Reproductive tactics in the kestrel, Falco tinnunculus

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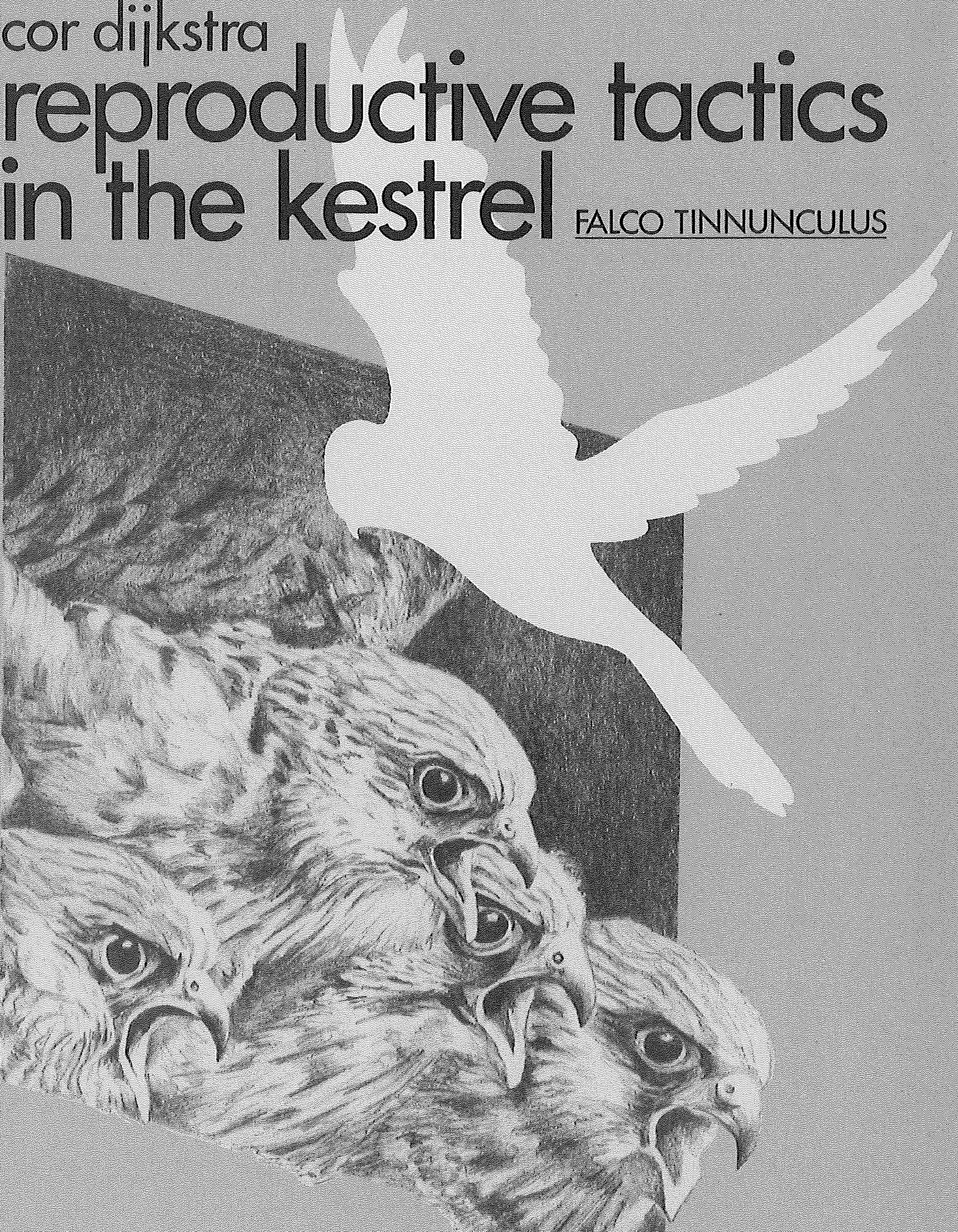
reproductive tactics in the kestrel

FALCO TINNUNCULUS



A STUDY IN EVOLUTIONARY BIOLOGY

REPRODUCTIVE TACTICS IN THE KESTREL
Falco tinnunculus
A study in evolutionary biology

RIJKSUNIVERSITEIT GRONINGEN

REPRODUCTIVE TACTICS IN THE KESTREL
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PROEFSCHRIFT

ter verkrijging van het doctoraat in de Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de Rector Magnificus Dr. S. K. Kuipers
in het openbaar te verdedigen op vrijdag 17 juni 1988
des namiddags te 2.45 uur precies
door

CORNELIS DIJKSTRA

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GRONINGEN

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voor Margriet, Jasper en Eelco

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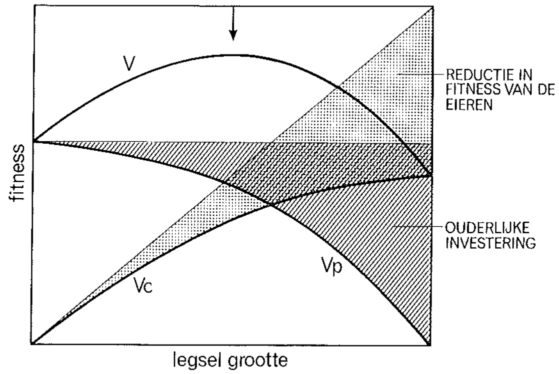
Chapter 1

OVERZICHT VAN HET ONDERZOEK

Achtergrond

In dit proefschrift worden de resultaten besproken van een populatie onderzoek aan torenvalken, uitgevoerd binnen de werkgroep Dieroecologie van het Zoologisch Laboratorium der Rijksuniversiteit Groningen. Dit project (onder leiding van Serge Daan) heeft ten doel de adaptieve betekenis van de temporele organisatie van gedrag in de dagelijkse, jaarlijkse en levens-cyclus van een vrijlevende diersoort te analyseren. In dit kader werden de timing en intensiteit van de investering in nakomelingschap door mij onder de loupe genomen.

Een belangrijke inspiratiebron voor veel vergelijkbaar onderzoek vormen de theorieen van David Lack (1966). Lack lanceerde de hypothese dat de legselgrootte bij vogels onder invloed van de natuurlijke selectie zo geëvolueerd is dat zij overeenkomt met het maximale aantal jongen dat de ouders kunnen voeden. Ook stelde hij dat de timing, d.w.z. de legdatum, zodanig is aangepast dat de tijd van maximale voedselbehoefte, als de jongen in het nest verzorgd worden, overeenkomt met het seizoen waarin het voedselaanbod zijn top bereikt. Deze hypothesen moesten later in hun oorspronkelijke vorm herzien worden. Enerzijds werd theoretisch duidelijk dat ouders niet alleen het aantal jongen in een bepaalde broedpoging zullen maximaliseren, maar de totale produktie van nakomelingschap over meerdere seizoenen. Elke "investering" in een broedsel die ten koste gaat van de ouderlijke overlevingskans en dus van de verwachte toekomstige reproduktie, zal betekenen dat het "optimale" aantal jongen per broedsel onder het maximale aantal ligt dat ze groot kunnen brengen (Williams 1966; Charnov & Krebs 1974). Deze gedachte is schematisch weergegeven in Figuur 1.



Figuur 1. Schematische weergave van het veronderstelde verband tussen fitness en de legselgrootte. De totale fitness (V) = fitness van de eieren (Vc) + fitness van de ouders (Vp). De pijl geeft de optimale legselgrootte aan, waarbij V maximaal is.

Anderzijds wezen empirische gegevens er op dat het gemiddelde legsel later gelegd wordt en minder eieren bevat dan dat met de meeste overlevende nakomelingen (Cavé 1968, Perrins 1966). Dit impliceerde, uitgaande van de oorspronkelijke visie van Lack, dat de meerderheid van de populatie zich suboptimaal zou gedragen. Wel zijn deze resultaten in overeenstemming met de optimalisatiegedachte als legselgrootte en legdatum door individuen kunnen worden afgestemd op hun eigen voedselsituatie (Drent & Daan 1980). In deze visie worden variaties in voortplantingsgedrag dus als fenotypische aanpassingen gezien. Individuen in slechte voedsel omstandigheden zouden pas laat in het seizoen in leg conditie moeten komen en een relatief klein legsel maken. Om deze meer gedetailleerde theorieen over voortplantingsgedrag aan een empirische toetsing te onderwerpen is het noodzakelijk over uitgebreide beschrijvende en experimentele gegevens te beschikken, niet alleen over de opgroeiende jongen in verschillende legsels, maar ook over individueel voedselaanbod van de ouders, hun conditie, inspanning bij de voedselvoorziening van de jongen, overleving en latere reproductie. Dit alles bleek bij de torenvalk in het open landschap van de jonge Nederlandse polders te verwezenlijken.

