vertical lines indicate standard deviations.

lity is high. If values had only been taken of chicks known to have survived until fledging, the average weight values at the lower ages would have certainly been higher. For age determination however, the values of chicks not surviving have to be included.

Growth and survival in relation to timing

In Fig. 6 spring development of 'available time' is shown (5-day running mean over average values for 10 years, 1976-1985), defined as dry hours above 15°C between sunrise and sunset, (data National Weather Forecasting Institute KNMI, De Bilt; observations per two hours). Fig. 6 also shows the hatching season of the Lapwing, Black-tailed Godwit, and the Redshank, and also of the Curlew and Ruff, which nest in similar habitats in The Netherlands. In all species, the majority of the chicks hatch when the number of hours 'available time' rapidly rises to values above four to five hours, i.e. 25% or more of the daylight period. This is the minimum time required for small chicks to survive and start growing (Beintema & Visser 1989).

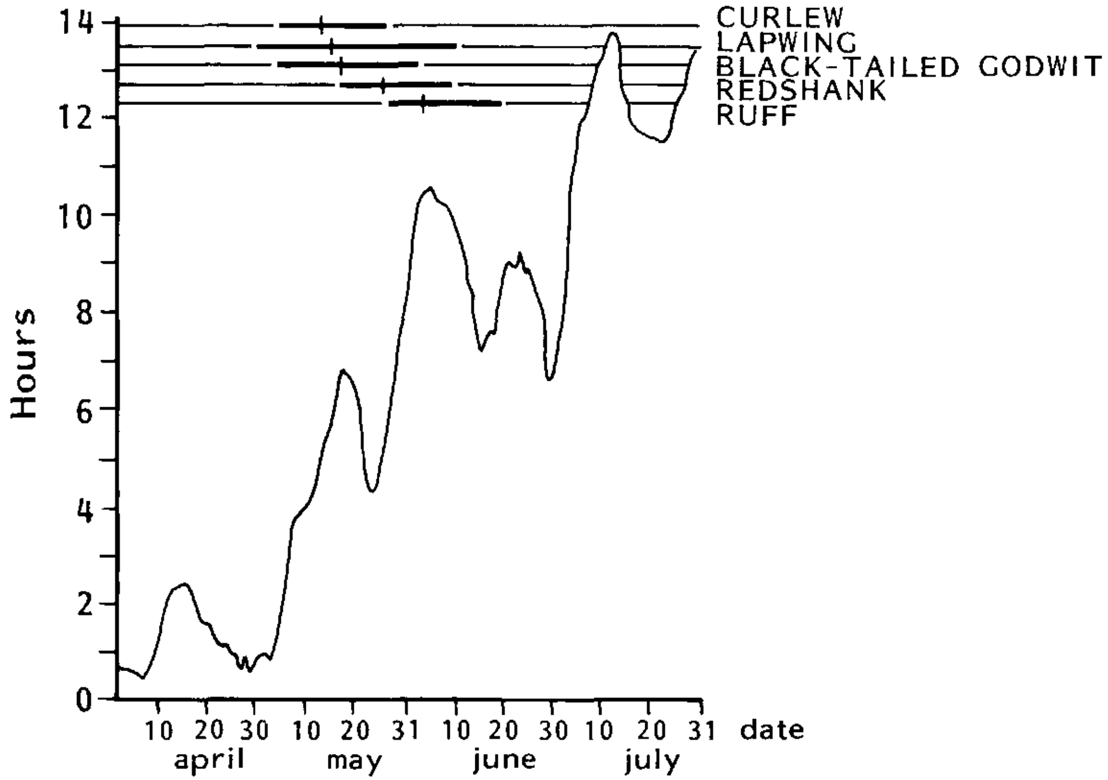

Fig. 6. 'Available time' for foraging in spring, defined as dry hours above 15°C between sunrise and sunset. Average of ten years (1976-1985). Five-day trend shown. Bars indicate hatching seasons, between 10% and 90% percentiles. Vertical line in bar indicates median hatching date.

The Black-tailed Godwit and later-nesting species rarely encounter weather problems, but the first 10% of Lapwing hatchlings have little chance of surviving in most years. Curlew chicks have a still higher cold tolerance than Godwit chicks, and reach thermal independence in only a few days (Visser, unpublished data). Over the past 50 years, the Lapwing, Black-tailed Godwit, Redshank, and Ruff have advanced their nesting season in The Netherlands by approximately two weeks, as a result of increased fertilisation of the agricultural grasslands in which they nest (Beintema *et al.* 1985). So far this seems to have led to a conflict with the possibilities of chicks surviving early spring cold weather only in the Lapwing. The earliest 'safe' hatching date for the Lapwing is around May 8th (Fig. 6), or, when newborn chicks can survive two days on yolk reserves, May 6th. This corresponds with incubation beginning on April 8th, or a laying beginning on April 3rd. Lapwing chicks born in March probably perish in most years. During cold springs, Lapwings may encounter problems until much later. In 1977 the number of dry hours above 15°C remained practically zero until May 22nd, resulting in retarded growth and increased mortality (Beintema 1978). However, if early chicks manage to survive during mild springs, they will benefit from being more mature when starting autumn migration. It has been shown that early-born Black-tailed Godwits are more likely to return to the breeding grounds from their African winter quarters the next year, instead of after two years, than those born later (Beintema & Drost 1986), which may give them an extra reproductive season. Another advantage of early laying is that the clutch have a better chance of surviving cattle and machines, and extra time for replacement clutches in the event of nest loss (Beintema & Müskens 1987).

Interaction between weather and food availability

It is possible that in a habitat rich in insects suitable as food, chicks need to spend less than 25% of their time on feeding, while in a poor habitat they may need much longer. In warm weather, chicks may grow and survive equally well in both habitats, but when bad weather limits the time available for feeding to about 25%, the chicks may survive in the rich habitat, but starve in the poor one. These relationships have to be further investigated. The prediction of chick survival from weather station data is not very accurate, since this data differs considerably from the microclimate close to the ground. In general, the microclimate shows larger variations in temperature. In addition, the microclimate depends on the habitat. Tall, dense vegetation is cool and moist, as compared to lower, more open vegetation (Barkman & Stoutjesdijk 1987).

Growth rates of Charadriidae and Scolopacidae

Growth data of other species was collected from the literature (Table 2). Information of many more species than Ricklefs (1973) used when comparing species groups is now available. In figure 7 the relation between the asymptotic weight (A) and the Gompertz coefficient of growth (K) is given for all species from table 2. The upper and lower line are Ricklefs' (1973) fitted curves for altricial and precocial landbirds respectively. The precocial Charadriidae and Scolopacidae have higher K values than precocial landbirds in general (which include many Galliformes). The line fitted has the formula $K = 0.390 * A^{-0.312}$ ($N = 19, r^2 = 0.75$, asymptotic weight in g). Charadriidae are represented by open symbols, Scolopacidae by closed ones. In Fig. 7 there is little difference in growth rate between Charadriidae and Scolopacidae. In both Scolopacidae and Charadriidae, there is a tendency

Table 2. Growth characteristics of Scolopacidae (1-15) and Charadriidae (19-26). Species number corresponds with Table 3 and Fig. 7. A = asymptotic weight (g), K = growth coefficient (Gompertz), T = time (days) at inflection point. Source Glutz = Glutz von Blotzheim *et al.* (1975, 1977).

species		*A*	*K*	*T*	source
1	*Calidris alpina*	40	0.138	5.8	Soikkeli (1967)
3	*Calidris alba*	81	0.085	11.1	Parmelee(1970)
4	*Calidris pusilla*	26	0.151	5.5	Safriel (1975)
7	*Calidris bairdii*	48	0.120	8.0	Norton (1973)
8	*Calidris fuscicollis*	37	0.158		Ricklefs (1973)
9	*Calidris melanotos*	60	0.106	8.0	Norton(1973)
10	*Philomachus pugnax* f.	125	0.092		Ricklefs (1973)
10a	*Philomachus pugnax* m.	210	0.085		Ricklefs (1973)
11	*Limosa limosa*	273	0.085	11.0	this study
11a	*Limosa limosa*	290	0.055		Ricklefs (1973)
14	*Numenius arquata*	990	0.051	22.9	this study
15	*Tringa totanus*	137	0.070	12.0	this study
19	*Charadrius dubius*	41	0.099	10.5	Glutz
21	*Charadrius hiaticula*	55	0.091		Ricklefs(1973)
21a	*Charadrius hiaticula*	67	0.108	8.6	Pienkowski (1984)
23	*Pluvialis apricaria*	261	0.059	17.0	Glutz
25	*Eudromias morinellus*	111	0.118	7.9	Glutz
26	*Vanellus vanellus*	225	0.079	23.8	Redfern (1983)
26a	*Vanellus vanellus*	236	0.054	20.5	this study

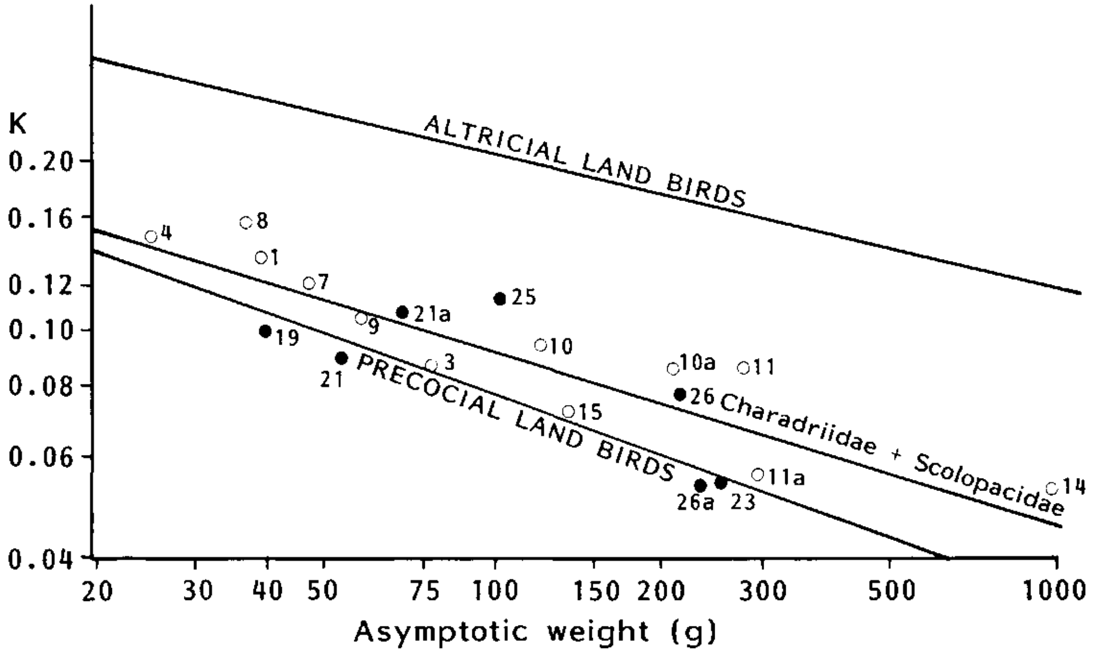

Fig. 7. Gompertz growth coefficient (K) as a function of the asymptotic body weight (A), for different wader species (table 2). Open symbols: Charadriidae, closed symbols: Scolopacidae. Lines shown for altricial and precocial land birds after Ricklefs (1973).

for arctic species to have slightly higher growth coefficients than temperate ones.

The difference between Scolopacidae and Charadriidae with respect to relationship between egg weight and fledging period has also been studied. This relationship is given in Fig. 8, for the species given in table 3. Three lines are given: the top line is the fitted curve for precocial birds in general (Calder 1982), the middle line is the fitted curve for the Charadriidae (open symbols), the lower line is the curve for the Scolopacidae (closed symbols). In accordance with the relatively high growth coefficients, the charadriiform chicks grow up faster than Calder's (1982) precocial birds, in relation to egg weight. In Fig. 8 there is a marked difference (c. 40%) between Charadriidae and Scolopacidae. It is

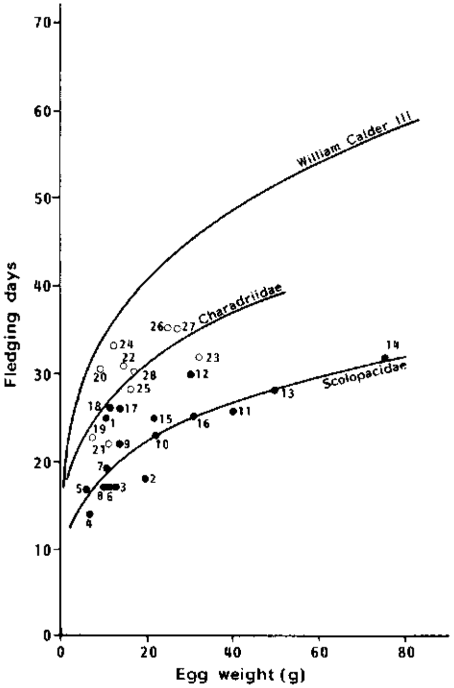

Fig. 8. Fledging period as a function of egg weight for different waders (table 3). Open symbols: Charadriidae, closed symbols: Scolopacidae. Line shown for precocial birds after Calder III (1982)

Table 3. Egg weights (*E*) in g, incubation periods (*I*) in days, fledging periods (*F*) in days, and percentage of asymptotic weight (%) at fledging, of Scolopacidae (1-18) and Charadriidae (19-28). Species number corresponds with Fig. 8. Sources: Glutz = Glutz von Blotzheim *et al.* (1975, 1977), RIN = own data Research Institute for Nature Management.

species		*E*	*I*	*F*	%	source
1	*Calidris alpina*	10.2	22	25	78	Glutz
2	*Calidris canutus*	19.3	22	18		Glutz
3	*Calidris alba*	11.2	24	17	55	Glutz
4	*Calidris pusilla*	7.3	19	14	76	Glutz
5	*Calidris temminckii*	6	21	17		Glutz
6	*Calidris himantopus*	11.2	20	17		Glutz
7	*Calidris bairdii*	10.1	20	19	77	Glutz
8	*Calidris fuscicollis*	9.8	22	17		Glutz
9	*Calidris melanotos*	12.9	22	22	80	Glutz
10	*Philomachus pugnax*	22	23	23		RIN
11	*Limosa limosa*	40.5	23	23	76	RIN
12	*Bartramia longicauda*	25.2	26	30		Glutz
13	*Numenius phaeopus*	50	27	28		Glutz
14	*Numenius arquata*	75	28	32	53	Glutz
15	*Tringa totanus*	22	23	23	76	RIN
16	*Tringa nebularia*	30.5	24	25		Glutz
17	*Xenus cinereus*	13.2	21	26		Glutz
18	*Actitis hypoleucos*	12.8	21	26		Glutz
19	*Charadrius dubius*	7.7	25	23	74	Glutz
20	*Charadrius alexandr.*	9.1	26	31		Glutz
21	*Charadrius hiaticula*	11.5	24	22	79	Glutz
22	*Charadrius vociferus*	14.5	27	31		Glutz
23	*Pluvialis apricaria*	32	31	32	66	Glutz
24	*Charadrius mongolus*	12.4	23	33		Glutz
25	*Eudromias morinellus*	16	26	28	91	Glutz
26	*Vanellus vanellus*	25	28	35	63	RIN
27	*Chettusa gregaria*	26.5	25	35		Glutz
28	*Chettusa leucura*	15.7	23	30		Glutz

therefore somewhat puzzling that so little difference is seen between the two groups in Fig. 7, as no systematic difference could be detected in the average percentage of the adult weight at which the birds fledge, nor in the relationship between this percentage and egg weights. We will have to await data on more species, especially Charadriidae, to solve this riddle. The discrepancy is mainly caused by the Ringed plover *Charadrius hiaticula*, and the Dotterel *Eudromias morinellus*, both showing relatively rapid growth, and due to a sample of Scottish Lapwings (one-year study only) which appeared to grow much faster than Dutch ones generally do (Redfern 1983). Differences in development rates between species living under different climatic conditions have been explained in terms of adaptive growth strategies in the accompanying paper (Beintema & Visser 1989).

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SAMENVATTING

Groeicurven worden gepresenteerd voor diverse parameters, voor drie soorten: de Kievit *Vanellus vanellus*, Grutto *Limosa limosa* en Tureluur *Tringa totanus*. Voor alle curven wordt de groeicoëfficient volgens de formule van Gompertz gegeven. Kuikens in gevangenschap blijken doorgaans sneller te groeien dan kuikens in het veld. In het veld lopen kuikens vaak groeivertraging op als gevolg van slecht weer. Bij koude gaat dan zoveel tijd verloren met het door de ouders warm gehouden worden, dat onvoldoende tijd over blijft om genoeg voedsel op te nemen. Groeivertaging blijft bij Kievitkuikens tot latere leeftijden optreden dan bij de Grutto. Bij de verschillende soorten weidevogels valt het geboorteseizoen juist samen met het die periode in het vroege voorjaar, waarin gewoonlijk het aantal droge uren boven 15°C tussen zonsopgang en zonsondergang, en daarmee de beschikbare fourageertijd voor kleine kuikens, plotseling sterk stijgt. Voor de snavellengten worden ijkkrommen gepresenteerd, die gebruikt kunnen worden om in het veld leeftijden van kuikens te schatten. Groeisnelheden tussen verschillende soorten Charadriidae en Scolopacidae worden vergeleken. In het algemeen groeien Charadriidae langzamer dan Scolopacidae. Verschillen in ontwikkelingssnelheid houden verband met opgroeistrategieën onder verschillende klimatologische omstandigheden.

Chapter 5

The effect of weather on time budgets and development of chicks of meadow birds.

A.J. Beintema & G.H. Visser

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THE EFFECT OF WEATHER ON TIME BUDGETS AND DEVELOPMENT OF CHICKS OF MEADOW BIRDS

A.J. BEINTEMA[1] & G.H. VISSER[2]

ABSTRACT Time budgets of chicks of the Lapwing, Black-tailed Godwit, and Redshank consist of alternating bouts of foraging freely, and being brooded by a parent. The lengths of brooding and foraging bouts depend on temperature and age. The foraging percentage, defined as percentage of time available for feeding, increases with the ambient temperature, as brooding bouts decrease in length, and foraging bouts increase in length. Foraging percentages also increase with age, when the chick improves its own thermoregulation. Above a threshold temperature brooding ceases. This threshold temperature decreases with age. Rain has an extra cooling effect, which cannot be expressed as a simple chilling factor, as the effect itself changes with age.From the data, a model has been derived, which can be used to predict the percentage of time available for feeding, based on the chick's age, and weather conditions. In adverse weather conditions, small chicks may need so much brooding, that too little time remains to feed. Chicks then show retarded growth, and may eventually die of starvation.

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INTRODUCTION

The Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, and Redshank *Tringa totanus*, are representatives of a bird community known as meadow birds in The Netherlands. They form an important and characteristic element of the Dutch avifauna (Van Dijk 1983, Piersma 1986). At present their numbers are declining because of the intensification of the agricultural management of their grassland habitat (Beintema 1983, 1986). The breeding biology of these species has been well studied (Van Balen 1959, Byrkjedal 1985, Grosskopf 1958, 1959, Klomp 1954, Lind 1961), but much remains to be learnt about the chick stage. In the chick stage most losses occur: while adult mortality ranges between 10% and 30% per year, and egg losses vary between 10% and 50% (Beintema & Müskens 1987), chick losses may exceed 75% (Beintema & Drost 1986). Causes of chick mortality include: lack of suitable food (insects), being killed by mowing, and adverse weather conditions for feeding. Food and feeding habits of chicks have been studied, but a relationship between food supply and mortality has not yet been established. The quantitative impact of mowing has not been estimated, but most observers suspect that losses among chicks, of at least the Black-tailed Godwit, are heavy. Weather is an important factor: in the Lapwing cold spells lead to retarded growth and increased mortality (Beintema 1978, Beintema & Visser 1989), in the Capercaillie Schröder *et al.* (1982) explain fluctuations at population level by weather-induced chick mortality, and Koskimies & Lathi (1964) even consider cold tolerance in chicks as a key factor explaining northern and southern limits of the species' distributions.