De ontwikkeling van een veldproject

Het hier beschreven onderzoek aan de broedbiologie van de torenvalk beslaat een periode van tien jaar (1976/87). Dit is kort, niet alleen in vergelijking met de termijn waarop natuurlijke selectie opereert, maar ook met populatieonderzoekingen zoals aan de Koolmees (Tinbergen et al 1987), Drieteenmeeuw (Coulson & Thomas 1985) en Sneeuwhoenders (Moss & Watson 1985). Maar wij hoefden niet bij het begin te beginnen. In de jaren 1959/65 had Cavé (1968) de basis voor ons veldwerk gelegd met zijn klassieke studie over de torenvalk in het toen net drooggelegde Oostelijk Flevoland. Dit was in wezen het eerste op moderne leest geschoeide onderzoek aan een roofvogelpopulatie. Cavé liet zien hoe het gebruik van nestkasten het mogelijk maakte grote gegevensbestanden over de reproductie en overleving van vrijlevende torenvalken te verzamelen en hoe na een gedegen beschrijvende fase ook experimenteren op populatieniveau mogelijk werd. Het is jammer dat dit onderzoek niet langer dan vijf jaar kon worden voortgezet. Hierdoor ontstond er een lacune in de gegevens tot het onderzoek door ons in de Lauwersmeer in 1976 weer werd opgevat. In feite werden daar dezelfde technieken gebruikt als door Cavé. Nestkasten werden op palen in open landschap opgesteld, valken met *bal-chatri* en schepnet frequent gevangen, zodat vanaf 1979 de gehele broedpopulatie jaarlijks geheel geidentificeerd werd. Legselgrootte, legdatum, en broedsucces werden van elk paar valken geregistreerd. Inmiddels was ook een soortgelijk onderzoek aan het Institute of Terrestrial Ecology in Schotland opgezet (Village 1980). Van Village konden wij in een latere fase van het onderzoek de door hem ontwikkelde vleugelmerk-methode overnemen. In aanvulling en ook voortbouwend op deze onderzoekingen werd in het Groningse project de nadruk gelegd op gedragswaarnemingen aan de valkenpopulatie. Dit was mogelijk dankzij de openheid van het landschap in de nog jonge Lauwersmeer en dankzij het grote aantal studenten dat bereid was lange zomerdagen van voor zonsopkomst tot na zonsondergang individuele vogels ononderbroken te volgen. Dit gedragsonderzoek gecombineerd met moderne energetica technieken leidde tot een quantificering van het dagelijkse en jaarlijkse energieverbruik, ook van ouders die voor hun jongen zorgen (proefschrift D. Masman 1986). Manipulaties van het voedselaanbod in het voorjaar (Dijkstra et al 1982) en de jongentijd (zie hoofdstuk 3) maakten al spoedig experimentele analyse van proximate en ultimate factoren in de voortplantingsbeslissingen mogelijk. Door valken zich in gevangenschap te laten voortplanten deden zich nieuwe mogelijkheden voor om achter de sturende, proximate factoren te komen (proefschrift T.Meijer 1988). De in dit proefschrift behandelde gegevens hebben betrekking op de ultimate aspecten van de broedbiologie. Ze zijn behalve op onze eigen veldstudie gebaseerd op de originele gegevens van Cavé (1968), die ten dele (wat betreft de gewicht-gegevens) niet eerder gepubliceerd waren. We hebben verder dankbaar gebruik gemaakt van het uitgebreide databestand aanwezig bij het Vogeltrekstation te Heteren en van de speciale moeite die een groep ringers van dit station zich gegeven heeft om stuitveren van nestjongen te verzamelen, op grond waarvan de sexe-allocatie binnen het broedsel kon worden uitgewerkt.

Voedsel, gewicht en reproduktie

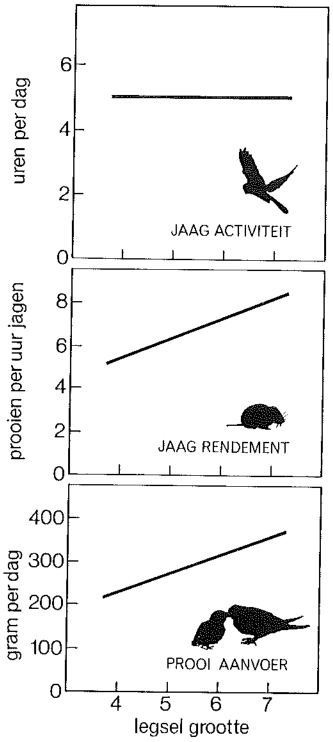
In gebieden als de Lauwersmeer en Flevoland leeft de torenvalk vrijwel uitsluitend van veldmuizen. Door de duur van alle maaltijden met de stopwatch vast te stellen was het mogelijk de dagelijkse voedselopname precies te meten (Masman et al 1986). Veldmuizen varieren sterk in aantal van jaar tot jaar, en deze wisselingen zijn bepalend voor de hele broedbiologie (Cavé 1968). Het was daarom in onze analyse allereerst noodzakelijk een vaste veldmuis-census uit te voeren. Dit werd gedaan met behulp van klapvallen op tien proefterreinen in de Lauwersmeer, elke twee maanden vanaf Maart 1981 tot Maart 1988. De gevangen muizen werden gebruikt voor vele doeleinden: o.a. voor het vaststellen van verteringsefficienties (Masman et al 1986) en voor de analyse van de incidentie van parasieten, *Sarcocystis cernae*, die de veldmuis als tussengastheer, de torenvalk als eindgastheer hebben (Hoogenboom & Dijkstra 1987). Het aantalsverloop wordt beschreven in hoofdstuk 2. In de Lauwersmeer bleek zich een duidelijke 3-jarige cyclus voor te doen, met pieken in de veldmuisstand in 1980, 1983, 1986. Deze variaties hadden hun gevolgen voor de conditie van de torenvalken. Deze conditie werd geanalyseerd aan de hand van circa 3000 gewichten van in het wild gevangen vogels. Voor deze analyse was het allereerst noodzakelijk de gewichten te corrigeren voor tijd van de dag. Dagactieve vogels zoals de torenvalk nemen in de loop van de dag gewoonlijk in gewicht toe, en 's nachts door vertering en verdamping af. De gemiddelde toename varieerde van 0 in de nestjongentijd tot 2.3 gram/uur in het najaar, als de nachten lang worden en de vogels vet opslaan. De muizenstand bleek zijn duidelijkste effecten te hebben op de jonge vogels in hun eerste levensjaar: alleen in de slechte voedseljaren zijn deze gemiddeld lichter dan de volwassen vogels. Dit is van betekenis voor hun reproduktiekansen. De seizoensvariatie in lichaamsgewicht ontstaat waarschijnlijk ten dele door variaties in voedselaanbod en energieverbruik. Valken die in gevangenschap werden gehouden onder een *ad libitum* voedselregime, waar ze niet voor hoefden te werken, waren bijna het gehele jaar ca 10 % zwaarder dan hun soortgenoten in de natuur. Alleen vrouwtjes tijdens de balts-, eileg- en broedfase waren even zwaar in het veld. Dit zijn dan ook de fasen waarin het mannetje exclusief de taak van voedselvoorziening uitvoert, zoals L.Tinbergen (1940) als eerste in detail beschreef.

Naast het effect op juveniele vogels was er een belangrijk effect van de muizenstand aantoonbaar in de gewichten van broedende vrouwtjes. Het lichaamsgewicht van vrouwtjes, ook in de winter al ca 30 gram zwaarder dan de mannetjes, nam gedurende de baltsfase met nog eens 70 gram toe, tot ca 300 gram tijdens de eileg. Het broedgewicht, gemiddeld ca 270 gram, was lager naarmate de valken later in het jaar met de eileg begonnen, en daardoor lager in jaren met lage veldmuisstand, wanneer de populatie later tot broeden kwam. In alle fasen van de reproduktie bleek dit verband tussen legdatum en gewicht aantoonbaar.

Niet broedende vrouwtjes hadden een spontane afname in gewicht terwijl de broeders zwaar werden. De taakverdeling tussen de sexen tijdens de voortplanting wordt door ons geinterpreteerd als een strategie waarbij het mannetje op een minimum gewicht, energetisch zo goedkoop mogelijk kan jagen, terwijl het vrouwtje door haar vetvoorraad gebufferd is tegen perioden van slecht weer en voedseltekort (zie ook Mosher & Matray 1974 en Wijnandts 1984). Het lagere gewicht van het vrouwtje bij latere legdatum bleek geen directe oorzakelijke rol in de bepaling van legselgrootte te spelen (Meijer et al 1988), en is vermoedelijk te interpreteren als een strategische verandering in de mate van buffering later in het jaar (hoofdstuk 2).

Experimenten met het broedsel

Om de verschillen in legselgrootte, die aangepast leken aan de jaarlijkse verschillen in muizenstand, functioneel te begrijpen, werd een nauwkeurige analyse gemaakt van het gedrag van de ouders in de nestjongentijd. Deze fase was al door Lack (1966) gezien als de flessehals van verhoogde vraag naar voedsel waarop de reproduktie van vogels zou zijn afgestemd, en is voor de torenvalk ook de fase van maximaal energieverbruik door de ouders (Masman et al 1988). Bij "complete" broedsels, d.w.z. broedsels waar geen sterfte is opgetreden, bleek dat de vaders steeds gemiddeld ca 4.75 uur per dag in de lucht waren om voedsel te vergaren, onafhankelijk van de broedselgrootte (Fig. 2). Echter, mannetjes met een hoge jaagopbrengst (ca 8 muizen/uur jagen) hadden 6 of 7 jongen in het nest, die met een laag rendement (ca 5.5 muizen/uur jagen) slechts 4. Uiteindelijk was de totale prooiaanvoer per nestjong niet verschillend.



Figuur 2.
Overzicht van de vliegaktiviteit (uren per dag) en de jaagopbrengst (prooien per uur jagen) van mannetjes Torenvalken in de nestjongenfase, als functie van de broedselgrootte (alleen complete broedsels). Tevens is de totale prooiaanvoer (gram per dag) naar de jongen weergegeven.

Door nestkasten te bevestigen aan verrijdbare schaftketen in het veld, en van achteren toegankelijk te maken voor een waarnemer, kon het hongerniveau van de nestjongen gewijzigd worden. Door waarnemers buiten, die met de waarnemer binnen in voortdurend radiocontact waren, werd vastgesteld dat valkenouders van hongerige broedsels wel hun totale jaaginspanning opvoeren maar niet het jaagrendement (muizen/uur jagen). Dit betekent dat zij van nature al het rendement maximaliseren en dus dat de broedselgroottes op voorhand op het jaagrendement zijn afgestemd (hoofdstuk 3).

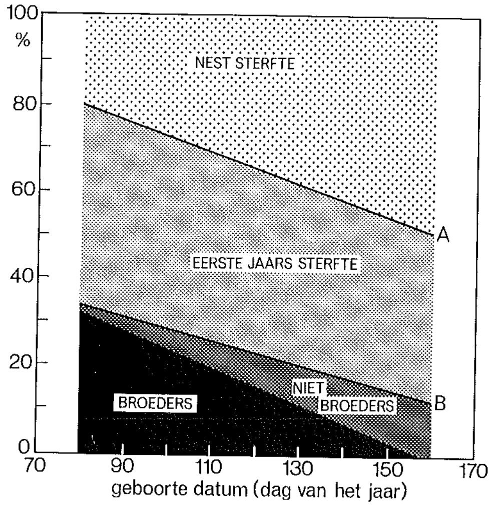
De grens waartoe de ouders bereid waren te gaan lag bij ca 8 uur jagen en vliegen per dag. Dit komt overeen met een maximale inspanning van ruim 500 kJ/dag. Bij deze inspanning werden door een ouderpaar dat gedurende 11 dagen onder druk gezet werd de energetische uitgaven gedekt door een overeenkomstig verhoogde voedselopname. Een analyse van literatuurgegevens over met dubbel gemerkt water gemeten energieuitgaven van oudervogels toont aan dat grotere vogels in het algemeen tijdens de jongenverzorging beneden een allometrisch voorspelde limiet aan de energieopname blijven. Deze experimenten suggereren dat een hoger inspanningsniveau mogelijk nadelige repercussies voor de ouders heeft op langere termijn, zoals door theoretici als Williams (1966) geopperd.

Om zulke repercussies nader te onderzoeken werd een reeks experimenten in de Lauwersmeer en Flevoland opgezet waarbij broedsels op de tiende dag na het uitkomen van de eieren met twee jongen verkleind of met twee vergroot werden (hoofdstuk 4). In de vergrootte broedsels vlogen meer jongen uit dan in controle en in verkleinde nesten. Kennelijk waren ook deze valkenouders in staat hun jaaginspanning zodanig te verhogen dat zij meer jongen konden grootbrengen dan zij van nature hadden. Wel was er iets grotere sterfte in de vergrootte broedsels, en vlogen de jongen met een wat lager eindgewicht uit. Geen aanwijzingen werden gevonden dat de ouders na het uitvliegen langer voor hun jongen zorgden. Het belangrijkste resultaat van deze experimenten was wel dat de locale overleving na een jaar hoger was bij ouders van verkleinde broedsels, en lager bij ouders van vergrootte broedsels. Deze gegevens vormen met de resultaten van andere onderzoekers aan Bonte Vliegenvangers (Askenmo 1979), Roeken (Røskaft 1985) en Koolmezen (Tinbergen 1987) de meest directe steun voor de theorie van Williams (1966).

Reproductieve waarde

Om de ultimate betekenis van de verschillende keuzen die vogels in het voortplantingsproces maken te evalueren, is het nodig hun consequenties voor de kansen op nakomelingschap te bepalen. Het proces van natuurlijke selectie is uit te drukken in termen van de verwachte bijdrage van de ouderlijke genen aan volgende generaties. Deze bijdrage kan worden samengevat in de "Reproductieve Waarde" volgens Fisher (1930). Om deze voor verschillende subgroepen in de populatie te bepalen, is het noodzakelijk de overlevingskansen en de kansen op reproductie zo nauwkeurig mogelijk te schatten.

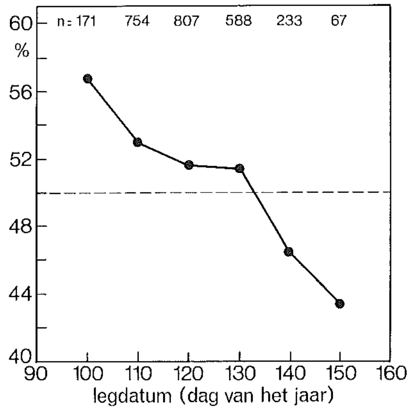
In hoofdstuk 5 wordt dit gedaan voor legsels begonnen op verschillende data in het jaar. Hiervoor was het noodzakelijk het uitgebreide ringmateriaal van het Vogeltrekstation te bewerken. Dit leverde een duidelijke afhankelijkheid op van zowel produktie- als overlevingscijfers van de 3-jaren cyclus in de veldmuizenstand, die zich kennelijk over grotere gebieden dan alleen de Lauwersmeer uitstrekten. De volgende componenten van de Reproduktieve Waarde van de eieren bleken te varieren met de legdatum: Kans op overleven tot uitvliegen (in de studiegebieden in Lauwersmeer en Flevoland, inclusief de onderzoeksjaren van Cavé); Kans op overleven tot de leeftijd van één jaar; Kans op overleven van jaar 1 tot jaar 2 (beide uit landelijk ringmateriaal); en tenslotte de kans op reproduktie op 1-jarige leeftijd (Fig. 3). De laatste component kon bij benadering worden geschat uit de verdeling van geboortedata van broedvogels in de populatie: de vroeggeborenen waren hierin oververtegenwoordigd, ook na verdiskontering van de verschillen in sterfte.



Figuur 3. Het percentage van de gelegde eieren dat overleeft tot het moment van uitvliegen (A); tot de leeftijd van één jaar is bereikt (B); en het pecentage dat als éénjarige aan het broedproces deelneemt, als functie van geboortedatum (dag waarop het eerste ei van het legsel werd gelegd). Lineaire regressies door de gemiddelde waarden per tiendaags interval.

De uiteindelijke reproduktieve waarden van de eieren berekend per tien-dagen interval vertoonden een scherpe daling met toenemende legdatum. Naast de principes van synchronisatie van voortplanting met de piek in voedselaanbod (Lack 1966), en van synchronisatie met de soortgenoten bij kolonievogels (Fraser Darling 1938), lijkt het principe van "zo vroeg mogelijk" broeden evolutionair voordeel op te leveren.

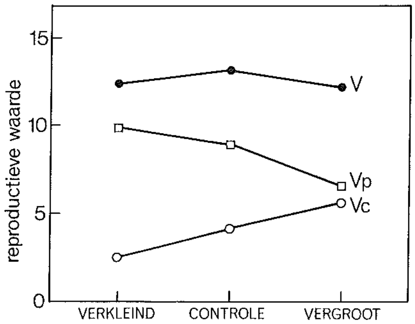
Bij deze analyse werd nog geen rekening gehouden met de verschillen in kansen voor mannelijke en vrouwelijke eieren. Sinds 1981 is een programma op gang gekomen waarbij op grote schaal de sexe van torenvalknestjongen in Nederland wordt vastgesteld. Een eerste analyse hiervan (hoofdstuk 6) leidde tot de conclusie dat de kansen op voortplanting van eerste jaars mannetjes sterk afhankelijk zijn van hun geboortedatum, die van de vrouwtjes niet. Vroeg geboren mannetjes hebben waarschijnlijk meer tijd beschikbaar om het jaagmétier te leren en territoria te veroveren. Hierdoor is het evolutionair voordelig om in vroege legsels vooral mannelijke, in late legsels vooral vrouwelijke eieren te produceren. Doordat het sexe-programma nog niet lang genoeg loopt is het thans nog niet mogelijk deze evolutionaire voordelen in termen van reproductieve waarde te kwantificeren. Wel is vastgesteld dat vroege torenvalkbroedsels inderdaad meer mannetjes, late broedsels meer vrouwtjes bevatten (Fig. 4).



Figuur 4. Sex ratio (percentage mannetjes; gesexed ± 25 dagen na uitkomen) in broedsels met verschillende legdatum.

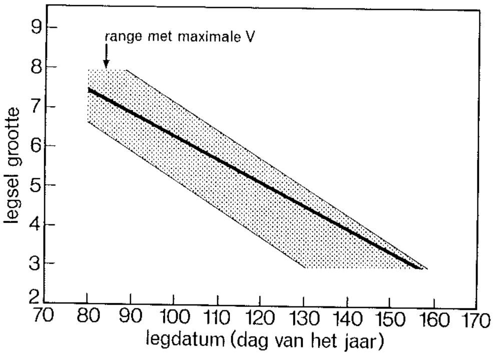
Ook vonden wij, door bij een reeks legsels nauwkeurig de volgorde van leggen en van uitkomen te scoren, en zo de sexe-volgorde bij de leg te bepalen, dat vroeg in het jaar de eerste eieren van het legsel statistisch gezien vaker mannetjes zijn, en laat in het jaar vaker vrouwtjes. Door de kans op mannelijke of vrouwelijke eieren met de legvolgorde en met de datum te varieren, bereiken de valken dat steeds het geslacht met de beste kansen voor de toekomst oververtegenwoordigd is. Dit fenomeen is nieuw in de ornithologie.

De uiteindelijke weging van voortplantingstrategieen (zoals keuze van legdatum en legselgrootte) door de natuurlijke selectie gebeurt niet alleen op de reproduktieve waarde van de jongen (V_c in figuur 1) maar ook op de "residual reproductive value" (Williams 1966) van de ouders (V_P). In hoofdstuk 7 wordt een poging gedaan de effecten van legsel/broedselgrootte op de totale reproductieve waarde, en dus op de fitness onder natuurlijke omstandigheden te berekenen. Doordat in de broedselgrootte experimenten V_c met de broedselgrootte toenam terwijl V_P vergelijkbaar afnam, kwam de totale reproduktieve waarde bij onbeinvloedde broedsels nauwelijks uit boven die van vergrootte en verkleinde (Fig. 5). De analyse doet vooralsnog vermoeden dat de optimale legselgroottes niet



Figuur 5. Reproductieve waarde van het legsel (Vc), van de ouders (Vp), en de totale reproductieve waarde $V = Vc + Vp$, van experimenteel vergrootte en verkleinde broedsels en controles.

zeer nauw begrensd zijn. Een stap verder voert de analyse van reproductieve waarde in combinatie met het aantal jongen dat ouders met constante inspanning (zie Fig. 2) kunnen grootbrengen. Dit aantal neemt ook voor individuele torenvalken toe naarmate ze later leggen, doordat het jaagrendement systematisch stijgt als de veldmuis zich gaat voortplanten en in aantal toeneemt. Bij gelijk blijvende inspanning van ca 6 uur jagen per dag door de vader en moeder samen, kan elke 14 dagen een jong meer worden grootgebracht. Intussen daalt echter de reproduktieve waarde van eieren naarmate ze later worden gelegd. Het is dit belangenconflict tussen meer (later broeden) en "betere" (eerder broeden) jongen waardoor bij hoog voedselaanbod grote vroege legsels, bij laag voedselaanbod kleine late legsels voor het individu de reproduktieve waarde maximaliseren. Het bleek dat de preciese voorspelling van de maximaliserende strategie afhangt van de wijze van berekening. De beste passing met de waargenomen verdeling van de legsels in het datum-legselgrootte vlak vertoonde een op simpele lineaire regressie door de reproduktieve waarden gebaseerde berekening. Bijna driekwart van de waargenomen legsels voldeed aan deze criteria en de gemiddelde relatie tussen datum en legselgrootte als geschat door de gereduceerde hoofdas lag nagenoeg midden tussen de voorspelde onder- en bovengrenzen (Fig. 6).



Figuur 6. Range van legselgrootte en legdatum combinaties die een maximale reproductieve waarde (V) opleveren. De lijn geeft de gereduceerde hoofdas aan, berekend door alle waargenomen legsels.