In the present paper we investigate the effect of weather on the time budgets of chicks (feeding versus brooding bouts), and we present a descriptive model to predict the lengths of feeding and brooding bouts from the age of the chick, and the ambient temperature.

METHODS

Study area and study design

The study was carried out in 1981 (Visser 1983) and 1984, in the meadow-bird reserve 'Kievitslanden' in Oostelijk Flevoland (52°24'N, 5°40'E). The reserve consists of 98 ha of wet grasslands, intersected at regular intervals by drainage channels. The reserve is heavily grazed by wild geese during the winter. The western part is mown in June, while the eastern part is grazed by cattle in summer. For details on management see De Jong (1972) and Zijlstra (1986).

The behaviour of meadow bird families with chicks was studied. As families wander considerably, and are susceptible to disturbance in their movements, a group of nests was fenced in, and a hide was erected just outside the enclosure, 2 m above the ground. Enclosures were 55-65 m wide, and 130-180 m long. They were constructed from wire-netting (mesh 1 cm), which was 50 cm high and firmly pinned to the ground. In order to minimize disturbance, construction work was limited to a daily maximum of three periods of one hour,during the middle of the day. The fence was completed within three days, in late April, before the first hatchlings appeared. Hatching dates were estimated with an 'incubometer', using flotation of the eggs (Van Paassen *et al.* 1984).

The wire-netting caused an unexpected problem: the adult birds sometimes took up a brooding posture just outside the fence, and called their chicks, which then tried to reach them in vain. Thus, one Godwit brood died of exposure. The problem was solved by attaching a 25 cm wide strip of black plastic foil to the fence, which made the chick invisible to a parent sitting on the other side. The fence did not deter the birds: additional pairs of Lapwing, Black-tailed Godwit, and Redshank started to nest within the enclosure. However, the set-up possibly repelled predators, as no eggs or chicks were lost to predation in either 1981 or 1984. In 1981, four pairs of Lapwings, four pairs of Black-tailed Godwits, and one pair of Redshanks nested within the enclosure. In 1984, there were four, two, and one pair(s), respectively. The chicks were never seen to favour the vicinity of the fence, where they may have profited from shelter or an improved microclimate.

Definition of terms

In the time budget of the chicks we simply distinguish between brooding bouts and foraging bouts. A brooding bout is an uninterrupted period of time spent being brooded by a parent. A foraging bout is the time spent between two brooding bouts. This time is not necessarily spent in continual foraging; in fact it is the 'time available for foraging'. However, smaller chicks do spend all of it foraging. Foraging and brooding bout lengths are not complementary (theoretically, a system with fixed-length brooding bouts and variable foraging bouts could exist). Therefore, brooding and foraging bouts are treated separately.

Observations

It was possible to observe the families in all corners of the enclosure from the hide. Observations were impaired by growing vegetation, and could not be continued beyond the first week of June. Observations began half an hour before sunrise and ended half an hour after sunset. The start of each brooding or foraging bout was registered. In all Lapwing and Redshank pairs, and in all Godwit pairs except one, the sex of the brooding parent could be distinguished by colour and size. One observer could monitor four families simultaneously.Total observation time was 687, 467, and 64 hours for the Lapwing, Black-tailed Godwit, and Redshank respectively. Seven Lapwing broods were followed, four of these being followed up until fledging. Six Black-tailed Godwit broods were followed, five up until fledging. One Redshank family was followed up until fledging. The other brood could not be observed in the tall grass, although the chicks were repeatedly captured. Chicks were ringed as soon as possible after hatching. Chicks were recaptured and weighed approximately every two days. Captures were done during the warm part of the day, and the procedure never lasted longer than 45 minutes. Usually it was possible to obtain 75% of all chicks during one round. Ambient temperature was recorded with a thermograph, in the vegetation at 'chick level', i.e. 10 cm above the ground. The registrations permitted readings up to every 2.5 minutes. Changes in the weather (cloudiness, rainfall) were noted.

Data analysis

The average air temperature was calculated for each brooding or foraging bout. Only fully observed, undisturbed bouts were used for analysis. The data were divided into two sets for each species: a 'dry' set without, and a 'wet' set with rain. The effect of the ambient temperature and the age of the chick on the length of brooding or foraging bouts was estimated in a regression model, for both the dry and wet data set.

RESULTS

Behaviour of parents and chicks

Most brooding was done by the female in the Lapwing and Black-tailed Godwit, while in the Redshank both sexes shared the duties (Table 1). In the Lapwing, the share of the male increased after two weeks, allowing the females to feed elsewhere. In the Black-tailed Godwit males were only seen brooding during the first week. In one case, when a family with small chicks was exposed to three cold, rainy days, the share of the male increased from 0% on the first day to 14% on the third. The chicks spent 24% of their time feeding during this day. The female spent all this time, and all extra time when the male relieved her, feeding. In all species the initiative for brooding could be taken by the parent, or by the chicks. In the first case, a parent started to walk around the chicks, and took up brooding posture. In the second case chicks started calling, and walked towards the parent, which then took up a brooding posture.

Table 1. The share of the female (% of total brooding time by male and female) in brooding of the chicks, during the daylight hours.

Age days	Lapwing (%)	Black-tailed Godwit (%)	Redshank (%)
1- 7	96.8	94.4	50
8-14	97.5	100	
8-10	-	-	50
5-21	89.2	-	-

Brooding was often done at the edge of a ditch, providing escape possibilities for the chicks, when disturbed by man or predator. Chicks were mostly brooded together. In one case, a Lapwing chick, when suddenly caught up in bad weather, failed to reach the brooding parent in time, and became immobile through hypothermia. The partner found the chick, and brooded it. Mortality on account of acute exposure was never observed. Brooding stopped when the chicks emerged to feed, or the parent got up and walked away. In the Lapwing and Black-tailed Godwit the female was mostly on guard when the chicks were foraging. The female left to feed elsewhere, when the male took over. In the Redshank both parents were often present.

Other animals (i.e. mammals, birds) were kept at least 20 m away from the chicks, and were chased by the male, and in severe cases of intrusion the female became involved in chasing as well. Mobbing a weasel attracted parents from a dozen other families of different species from throughout the area. Neighbouring families of the same species were often chased away, chicks being severely pecked. However, sometimes families tolerated each other, and allowed their chicks to mix. One Godwit chick permanently changed family, and was also brooded by the foster parent. Adoption has previously been observed in the Lapwing, under high density conditions (own data).

Growth and survival of chicks

Fig. 1 gives the growth curves for the chicks in the enclosures. Growth parameters are dealt with in the accompanying paper (Beintema & Visser 1989). In four Lapwing families followed until fledging, 4 of the 15 chicks died, at ages varying from 4 to 13 days. Three of these chicks showed retarded growth. All chicks fledged (16 in total) in five Godwit families followed up until fledging. This

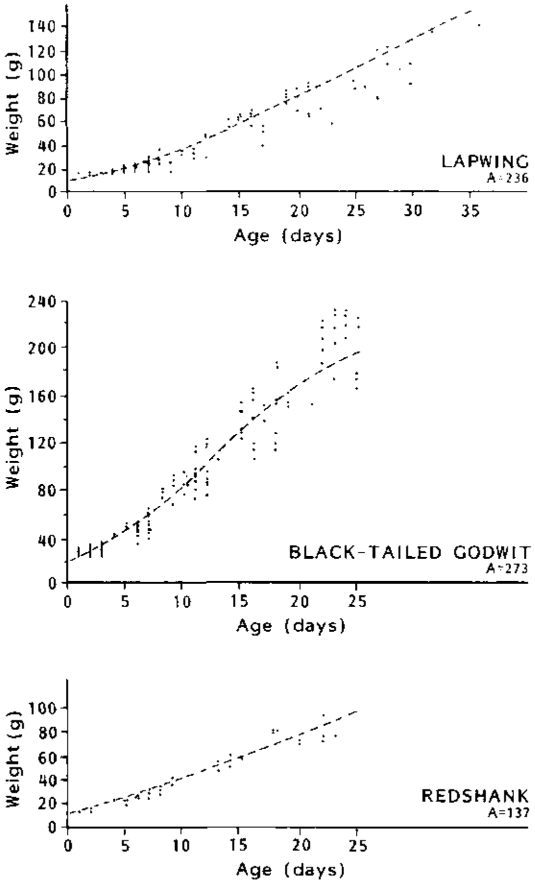

Fig. 1. Development of the weights of chicks in the enclosure. For comparison with average growth in The Netherlands, lines give fitted Gompertz' growth curves, based on all available Dutch data (Beintema & Visser 1989). A = asymptotic value of Gompertz' curves.

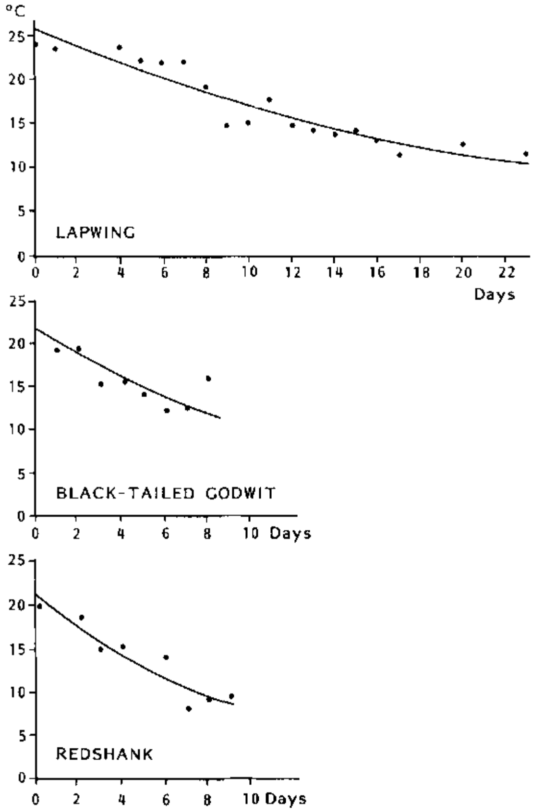

Fig. 2. Threshold temperature, above which no brooding by a parent takes place, as a function of age.

is a remarkably high value since the average survival rate of Godwit chicks up until fledging has been estimated at 21% (Beintema & Drost 1986).One of the eight Redshank chicks died after 3 days. It did not differ in body weight from its surviving siblings.

The model

As the chicks grow, they require less brooding by their parents. A striking change in brooding behaviour was the increase in the period without any brooding during the middle of the day. A threshold temperature was observed, above which there was no brooding. In Fig. 2 the highest temperature which brooding has ever been observed is given for each age (age given in days). Lines were fitted as

$$\log(\text{threshold}) = C + a * \text{age}$$

C = 3.284, 3.142, and 3.159, a = -0.034, 0.071 and -0.101 for the Lapwing, Black-tailed Godwit, and Redshank,respectively. Below this threshold, brooding and foraging bouts alternated. This threshold decreased rapidly with age in the Godwit and Redshank, and decreased much more slowly in the

Lapwing.Below the threshold, the length of both brooding and foraging bouts varied with the ambient temperature. At lower temperatures, brooding bouts increased, and foraging bouts decreased in length. Bout lengths were fitted against ambient temperature, and the age of the chicks. A simple logarithmic model was assumed based on the supposed asymptotic nature of the relationship between both factors and the length of foraging or brooding bouts:

$$\log(\text{timespan}) = \text{constant} + a * \text{temperature} + b * \text{age}$$

in which timespan stands for bout length (in decimal hours * 1000), temperature is given in °C and age in days. The model only serves to describe the data, not to explain it. In a more explanatory model, the temperature relative to the threshold would seem more appropriate, as a relevant parameter. However, the threshold was left out of the equation, because it would make the model very sensitive to the accuracy with which the threshold can be estimated, and it would introduce a strong interaction between the parameters.

The variation in the data was reduced (smoothed) by calculating two-dimensionally running mean bout lengths for each block of nine cells (three age values in days against three whole-degree temperature values), discarding means based on less than five observations. The model was fitted through the running means, for the three species, and for the dry and wet data set separately. Coefficients are given in Table 2. Residuals were calculated by subtracting the calculated fitted value (after smoothing) for the corresponding age and temperature from each observed value (before smoothing). The same model (timespan = residual) was fitted through these residuals, to estimate the mean deviation, for the positive and negative residuals separately.Foraging percentages were calculated for each combination of age and temperature from the fitted values for brooding and foraging bouts. The effect of rain was estimated by comparing foraging percentages for the dry and wet data set.

Simulation of foraging percentages

The model can be used to predict foraging percentages for chicks of various ages, under various weather conditions, using the coefficients from Table 2. This was done for our own data, to test the model. This looks like 'circular reasoning', as these data have been used to estimate the parameters in

Table 2. Coefficients in the model log(timespan) = $C + A * \text{temperature} + B * \text{age}$. BR is timespan = length of brooding bout, FO is timespan = length of foraging bout, DRY in dry weather, WET in rainy weather. Values for WET only applicable below 22°C for the Lapwing, and below 13°C for the Black-tailed Godwit. Timespan in decimal hours * 1000, temperature in °C, age in days. Age at birth defined as age 1, etc.

			A	*B*	*C*
Lapwing	DRY	BR	-.03985	-.00769	5.7035
	DRY	FO	.06002	.04014	3.9943
	WET	BR	-.081	.00655	6.1956
	WET	FO	.0517	.04328	3.7469
Black-tailed Godwit	DRY	BR	-.02889	-.11141	5.7498
	DRY	FO	.07178	.2263	3.7353
	WET	BR	-.0827	-.132	6.676
	WET	FO	.1784	.2363	2.6113
Redshank	DRY	BR	-.02214	-.0113	5.082
	DRY	FO	.1495	.1994	2.0476

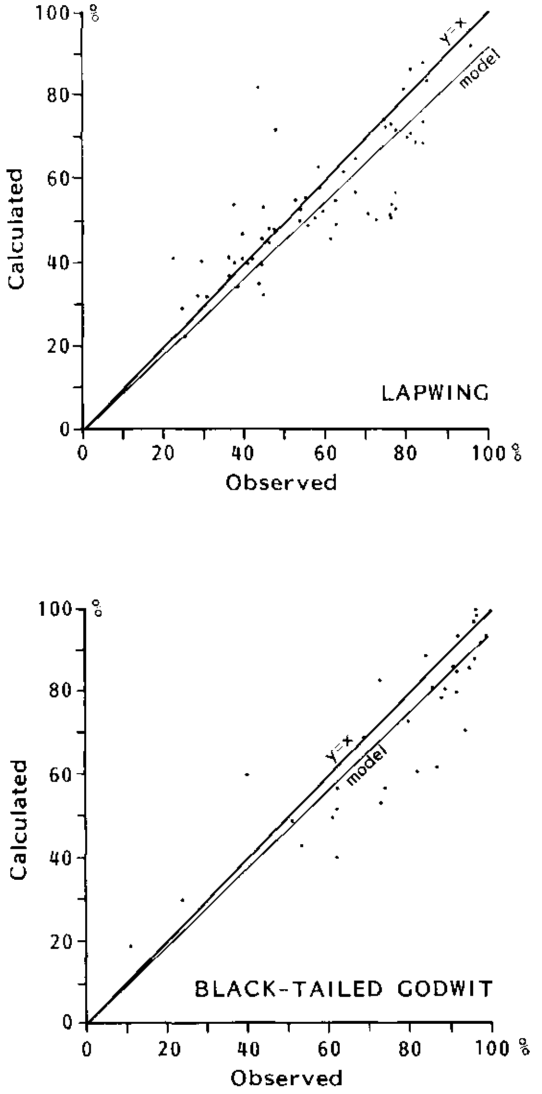

Fig. 3. Relationship between observed and predicted foraging percentages.

the model. However, the true foraging percentages have not been used in the analysis, only the lengths of brooding and foraging bouts, which may vary independently, as has been pointed out earlier. The actual percentage of time available for foraging was calculated from the field observations, for each day for each family under observation. Predictions were made for the same days (only for the ages observed), using the formulae derived above, and the weather recordings of these days. The day was divided into periods of five minutes from sunrise to sunset. The foraging percentage was predicted for each period, during which the temperature was assumed to have been constant. These figures were then accumulated into a percentage for the day. Simulations were only performed for the Lapwing and Black-tailed Godwit. Fig. 3 shows the relationships between observed and calculated values. Lines fitted through the origin did not differ significantly from the line of equivalence, $y = x$ ($P < 0.01$, F-test on sum of least squares).

Brooding and foraging bouts in dry weather

The relationships between bout length, age, and temperature are presented in Fig. 5 (brooding bouts) and 6 (foraging bouts). Fig. 4 demonstrates the three-dimensional relationship between timespan, age, and temperature, and how the two-dimensional representation in Fig. 5 and 6 has been derived from this, giving the bottom plane with isorythms of timespan values, and two vertical cross sections. The effect of the ambient temperature on the time budget for small chicks did not differ much between the species. As the chicks grew older, the length of brooding bouts decreased, and the length of foraging bouts increased, at a given temperature. This change took place rapidly in the Black-tailed Godwit, but slowly in the Lapwing. Thus, in cold weather Lapwing chicks remain dependent on their parents much longer

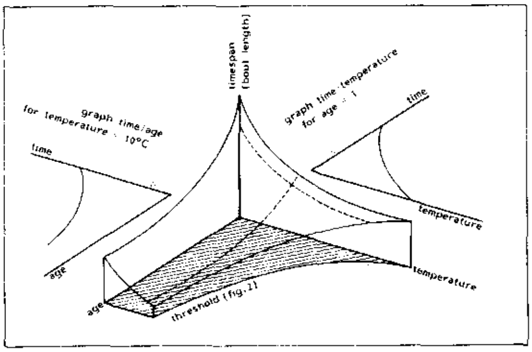

Fig. 4. Three-dimensional diagram of the relationship age-temperature-timespan, illustrating composition of figs 4 and 5.

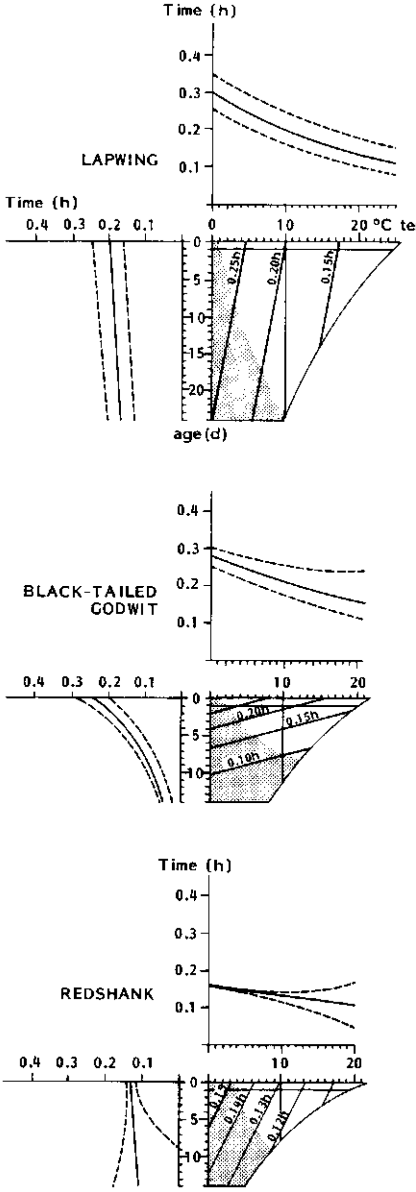

Fig. 5. Length of brooding bouts as a function of ambient temperature, and age of the chick. The diagram only shows the temperature range between the freezing point and the threshold temperature (Fig. 2). Diagonal lines connect points (age-temp. combinations) with equal bout lengths (decimal hours). No observations are available in shaded areas (values have been extrapolated here). Graphs give two sample sections through diagram, with mean deviation.

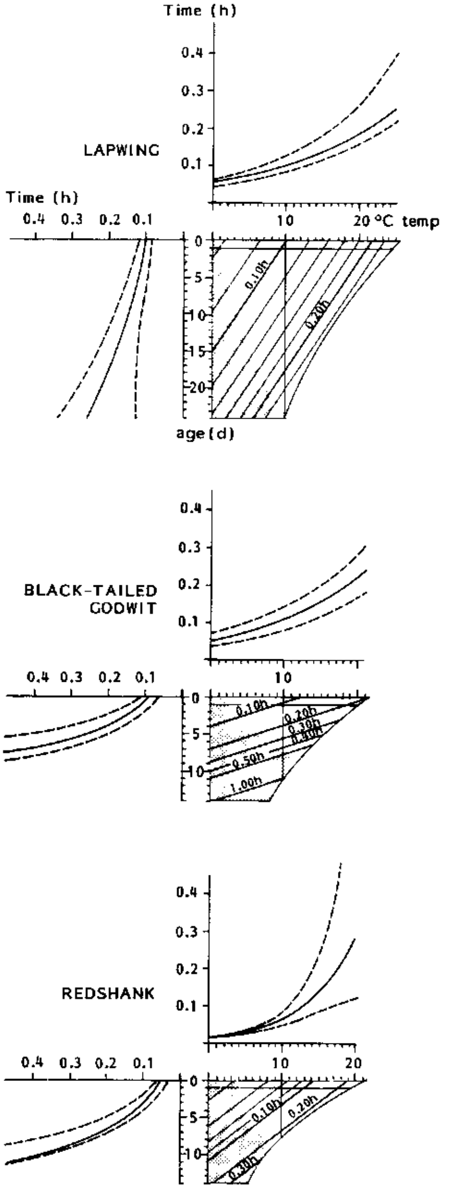

Fig. 6. Length of foraging bouts as a function of ambient temperature, and age of the chick. Explanation as Fig. 5.

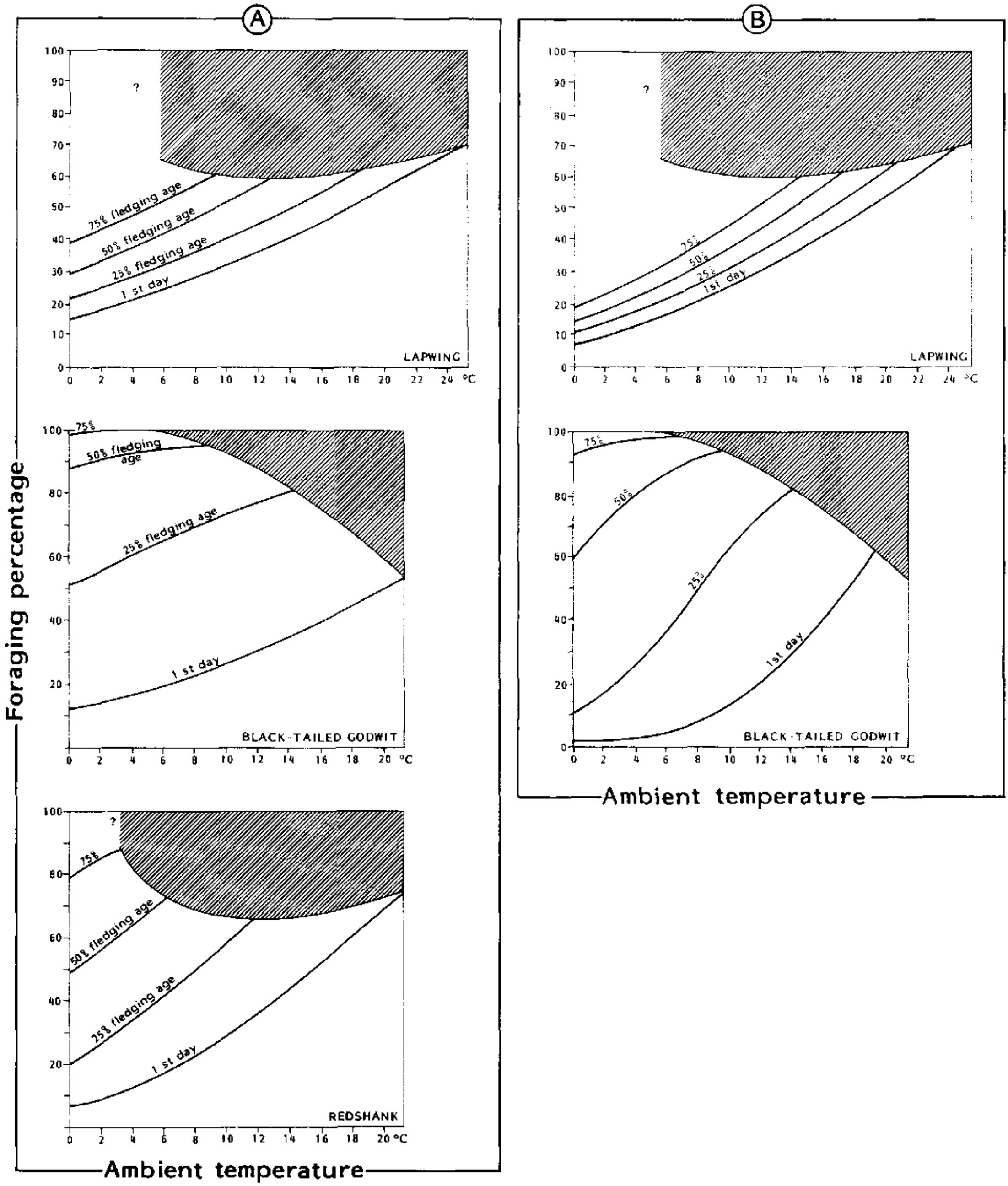

Fig. 7. Foraging percentages in dry weather (7a), and rainy weather (7b), calculated with the coefficients from Table 2, as a function of ambient temperature, for four different relative ages. Values in shaded area are always 100%, because temperatures exceed threshold (Fig. 2). Data are insufficient to calculate separate threshold temperatures for rainy weather.

than Black-tailed Godwit chicks. In the Black-tailed Godwit, the lengths of brooding and foraging bouts greatly depend on age, and less on temperature, while in the Lapwing the reverse applies. The Redshank holds an intermediate position.To further visualize the different responses of the species, Fig. 7 has been constructed, using the coefficients from table 2. Fig. 7a shows the percentage of the time available for foraging, as a function of the ambient temperature, in dry weather, for four different relative ages, expressed as a percentage of the fledging age. Fledging age is 35, 27, and 26 days in the Lapwing, Black-tailed Godwit, and Redshank, respectively (own data).In cold weather (below 5°C) small chicks (1-3 days) of all three species, did not have more than 10 - 20% of their time available for foraging. At the same temperatures, half grown Black-tailed Godwits are virtually independent of brooding, half grown Redshanks can spend over 50% of their time feeding, and halfgrown Lapwings only 35%.

The effect of rain

For the 'wet data set', brooding bouts, foraging bouts, and foraging percentages were calculated. Rain has a chilling effect, because at the same temperatures brooding bouts tended to be longer, and foraging bouts shorter, than under dry conditions.In the Lapwing, brooding bouts did not increase in length at temperatures above 15°C, but were almost doubled at the freezing point, for all age classes. Foraging bouts were reduced by 25-45%, with little difference between age classes or temperatures. This resulted in a considerable reduction in foraging percentages (Fig. 7b). The effect of rain decreases with higher temperatures, and is only discernable when the temperature falls to below 22°C. The effect is rather independent of age.In the Black-tailed Godwit the effects of rain were about equally strong on brooding and foraging bouts. Brooding bouts could be doubled, and foraging bouts reduced to 50% at lower temperatures in small chicks. No reduction in foraging percentage was found at temperatures above 13°C. In this species there is a strong age effect: the chilling effect of rain diminishes with age.For the Redshank, there are insufficient observations in rainy conditions to allow analysis. Values could only be calculated in the temperature range 7-9°C for ages 4-6 days.Within this range, reductions of foraging percentages of 29-57% were found. Within the same range, the reduction in foraging percentage varied from 20-47% in the Black-tailed Godwit, and from 28-35% in the Lapwing.The rain effect cannot be expressed as a simple 'chilling factor', analogous to usage in human Physiology (Leblanc 1975), as the effect itself changes with age.

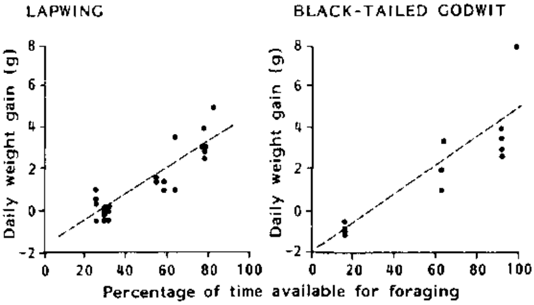

Fig 8. Relationship between growth (daily weight gain) and observed foraging percentages, in chicks of less than a week old.

Foraging percentages needed for growth

Weight increase per day was plotted against the foraging percentages observed in the field for the Lapwing and Black-tailed Godwit chicks, during their first week of life (Fig. 8). In both species, small chicks cannot maintain weight at foraging percentages below 25-30%. Growth is hampered at percentages below 50.The accompanying paper (Beintema & Visser 1989) shows how weight gain is related to the number of daylight hours above a certain temperature (15°C) in small chicks.

DISCUSSION

Development of thermal independence

As the surface area of birds is related to the two-third power of weight (Calder & King 1974), the ratio of heat production (mass related) to heat loss (surface related) in newborn chicks is most favourable in the Black-tailed Godwit (29 g at hatching), and least favourable in the Redshank (16 g): the Lapwing (18 g) is intermediate. In spite of this, Redshank chicks forage at lower temperatures than Lapwing chicks and are almost as hardy as the much heavier Godwit chicks, indicating that Redshank chicks spend more energy on heat production than Lapwing chicks, or have better insulation. In addition to this, thermoregulation develops more slowly in the Lapwing. The Black-tailed Godwit and Redshank reach thermal independence at 40-50% of the fledging age, the Lapwing at 70%. In the Semipalmated Sandpiper, studied at Point Barrow, Alaska, brooding has been observed up until 65% of the fledging age (Ashkenazie & Safriel 1979), and in the Ringed Plover,studied in Greenland, until 75% (Pienkowski 1984). Wader chicks perform normal behaviour at body temperatures far below the adult's temperature, which reduces heat loss, and the cost of thermoregulation (Norton 1973, Ricklefs 1974, 1979, 1983). For example, small Lapwing chicks, when brooded, won't even let their temperature rise above 37.5°C (Myhre & Steen 1979), and let their temperature drop to almost 30°C when feeding (Visser, unpubl. data).

The role of the parents

Brooding of chicks may affect the time and energy budgets of the parents, as time spent brooding or standing guard cannot be used for foraging. Some weights of the Redshank parents are available up until 16 days after hatching (Visser unpubl. data), but no change could be detected in weights of either females or males during development of the chicks. When not on guard, parents often went feeding in other habitats to these that the chicks frequented. Ashkenazie & Safriel (1979) assumed that this avoids food competition between parents and chicks in arctic waders. This is not likely in our species as chicks and parents have different diets: chicks hunt for insects in the vegetation, while the adults probe for soil fauna. Later in the nesting season, the meadows may become a rather poor feeding habitat for adults, as the soil fauna retreats to greater depths, especially in well drained places (Visser 1982). When they have no chicks, the adults leave such areas, to gather in wetter places.

Zoogeographical aspects

Interspecific differences in cold tolerance have a zoogeographical and taxonomic perspective. Koskimies & Lahti (1964) have shown a relationship between cold-hardiness of ducklings, and the north-south extent of the species' distribution. They also found that chicks of gallinaceous birds are more sensitive to cold than those of ducks.Early development of thermoregulation in chicks has its costs. Energy intake has to be high, and problems of high metabolic rates in warm weather may even put a southern limit to the distribution of species (Koskimies & Lathi 1964). Less hardy chicks do not face these problems, but under cold conditions the time available for foraging is reduced, as the parents have to brood them. This does not prevent species with more sensitive chicks from penetrating far north. Koskimies & Lahti (1964) concluded that species with chicks of different cold-hardiness do not differ much in the northern limit of their distribution, but differ much more in their southern limit. They considered low energy-expending young as being ecologically more plastic, and generally more successful, with the Mallard *Anas plathyrhynchos* as a typical example within the duck family. The northern tetraonids have the more 'expensive', cold-tolerant chicks among the gallinaceous birds. The chicks of the Capercaillie are more sensitive than those of the Black Grouse, *Tetrao tetrix* (Moss 1986), in spite of being bigger. Whether the Capercaillie is indeed a more southerly species than the Black Grouse by origin, cannot be judged from its present distribution, which has been severely restricted by man.

The three wader species in the present study range more widely from south to north than most other (more northern) wader species, which fits the ideas of Koskimies & Lathi (1964). Although the differences in range are small, the Lapwing is the least northern, the Black-tailed Godwit the least southern, and the Redshank embraces both regions. This is in accordance with the differences in their development of thermoregulation. There is an interesting difference between the Plover family (Charadriidae), to which the Lapwing belongs, and the Sandpipers (Scolopacidae), to which the Black-tailed Godwit and Redshank belong. Plovers have longer incubation periods, longer fledging periods, and longer total life spans than sandpipers (Beintema & Visser 1989), and the chicks depend on brooding far longer. Sandpipers have mostly northern distributions, in colder climates, whereas plovers occur all over the world, in many climates, with only few representatives in the arctic. One may suppose that not only weak thermoregulation, but also slow development is an adaptation to keep the running costs of chicks low. This may be less advantageous in cold areas than in arid habitats, where food is more likely to be scarce or thinly distributed at times. Latitudinal trends in growth rates have been shown by various authors (see Drent & Klaassen 1989). Slow development as a buffer against unpredictable food resources has also been postulated for a variety of seabird species (Drent & Daan 1980).

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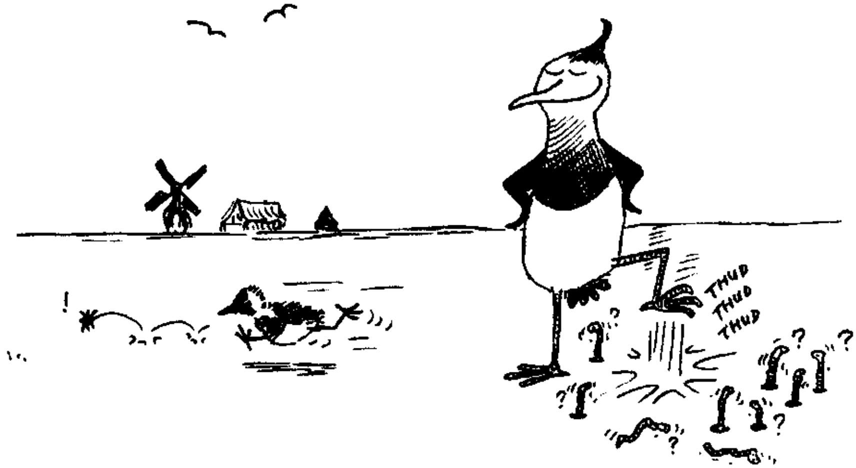
SAMENVATTING

De tijdsbesteding van kuikens van drie weidevogelsoorten (kievit, grutto en tureluur) werd bestudeerd, in samenhang met de weersomstandigheden. De tijdsindeling van een kuiken bestaat uit een afwisseling van periodes waarin zij vrij lopen te fourageren en periodes waarin zij door een ouder worden opgewarmd. De lengte van opwarm- en fourageerperioden hangt af van de omgevingstemperatuur en de leeftijd van het kuiken. Het fourageerpercentage, ofwel het percentage van de tijd dat voor fourageren beschikbaar is, neemt toe bij stijgende temperatuur, omdat dan de opwarmperioden korter worden en de fourageerperioden langer. Het fourageerpercentage neemt ook toe met de leeftijd, omdat de eigen warmteregulatie van het kuiken zich beter ontwikkelt. Regen geeft een extra afkoelingseffect. Hiervoor kan niet met een eenvoudig 'behaaglijkheidscijfer' gecorrigeerd worden, omdat het effect zelf met de leeftijd verandert. Uit de gegevens is een model afgeleid waarmee fourageerpercentages voorspeld kunnen worden, als de leeftijd van het kuiken en de weersomstandigheden (temperatuur en neerslag) bekend zijn. Bij slecht weer kan het voorkomen dat kleine kuikens zoveel tijd nodig hebben om warm gehouden te worden, dat te weinig tijd overblijft om te fourageren. Kuikens lopen dan groeivertraging op en kunnen uiteindelijk van honger omkomen.

Chapter 6

Feeding ecology of charadriiform chicks in agricultural grassland.

A.J. Beintema, J.B. Thissen, D. Tensen & G.H. Visser



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FEEDING ECOLOGY OF CHARADRIIFORM CHICKS IN AGRICULTURAL GRASSLAND

A.J. BEINTEMA[1], J.B. THISSEN[1], D. TENSEN[1] & G.H. VISSER[2]

ABSTRACT Diets of chicks of the Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus*, Ruff *Philomachus pugnax*, and Oystercatcher *Haematopus ostralegus* were studied by faecal analysis. Lapwing chicks feed on surface dwelling organisms, and exploit fauna living inside cow-dung pats. Black-tailed Godwit chicks hunt for more mobile prey species, higher in the vegetation. Redshank and Ruff take intermediate positions. Oystercatcher chicks are fed on tipulid larvae and earthworms. To obtain information on food availability, macrofauna was sampled. In May, the number of arthropods in grassland rapidly increases. In June, arthropod abundance may temporarily decrease. Chicks show retarded growth from mid-May onwards, before prey abundance peaks. A hypothesis is proposed that from the energetic point of view, chicks cannot grow up on arthropod fauna alone, but have to switch to earthworms, which may become progressively difficult to obtain later in the season.

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INTRODUCTION

This paper deals with dietary studies, based on faeces analysis, of five charadriiform species (collectively known as meadow birds in The Netherlands; Beintema 1983) which nest in Dutch agricultural grasslands. Four of these species, the Lapwing, Black-tailed Godwit, Redshank, and Ruff, are nidifugeous, and their chicks have to find their own food. Thus, they are totally dependent on the prey fauna present in the grassland itself. Furthermore, they can only feed when they are not being brooded by a parent, which may become a problem in cold weather (Beintema & Visser 1989b). Chicks of the fifth species, the Oystercatcher are mainly fed by their parents. Thus they can be fed on items brought from elsewhere, and on soil fauna living out of reach for small, short-billed chicks. In addition, feeding can continue during adverse weather, when the chick has to be kept warm by a parent.

Within the group of nidifugeous species, there are differences in growth strategies (Beintema & Visser 1989a), which may have consequences for the amount of food needed, and for the choice of food items. Since all the species mentioned exploit the same resource, and can often be found at the same locations, it is interesting to investigate how they differ in their ways of feeding.

This paper presents data of a rather basic nature, but in one direction there are links to further studies on the ecology of grassland fauna, in the other direction there is a link to more quantitative studies on feeding and energetics in chicks.

MATERIAL AND METHODS

Samples of arthropod fauna

In 1981, fauna was sampled in an enclosure where families with chicks were kept under observation. Samples were collected using a sweep net, and pitfalls with ethylene-glycol (Southwood 1978, Stammer 1949, Tretzel 1955). Ten pitfalls were used, in two rows of five, at 10 m intervals. At 12 points between the pitfalls, a sample was taken with the sweep net, each time making three sideways sweeps when walking. Sweep net samples were taken on 14 May, and on 3 June. Pitfall samples were emptied on 12 May and 2 June, each time after having been in the field for 7 days. To obtain a better impression of the food availability through the chick season, fauna was sampled in the Arkemheen Polder in 1984 (Tensen 1984), using pitfalls, sweep net, and a small, battery-powered exhauster (a suction apparatus, based on a small fan, sucking air through a narrow nozzle). With the exhauster, as many insects as possible were removed during five minutes, in a 50x50 cm quadrant. Exhauster samples were taken every half hour, between sunrise and sunset, on 11 days, from April 14 to July 5. During sampling, notes were taken on cloud cover, wind, moisture, temperature, and vegetation length.

Diet samples

During ringing activities from 1977-1981 790 faeces samples of charadriiform chicks were collected: 309 from the Lapwing, 191 from the Black-tailed Godwit, 177 from the Redshank, 71 from the Oystercatcher, and 42 from the Ruff. All samples were collected in agricultural grasslands, utilised for dairy farming, mostly in the provinces of Friesland, Utrecht, and Gelderland. For each sample the following parameters were noted: the bill length of the chick as age estimator (Beintema & Visser 1989a), date and locality, predominant soil type (clay, sand, peat), a judgement of the moisture conditions of the field on a three-point scale (dry, moist, wet), and a judgement of the level of intensity of agricultural management, also on a three-point scale. All samples were conserved in 70% alcohol.