Het kwantificeren van reproduktieve waarde als afhankelijk van phenotypische eigenschappen van dieren is een moeizame weg, die alleen begaan kan worden als er een uitgebreid databestand beschikbaar is, verzameld onder de omstandigheden waaronder natuurlijke selectie optreedt, dat wil zeggen in de natuur. Als we ondersteuning willen vinden voor het idee dat reproduktie-eigenschappen als individuele taktiek kunnen worden beschouwd, lijkt het de enige weg.

LITERATUUR

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Chapter 2

DAILY AND SEASONAL VARIATIONS IN BODY MASS OF THE KESTREL IN RELATION TO FOOD AVAILABILITY AND REPRODUCTION.

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1. SUMMARY

We measured variation in body mass in male and female kestrels in relation to age, food availability and reproduction. All body mass data were corrected for time of day by transforming them to morning weights, since there was a significant daily increase throughout most of the year in both sexes. Juveniles weighed less than adults, especially in low vole years. Both sexes had higher body mass in winter than in summer. Breeding females had maximum body mass during reproduction, whereas non-breeding females maintained a relatively low body mass throughout the reproductive season. *Ad lib* fed kestrels, held in captivity, showed the same difference in body mass between breeding and non-breeding females. This indicates a different body mass set point for breeders and non-breeders. Females rapidly increased in mass two weeks before laying. After laying they lost ca. 30 g of body mass and maintained the same level until the young hatched. From hatching onwards female weights dropped sharply to a minimum level during moult. Males showed a gradual decrease in body mass of about 10 g during the whole reproductive phase. *Ad lib* fed kestrels held in captivity showed the same annual variations in body mass, but were heavier then free-living birds throughout the year except during laying (both sexes) and incubation (only females). Late-laying females produced smaller clutches and weighed less than early layers during the entire reproductive phase and the same trend in body mass showed up in males. Females layed at an earlier date in high vole years and attained higher body mass during incubation compared with low vole years. Analysis of covariance indicated that the dependence of body mass on laying date was the same in low and high vole years, and thus reflects variation within years related to individual nutritional conditions rather than spurious correlation between general effects of annual vole density on both mean laying date and mean body mass. Deposition of fewer body reserves by late females may let them gain time to advance laying date, maintaining more reserves may buffer early females against adverse weather.

2. INTRODUCTION

Patterns of variation in avian reproduction are both ultimately adapted to and proximately generated by variations in food supply (Lack 1966; Daan et al 1988a). Food availability may affect both ultimate reproductive success and proximate reproductive decisions either directly through the rate of energy input or via energy storage in the body. Variations in body reserves are therefore expected to be associated both with food abundance and with reproductive strategies (Jones & Ward 1976, Drent & Daan 1980). Natural variations in body mass have not often been analysed in this context (e.g., Järvinen & Väisänen 1984). Raptors are particularly suited for such analysis, on account of their large natural variations in body mass related to season and sexual task differentiation. Detailed studies are available for the Sparrowhawk *Accipiter nisus* (Newton et al. 1983), a diurnal bird feeder, the Tawny Owl *Strix aluco* (Hirons et al. 1984) and the Ural Owl *Strix uralensis* (Pietiäinen et al. 1986), both nocturnal mammal hunters. These studies present correlative evidence for associations between food abundance, body mass and reproductive investment. We have carried out a complementary study on a diurnal mammal hunter, the European Kestrel *Falco tinnunculus*. More than 3000 body weights were taken of birds in their natural situation and under experimentation with food supply both in the natural habitat and in captivity.

The pattern of reproduction in relation to food is well-known in the kestrel (Cavé 1968) and is probably representative for many species of raptors. The predominant food of kestrels is microtine mammals, which typically undergo large population fluctuations from year to year, often in pronounced 3-4 year cycles. In years with high vole abundance, kestrels breed early and lay large clutches. In low vole density years, they breed later in the season and produce smaller clutches (Cavé 1968, Village 1986, Daan & Dijkstra 1988, chapter 5). To analyse how body mass varies in association with food supply and reproduction, it is necessary to evaluate several other sources of variation: time of day, time of year, age and body size. Seasonal variation in body mass of the kestrel has previously been reported (Village 1983), albeit not in relation with food supply and reproductive strategy. On the basis of our data we address the question to what extent such variations in body mass reflect changing regulatory set points, and to what extent they are the immediate consequence of the environmental situation. In a following paper (Meijer et al. 1988b) we use these descriptive data as a background to evaluate the results of experimental food manipulation.

3. METHODS

The data were obtained in two recent land reclamations in the Netherlands: Oostelijk Flevoland (52°30'N, 5°49'E) and Lauwersmeer (53°20'N, 6°16'E). In Flevoland data were collected in 1960-65, (Cavé 1968) and again in 1985-86. Lauwersmeer data stem from the years 1977-86. For general descriptions of the areas we refer to Cavé (1968) and Joenje (1977).

3.1 Catching and weighing procedures

The studies in both areas used similar methods. In flat and rather unstructured areas undergoing rapid vegetational succession with little human interference, nestboxes (usually 40x30x30 cm) were mounted on poles 2-5 m high. The rapid development of common vole (*Microtus arvalis*) populations in the new polders attracted considerable numbers of kestrels to the nestboxes. Laying dates (expressed throughout as day of the year), clutch sizes, initial brood sizes and numbers of fledglings could be determined by regular checks of the nestboxes. Kestrels are partial migrants in the Netherlands, and birds that stay during winter make further use of the boxes as a night roost. Kestrels could be caught by silently approaching a nestbox from behind and suddenly closing its entrance with a deep net. In the breeding season the same technique was used when the female incubated the eggs or the male attended the clutch while the female took a short meal break. A technique we used more frequently was the '*bal-chatri*' (Cavé 1968), a double wire mesh cage with live mice inside and nylon nooses on top in which birds approaching the bait became entangled with their talons. The *bal-chatri* was usually operated from a car and remained under observation until the bird was caught. While most kestrels rapidly respond to the *bal-chatri* when it is offered for the first time, it is rarely possible to recapture them with the same method. Nestbox trapping allowed repeated captures. Birds trapped were ringed with aluminium rings of the Bird Ringing Station (Heteren). Colour rings, and in a later stage of the Lauwersmeer study wing tags (Village 1982), were used for remote individual recognition. Body weights were taken to the nearest gram, using Pesola spring balances. In the Lauwersmeer study we further recorded wing length, plumage coloration, moult scores and crop filling before the birds were released. Birds collected during darkness were released the next morning to avoid risks in having them stray during the night.

In addition to trapping, kestrels were weighed using electronic balances mounted in the entrance of the nestbox. These balances were wired such that each time a bird landed in the entrance or left the scale its mass would be recorded, together with time of day, on a paper chart recorder underneath the nest. Male and female of a pair could be distinguished by their weight difference, and multiple weights could be obtained throughout the daylight period.

3.2. Common vole census

In order to evaluate food conditions, densities of the common vole *Microtus arvalis*, the major food source of kestrels in the Netherlands (Cavé 1968, Masman et al. 1986), were assessed in a periodic breakneck trap census. Methods and results for the years 1960/64 in Flevoland have been described by Cavé (1968). In the Lauwersmeer a trap census was carried out every two months from March 1981 until January 1987, adopting the method of Hörnfeldt (1978) with minor modifications. Ten plots of one hectare each were selected in open areas where kestrels were seen hunting regularly. In every plot, six traplines were set up, 20 meters apart, one randomly assigned to each of the six trapping times per year. On each trapline ten trapping stations were situated ten meters apart. At each trapping station five breakneck traps, baited with carrot, were placed in a radius of two meters around the station mark. The traps were placed where possible near holes or runways. One trapline consisted of 10x5=50 traps, and thus a total of 500 traps were set every two months. Traps were checked on three successive days and then removed.

4. RESULTS

4.1 Daily variations in body mass

Weighing scales in the nestbox entrance allowed us to record daily variations in body mass in individuals only during the reproductive season. Examples of such individual records in the field are given in Fig. 1. The lowest weights in most birds were measured early in the morning just after the kestrels left their roost. During daytime a variable increase in body mass occurred and peak weights were usually reached just before nightfall. The differences in body mass between the individuals in Fig. 1 are partly due to the different phases of the reproductive cycle.

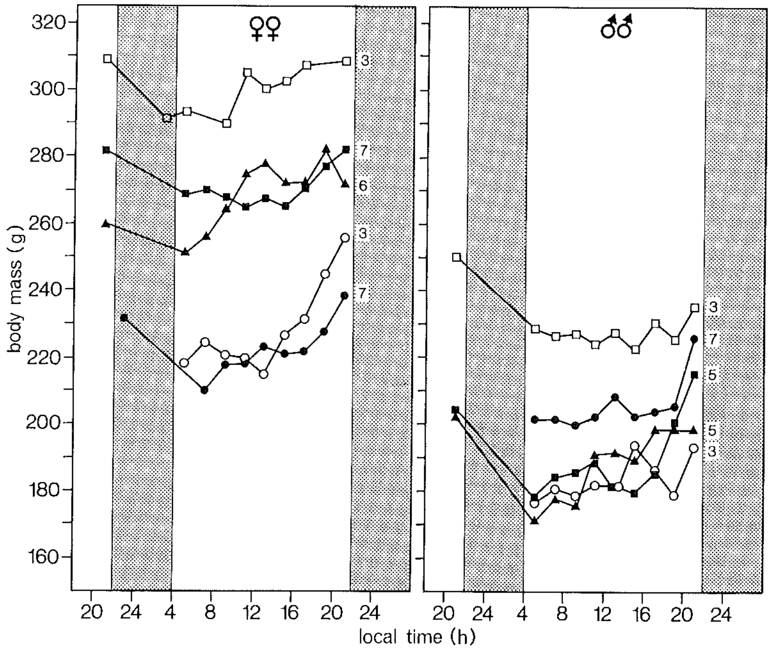

Figure 1. Examples of body mass recordings of female (left panel) and male kestrels (right panel) on electronic balances mounted in the entrance of nest boxes. Shaded areas indicate approximate time of darkness. Numbers indicate phase of the breeding cycle.