Diet samples in enclosure

In 1981 and 1984 several pairs of Lapwing, Black-tailed Godwit, and Redshank raised their chicks in an enclosure, where their development was observed (Beintema & Visser 1989b). From these chicks, 60 additional faeces samples were obtained: 20 of Lapwing, 23 of Black-tailed Godwit, and 17 of Redshank. These samples were of special interest for comparison of species' diets, as they originated from the same field.

Sample analysis

Samples were examined under a microscope, using magnifications of 10, 20, or 40x. If samples were too obscured by fine debris, they were sieved, using four successive sieves, with a mesh of 1.0, 0.5, 0.25, and 0.125 mm, respectively. To eliminate the effect of increased experience during identification, analysis of all samples was started all over again after the first 150 had been examined. This was done again after 300 samples. After this, hardly any new taxa were identified. Identification was usually possible at the family level (Chinery 1975, Colyer & Hammond 1951, Freude *et al.* 1965-1983, Reitter 1908-1916, Locket & Millidge 1951-1953). Larvae and imagines were treated as separate groups.

Twenty samples from Redshank chicks did not contain any recognisable fragments. These were all from chicks with a bill length of 19 mm or more. This corresponds with an age of 6-7 days (Beintema & Visser 1989a). At this age, the chicks probably start to produce regurgitated pellets. Such pellets were produced twice by an older chick during capture. Consequently, all samples from Redshank chicks with bill lengths of 19 mm or more were excluded from analysis. Two samples from the Lapwing, and one from a Ruff, did not contain recognisable fragments, and were also excluded from analysis. These were from very small chicks, which were probably still surviving off yolk reserves. A further ten samples from the Ruff, and 12 from the Redshank were excluded, since they were too small to be representative. Finally, when more samples were taken within one family, only one was chosen (randomly) for analysis. Thus, 262, 144, 23, 56, and 24 samples remained, for Lapwing, Black-tailed Godwit, Redshank, Oystercatcher, and Ruff, respectively. Samples were mainly examined on a qualitative basis (absence or presence).

To determine the relationship between food composition and explanatory variables, canonical correspondence analysis was used (Ter Braak 1986).

Growth data

To investigate the possible relationships between date, food availability and chick growth, daily weight gain was calculated from recaptures of chicks, using the material obtained with the aid of many bird ringers, during a 10-year chick-ringing programme (1976-1985). The same data has been used earlier (Beintema & Visser 1989b) to show a relationship between weight gain (in small chicks only) and the amount of dry, warm weather.

Digestion experiments

Chicks raised in captivity for other purposes (Beintema & Visser 1989a, 1989b) were used to measure the time elapsing between consumption of insects and their appearance in the faeces, in order to obtain an impression of the probability of a sample representing the fauna found in the same field where a chick was captured. After having been fed for some time on commercial food, which yielded no recognisable fragments, chicks of four and eleven days old, of both Lapwing and Black-tailed Godwit, were offered ten flies (*Musca domestica*), ten beetle larvae (*Tenebrio molitor*), and ten caterpillars (*Galleria mellonella*). Faeces were collected every hour during the next ten hours, and examined for four types of fragments: wings (20 items) and legparts (360 items) of the flies, and jaws (20 items) of the beetle larvae and caterpillars.

RESULTS

Treatment of taxa

About 120 taxa could be distinguished in the faeces, mostly to family level, sometimes to genus level (e.g. *Scatophaga*). The number of taxa found in fauna samples is even higher. In the results presented, taxa are grouped in different ways: in Table 1 only the larger taxa are given, to illustrate a general change in abundance. In Table 2 the main criterium for splitting up larger taxa was the amount of variation in size classes: this is the case within the Nematocera and Brachycera. Coleoptera have not been split up, as all families found fall into the largest size class distinguished. In Table 3 the three important groups Nematocera, Brachycera, and Coleoptera have been partly split up, for those families commonly eaten, as these families show considerable differences in their ecology.

Table 1. Pitfall and sweep net samples of fauna, in the Kievitslanden. Figures give the average number of representatives of larger taxa per sample.

	pitfall 5-12 May	sweepnet 14 May	pitfall 27 May-2 June	sweepnet 3 June
Lumbricidae	6.4		2.4	
Gastropoda	7.8		33.5	
Auchenorrhyncha	1.4		5.3	
Sternorrhyncha	1.1		1.5	
Nematocera	3.9	4.8*	2.4	35.8*
Brachycera & Cyclorrhapha	10.5	9.1	11.2	33.3**
Hymenoptera	3.0	0.8	9.2	4.2
Coleoptera	25.4		31.9	
Araneida	61.7		32.8	
Larvae	0.9			
Other insects	0.1	0.7	0.1	3.8

* >90% Chironomidae

** mainly *Oscinella frit*

Table 2. Presence (in percentage of samples) of taxa in faeces (bird species combined) and in exhauster samples. Size class 1: taxa in which most common species range between 0 and 4 mm; size class 2: 2-6 mm, size class 3: 4-20 mm (or larger).

	size class	faeces	exhauster
Lumbricidae	3	9.7	0.6
Gastropoda	3	22.2	4.1
Sminthuridae	1	1.2	24.8
Auchenorrhyncha	3	3.2	49.7
Aphidoidea	1	7.6	53.8
Tipulidae	3	44.9	4.5
Mycetophilidae	1	5.9	9.6
Chironomidae	2	60.5	54.5
Tabanidae	3	1.6	1.0
Empididae	2	30.3	18.8
Rhagionidae	3	0.5	3.5
Dolichopodidae	2	49.7	9.6
Syrphidae	3	6.5	1.0
Sepsidae	1	2.7	7.3
Opomyzidae	2	1.1	2.2
Ephydridae	2	2.2	8.6
Chloropidae	2	12.4	26.4
Drosophilidae	1	0.5	0.6
Agromyzidae	1	3.8	1.6
Muscidae	3	40.0	3.5
Scatophaga	3	71.4	2.9
Hymenoptera	2	81.1	27.7
Tenthredinidae	3	38.4	0.6
Coleoptera	3	89.2	14.0
Araneida	3	16.2	36.3

Food availability

The fauna samples from the enclosure in the Kievitslanden are summarised in Table 1. Most noticeable is the increase in the number of midges (Nematocera), and flies (Brachycera & Cyclorrhapha). This is mainly attributable to Chironomidae and Chloropidae, which together made up 77% of the catches on 3 June. An increase in available food items is less evident from the pitfall samples.

The relative abundance of arthropods obtained using pitfalls, a sweep net, and an exhauster, in Arkemheen, is given per 10-day period (Fig. 1). The samples obtained with pitfalls appeared to be the most unpredictable and showed too much variation in composition to allow much comparison with the other methods. As in the Kievitslanden, pitfall samples show that food may be more abundant than suggested by sweep net samples earlier in the season. Both sweep net and exhauster samples showed a marked increase (the former starting in early May, the latter during late May) followed by a decrease during the second half of June. The sweep net gave poor results in April, followed by an explosive development in May. The exhauster samples showed a more steady increase, during April and May. The number of arthropods in the samples were fitted (simple linear regression) against vegetation length, and three temperature parameters: actual temperature, cumulative daily average, and cumulative daily minimum. The variation in the number obtained by sweep net could be best explained by the variation in vegetation length (determination coefficient $R^2 = 0.9824$, $p < 0.01$; Sokal & Rohlf 1981), with the cumulative average daily temperature as second best explanatory variable ($R^2 = 0.5248$, $p < 0.05$); relationships with the other temperature variables were not significant. In the exhauster samples the cumulative average daily temperature gave the best fit ($R^2 = 0.6293$, $p < 0.05$), followed by the other temperature variables and finally the vegetation length ($R^2 = 0.4596$, $p < 0.05$). The peak in the sweep net samples is found to be later than that in the exhauster samples, but this is mainly attributable to tiny flying insects which may not provide much profitable prey. When only arthropods with a length of more than 3 mm are considered, both methods show a peak around the first week of June (period 16, Fig. 1). Yalden (1986), who studied food availability for Common Sandpipers in a riparian habitat in Britain, found similar peaks, both in numbers and weights of insects, in the last days of May and the first days of June.

From a methodological point of view, the results suggest that the exhauster method is best suited to assess a relative measure of prey availability for wader chicks, also because this method (unlike the use of a sweep net) is not dependent on dry weather conditions.

Table 2 gives the presence of taxa (expressed

Table 3. Occurrence (% of samples) of food items in faeces of chicks. S: soil, V: vegetation, D: cow dung (habitat codes for prey taxa). Difference between Lapwing and Black-tailed Godwit: **: $p < 0.01$ (c^2-test).

	habitat code	Oyster-catcher	Lap-wing		Bl.-td. Godwit	Ruff	Redshank
N		56	262		144	24	23
Seeds		5	9	**	13	25	-
Lumbricidae	S	68	81	**	13	29	22
Gastropoda	S	7	24	**	17	21	13
Auchenorrhyncha	V	-	2		3	8	-
Sternorrhyncha	V	2	5		6	13	13
Neuroptera	V	-	1	**	8	8	-
Nematocera	V	4	30	**	83	63	48
Tipulidae	V	2	10	**	42	13	-
Chironomidae	V	2	13	**	58	58	44
Dilophus	V	-	4	**	21	4	13
Brachycera & Cyclorrhapha	V	18	49	**	94	88	56
Empidinae	V	-	2	**	29	21	17
Dolichopodidae	V	2	3	**	42	50	17
Chloropidae	V	-	1	**	7	13	9
Muscidae	V	-	4	**	40	13	4
Scatophaga	VD	5	21	**	73	33	17
Unidentified Diptera		2	4		5	13	-
Hymenoptera	V	-	21	**	78	88	26
Coleoptera		55	92		87	92	83
Carabidae	S	27	49	**	22	67	17
Helophorus	S	-	31		26	46	26
Staphylinidae	S	5	32	**	7	58	4
Aphodius	SD	9	30	**	18	29	9
Elateridae	V	4	21		29	33	4
Curculionidae	V	7	49	**	66	46	26
Araneida		-	10		10	38	17
Tipulidae, larvae	S	89	37	**	4	8	-
Stratiomyidae, larvae	SD	2	49	**	1	13	4
Other Diptera, larvae	S	4	26	**	6	-	9
Coleoptera, larvae	S	5	24	**	2	8	9
Tenthredinoidea, larvae	V	-	2	**	34	21	4
Other arthropods		11	16		10	29	-

as the percentage of samples containing these taxa) in all faeces (species combined) and exhauster samples. With the exception of Auchenorrhyncha and Araneida, large prey items seem clearly to be favoured.

Diets of species

There are striking differences in the most important food items between the species. The combined results for all chicks, are presented in Table 3. Among the species of which the chicks search their own food, Lapwing and Black-tailed Godwit show the most pronounced specialisation as consumers of

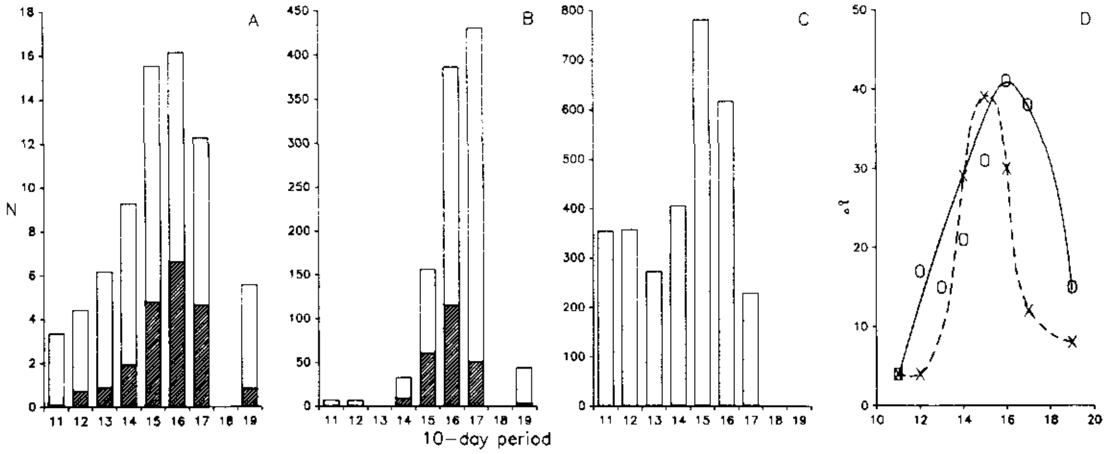

Fig. 1. Abundance of insects in grassland, according to different sampling methods. A: exhauster, B: sweep net, C: pitfalls. Hatching indicates insects > 3mm. D: relative abundance of insects > 3mm in Sweep net (continuous line) and exhauster (broken line) samples. Ten-day periods numbered from January 1st (13: 1-10 May).

soil fauna and vegetation dwellers, respectively. For most of the prey taxa, the diets of these two species differ at the 1% level (c^2-test; Table 3).

Lapwing chicks specialize on fauna living on, or just beneath, the surface and fauna living in cow dung pats. Important food items are earthworms, carabid beetles, staphylinid beetles, dung beetles (especially *Aphodius*), tipulid larvae and stratiomyid larvae (which live in cow dung).

Black-tailed Godwit chicks consume fauna from taller vegetation, living well above the ground. Important food items are curculionid beetles, tenthredionid larvae and many flying insects, like Tipulidae, Chironomidae, Bibionidae (especially *Dilophus*), Empidinae, Dolichopodidae, Muscidae, Scatophagidae and Hymenoptera.

The Ruff and Redshank have diets more or less intermediate between those of the Lapwing and Black-tailed Godwit. A comparatively large number of spiders and many surface-dwelling beetles, such as Carabidae, Staphylinidae, and *Helophorus* sp, are found in the Ruff. The high percentages of occurrence of many taxa reflect a high degree of variation in the Ruff's diet.

Oystercatcher chicks do not search for their own food, but are fed by their parents on earthworms, tipulid larvae and beetles.

Age and season

The samples from the enclosure have been quantitatively examined in more detail. Fragments were counted and matched to give 'entire animals'. This was not possible for earthworms and snails because these produce very large numbers of tiny fragments, but the abundance of earthworm bristles was recorded on a relative basis.

The differences between the Lapwing and Black-tailed Godwit correspond with those found in Table 3. There was no noticeable change in presence of arthropods in the diet of the Lapwing with age or season, but a gradual increase in abundance of earthworm bristles with age was seen.

The most noticeable change in diet of the Black-tailed Godwit is the increase in chironomids in the last week of May, both in large and small chicks. This corresponds with a sudden rise in the number of chironomids in sweep-net samples, indicating that the change in diet is not a matter of age but merely a matter of availability. A similar rise in the number of available chloropids is not reflected in the diet. The rise in chloropids can almost entirely be attributed to one species, *Oscinella frit*, which is very small (2 mm), and probably considered unprofitable by the chicks. Development in the Redshank diet cannot be studied from faeces, as they start to regurgitate pellets after one week.

Region, habitat and management

Since considerable differences in food composition were found between regions, further analysis had to be done on a regional scale. Only three categories were found to contain enough samples to allow this: Black-tailed Godwits from Frisia (BTGF), Lapwings from Frisia (LAPF), and Lapwings from the river district (LAPR). When comparing the latter two, it is seen that significantly more Lumbricidae, Gastropoda, Sternorrhyncha, Elateridae, and Curculionidae were eaten in LAPR, while significantly more Hymenoptera, *Helophorus*, *Aphodius*, Araneida, and Tipulidae (c^2-test) were eaten in LAPF. Within the beetle families, LAPR showed more taxa living in the vegetation, LAPF more typical soil surface dwellers.

A canonical correspondence analysis was performed within each of the categories BTGF, LAPF and LAPR, using the computer programme CANOCO, developed by Ter Braak (1986), to investigate the effects of the following factors: management intensity, soil humidity, soil type, ambient temperature, rainfall, wind speed, age of the chick and date.

Only the date has a significant effect ($p < 0.01$) on the food composition in all categories. Tenthredinoidea larvae, *Helophorus* and Dolichopodidae are eaten significantly more often after June 5th in BTGF, while *Dilophus*, Empidinae and Hymenoptera are eaten significantly earlier. Lumbricidae are eaten significantly later in LAPF, while *Helophorus* are eaten significantly earlier. Curculionidae and *Aphodius* are eaten significantly early in LAPR.

A significant age effect ($p = 0.01$) is only found in BTGF, after correction for date and other factors. The difference is only significant for *Dilophus* (eaten by young chicks).

Management intensity is almost significant ($p = 0.09$) in LAPF. This variable is strongly correlated with soil humidity ($r = 0.71$). Therefore, correction for humidity possibly obscures the effects of management intensity. When the correction for soil humidity is left out, significance of the effect of management intensity increases ($p = 0.04$). Tipulids, lumbricids and stratomyids are typical intensity (notably fertilisation level) indicators, and are more frequently eaten at high levels of management intensity (for stratiomyid larvae $p < 0.05$). It should be noted that the larvae of Stratiomyidae are typically taken out of decaying cow dung. Lapwing chicks are often seen actively exploiting cow dung pats.

Growth and season

It has been shown earlier (Beintema & Visser 1989b) that daily weight gain in small chicks is positively correlated with the number of dry hours above 15°C per day. When they get older, this relationship is lost, as the chicks become temperature independent. When the same weight gain data is plotted against the date, instead of 'dry, warm hours', a different pattern is seen (Fig. 2, average value per 10-day period). Small chicks grow better late in the season, and this is the effect of the temperature, as explained above. Large chicks however grow less well, as the season progresses. Daily weight gain was fitted against date for all recaptures during the linear phase of growth. The decrease was significant ($T = -5.06$ for $N = 237$; $p < 0.01$) for the Black-tailed Godwit (3 days and older). Trends were negative, but not significant, for Lapwing (6 days and older) and Redshank (4 days and older). Since chick condition is positively correlated with rainfall in May (own data), an attempt was made to test reduced growth for dry and wet springs separately (the 5 driest versus the 5 wettest out of the 10 years of observation). Such a division appeared not to be possible for the Black-tailed Godwit and Redshank, since by coincidence hardly any recaptures were made during the dry springs. The decrease of daily weight gain was significant for the dry springs ($T = -3.16$ for $N = 99$; $p < 0.01$) in the Lapwing; in the wet springs no trend could be seen.

Digestion experiments

No fragments were encountered in the faeces one hour after the chicks had started to feed on insects.