The mean body mass of male and female kestrels, based on all scale recordings, is shown in Fig. 2 (solid dots) as a function of time of day. Data were only included in this analysis if at least three data points were obtained and if the time between first and last weights was at least half a day. The data refer to the courtship and laying phase (phases 3, 4), the

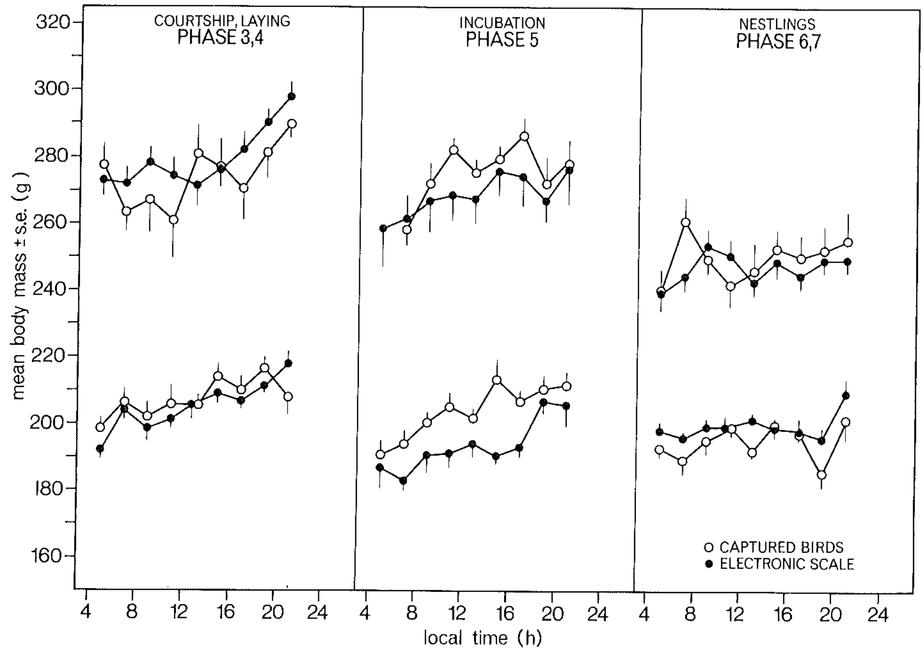

Figure 2. Variations over the daylight period in mean body mass of all free-living birds recorded by electronic scales in the field (solid symbols) and of those captured and weighed on spring balances. Upper curves: females; lower curves: males.

breeding phase (phase 5) and the nestling phase (phases 6, 7). The bulk of our data was collected by catching the kestrels, which resulted in at most one record of an individual per day. Indeed the majority was caught only once or twice a year. The data collected in this way are again shown as a function of time of day in Figure 2 (open symbols). The trends in body mass change in the course of the day are approximately the same for the two sampling methods. In the females the largest daily increase in weight occurred in the courtship and laying phase. In the nestling stage there was only a slight increase. The males also showed the smallest increase in the nestling phase. During incubation (phase 5) the males weighed by the scale method appeared lighter than the birds caught, but this is merely due to the small number of individuals recorded on the scale. Even in this case the trend in body mass during daytime was the same with both methods.

In the analysis of seasonal changes in body mass we have to eliminate time of day as a source of variation. Since during reproduction the figures based on single catches of a large number of birds revealed the same trend in body mass as individual recordings (Fig. 2) we

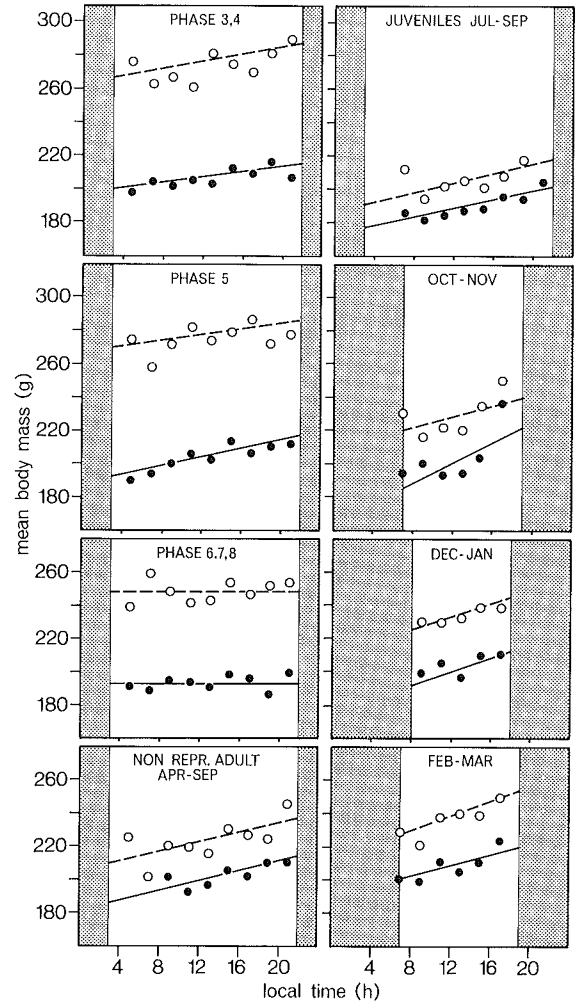

Figure 3. Mean body mass of captured free-living kestrels in two-hourly intervals of the daylight period in different phases of the annual cycle. Open symbols: females; solid symbols: males. Lines show linear regressions (see table 1).

assumed the data outside the breeding season also to be representative for individual body mass change in the course of day. A summary of daily mass change in the course of the year is shown in Fig. 3 and Table 1. In all stages except the nestling-fledgling phase, males and females showed a significant increase in body mass in the course of day. Linear regressions sufficiently describe these data since adding a quadratic term did not improve the fit. We used the equations from Table 1, to correct for time of day effects. Weights recorded were transformed to morning weights, since the time of leaving the roost appeared to show the lowest weight during the daily cycle (Table 1). Morning weights were used in all further calculations.

Table 1. Regressions of body mass (g) on hour of the day during daylight (t, Central European Time) of wild caught kestrels in the Netherlands. Significance of the increase over the day: * p<.05; ** p<.01; *** p<.001; one-tailed t-test).

Phase of the cycle	Females			Males		
	mass	n	p	mass	n	p
Courtship(3)/Laying(4)	263+1.0t	168	**	197+0.8t	142	***
Incubation(5)	268+0.7t	255	*	189+1.2t	141	***
Parental care(6,7,8)	248	201		194	140	
Summer adults non-rep	206+1.4t	99	**	181+1.5t	97	***
July-Sept fledglings	184+1.6t	299	***	173+1.2t	215	***
October/November	210+1.6t	78	**	176+2.3t	71	***
December/January	217+1.4t	80	*	185+1.5t	85	*
February/March	215+2.0t	76	**	188+1.8t	63	***

4.2 Seasonal changes in body mass

In individual female kestrels, repeatedly caught during three successive years, highest body masses were recorded during the reproductive season, about 50-100 g higher than during winter (Fig. 4). The same pattern emerges in all the female body mass data, pooled per

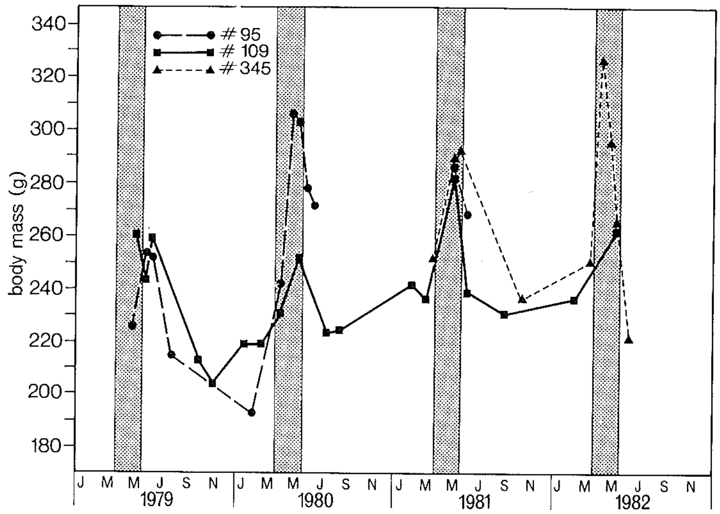

Figure 4. Examples of body mass measurements taken in three individual free-living female kestrels captured repeatedly in the course of three years. Shaded areas indicate the breeding season.

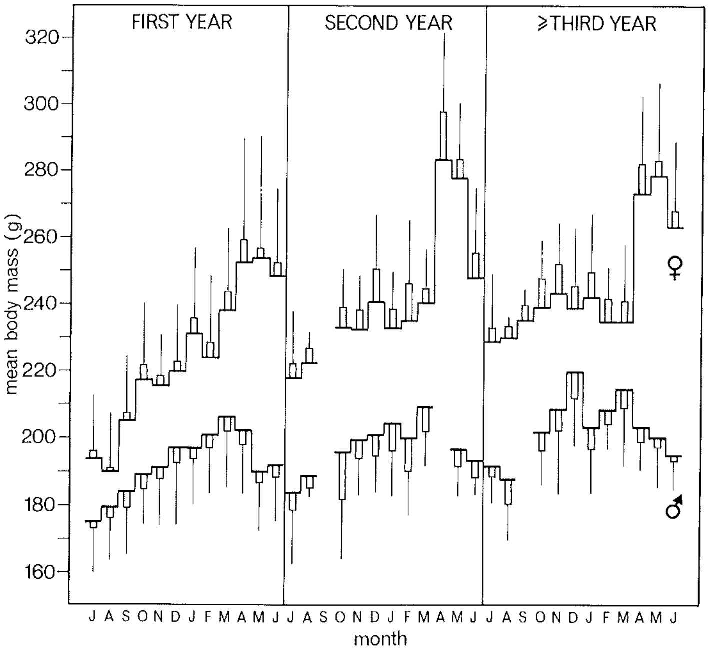

Figure 5. Mean body mass per month of known-age wild caught kestrels as a function of age in their first and second year of life, and as a function of time of year in older birds. Rectangles indicate 1 s.e.m., lines 1 s.d.

month and age class (Fig. 5). Lowest body mass in all age classes and both sexes was measured in July/August. This coincides with moult in adult birds and with reaching independence in juveniles. In autumn there was a gradual increase in all cases, followed by a stabilisation during winter. The males reached their peak weights in early spring just before the start of reproduction, and lost weight from April until July. Female peak weights were reached in April and May when most birds incubated, followed by a steep drop in June and July. First-year birds, just after becoming independent of their parents in July/August, were considerably lighter then the yearlings and older birds (see also Table 2). The juveniles surviving the summer months grew rapidly in autumn. However, even in May and June after their first winter the peak weights of the first-year females were still somewhat lower than those of the adults (Fig. 5). Since these data concern all individuals caught or recorded, including non-breeding birds, the lower peak weight of the first-year females might be caused by a larger fraction of non-breeders, since non-breeding birds weighed considerably less then the breeding birds (see section 4.4).

Apart from seasonal and age related variations in body mass one may expect that some of the variation is related to skeletal size differences. As a potential mass independent measure

Table 2. Monthly averages of body mass (g) in and after the first year of life. Means ± s.d (n).

Month	Females		Males	
	Juveniles	Adults	Juveniles	Adults
July	193±19(44)	220±19(43)	174±16(30)	187±15(48)
August	189±18(184)	222±12(13)	178±16(134)	190±11(6)
September	204±20(47)	227±17(5)	182±19(30)	202± 9(4)
October	216±24(16)	232±17(27)	188±15(16)	198±19(19)
November	215±15(30)	236±19(26)	190±18(35)	203±20(35)
December	219±20(26)	239±21(31)	196±23(29)	210±21(40)
January	230±26(28)	236±20(50)	196±16(28)	204±21(44)
February	223±24(25)	237±26(36)	200±18(25)	202±19(44)
March	237±25(30)	240±25(53)	206±22(21)	209±18(42)
April	253±37(30)	262±32(40)	202±19(24)	200±14(28)
May	254±37(110)	276±26(116)	189±18(45)	197±15(88)
June	248±27(53)	252±29(56)	191±17(28)	192±11(49)
Total	219±36(623)	248±30(496)	187±20(445)	200±18(447)

Table 3. Regressions of body mass (g) on winglength (w, in mm) and significance levels for the difference of the slope from zero (* p<.05; ** p<.01; *** p<.001; one tailed t-test) in kestrels during various phases of the cycle. Number of birds in parentheses.

Age group	Phase	Females Mass	Sign	n	Males Mass	Sign	n
Juveniles	Jul/Sep	- 68+1.0w	***	(245)	- 12+0.8w	***	(179)
Juveniles	Oct/Mar	205+0.1w	--	(92)	- 83+1.1w	**	(84)
Adults	Oct/Mar	217+0.1w	--	(114)	- 19+0.9w	**	(102)
All	3/4	- 11+1.1w	--	(46)	116+0.4w	--	(38)
All	5	- 102+1.5w	***	(114)	83+0.5w	--	(65)
All	6/7/8	188+0.2w	--	(60)	144+0.2w	--	(42)
All	non-rep	205+0.0w	--	(56)	2+0.7w	*	(61)

of size, we measured wing length in all kestrels caught, and analysed the regression of body mass on wing length for all phases of the annual cycle (Table 3). In the males a significant positive correlation between body mass and wing length existed during winter and in summer, both for juveniles and adults. Only during the breeding season no correlation was found. In the females a different pattern emerged, since only juveniles just after independence and incubating birds showed a significant positive correlation. However, standard deviations of wing lengths in the complete data set were only 1.1 in females and 0.7 in males. Correction for such small variation would lead only to minor changes in body mass estimates (on average 4.3%). We thereby feel justified in neglecting size differences here.

4.3. Variations in body mass with food availability

In Fig. 6A the total number of voles trapped in the break neck census in the Lauwersmeer is plotted as a function of the time of year, for six consecutive years. In every year the lowest numbers were trapped in spring (March/May) at the start of the reproductive season of the voles, and peak numbers in September at the end of reproduction. In March only adult voles were caught. In May the first juveniles were trapped. Vole population size in May is probably underestimated in trap censuses due to low trappability of the voles in this period, compared with other times of year (Hoogenboom et al. 1984). In addition to this annual cycle in numbers another well known feature in voles is a three-year cycle in population size (e.g. Van Wijngaarden 1957, Hörnfeldt 1978). We found an increase in autumn numbers from 1981 till 1983, followed by a drop in 1984 and again an increase through 1985 and 1986 (Fig. 6A).

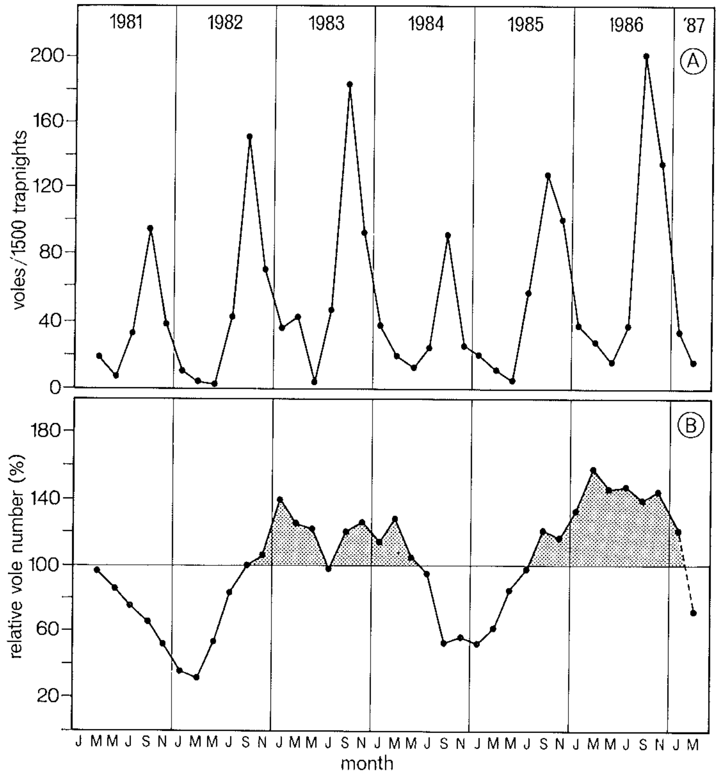

Figure 6. A. Number of common voles (*Microtus arvalis*) trapped per 1500 trapnights in a standard bimonthly trapping census in the Lauwersmeer over a six-year period. B. Vole numbers expressed relative to the mean (100%) of all values obtained in the same month over six years.

For better visualisation of these longterm changes we expressed the actual number of voles caught in each trapping episode as a percentage of the mean number trapped in the same month over six years (Fig. 6B). In 1981 and 1982 vole numbers were well below average, whereas 1983 until May 1984 was a relatively high density period. The same pattern returned in the last three years of the trapping census.

To analyse body mass variation of the kestrels in relation to food abundance, months were grouped in "high" (above 100%) and "low" (below 100%) vole abundance periods on the basis of Fig. 6B. The same method was used for the vole census results from Cavé (1968) in 1960-1964. Kestrel body mass data were grouped accordingly. During 'high' vole periods, juvenile kestrels had a higher body mass than during 'low' periods. In the adults mean body mass was the same in both cases (Fig. 7). So the difference in body mass between juveniles and adults as described earlier (Fig. 5) is at least partly due to an effect of vole abundance. But even in rich vole periods the juvenile females attained the body mass of adults only after their first winter. Peak weights in the females were reached in April-June both in first year birds and in the adults. This rapid increase in mean body mass is due to those females taking part in reproduction (see section 4.4).

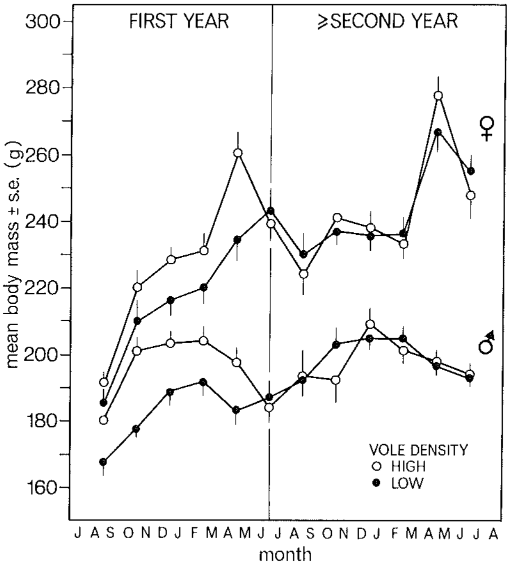

Figure 7. Two-monthly mean values for body mass of male and female kestrels trapped as juveniles or adults in months with high and with low common vole densities.

4.4. Variations in body mass during reproduction

Body mass variation during reproduction is analysed in more detail in Table 4 and Fig. 8. Males showed a gradual decrease in body mass during reproduction. At the start of courtship they weighed on average slightly more than 200 g and at the end of the nestling stage about 190 g. Reproducing females showed a rapid increase in body mass during courtship (Fig. 8). This increase started about twelve days before egg-laying. Females reached peak weights of about 300 g during laying and body mass stabilised during incubation around a mean of 275 g. After the young hatched the females rapidly lost weight. This weight loss during the 30 days of the nestling stage amounted to about 50 g, or about 20% of the body mass during incubation. Non-breeding females did not show these large variations in body mass but maintained a relatively low body mass throughout the breeding season (Table 4).

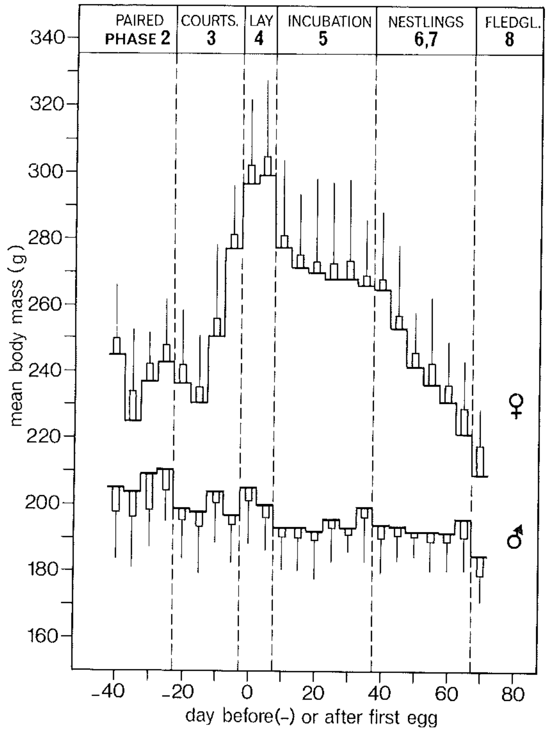

Figure 8. Mean body mass per five days relative to the laying date of the first egg for breeding male and female kestrels trapped or recorded in the field. Rectangles: 1 s.e.m.; lines: 1 s.d.