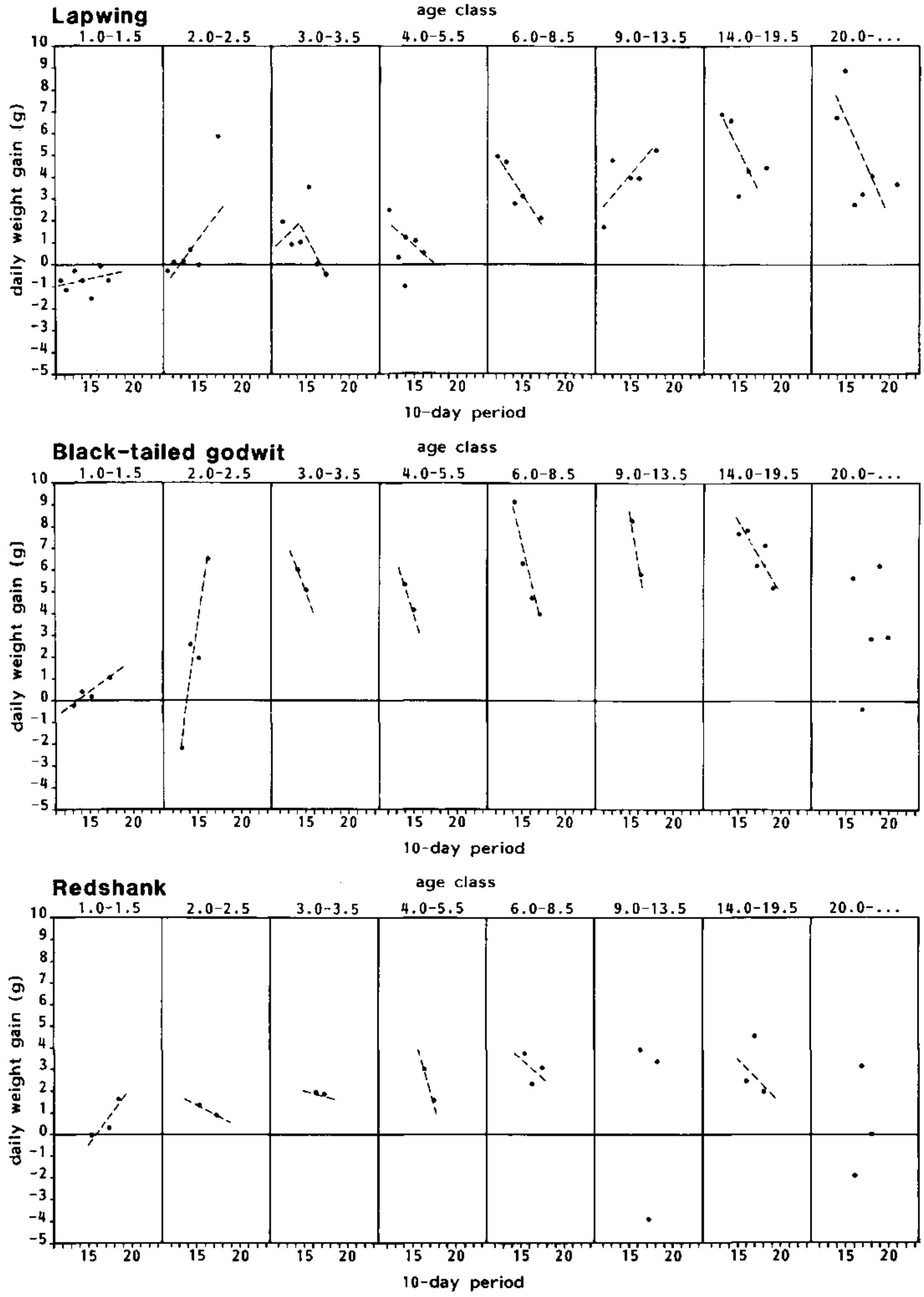

Fig. 2. Daily weight gain of chicks of different age classes as a function of season (10-day periods numbered from January 1st).

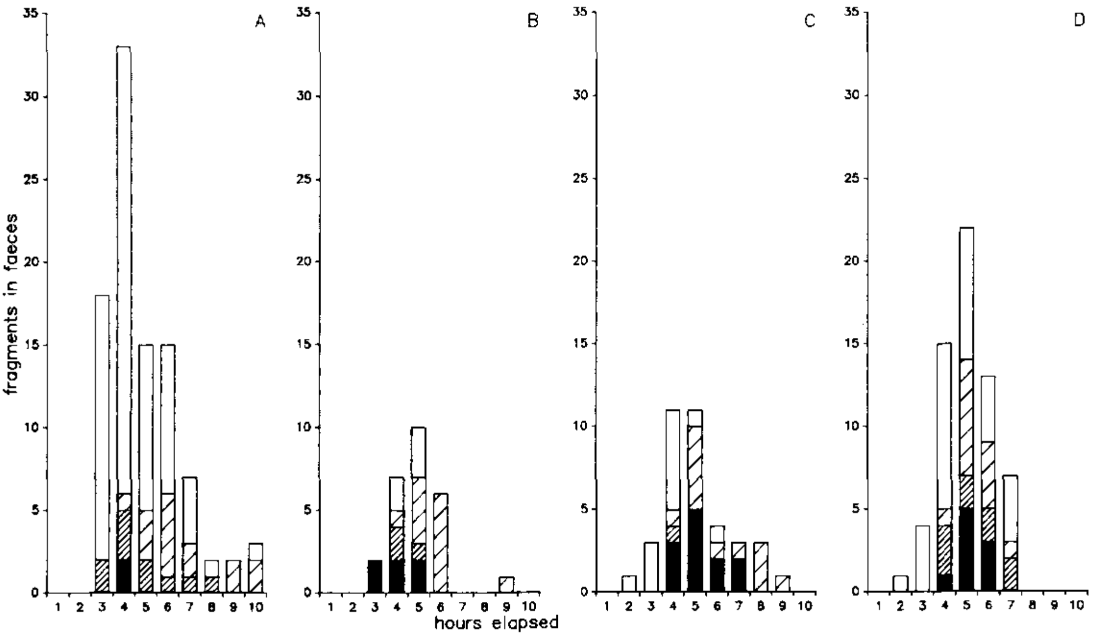

Fig. 3. Number of prey fragments found in faeces, per hour after feeding. A: Lapwing chicks of 4 days old, B: Lapwing chicks of 11 days old, C: Black-tailed Godwit chicks of 4 days old, D: Black-tailed Godwit chicks of 11 days old. Black bars: jaws of *Tenebrio molitor*, fine hatching: jaws of *Galleria mellonella*, coarse hatching: wings of *Musca domestica*, open: legparts of *M. domestica*.

Over 90% of all fragments found stayed in the alimentary tract for between two and seven hours. Peak occurrence in the faeces was after four or five hours (Fig. 3). There is little difference between the bird species or age classes.

The results indicate that the faeces may be considered as a sample originating from the fauna in the vicinity of the locality where a chick has been captured.

DISCUSSION

Food availability

Although arthropod abundance and species composition may vary considerably between localities and between years (Van de Bund pers. comm.), the general pattern of increase in April and May, corresponds with the patterns usually found in Dutch grasslands (Siepel pers. comm.). A decrease in June is not always as pronounced as we found in 1984, as insect abundance in general reaches its maximum in late summer. A temporary decrease in late spring is caused by mowing and intensive grazing (Siepel pers. comm.).

Ecological differences between species

The dietary differences between species reflect their different ecological requirements for feeding. Lapwing chicks are typical soil feeders, greatly dependent on arthropod fauna living on, or just below the soil surface, and on fauna living inside decaying cow dung pats. They are not very agile and therefore rely on less active fauna, such as beetles and larvae. During feeding, they usually stand motionless when looking for prey. Lapwing families with chicks have a preference for very short vegetation (e.g. grazed fields).

Black-tailed Godwit chicks are very active feeders, running through the vegetation, pecking in the higher strata of the vegetation. Consequently, their prey includes many flying species, and Godwit families with chicks have a preference for taller vegetation.

Which prey species is actually taken, depends on both its availability in the habitat, and the active choice of the chicks themselves. The large variation in the diet of the Ruff, for example, probably reflects the richness of the habitats in which the species is found, rather than the need for such a variation in its diet.

Timing and conditions for growth and survival

The question as to whether the chick stage should be synchronised with maximum food availability, or whether females should start to produce eggs just as early as possible, has long been subject to discussion (Lack 1954, 1968, Perrins 1970, Drent & Daan 1980, Beintema *et al.* 1985). Chicks hatched late in the season tend to survive less well than those hatching earlier on in many bird species nesting in temperate regions (Klomp & Speek 1971). This has also been shown to be the case for the Oystercatcher (Harris 1969, Heppleston 1972) and the Lapwing (Galbraith 1988). Not only the food availability but also the amount of time they can spend feeding is of importance for small chicks. This depends on weather conditions. Too much time may be lost, while chicks have to be kept warm by a parent. Time budget problems in small chicks, caused by cold weather, mainly occur early in the season (Beintema & Visser 1989b), while growth reductions in larger chicks (Fig. 2) occurs later in the season, especially in dry springs. Reduced growth does not correspond with a decrease in insect abundance, which takes place later. An explanation may be found in prey profitability, and a necessary change in diet during the chick stage. It can be calculated for the larger species that it is not very likely that a chick could grow up on insects alone. This is illustrated in Table 4 and Figure 4. Table 4 gives the energy intake of chicks, measured in captivity, in the thermoneutral zone (*ME* = consumed food minus faeces produced, expressed in kJ day^{-1}), and the number of insects (g dry-weight) needed for that, supposing an average energy content of 23kJ g^{-1} dry-weight (Bryant 1973), and an digestion efficiency of 74% (Castro *et al.* 1989). From this, the required intake rates can be calculated as a function of average prey size (Fig. 4). Although much depends on size class distribution of prey and selection by chicks, there is a strong suggestion that it may become very difficult for chicks near fledging to sustain themselves on the insects present (Fig. 1) in grassland. Thus, they may have to switch to more profitable prey, such as earthworms. Earthworms are not yet available to small chicks, simply because their bill is not long enough to catch them. In Lapwing chicks, a gradual increase in the amount of earthworms in the diet can certainly be seen. The availability of earthworms as prey decreases with date, as the soil dries out, and the worms retreat to a greater depth, beyond reach of many bills, especially in dry springs. Thus, the perfect timing for optimal growth can be seen as an interesting dilemma.

At what moment it will become unprofitable (or impossible) to feed on insects alone may also be influenced by grassland management. The average body mass of insects present in grassland has been shown to decrease with increasing levels of fertilization (Siepel 1990). This, combined with an earlier retreat of the earthworms as a result of improved drainage, may render improved meadows with intensified agricultural use unsuitable as feeding areas for chicks too early in season.

Such a change in feeding habits cannot be derived from the data on the diet of Black-tailed Godwit chicks. Another possible explanation may be that the larger chicks especially are more sensitive to overheating in warm, sunny weather and therefore can feed less efficiently, as has been shown for adult Starlings (Clark 1987). Godwit chicks have little possibility of seeking shade. During observations of families with chicks in the enclosures, we often noted that chicks spend time laying down, dozing, during the heat of the day. However, at that time we were not yet aware of possible implications.

Finally, there is evidence that birds have difficulties digesting food when drinking water is short, especially at higher temperatures. Van Kampen (1981) found that the water: food intake ratio increases from 1:1 to 6:1, when the ambient temper-

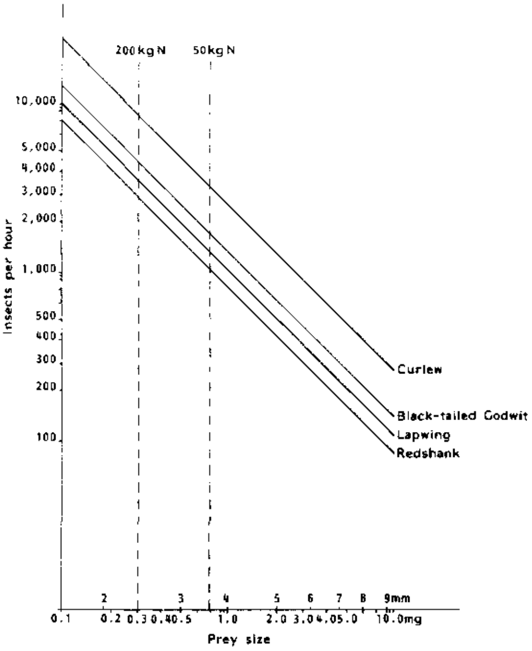

Fig. 4. Required hourly intake rates of insect prey to meet energy demands, as a function of prey size, assuming 16 h day^{-1} available for feeding. Conversion of body mass to length (*X*-axis) according to Rogers *et al.* 1976. Vertical dotted lines indicate average size (mass) of insects found a fertilization levels of 200 kg ha^{-1}, and 50 kg ha^{-1} (nitrogen), according to Siepel (1990).

ature is raised from 5 to 35 °C. In the hot humid tropics, food intake of broiler chickens appears to be just a function of water availability (Kese & Baffour-Awuah 1979). Chicks of Lapwing, Black-tailed Godwit, Redshank, and Curlew raised in captivity simply stopped feeding entirely, when no drinking water was readily available. The total daily water intake (in food plus drinking water) in chicks near fledging was 75, 100, and 50 g day^{-1}, for Lapwing, Black-tailed Godwit, and Redshank, respectively. Assuming an average water content of 67% for insects (Ricklefs 1974), they would obtain 36, 45, and 29 g day^{-1}, respectively from insect food in the field. This suggests that in the field they also need additional drinking water, which may become more difficult later in the season.

Problems of draught (lack of drinking water, retreating earthworms) not only apply to chicks. In the exceptionally hot and dry summer of 1959 mass mortality of adult lapwings was reported in The Netherlands (Voous 1962).

In order to fully understand the factors affecting growth and survival we need more careful research into the feeding ecology of chicks in relation to their environment, with special attention to the thermal and energetic aspects.

ACKNOWLEDGEMENTS

Identification of insect fragments would not have been possible without the help of Chris van de Bund, who checked and confirmed most identifications, and often gave sound methodological advise. Leo van den Bergh collected a large part of the faeces samples. Recapture data of chicks could only be obtained with the voluntary aid of many bird ringers.

Table 4. Daily food requirements of chicks in captivity. Fledging stage: half is half the fledging age, full is fledging age. *ME*: metabolised energy, in kJ day^{-1}.

species	stage	age (d)	weight (g)	*ME* (kJ)	insects (g dry)
Lapwing	half	18	80	230	13.5
Lawping	full	35	150	300	17.6
Black-tailed Godwit	half	12	115	310	18.2
Black-tailed Godwit	full	24	200	380	22.4
Redshank	half	12	45	160	9.4
Redshank	full	24	80	240	14.1
Curlew	Half	15	250	480	28.2
Curlew	Full	30	450	720	42.4

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SAMENVATTING

Het dieet van de kuikens van Kievit, Grutto, Tureluur, Kemphaan en Scholekster werd bestudeerd aan de hand van faecesanalyses. Kievitkuikens verzamelen in hoofdzaak ongewervelden die op of vlak boven de bodem leven. Daarnaast graven zij in halfverteerde koeievlaaien naar mestkevers en larven van wapenvliegen. Gruttokuikens zijn veel aktiever in hun gedrag en jagen op insekten die zich hogerop in de vegetatie bevinden. Hun dieet bevat dan ook meer vliegende insekten. De kuikens van Tureluur en Kemphaan nemen een intermediaire positie in. Scholeksterkuikens worden door hun ouders gevoerd met emelten en regenwormen.

Om een indruk te krijgen van het voedselaanbod voor kuikens, werd de graslandfauna bemonsterd. Tot eind mei neemt het aantal arthropoden in het grasland sterk toe. In juni kan weer een daling optreden. De samenstelling van het dieet wordt niet alleen door de voedselkeuze bepaald, maar ook door het aanbod. Veranderingen in de loop van het seizoen en verschillen tussen gebieden en biotopen kunnen in hoofdzaak verklaard worden door verschillen in voedselaanbod.

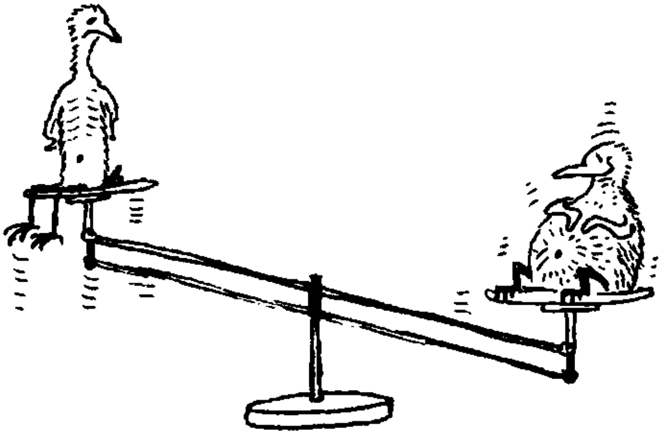
Hoewel het insektenaanbod niet voor juni begint te dalen, is bij de kuikens al vanaf half mei verminderde groei te constateren. Wij veronderstellen dat de kuikens om energetische redenen niet in staat zijn geheel op een dieet van insekten op te groeien. Noodgedwongen moeten zij voor het vliegvlug worden omschakelen op grotere, energierijkere prooien: regenwormen. Later in het seizoen zou deze omschakeling steeds moeilijker worden omdat de wormen zich in de uitdrogende grond steeds dieper terugtrekken. Dit probleem kan zich vooral in droge voorjaren voordoen. Het effect zal versterkt worden door ontwatering en verbeterde drainage.

Ook de bemestingsgraad van het grasland speelt een rol. Deze is van invloed op de gemiddelde prooigrootte. Bij een hogere bemestingsgraad worden de prooien kleiner en zal een omschakeling op regenwormen eerder noodzakelijk zijn.

Chapter 7

A condition index for chicks of Lapwing, Black-tailed Godwit, Redshank, and Oystercatcher.

A.J. Beintema



A CONDITION INDEX FOR CHICKS OF LAPWING, BLACK-TAILED GODWIT, REDSHANK, AND OYSTERCATCHER

A.J. BEINTEMA

ABSTRACT Growth in nidifugeous chicks of waders greatly depends on their feeding possibilities. When chicks find insufficient food, growth rates may be considerably reduced. Bill length and body weight respond differently to reduced growth, and to recovery after a period of reduced growth. Therefore, a condition index *CI* can be derived from the relationship between bill length and body weight. *CI* = *WO/WE*, where *WO* is the observed weight, and *WE* is the expected weight for the observed bill length. Standard weigths for observed bill lengths are given for Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus*, and Oystercatcher *Haematopus ostralegus*. Annual variations in *CI* in these four species follow very similar patterns. Annual variations in the Lapwing are correlated with total rainfall in May. Similar fluctuations in fledging success are also correlated with rainfall in May, indicating that a relationship between *CI* and chick survival does exist.

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INTRODUCTION

Contrary to human beings, birds are supposed to be in good condition when they carry a lot of fat. Condition in free living birds is often estimated by judging the body weight relative to a linear measurement, such as bill length. A condition index *Q* could be BodyWeight/BillLength. In growing chicks the matter is more complicated. If food shortage results in growth reduction, both body weight and bill length could be lagging behind, so the question is: does the index *Q* have any significance? Years ago I have tried to investigate this, based on the philosophy that a chick can loose weight, but a bill can never shrink. Thus, a very low value of *Q* would indicate a chick suffering growth problems. However, when a chicks stops gaining weight, the bill also stops growing. When a chick recovers after surviving a period of reduced growth, it picks up the original growth rates again; it only looks younger than it really is. It turned out that such chicks may have very high values of *Q*, indicating that recovering from reduced weight gain may go faster than recovering from reduced bill growth. This makes it impossible to distinguish between truly fast developing chicks and the ones that have recovered from a bad period, but still are too small for their age. This finding put an end to the exercise, at that time.

Recently, I saw data from a study area in Western Germany, where "*Q*-values" in Lapwing chicks differed consistently and significantly between two years (Schwöppe, pers. comm.). Furthermore, we found that chicks in captivity (which never experience bad periods) gain weight much faster than chicks in the wild, whilst their bills grow only a little faster (Beintema & Visser 1989a). These observations lead to the conclusion that *Q* must have some meaning, after all.

METHODS

From 1976 - 1985, over 41,000 age estimates of wild meadow-bird chicks were collected all over the Netherlands, with the aid of many voluntarily cooperating bird ringers, in an effort to obtain information on chick mortality. Participants were asked to record the bill length, as this was found to be the most convenient age estimator (Beintema & Visser 1989a). A limited number of participants also recorded body weight. Thus, both weight and bill length were collected on 5,715, 2,272, 1,048, and 1,520 chicks of Lapwing, Black-tailed Godwit, Redshank, and Oystercatcher, respectively. Of particular interest are the recaptures, especially of chicks of known age (those ringed as hatchlings, while still in the nest; this is not normally done in Oystercatcher hatchlings, because their legs are too small). We have 277, 177, and 76 of such recaptures, of Lapwing, Black-tailed Godwit, and Redshank, respectively.

RESULTS

Condition in chicks of known age

Since body weight and bill length follow different growth patterns, the absolute value of Q, as defined above, is age dependent. Therefore, we must use the relative value of Q:

Estimated Condition (EC) =
observed Q / expected Q (1)

in which for each age the expected Q = average weight / average bill length for that age. If a chick is relatively heavy for its bill length, observed Q will be larger than expected Q, and EC will be larger than 1. Similarly, when a chick is relatively light for its bill length, EC will be less than 1. For chicks of known age, we could define the 'true' condition as:

True Condition (TC) =
observed weight / expected weight (2)

in which the expected weight is the average weight, for each age. TC will be larger than 1 if a chick is relatively heavy for its age, and less than 1 if it is relatively light for its age. Fig. 1 shows the relationship between EC and TC, for chicks of known age, of three species (statistics in table 1). The strong positive correlation proves that indeed, chicks which are relatively heavy for their age, are relatively heavy for their bill length as well. The question remains: are chicks, which are relatively heavy for their bill length, always heavy for their age too?