Whether these differences between breeding and non-breeding free-living kestrels are a direct result of food availability, or reflect differences in regulatory setpoints cannot be deduced from these data. However, body mass data from pairs of kestrels, held in captivity and fed *ad lib.* (Meijer et al. 1988a) also showed a marked difference in mass between breeding and non-breeding females (Fig. 9A).

Table 4. Average body mass (g) during the various phases of reproduction, for yearling and adult breeders and for non-breeders. Means ± s.d. (n).

	Females		Males	
Phase	Yearlings	Adults	Yearlings	Adults
3 Courtship	254±28(31)	255±24(29)	208±20(9)	200±14(31)
4 Laying	302±23(14)	307±22(19)	210±13(5)	203±14(22)
5 Incubation	268±25(93)	275±24(113)	194±13(25)	196±14(70)
6 Nestl. < 10d.	258±19(28)	267±24(37)	193±18(6)	195±12(28)
7 Nestl. > 10d.	238±24(16)	239±22(30)	194±16(8)	193±11(28)
8 Fledglings	193 (1)	237±26(5)	(0)	192±15(11)
9 Moult	214±15(11)	227±21(8)	184±22(16)	190±11(10)
1 Non-breeders (April/Sept)	199±16(30)	222±10(6)	186±19(34)	186±16(7)

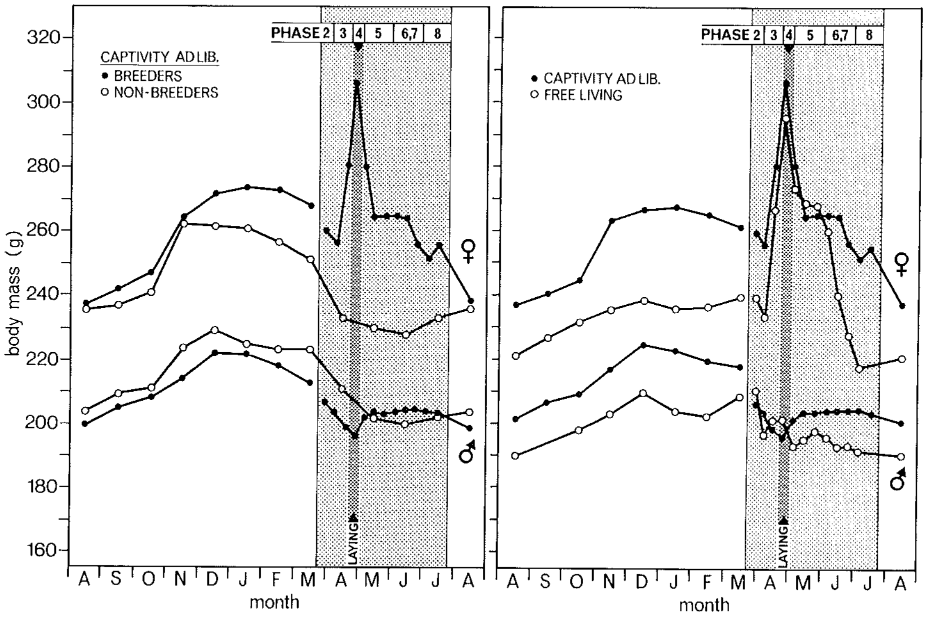

Figure 9. Comparison of mean body mass of breeding and non-breeding kestrels in captivity fed *ad lib.* (A, left panel). Comparison of mean body mass in captive birds and in free-living breeding kestrels in the course of the year (B, right panel).

Kestrels in captivity weighed considerably more than free-living birds (Fig. 9B). Only during laying and incubation the free-living females reached body mass levels of the *ad lib.* fed group in captivity, whereas the males showed the same levels only during courtship and the laying phase.

Within the breeding population there is large variation in timing of reproduction (Cavé 1968). Mean laying dates of the kestrels in different years were negatively correlated with both clutch size and indices of vole abundance (Daan & Dijkstra 1988, chapter 5). It is therefore of interest to analyse body mass as a function of laying date, clutch size and vole abundance. Late laying females weighed less than the other groups throughout the reproductive cycle (triangles in Fig. 10). Regression of female body mass on laying date (Fig. 11) revealed a significant negative correlation during egg-laying (phase 4), incubation (phase 5), and the nestling-fledgling stage (phases 6, 7, 8). The same trends show up in the males although the correlation was significant only during incubation (Fig. 11).

The decline in body mass with laying date may be partly due to variation between rather than within years. Therefore we distinguished three groups: high vole years (vole trapping index presistently above mean) low vole years (persistently below mean) and vole crash years (switch from high to low occurred during the reproductive season).

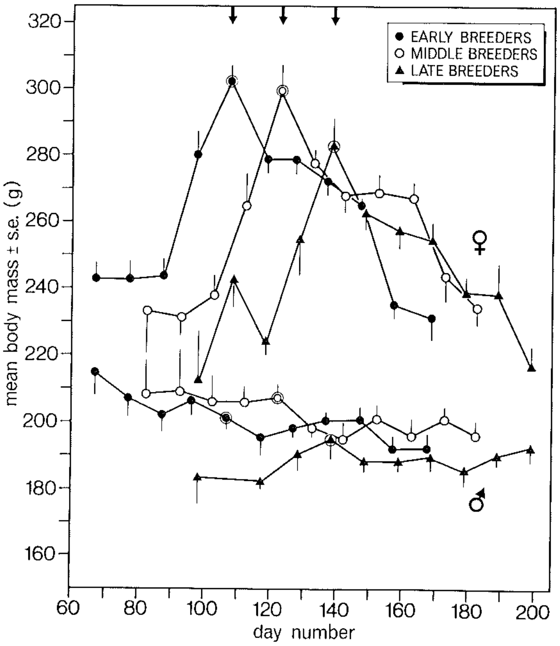

Figure 10. Mean body mass per ten day interval in early, middle and late breeding free-living kestrels, based on both captured and electronically recorded birds. Data are plotted relative to the mean laying date (arrows).

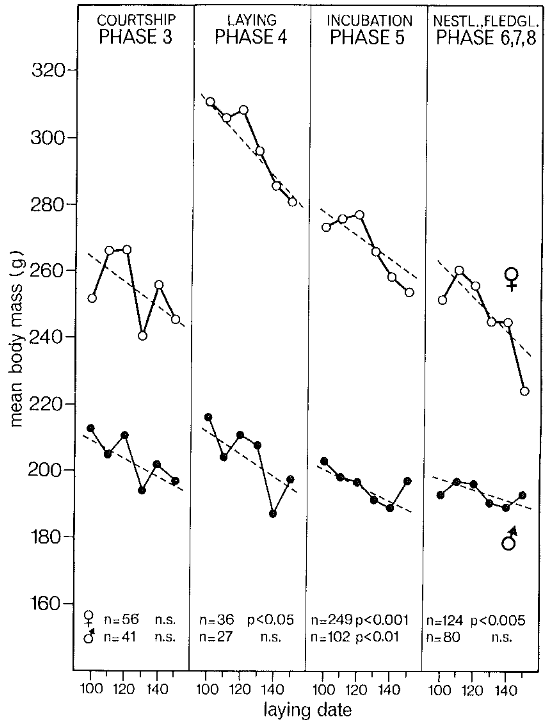

Figure 11. Mean body mass of free-living kestrels during the major phases of reproduction per ten day interval of laying dates. Dashed lines show individual linear regressions for females (upper) and males (lower). p-values indicate significance levels for the difference between regression slopes and zero.

Table 5 shows for these year categories mean female body mass during incubation, mean laying date and clutch size. High and low vole years were statistically distinguishable in all three parameters. Incubating females weighed on average 10 g less in low than in high vole years. Mean body mass in crash years was not significantly different from either high or low years in spite of the considerably earlier laying date and corresponding larger clutches in crash than in low years.

Table 5. Mean body mass (g) ±s.d. (n) of incubatig females, laying date and clutch size in years with high and low vole density as well as in years when the vole population crashed during the kestrel's reproductive season. Levels of statistical significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. (Mann Whitney U-test).

Voles	Mass			Laying date			Clutch size		
High	278.5±23.7(59)	*		116.7±14.3(59)	***		5.51±0.80(59)	***	
Low	268.2±22.9(51)		ns	131.1±14.0(51)		*	4.57±0.98(51)		ns
Crash	270.9±20.9(61)	ns		110.0±11.9(61)	***		5.43±0.74(57)	***	

The comparison of mean body mass between years does not answer the question whether birds with the same reproductive behaviour (in terms of laying date and clutch size) varied systematically in body mass between year groups. Therefore, we analysed the dependence of body mass on laying date (in intervals of ten days) as well as on clutch size for the three year groups separately (Fig. 12). In all groups similar declines of incubation body mass with laying date and positive relations of body mass with clutch size were found. Regressions had slopes significantly different from zero in all cases except the increase of mass with clutch size in crash years (Table 6). Analysis of covariance revealed no significant differences between year groups in the slopes of the regressions on either laying date or clutch size. However the elevation of the regression on laying date was significantly lower in the crash years than in the other year groups. Low and high vole years had the same elevations, both in the regression on laying date and on clutch size (Table 6). Thus, the differences between

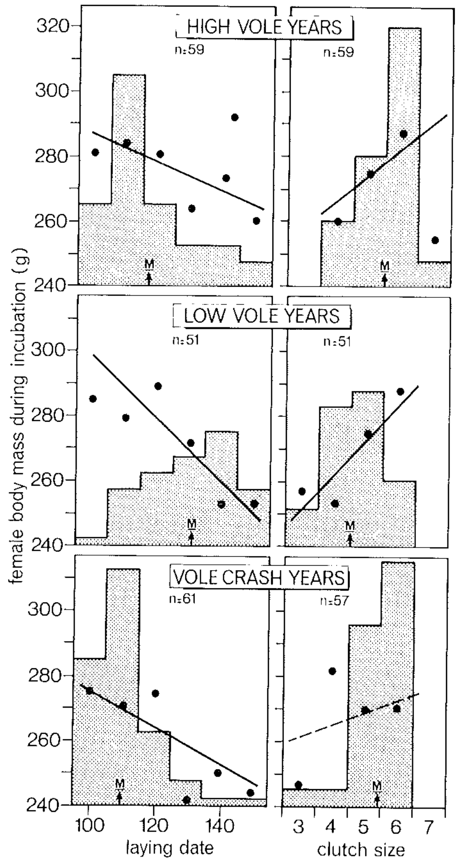

Figure 12. Mean body mass (dots) per ten day interval of laying dates (left panels) and per clutch size (right panels) in high vole years (upper), low vole years (middle) and vole "crash years" (lower). Lines indicate linear regressions through individual data points. (see Table 6). Histograms show the distribution of laying dates and of clutch sizes for those females whose mass was included in the data points, arrows the mean of the distributions.