Condition in chicks of unknown age

Now let us suppose that we have no known age available for our estimate of EC, and have to base our age estimate on bill length. In that case, expected Q in formula (1) is not "average weight for that age" / "average bill length for that age", but "average weight for that bill length" / "that bill length". As a consequence, both observed

Table 1. Statistics from Figure 1 and 2. *%var* = percentage of variance accounted for, T = T-value of regression coefficient, df = degrees of freedom (identical in Fig. 1 and 2).

	Figure 1		Figure 2		
	%var	*T*	*%var*	*T*	*df*
Lapwing	79.9	33.15	23.4	9.23	276
Black-tailed Godwit	60.0	16.00	6.2	3.51	170
Redshank	60.8	10.84	20.5	4.50	75

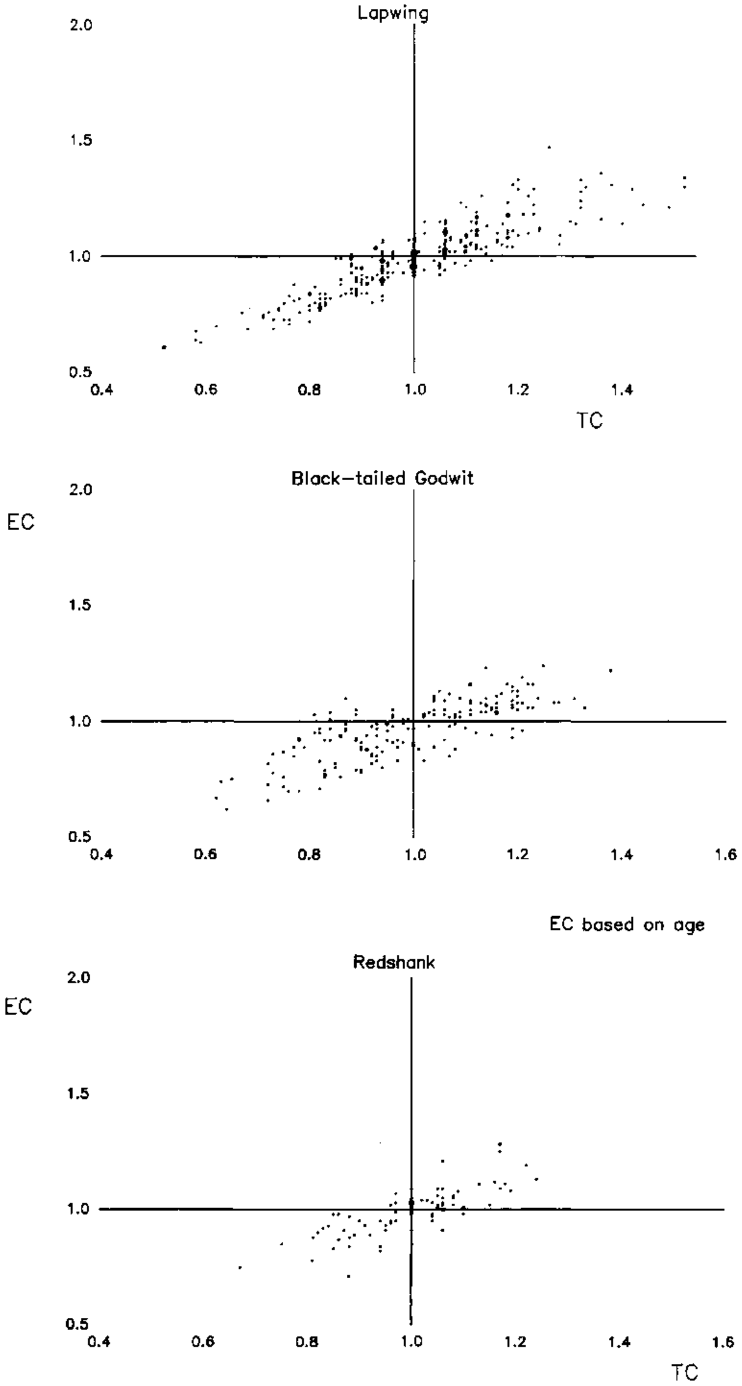

Fig. 1. Estimated condition (formula 1 in text) as a function of 'true' condition (formula 2 in text) in chicks of known age.

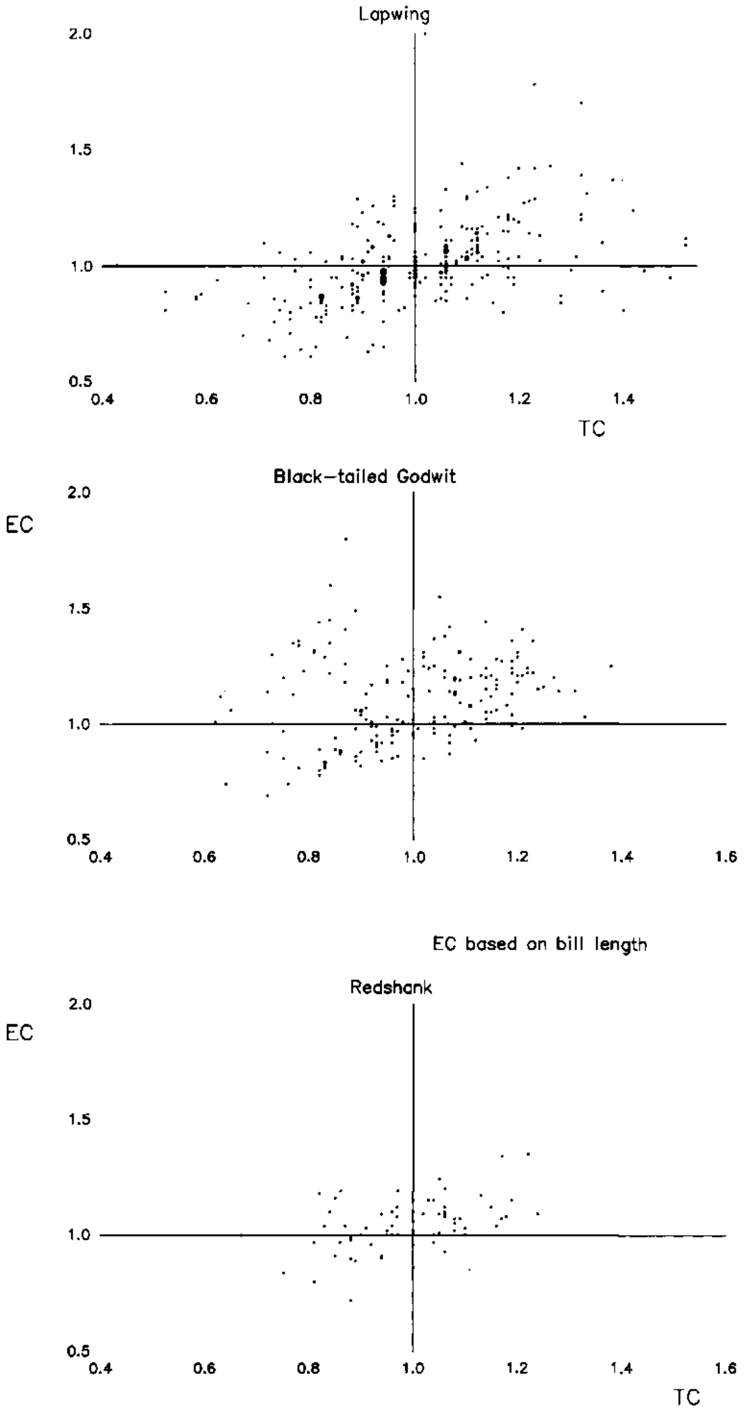

Fig. 2. Estimated condition (formula 3 in text) as a function of 'true' condition (formula 2 in text) in chicks of known age, when not the true age is used, but the age estimated according to bill length.

and expected Q are based on the observed bill length, which can therefore be eliminaed from the formula, which then becomes:

$$EC = \text{observed weight} / \text{expected weight} \quad (3)$$

which differs from (2) in the expected weight being based on bill length, instead of known age. The relationship between EC based on bill length, and TC (based on age), is shown in Fig. 2. Although the percentage of variance accounted for is greatly reduced (table 1), the correlation is still significant. Closer observation reveals that the main difference between the figs 1 and 2 lies in the number of points in the upper left-hand quadrant of the diagrams. These are the chicks which have presumably recovered from a bad period: they are too

Table 2. Standard body weights of chicks of Lapwing. Bill = bill length in mm, weight = average body weight in g, *SE* = standard error of body weight, *N* = number of observations, Standard = smoothed 'Standard Weight'.

bill	weight	*SE*	*N*	Standard
7	16.0	*	1	16
8	15.0	*	1	16
9	16.0	*	1	16
10	16.2	1.6	91	16
11	16.9	2.3	465	17
12	18.5	3.4	634	19
13	21.3	4.7	569	21
14	27.5	7.0	432	28
15	35.7	7.8	364	36
16	44.5	10.5	265	45
17	53.9	12.5	311	54
18	65.1	15.9	343	65
19	80.4	22.8	386	80
20	96.2	22.2	474	96
21	113.7	25.1	492	114
22	128.0	25.9	464	128
23	135.3	24.7	301	135
24	141.1	22.4	97	141
25	147.3	22.9	22	147
26	162.5	2.5	2	153

Table 3. Standard body weights of chicks of Black-tailed Godwit. Legenda as Table 2.

bill	weight	*SE*	*N*	standard
14	23.3	3.1	3	24
15	25.0	*	1	25
16	26.4	2.0	12	26
17	28.1	3.1	49	27
18	28.3	3.5	63	28
19	30.8	4.9	84	31
20	33.7	8.0	83	34
21	36.0	6.2	54	37
22	41.1	7.9	68	41
23	48.4	9.9	60	46
24	49.8	10.0	58	52
25	57.7	11.4	75	57
26	64.1	13.9	50	63
27	71.2	13.3	65	69
28	74.3	13.5	59	75
29	80.7	13.9	62	82
30	88.5	15.4	58	88
31	94.9	14.7	75	95
32	101.9	14.0	41	102
33	109.7	19.1	70	107
34	111.4	18.3	67	113
35	116.3	19.1	50	118
36	125.0	18.8	58	124
37	127.8	18.5	56	129
38	132.7	21.5	68	135
39	140.5	25.0	70	140
40	150.0	26.6	74	146
41	153.1	19.3	62	151
42	157.0	23.0	64	157
43	157.1	19.6	72	161
44	166.1	25.0	63	165
45	169.5	22.1	57	170
46	170.4	23.6	71	174
47	179.8	23.7	56	179
48	179.3	20.6	61	183
49	184.1	28.0	42	187
50	198.1	26.6	39	191
51	197.4	25.0	31	196
52	204.7	23.1	40	200
53	201.7	25.4	28	205
54	209.9	22.8	17	209
55	213.0	22.6	10	214
56	217.6	16.0	9	218
57	222.1	30.9	7	222
58	237.5	7.5	2	224
59	265.0	*	1	226
60	235.0	12.2	3	228
61	225.0	*	1	230
62	217.5	17.5	2	232
63	*	*	0	234
64	160.0	*	1	236

Table 4. Standard body weights of chicks of Redshank. Legenda as Table 2.

bill	weight	*SE*	*N*	standard
11	13.0	*	1	13
12	13.4	1.6	9	14
13	15.2	2.1	34	15
14	15.8	1.9	66	16
15	16.0	2.7	56	17
16	19.3	2.8	51	19
17	21.7	3.3	50	21
18	24.1	3.0	53	24
19	28.5	4.2	59	28
20	31.4	4.8	44	32
21	36.2	5.5	57	36
22	42.0	5.6	53	41
23	46.2	6.5	54	46
24	50.8	6.8	55	51
25	56.3	6.8	55	56
26	62.1	8.2	45	60
27	63.2	8.1	38	65
28	69.2	7.4	46	69
29	72.2	7.0	61	73
30	75.7	7.7	45	77
31	83.3	7.5	37	81
32	84.5	7.4	38	84
33	87.3	6.3	26	87
34	91.4	4.2	7	90
35	89.8	5.8	5	92
36	98.0	*	1	94
37	*	*	0	96
38	93.0	*	1	98
39	*	*	0	100
40	*	*	0	102
41	*	*	0	104
42	*	*	0	106
43	110.0	*	1	108

light-weighted for their age (low *TC*), but are heavy in relation to the length of their bill (high *EC*), which is too short for their age. The lower right-hand quadrant of the diagrams remains rather empty, indicating that a low *EC* still is a good estimator for (low) *TC*.

Fig. 2 suggests that Black-tailed Godwit and Redshank have a higher capability of recovering from a period of reduced growth than the Lapwing.

Table 5. Standard body weights of chicks of Oystercatcher. Legenda as Table 2.

bill	weight	*SE*	*N*	standard
16	37.3	2.9	8	38
17	41.1	3.4	13	41
18	44.3	9.5	19	44
19	50.1	5.8	15	50
20	58.6	17.8	39	57
21	61.1	11.2	37	63
22	69.8	13.9	41	70
23	77.3	17.2	46	77
24	87.9	16.0	30	84
25	92.9	16.5	64	91
26	99.8	16.8	58	98
27	103.8	16.3	48	107
28	117.4	16.2	32	116
29	129.1	26.0	49	126
30	137.7	26.0	58	136
31	145.1	32.9	45	147
32	155.4	30.0	59	158
33	173.8	32.2	52	170
34	188.2	30.8	54	181
35	196.8	32.2	60	192
36	206.2	37.8	58	204
37	213.1	37.0	64	215
38	218.6	33.3	58	226
39	229.7	32.3	46	238
40	248.6	40.3	52	249
41	263.8	41.1	49	261
42	270.9	37.6	50	272
43	280.5	42.2	51	280
44	287.1	47.1	38	288
45	289.0	36.8	43	296
46	308.2	37.0	44	304
47	307.5	28.3	24	312
48	320.9	32.2	22	320
49	336.8	27.9	14	328
50	327.5	36.0	26	336
51	357.7	43.0	15	344
52	352.4	36.9	15	352
53	374.4	13.1	8	360
54	388.3	27.2	3	367
55	358.0	18.3	5	374
56	345.5	26.5	4	376
57	392.5	7.5	2	378
58	430.0	*	1	380
59	*	*	0	382
60	365.0	*	1	384

Condition index and standardized weights

The results show that a Condition Estimate based on body weight and bill length does have a meaning, after all. Standardized values for expected weight (smoothed graphically) for four bird species are presented as tables (2 - 5), to enable further use by the reader. As condition index, formula (3) can be rephrased as:

Condition Index (CI) =
observed weight (OW) / expecteded weight (EW) (4)

Condition index in wild chicks

Like in the case of our German colleagues, the average condition index showed considerable variations from year to year (fig 3). When comparing years within one species, all differences larger than 0.03-0.05 (depending on sample size) are significant at the 1% level (two-sided test of Z-statistic; large-sample test). Fig 3 further reveals that changes from year to year are very similar in different species. Thus, 1980, 1982, and 1985 could be classified as 'bad' years, and 1977, 1979, and 1981 as 'good' years, in terms of average chick condition. Good and bad years coincided nicely with wet and dry springs (fig. 3), defined as total rainfall in May ($p < 0.05$ for Lapwing and Black-tailed Godwit, Redshank almost significant, Oystercatcher n.s.; T-test on linear regression). Rainfall in June showed no relationship, but when the first two weeks of June were added, the correlation between rainfall and CI became significant ($p < 0,05$) for the Redshank, which nests later than Lapwing and Black-tailed Godwit (for these two species p increased, but remained < 0.05, Oystercatcher remained n.s.). In Great Britain, Baines (pers. comm.) found that Lapwing chicks developed more slowly than usual in the dry springs of 1988 and 1989. In Germany, when comparing the springs of 1988 and 1989, Schwöppe (pers. comm.) found lower weight/bill-length ratios in the drier of the two.

There was no consistency in within-year trends in condition index. Some years showed upward, others downward trends, with no similarity between species, and no clue to good or bad years. All efforts to ex-

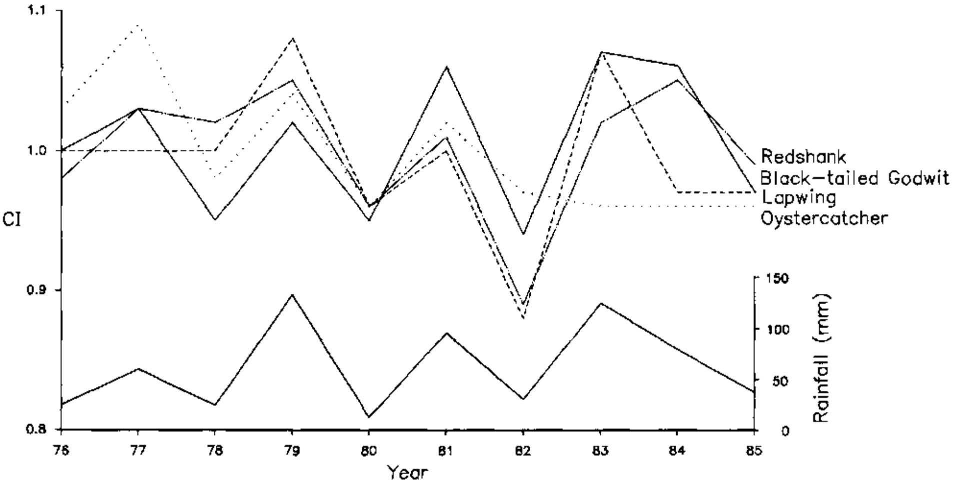

Fig. 3. Condition indices (formula 4 in text), and total rainfall in May, for 10 years.

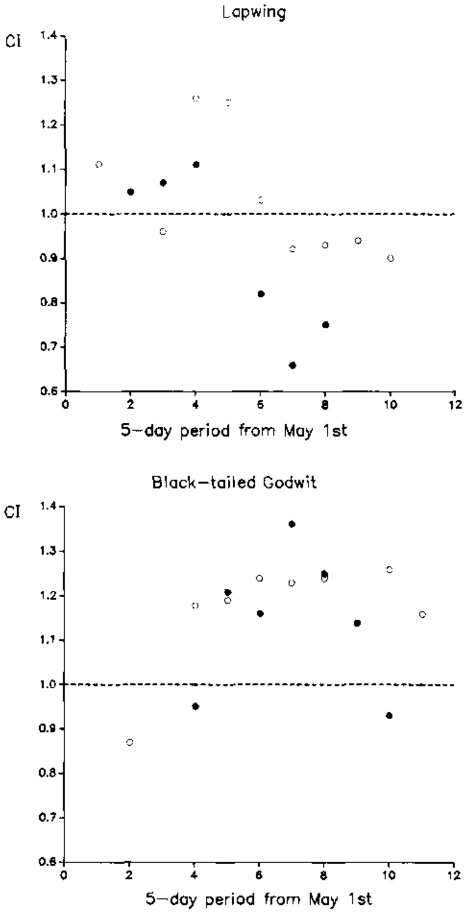

Fig. 4. Seasonal variation in condition index in chicks growing up in an enclosure, in 1981 (open symbols), and 1984 (closed symbols).

plain fluctuations in condition indices from weather parameters, failed. It is likely that a large, heterogeneous data set, contains too much bias to allow any interpretation, and that one should concentrate on detailed studies on a local scale. As an example, Fig. 4 gives the seasonal trends in condition index for Lawping and Black-tailed Godwit, for those chicks which grew up in an enclosure in the Kievitslanden Reserve, where families were kept under observation in 1981 and 1984 (Beintema & Visser 1989b). Low values early in the season correspond with small chicks not performing well because of adverse weather. It seems that in both years the conditions for Lapwing deteriorated quickly from the end of May onwards. This seems not to be the case for the Black-tailed Godwit, although the 1981 data suggest a best period in the first week of June.

DISCUSSION

Bill length in wader chicks is less affected by reduced growth than body mass. Dijkstra (1988) found a similar relationship between wing length and body mass in the kestrel. Differential response enables condition indices to be derived from growth parameters.

Weather has a great effect on the performance of chicks. Two hypotheses have been put forward earlier (Beintema et al. 1991): small chicks perfom less well early in the season, when adverse weather often prevents them from spending enough time on foraging, and larger chicks perform less wel later in the season, when feeding on insects becomes less profitable, and switching to soil fauna becomes more difficult, especially in dry springs. This puts forward an interesting dilemma in timing the chick season. There is also a contradiction in what the best weather for chicks should be: it should not rain, but at any moment it should just have rained. Obviously, not only the amount, but also the temporal distribution of rainfall is of great importance, but it is not yet clear how to best describe it, as an explanatory variable for condition.

One would expect a relationship between *CI* and chick survival, but a direct link has not yet been established. Annual fluctuations in chick survival in the Lapwing (own data) resemble those in *CI*, but there is no significant correlation. However, these fluctuations are correlated with rainfall in May, as is the case with *CI*, thus indicating that a relationship does exist.

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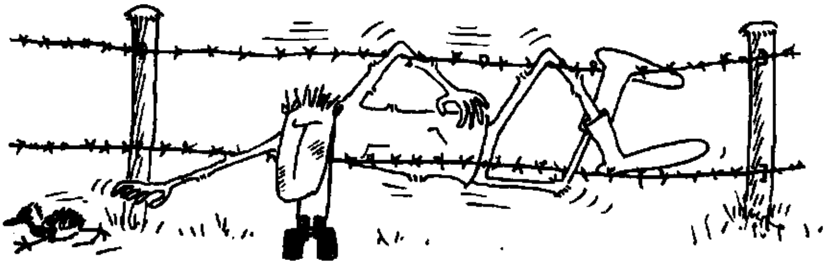
SAMENVATTING

Groei van weidevogelkuikens wordt in belangrijke mate bepaald door de mogelijkheden om aan voldoende voedsel te komen. Als onvoldoende voedsel opgenomen kan worden treedt groeivertraging op. Snavellengte en lichaamsgewicht reageren verschillend op groeivertraging en op herstel daarna. Daardoor is het mogelijk uit de verhouding tussen snavellengte en gewicht een conditie index af te leiden. Conditie index *CI = OW/EW*, waarbij *OW* het waargenomen gewicht en *EW* het verwachte gewicht is behorende bij de waargenomen snavellengte. Gestandaardiseerde verwachte gewichten voor iedere snavellengte worden gepresenteerd voor Kievit, Grutto, Tureluur en Scholekster. Jaarlijkse fluctuaties in gemiddelde *CI* zijn gecorreleerd met de totale regenval over de maand mei. Omdat jaarlijkse fluctuaties in de overlevingskans van kievitkuikens eveneens gecorreleerd zijn met regenval in mei is het aannemelijk dat *CI* van invloed is op deze overlevingskans.

Chapter 8

Fledging success of meadow bird (Charadriiformes) chicks, estimated from ringing data.

A.J. Beintema



FLEDGING SUCCESS OF MEADOW BIRD (CHARADRIIFORMES) CHICKS, ESTIMATED FROM RINGING DATA

A.J. BEINTEMA

ABSTRACT From 1976 to 1985, large numbers of chicks of Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus*, and Oystercatcher *Haematopus ostralegus* have been aged during ringing. Hatching dates have been calculated from ringing dates (corrected for estimated age at ringing). Distributions of hatching dates in the province of Frisia differ from elsewhere, because of egging (Lapwing eggs are taken), and the associated activities of nest protection. Hatching dates of Frisian Lapwings are strongly synchronised, not only because of a peak in replacement clutches after the closing of the egging season, but also as a result of nest protection, which precludes the occurrence of many late replacement clutches. Synchronisation also characterizes the other species. Age specific recovery rates from the same material have been used to estimate fledging success. Fledging success in the Lapwing is positively correlated with rainfall in May, which is a major factor indirectly affecting chick condition. Chicks born in the early and late parts of the season tend to survive less well than those born in the middle. Survival rates are relatively high for chicks born in the period between the 25th and 50th percentile of the distribution of hatching dates, with higher values for wet years than for dry years. Frisian chicks tend to survive less well than those elsewhere when still in the nest, but better when they are larger. These differences may be attributed to climatic differences, and to side-effects of the Frisian system of nest protection.

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INTRODUCTION

What makes a chick survive better or worse, and how many chicks typically survive anyway? This paper completes a series of papers on these questions, for chicks of the charadriiform representatives of the meadow bird community in The Netherlands (Beintema & Visser 1989a, 1989b, Beintema et al. 1991, Beintema 1991). Factors affecting growth, condition, and survival in chicks are complicated, and are much less readily influenced by management than those affecting habitat choice and hatching success. Very often, studies on breeding success of waders, including meadow birds, end with hatching success, simply because families with chicks disappear from view. Information on chick survival is scarce, or fragmentary. By using recoveries from a nation-wide ringing scheme, I hope to set a general background for chick survival, against which more local and detailed studies can be compared.

METHODS

To obtain nation-wide information on fledging success, an extensive chick-ringing programme was started in 1976, with the voluntary aid of many bird ringers. All participants were asked to record the bill length (exposed culmen) of each chick captured, since this measurement was found to be the most convenient age estimator (Beintema & Visser 1989a). The assumption was made that the numerical distribution of chicks over age classes would yield information on chick survival in relation to season, year and region. The ringing programme was suspended after 1985, when it became obvious that analysis of the ringing totals of different age classes would not meet the objectives (see discussion), and it was decided to wait for ringing recoveries after fledging. Ringing recoveries up to January 1st, 1990, were obtained from the Dutch Ringing Centre. Differences between recovery rates (after fledging) of different age classes directly reflect survival during the chick stage, assuming that there is no relationship between the age of ringing and the eventual life history after fledging (Beintema & Drost 1986).

Table 1 lists all chicks ringed and aged from 1976 through 1985, per age class. Chicks of Lapwing, Black-tailed Godwit and Redshank were aged using own observations on growth rates (Beintema & Visser 1989a), for Oystercatcher chicks data from the University of Groningen were used (Klaassen pers. comm.). Chicks in the youngest age class in the first three species have been ringed while still in the nest, and were assumed to be half a day old (0-1), irrespective of their bill length. Age classes correspond to millimeters bill length in the Lapwing. Bill lengths had to be grouped in the other species, to create sufficiently large samples.

To get around the problem of having too few recoveries for separate categories, an alternative, relative measure of survival *RS* was derived from the age distribution of the chicks captured, as the the quotient *RS* = *LARGE*/*SMALL*, where *LARGE* is the total number of chicks captured at an age of more

Table 1. Ringing totals (1076-1985) and recovery rates after fledging (up to January 1st, 1990) of chicks of known age.

Bill (mm)	Age (days)	Ringed (number)	Recovered (number)	Recovery rate (%)
Lapwing				
-	0.5	3809	57	1.50
<12	1.9	2787	38	1.36
12	3.2	2906	47	1.62
13	4.7	2167	39	1.79
14	6.4	1579	34	2.15
15	8.5	1475	38	2.58
16	10.6	1252	31	2.48
17	12.8	1414	38	2.69
18	15.0	1416	35	2.47
19	17.2	1459	32	2.19
20	19.5	1985	53	2.71
21	22.3	1672	60	3.59
22	25.0	1322	57	4.31
23	27.7	698	28	4.01
>23	30.0	304	11	3.63
Black-tailed Godwit				
-	0.5	272	35	1.27
<21	1.9	669	13	1.86
21-26	6.1	791	13	1.64
27-32	11.5	721	14	1.94
33-38	15.9	845	13	1.54
39-44	19.8	863	20	2.32
45-50	23.2	737	25	3.39
>50	24.0	267	7	2.62
Redshank				
-	0.5	906	17	1.88
<20	3.6	516	11	2.13
20-26	11.5	547	11	2.01
27-33	19.5	435	10	2.30
Oystercatcher				
<19	2.2	203	6	2.96
19-22	5.8	283	11	3.89
23-25	9.1	267	11	4.12
26-27	11.5	229	16	7.00
28-29	13.5	252	21	8.33
30-33	15.8	589	43	7.30
34-37	19.5	617	49	7.94
38-41	23.0	579	49	8.46
42-45	26.5	483	43	8.90
46-52	31.5	496	45	9.07
>52	37.5	106	11	10.38

than one week old, and *SMALL* is the number of chicks captured when smaller than that, excluding those chicks ringed in the nest, because numbers of these are strongly biased by the activities of a few specialists. The assumption is that when more chicks survive until fledging, there will be relatively more large chicks in the total sample.

RESULTS

Hatching season

The average seasonal distribution of calculated hatching dates is given in Fig. 1. Data for Frisia are treated separately, because the widespread tradition of egging in this province has a marked effect on hatching dates, not only directly, as a result of harvesting Lapwing eggs, but also indirectly through a change in attitude towards protection of nesting waders in general. Frisian Lapwings show a pronounced hatching peak from 12 to 18 May, particularly on 15 and 16 May, corresponding with replacement clutches started after the closing of the egging season on 12 April. Elsewhere in The Netherlands, the egging season closes one week earlier, and egg collectors cover the ground much less intensively. Therefore, the expected synchronisation of hatching around 8 and 9 May does not really show. Linked to egging, the Frisians have developed a tradition of taking special care of nests after the closing date of the egging season, thus reducing losses during the peak of incubation. This further enhances synchronisation, by reducing the number of replacement clutches later in the season. Thus, in spite of the postponed start, the median hatching date in Frisia averages one day earlier than in the rest of the country. Up to 1974, egging in Friesland was allowed until 19 April, i.e. one week longer

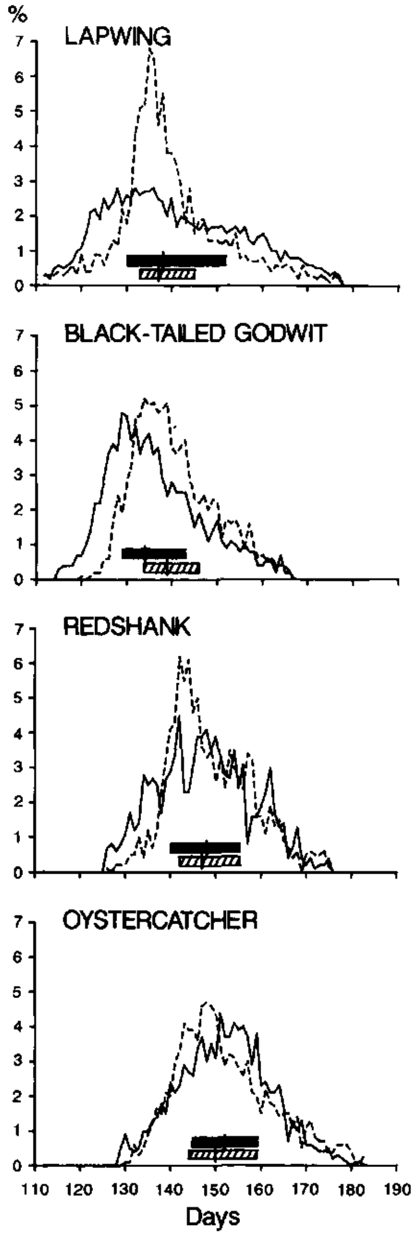

Fig. 1. Distribution (in %) of hatching dates for Frisia (dotted line) and elsewhere in the Netherlands (drawn line). Horizontal bars (hatched = Frisia, black = elsewhere) give timespan between 25th and 75th percentile of distribution; vertical line is median hatching date. Days numbered from January 1st.

than during the intensive study period. It is known that some Frisians still continue egg collecting until this date, which may explain why relatively high numbers of hatchings take place until 19-22 May. Synchronisation also reduces variation between years: from 1976 to 1985 the median hatching date in Frisia varied between 15 and 20 May, while it varied from 12 to 27 May elsewhere.

Frisian Black-tailed Godwits hatch about 5 days later than those elsewhere. This may partly be explained by climatic differences, but allegedly some egg collectors also take Godwit eggs during the egging season. In this species too, the Frisians synchronise hatching. The timespan between the 25 and 75 percentile of the hatching dates in Frisia averages two days shorter than elsewhere, and the hatching peak is slightly higher.

In both the late-nesting Redshank and Oystercatcher, synchronisation in Frisia is only discernable in the first half of the hatching season, not in the tail of the distribution. In Frisia, both species start a few days later, but have their median hatching date one or two days earlier than elsewhere.

Neonatal weights

Neonatal weights of Lapwing, Black-tailed Godwit and Redshank are 17.5 g (*SD* = 1.9, *N* = 1152), 28.6 g (*SD* = 2.6, *N* = 1431), and 15.6 g (*SD* = 1.6, *N* = 488), respectively (Beintema & Visser 1989a). No consistent seasonal patterns could be detected in these weights. Most years showed no trend, some years suggested an upward trend, others a downward one, with no accordance between species. On average, neither early born, nor late born chicks differed from those born during the hatching peak. The average neonatal weight did not differ between years.

Overall fledging success

Chick survival was estimated as a constant daily survival rate S by linear regression on the log(recovery rate) values of the different age classes (Table 1). Total fledging success is estimated as $F = S^f$, where f is the length of the fledging period in days. The results are given in Fig. 2 and Table 2. Fig. 2 suggests lower daily survival rates during the first part of the fledging period for Lapwing and Oystercatcher, but not for Black-tailed Godwit. The difference between Lapwing and Black-tailed Godwit is in accordance with the earlier finding that small Lapwing chicks are more vulnerable to weather-induced losses (Beintema & Visser 1989b).

Effect of neonatal weight and condition on fledging success

To test whether the neonatal weight has an effect on survival, recovery rates of Lap-

Table 2. Daily survival rates S and fledging success F (exponent of S is length of fledging period in days) calculated from the relationship between age and age-specific recovery rates. In brackets: 95% confidence interval. Lap = Lapwing, God = Black-tailed Godwit, Red = Redshank, Oys = Oystercatcher.

Species	S	F
Lap	0.9633 (0.9557-0.9709)	S^{35} = 0.270 (0.205-0.356)
God	0.9701 (0.9557-0.9847)	S^{23} = 0.498 (0.352-0.701)
Red	0.9917 (0.9830-1.0006)	S^{23} = 0.826 (0.674-1.148)
Oys	0.9684 (0.9558-0.9812)	S^{35} = 0.325 (0.206-0.515)

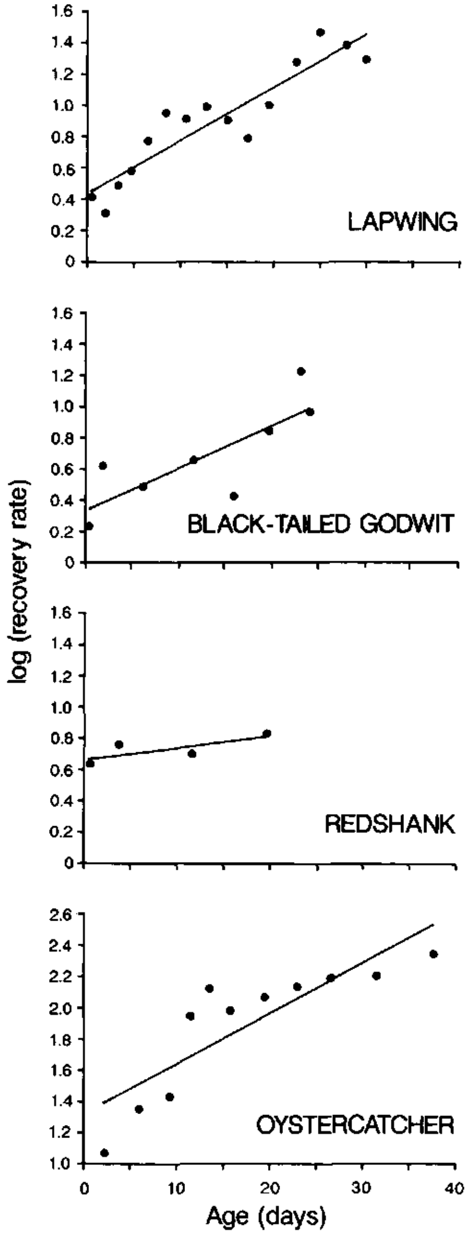

Fig. 2. Log(recovery rate) as a function of age.

Table 3. Recovery rates after fledging of neonate chicks of Lapwing (Lap) and Black-tailed Godwit (God), according to neonatal weight *M* (above average and below average, respectively). *T* = total ringed, *R* = number recovered, *r* = recovery rate (%).

Species	*M* above average			*M* below average		
	T	*R*	*r*	*T*	*R*	*r*
Lap	630	3	0.48	522	2	0.38
God	737	17	1.49	691	8	1.15

wing and Black-tailed Godwit were compared between chicks ringed as neonates with a body mass above the average, and below the average, respectively. Heavy neonates yield slightly higher recovery rates than light ones (Table 3), but the differences are not significant (Chi square).

From the relationship between bill length and body mass, a condition index *CI* can be derived (*CI* = observed body weight / expected body weight, where expected body weight is the average weight of chicks having the observed bill length). *CI* has an average value of 1 for each age class (Beintema 1991). To test the effect of condition on survival, ringing totals (all years combined) for *SMALL* and *LARGE* were divided into *LOW* and *HIGH*, where *LOW* is those chicks with $CI < 1$, and *HIGH* is chicks with $CI > 1$ (Table 4). None of the differences are significant (Chi square). However, annual variations in fledging success are indirectly linked with *CI*, through a relationship with rainfall (see below).

Annual variations in fledging success

Comparison of *RS* values between years was done for Lapwing and Black-tailed Godwit only. Numbers of Redshanks were too small in some years, and the number of small Oystercatcher chicks captured is heavily biased by a handful of bird ringers who catch them, and who did not participate in all years (most ringers wait until the chicks have large enough feet to carry adult

Table 4. Recovery rates after fledging of *SMALL* (up to 1 week old) and *LARGE* (> 1 week) chicks with *LOW* and *HIGH* condition index *CI*. T = number ringed, R = number recovered, r = recovery rate (%).

		LOW			*HIGH*		
		T	R	r	T	R	r
Lapwing	*SMALL*	1018	19	1.87	743	11	1.48
	LARGE	1641	46	2.80	1415	41	2.90
Godwit	*SMALL*	250	8	3.20	183	3	1.64
	LARGE	837	18	2.15	662	23	3.47
Redshank	*SMALL*	147	1	0.68	130	2	1.54
	LARGE	285	6	2.11	627	10	1.59
Oystercatcher	*SMALL*	97	6	6.19	63	2	3.17
	LARGE	604	45	7.45	596	49	8.22

ring size). Annual fluctuations in *RS* for the Lapwing (Table 5) follow a pattern superficially resembling the one for the annual average condition index *CI* for chicks, but the correlation is not significant. However, *RS* is positively correlated with total rainfall in May (figure 3; $T = 2.29$ for $N = 10$, $p < 0.05$), as is *CI* (Beintema 1991). Annual fluctuations in *RS* for Black-tailed Godwit (Table 5) cannot be explained from the present data.

Table 5. Annual fluctuations in relative chick survival *RS* for Lapwing and Black-tailed Godwit. *RS* = *LARGE/SMALL*, where *LARGE* is total of chicks captured at age > 1 week, *SMALL* is total for chicks up to 1 week (chicks ringed while still in the nest excluded).

Year	Lapwing	Godwit
1976	1.26	2.56
1977	1.24	3.11
1978	1.10	5.39
1979	1.52	2.79
1980	1.05	2.79
1981	1.91	3.23
1982	1.44	4.61
1983	1.64	3.06
1984	1.41	3.18
1985	1.67	2.85

Regional differences in fledging success

Within The Netherlands, Frisia is the meadow-bird province par excellence, with

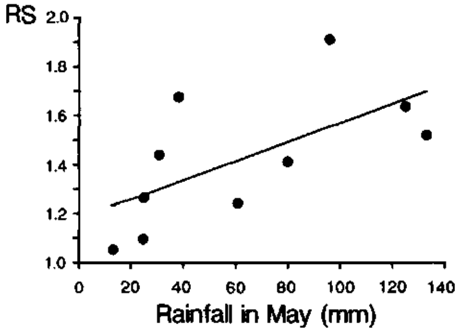

Fig. 3. Relationship between relative chick survival *RS* for the Lapwing and total rainfall in May, for 10 years (1976-1985). *RS* = *LARGE/SMALL*, where *LARGE* is ringing total for chicks captured at an age > 1 week; *SMALL* is up to 1 week.

Table 6. Comparison of numbers ringed and recovered between chicks ringed in Frisia and Elsewhere. T = total ringed, R = recovered, r = recovery rate, *NEST* = ringed in the nest, *SMALL* = up to one week old, *LARGE* = older than one week. *RS* = *LARGE*/*SMALL*. Lap = Lapwing, BtG = Black-tailed Godwit, Red = Redshank, Oys = Oystercatcher. Differences (chi square): * = $p < 0.05$, ** = $p < 0.01$.

		Frisia				Elsewhere				
	age	*RS*	T	R	r	*RS*	T	R	r	
Lap	*NEST*		2804	39	1.39		1005	18	1.79	
	SMALL		1283	21	1.64		8165	137	1.68	
	LARGE		2354	88	3.74		10616	295	2.78	*
		1.8				1.3				**
BtG	*NEST*		1691	17	1.01		1051	18	1.71	
	SMALL		373	8	2.14		794	13	1.64	
	LARGE		1885	41	2.18		1841	43	2.34	
		5.1				2.3				**
Red	*NEST*		648	6	0.93		258	11	4.26	**
	SMALL		252	7	2.78		264	4	1.52	
	LARGE		530	9	1.70		452	12	2.65	
		1.8				2.1				
Oys	*NEST*		1	0	0.00		51	2	3.92	
	SMALL		157	8	5.10		277	7	2.52	
	LARGE		1794	109	6.08		1824	179	9.81	**
		11.4				6.6				**

about 50% of the total Dutch Black-tailed Godwit population, and large proportions of the populations of the other species as well. To test whether Frisia is a better place for chicks to survive, recovery rates of Frisian chicks were compared with those from elsewhere, for three age categories: *NEST* (hatchlings still in the nest), *SMALL*, and *LARGE* (Table 6). *NEST* yields lower recovery rates in Frisia for all species, but only for the Redshank is this significant ($p < 0.01$, Chi square). *SMALL* yields no significant differences. *LARGE* gives no significant differences in recovery rates for Black-tailed Godwit and Redshank, but for the Lapwing Frisia yields a significantly higher rate ($p < 0.05$, Chi square), while for the Oystercatcher this is just the reverse ($p < 0.01$, Chi square).

RS values are significantly higher in Frisia for Lapwing, Black-tailed Godwit, and Oystercatcher ($p < 0.01$ for all three species, Chi square). There is no significant difference in the Redshank. The outcome for the Oystercatcher contradicts the outcome resulting from the recovery rates.

The combined results, although not quite consistent, suggest that Frisian hatchlings run a greater risk of dying in the nest, while the larger chicks are better off in Frisia. Both effects could be explained by a slightly colder and wetter climate in the northern part of the country. Early nestling mortality in Frisia may be enhanced by people intensively searching for, or checking nests during nest-protection activities (own observations), thus preventing chicks from being brooded by a parent.

Seasonal differences in fledging success

When comparing ringing recoveries of chicks ringed in different parts of the season, one has to correct for the increase in average age at ringing, through the season. Each capture was counted as $1/S^a$, where S is the daily survival rate (Table 2), and a is the age, thus yielding 'numbers originally present at birth'. These corrected hatching dates were divided into four periods: up to the 25th percentile of the date distribution, from 25-50 percentile, from 50-75 percentile, and from the 75th percentile onward (*cf* Fig. 1). Recovery rates based on corrected hatching dates (Table 7) are presented in Fig. 4, for the five wettest, and the five driest springs (based on total rainfall in May). Recoveries of Redshank were too few to allow subdivisions. Assuming a linear relationship between recovery rate and total fledging success, recovery rates can directly be translated into fledging success, when the average rate is set equal to the average fledging success.

Fig. 4 allows the following observations:

- Wet springs yield higher fledging rates than dry springs, for all three species.
- In four out of the six situations presented the second period (up to the median hatching date) gives the highest survival.
- All six situations suggest lower survival towards the end of the season.
- Five out of the six situations show also lower survival in the first period.
- The difference between wet and dry springs is most pronounced in the first half of the season, especially in the Black-tailed Godwit.
- In Black-tailed Godwit and Oystercatcher there is a general downward trend in survival through the season.
- In Lapwing there is no clear trend in wet springs, and even an upward trend in dry springs.

Table 7. Estimated number of hatchings *He*, calculated from ringing totals corrected for mortality, and number of recoveries *R*, for four periods: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, 4 = 75-100% of the hatching dates. Recovery rates in figure 4. *WET* = total of the 5 wettest springs, *DRY* = the 5 driest springs 1976-1985 (total rainfall in May).

		WET		*DRY*	
	period	*He*	*R*	*He*	*R*
Lapwing					
	1	5058	72	4601	55
	2	4869	80	4930	69
	3	5363	85	4667	73
	4	5226	79	5198	76
Black-tailed Godwit					
	1	1074	20	1345	15
	2	1063	18	1407	21
	3	1207	17	1568	20
	4	1179	12	1459	17
Oystercatcher					
	1	786	34	924	32
	2	980	50	1024	45
	3	968	34	1103	43
	4	914	40	1024	30

Decreasing survival towards the end of the season has been shown for many bird species (Klomp & Speek 1971), including Lapwing (Galbraith 1988) and Oystercatcher (Harris 1969, Heppleston 1972). Klomp & Speek (1971) reported an upward trend for the Lapwing, but in fact their conclusions were biased by the incorrect assumption that the average age at ringing did not change through the season.

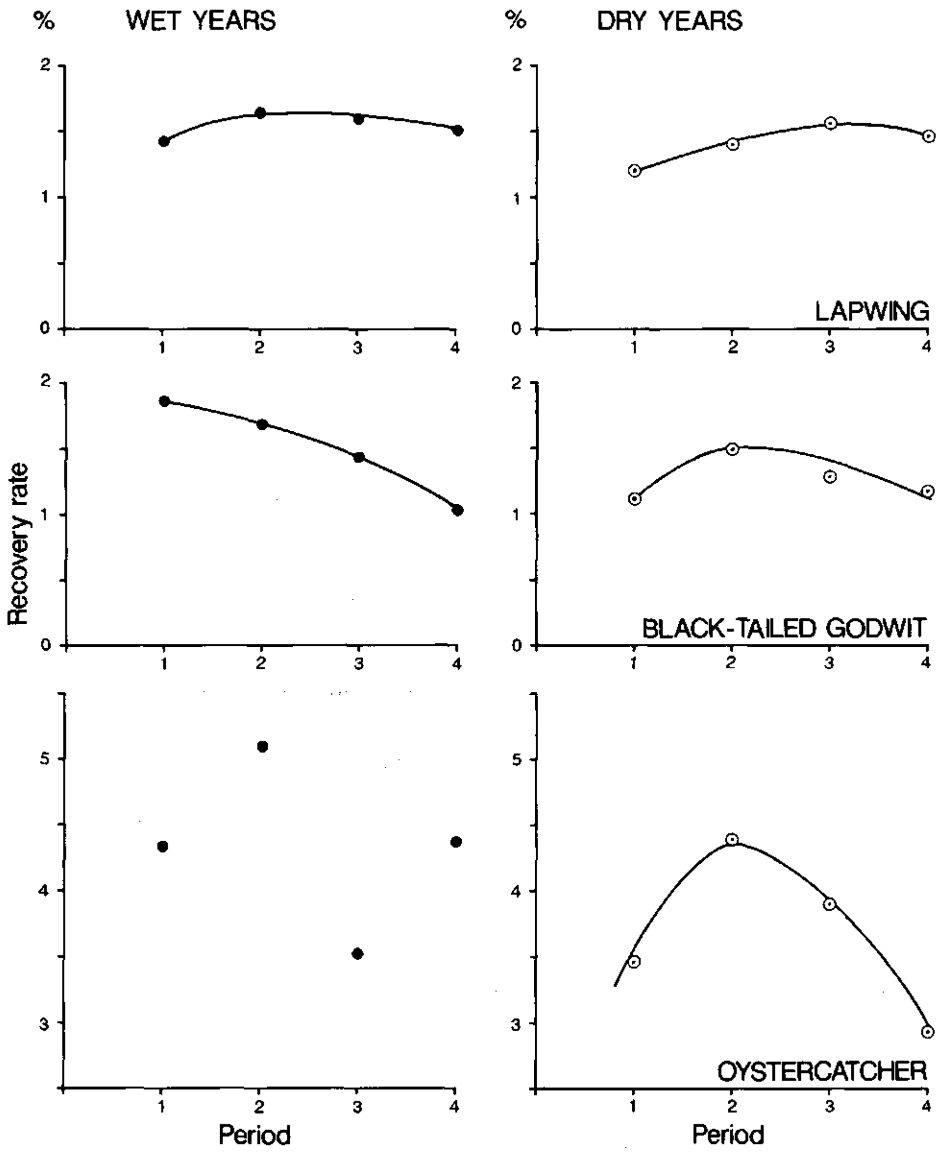

Fig. 4. Recovery rates corrected for chick mortality (standardized to recovery rates of newborn chicks) for 4 equal-size periods of the hatching season: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, 4 = 75-100% of the hatching dates. Lines fitted by eye.

DISCUSSION

Inferring mortality from time-age tables

To illustrate the problems of analysing time-age tables, table 8 presents a simplified example, with only three age classes (days), six days of capture, and a daily survival rate of 0.8. Column totals give traditional ringing totals, row totals show decreasing numbers due to mortality. Diagon-

Table 8. Hypothetical data set of chicks aged when captured.

		date						
		1	2	3	4	5	6	total
age	1	10	100	50	10			170
	2		8	80	40	8		136
	3			6	64	32	6	108
total		10	108	136	114	40	6	

al totals show distribution of hatching dates.

Reality is more complex: Dutch ringers catch c 50% of their total catch on Saturdays. In addition, there are some holidays producing large peaks in numbers caught. Row totals not only depend on numbers present, but also on catchability, which may change with age. Black-tailed Godwit chicks, for instance, are more easily captured when they are more than one week old, because they tend to frequent less tall vegetation, and often prefer to run away from ringers, instead of hiding. Worst of all, there probably is a general downward trend of ringing effort through the season. In the first half, ringers are very keen on catching what they can. In the later part, many of them quit when days slogging through polders produce no more than a handful of captures.

In theory, one can describe all cells in a table like Table 8 in one, very large likelihood formula, and estimate all the parameters, like hatching dates, mortality, ringing effort, catchability, etc. In such complicated likelihood models parameter estimates may wander wildly, making restrictions necessary. Eventually, Ter Braak obtained survival estimates for different cohorts within each year, but no explanatory factor could be correlated with them. Two problems could not be satisfactorily solved: firstly, a general downward trend in ringing effort in the course of the season can never really be distinguished from mortality, and secondly, in periods of reduced growth chicks may erroneously be switched from their true cohort to the neighbouring one (when the age is estimated on the basis of bill length), thus corrupting survival estimates for both.

The idea of estimating survival rates directly from the tables with ringing data, had to be abandoned for reasons given above (except the most simplified form of looking at *RS* values). Meanwhile, statisticians agree on the impossibility of estimating survival from this type of age-time tables in general (Ter Braak pers. comm.).

Daily survival rates

Theoretically, the model assuming a constant daily survival rate is too simple. Daily survival rates may be expected to increase towards fledging, eventually reaching the much higher values of adults, as has been found by Graul (1975) for the Mountain Plover (*Charadrius montanus*). In Fig. 2, the data for Oystercatcher suggest lower survival rates during the first two weeks ($S = 0.912$ for the period age 1-14), and higher values for the remaining period ($S = 0.986$ for age 17 and up). In fact, if all estimates are very accurate, fledging success can be calculated using only the first and the last point of the graph. The line through these two happens to run parallel to the fitted line through all points. Therefore, a model with an increasing *S* would (in this case) not much alter the estimate of total fledging success.

The situation is more complicated for the Lapwing. The data suggest two periods of increased mortality, from day 2-9, and from day 17-25, respectively. The first could be explained by the vulnerability of small Lapwing chicks to bad weather (Beintema & Visser 1989b), the second to postulated difficulties incurred by the dietary switch at this age (from insect food to earthworms, see Beintema et al. 1991). However, the period of virtually zero mortality from day 9-17 may not be realistic. It is quite likely that this is an artefact, caused by problems in age estimation from bill length. This estimate is most accurate in the first 10 days (Beintema & Visser 1989a). Towards the end of the fledging period, however, an inaccurate estimate would never lead to assigning an age of e.g. 80 days. Thus, the range of estimates narrows again towards fledging, leaving most mixed ages in the middle part. This is also seen in Table 1, where Lapwing chicks with a bill length around 20 mm are overrepresented, also when corrected for growth rates slowing down, and allowing for changes in catchability.

Factors affecting chick survival

Spring rainfall has been found to be an important factor affecting chick survival. Rainfall has two counteracting effects. On the one hand, feeding behaviour of tiny chicks, which cannot yet thermoregulate, may be hampered, on the other hand, rain may positively affect food availability. The effect of rain presumably also depends on the temporal distribution of rainfall (short showers vs. drizzle, rainfall at night vs. during the daytime, etc.). In the spring of 1984, which was not extremely wet, unusually high mortality of small chicks due to bad weather was reported (Buker & Winkelman 1987). This might be explained by showers during the daytime coinciding with the days on which most chicks were just born, and had to start feeding in tall, dense vegetation. From mid-May onwards, conditions seem to generally deteriorate: chicks start to show reduced growth (Beintema & Visser 1989a), chick survival decreases, and the positive effect of wet springs diminishes.

The results for the Lapwing are the most consistent. Redshank data seem, in spite of large numbers ringed, still to be insufficient to allow detailed analysis. Compared to Lapwing data, Godwit data are more biased by a smaller number of specialised ringers, whose activities are not evenly distributed in time or space. Furthermore, Godwit chicks are more likely to fall victim to agricultural practice (notably mowing) than Lapwing chicks. Mowing losses allegedly differ greatly between years, depending on mowing dates. Unfortunately, no reliable data on mowing dates could be obtained. The extent of chick losses due to mowing is virtually unknown. Some researchers report very low losses, and conclude that by far the most families with chicks wander away in time, when the farmer starts mowing (Van Paassen 1981), others state that eventual losses may be considerable, in spite of small losses at each plot actually being mown, because families with chicks repeatedly move to new plots which are just about ready to be mown (Kruk pers. comm.). The survival estimate for the Black-tailed Godwit from the age-specific recovery rates is lower than measured in the field under optimal conditions in the Schaalsmeerpolder reserve (Fabritius 1975) and the Kievitslanden reserve (Visser 1983), but higher than measured over 1984 and

1985 in the same Schaalsmeerpolder by Buker & Winkelman (1987). Also when compared to the other species, Godwit chicks do not seem to have particularly poor survival. This may suggest that mowing losses do not have a dramatic effect on chick survival in the average Dutch Black-tailed Godwit.

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SAMENVATTING

Tijdens een ringprogramma waaraan vele ringers vrijwillig meewerkten, werd van 1976 t/m 1985 van een groot aantal kuikens van Kievit, Grutto, Tureluur en Scholekster de leeftijd op het moment van ringen geschat aan de hand van de snavellengte. Met deze geschatte leeftijden werden de geboortedata teruggerekend. In de verdeling van de geboortedata zijn grote verschillen te zien tussen Friesland en de rest van Nederland, vooral bij de kievit. Door het rapen van eieren wordt de uitkomst van de eieren bij deze soort sterk gesynchroniseerd. Synchronisatie wordt verder bevorderd door nazorg, waardoor er minder vervolglegsels laat in het seizoen optreden. In mindere mate is synchronisatie in Friesland ook bij de andere soorten waarneembaar. Uit het verloop van het terugmeldingspercentage met het toenemen van de leeftijd bij

ringen werd de dagelijkse overlevingskans berekend, waaruit het totale opgroeisucces geschat kon worden. Bij de kievit is het opgroeisucces gecorreleerd met de totale regenval in de maand mei. Vroege kuikens en late kuikens blijken een geringere overlevingskans te hebben dan kuikens die halverwege het seizoen geboren worden. Over het algemeen lijken kuikens die in het tweede kwart van het seizoen (tussen de 25ste en 50ste percentiel in de verdeling der geboortedata) uitkomen, de beste kansen te hebben. Vooral in de eerste helft van het seizoen zijn de overlevingskansen in natte voorjaren hoger dan in droge. In Friesland lijken nestkuikens wat slechter te overleven dan elders, maar grote kuikens doen het er juist weer wat beter. Deze verschillen kunnen zowel met klimaat als met neveneffecten van het eierzoeken te maken hebben.

STELLINGEN

I

Klomp (1954) constateerde dat de kievit 'zich alleen op de onvruchtbare natuurgraslanden en overgangslanden thuis voelt' en fris-groene weilanden onbezet laat. In zijn conclusie 'dat de verbetering van het grasland een ernstige bedreiging vormt voor het voortbestaan van de kievitenstand van ons land' heeft hij echter het vermogen tot aanpassing van de kievit in hoge mate onderschat.

Klomp, H. 1954. De terreinkeus van de Kievit, *Vanellus vanellus* (L.). Ardea 42:1-139.

II

De achteruitgang van weidevogels in Nederland gedurende de laatste decennia kan geheel worden toegeschreven aan veranderingen in de landbouw in Nederland. Factoren als droogte in de Sahel, eierrapen in Friesland, jacht in zuidelijke landen en een toenemend aantal kraaien en meeuwen hebben daarbij tot nu toe geen aanwijsbare rol gespeeld.

III

Veel onderzoekers blijven gegevens over broedsucces presenteren in de vorm van een tabel waarin de verschillende verliesoorzaken van nesten als elkaar uitsluitende percentages gegeven worden. Het vasthouden aan deze principieel foutieve methode in plaats van de correcte benadering van Mayfield (1961) te volgen, waarbij het broedsuccess wordt uitgedrukt als een dagelijkse overlevingskans, is niet te rechtvaardigen met het argument dat zo'n tabel voor de lezer gemakkelijker te begrijpen is.

Mayfield, H.G. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

IV

Bij de besteding van fondsen voor bescherming en beheer van Nederlandse broedvogels die elders overwinteren dient meer rekening gehouden te worden met het feit dat het toekomstperspectief voor deze vogels mede bepaald wordt door ecologische en socio-economische ontwikkelingen in landen waar zij overwinteren; dit geldt in bijzondere mate voor West-Afrika.

V

Bij beschouwingen over verstoring door recreanten van groepen pleisterende wad- en watervogels wordt doorgaans voorbijgegaan aan de kern van het probleem, namelijk dat deze vogels zo storingsgevoelig zijn omdat zij door eeuwenlange bejaging schuw gemaakt zijn en schuw gehouden worden.

VI

Uit het feit dat pinguins zeer fel reageren op prederende grote jagers (*Stercorarius skua*), doch ternauwernood notitie nemen van eierrovende zuidpoolkippen (*Chionis alba*), zou men kunnen afleiden dat de zuidpoolkip zich in de evolutie eerst als aaseter heeft ontwikkeld en pas betrekkelijk recent als actieve predator.

VII

De snelle toename van de oppervlakte aan natuurreservaten in Nederland over de laatste tien jaar is geen indicatie dat het goed gaat met de natuur in Nederland, maar wijst eerder op het tegendeel.

Vereniging tot Behoud van Natuurmonumenten. Handboek Natuurmonumenten 1980, 1985, 1991.

VIII

Het natuurbeschermingsbeleid van de Nederlandse overheid en de praktische uitvoering daarvan worden al jarenlang gefrustreerd door de voortdurende opeenvolging van reorganisaties en de daarmee gepaard gaande ontmantelingsprocessen binnen de verantwoordelijke diensten.

IX

Uit het feit dat in het verkeer tussen landingsplaatsen en kolonies de keelbandpinguins (*Pygoscelis antarctica*) van de Zuid-Shetland Eilanden over het algemeen rechts houden zou men kunnen afleiden dat de Britse territoriale claim in Antarctica weinig draagvlak in de regio heeft.

Albert Beintema
26 april 1991