Table 6. Linear regressions of female body mass (W in g) during incubation on laying date (d, day of the year) and on clutch size (c) in years with different vole abundance. Differences in slope and intercept were tested with analysis of covariance (ANCOVA). * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

High		$W = -0.50\ d + 336.1$ (59)	*
Low		$W = -0.89\ d + 386.6$ (51)	***
Crash		$W = -0.55\ d + 332.5$ (61)	**
High/Low:	slope:	$F_{1,106} = 1.86$	n.s.
	intercept:	$F_{1,107} = 0.003$	n.s.
High + Low/Crash:	slope:	$F_{1,167} = 0.20$	n.s.
	intercept:	$F_{1,168} = 9.66$	**
High		$W = 8.68\ c + 230.2$ (59)	*
Low		$W = 10.62\ c + 219.8$ (51)	***
Crash		$W = 3.90\ c + 248.9$ (57)	n.s.
High/Low:	slope:	$F_{1,106} = 0.16$	n.s.
	intercept:	$F_{1,107} = 0.01$	n.s.
High + Low/Crash:	slope:	$F_{1,163} = 1.81$	n.s.
	intercept:	$F_{1,164} = 3.30$	n.s.

body mass in high and low vole years can be fully explained by the differences in reproductive behaviour, and there are no indications for additional between-year variations superimposed on the trends within years. However, the crash years showed a significant reduction of incubation body mass relative to both the low and high vole years. We surmise that this reduction is related to the crash phenomenon itself. With a sudden decline in vole population density it may not have been possible for most incubating birds to maintain the body mass at the same levels as when the normal spring increase in vole density occurred. The body mass data stem from the incubation phase, several weeks after the onset of laying, and may have been differently affected by the food situation subsequent to when reproductive decisions were taken in crash years. In other years, with both high and low vole density, kestrels in the field were able to maintain the same body mass during incubation as in captivity (Figure 9).

For these reasons we excluded the particular situation of the crash years from a multiple correlation analysis of the major reproductive parameters. Both simple and partial correlations between body mass during incubation, clutch size, laying date and vole year group are presented in Table 7. All four parameters are significantly correlated with each other if the other variables are not taken into account. However, when the relationship between each pair of variables was controlled for the effects of the other two variables, a highly significant partial correlation ($p<0.001$) remained only between laying date and clutch size. No partial

Table 7. Correlations of female body mass during incubation, clutch size, laying date and vole year category (high and low vole years). * $p<0.05$, ** $p<0.01$, **** $p<0.0001$.

Simple correlations coefficients:

	Clutch	Date	Year
Mass	0.408 ****	-0.448 ****	0.203 *
Clutch	---	-0.754 ****	0.475 ****
Date	---	---	-0.463 ****

Partial correlation coefficients:

	Clutch	Date	Year
Mass	0.124	-0.236 *	-0.033
Clutch	---	-0.631 ****	0.219 *
Date	---	---	-0.184 *

correlations could be established between body mass and vole abundance and with clutch size. Body mass was only significantly correlated ($p<0.02$) with laying date after controlling for clutch size and vole category. High and low vole years had weak ($p<0.05$) independent effects on both laying date and clutch size.

5. DISCUSSION

Before discussing any association of the variations in body reserves with food abundance and with reproductive strategies in the kestrel we have to comment on other sources of mass variation that may mask these relations. We found correlations of measured body mass with time of day, structural size and age of the bird and a general seasonal pattern in body mass.

Time of day

In studies reporting variations in body mass of free-living birds, time of day of weighing is rarely taken into account. In the kestrel, body mass was positively correlated with time of day during all phases of the annual cycle except during the phase of parental care for nestlings and fledglings (Fig. 3). Such an increase can generally be expected in diurnal organisms which feed during the day and lose weight overnight by metabolism, evaporation and excretion. The absence of an increase during parental care may have various interpretations. Female kestrels show a sharp decrease in body mass during this stage, and nocturnal decrease apparently is not fully compensated by diurnal food intake. Furthermore nights are short and temperatures relatively high in this phase, and one should therefore expect small weight losses overnight. Finally, due to the long days in summer kestrels caught before their first morning meal and after the last evening meal may be slightly underrepresented. In the other phases of the annual cycle the regression of body mass on time of day revealed increases between 1 and 2 g h^{-1}, resulting in an increase during daylight hours of 5 to 15%. This is obviously an important source of error, hence we corrected for time of day and used inferred dawn weights throughout.

Size

Correlations of body mass with wing length were less consistent than with time of day (Table 3). Males showed positive correlations only outside the breeding season, females only during incubation and juveniles just after independence. If wing length is an indicator of skeletal size, size is a predictor of body mass only at the annual high and low points in female body mass. This suggests that female body mass variation reflects variation in reserves rather than size during most of the year. Male body mass is much more stable throughout the year and the male correlations are consistent with the interpretation that males have less variation in body reserves than females. During reproduction, when the correlation is absent, males hunt also for the female and young, and variations in food demand from the nest possibly obscure correlations of size and body mass of the male.

Age

Kestrels in their first year weighed less than older birds (Fig. 5, Table 2). Juvenile body mass just after the parents ceased prey deliveries to their young (July/August) was the lowest of any age group. Juvenile mortality is high at this stage (Daan & Dijkstra 1988, chapter 5). The low body mass indicates that food shortage may be a major cause of the enhanced mortality. There is no firm evidence that selective mortality of the lighter birds causes the consistent increase in body mass observed until the next spring. It may, alternatively be regulated by temporal changes in body mass setpoints, such as experimentally demonstrated, e.g., in hibernators (Mrosovsky & Fischer 1970) and birds (Sherry et al. 1980). The differences found between mean body mass in the first winter for high and low vole years (Fig. 7) argues for a sensitivity of body mass to food conditions at least during the first year in both sexes. In birds after the first year of age, this difference could no longer be detected (Fig. 7).

Season

Minimum body mass in the kestrel was attained in both sexes in July/August, i.e. during moult. A relatively low body mass during moult of the primaries is a common feature in birds (e.g. Newton et al. 1983, Coulson et al. 1983, Hirons et al. 1984, Wijnandts 1984). It may partly be a consequence of increased difficulties in obtaining food and partly reflect an adaptive down-regulation of body mass adjusting the wing loading to the reduced wing surface area in moult. The former interpretation is supported by the reduced strike success and hunting yield of moulting kestrels (Masman et al. 1988), the latter by the occurrence of a minimal body mass during moult also in captive *ad lib* fed kestrels (Fig. 9). Males as well as females gained weight during autumn. This probably reflects the deposition of fat reserves. During winter body mass remained relatively stable until March, when males started to gradually lose weight again, while females rose sharply to peak weights during the breeding season (Figs. 5, 8).

Reproduction

A detailed analysis of female body mass during reproduction showed a ca 70 g increase during the last 20 days before egg laying (Figure 8). Peak weights were attained at the time of laying but a high and rather constant body mass was maintained during incubation. After hatching of the eggs, female body mass dropped steeply at a rate of ca 2 g day^{-1}. Non-breeding females showed neither the spring increase nor the summer decline after hatching (Table 4). The fact that this is true also in captive *ad lib.* conditions (Fig. 9) suggests that the reduced body mass of non-breeders is not merely a direct consequence of the fact that such females have to hunt for their own food instead of being nourished by the mate. On the other hand, breeding females in captivity showed only a minor 15 g drop in body mass while raising their brood, as compared to a 50 g drop in wild birds. Thus the weight loss after egg hatching should be partly interpreted as a consequence of the necessity for wild birds to collect their own food from the nestling phase onwards. In general, captive *ad lib.* fed and free-living breeding birds had essentially the same weights during laying and incubation, while they maintained a 20-40 g difference during the rest of the year.

Laying date, clutch size and food abundance

Females reproducing at different dates of the year went through essentially the same cycle of body mass changes. However, those reproducing early in the year started at higher levels and reached higher peak weights during laying (Fig. 10). In fact a negative correlation between body mass and laying date was found in all phases of the reproductive cycle in females and, interestingly also in males (Fig. 11). This was not a consequence of laying early in high vole years and late in low vole years, since the relationship is the same for all years (Fig. 12, Table 6). The results from partial correlation analysis suggest that the strong simple correlations of body mass with clutch size as well as with vole year group are fully explained by the corresponding variations in laying date. No residual effects of clutch or year group could be detected.

Between year effects of vole density on laying dates and clutch size were small, though significant, indicating that food availability may influence the start of reproduction. The effect of supplementary food, given before and during the start of the reproductive season, was that kestrels, experimentally supplied with food, layed earlier and larger clutches (Dijkstra et al. 1982). We show elsewhere that late breeding pairs have reduced male hunting yield, reduced frequency of prey transfer from male to female, resulting in reduced female energy intake (Meijer et al. 1988b). We interpret these results as indicating considerable within year variation in vole availability to reproducing kestrels which primarily exerted effects on laying date and secondarily, via laying date on clutch size and body mass of incubating females. Thus the date of laying seems a central and crucial parameter in the reproductive decision process. It can not be established at this stage whether late date and small clutches are mainly the result of lower male quality or of reduced food abundance in the territory. Due to the tight association between date of laying and clutch size, this has the consequence that pairs with lower reserves also produce fewer offspring to nourish.

Whether female condition itself is a causal factor in the proximate chain of events leading to the decisions on laying date and clutch size can only be established by experimental manipulation (Meijer et al. 1988a), not by correlation analysis. On the other hand the ultimate function of the association between female condition, laying date and clutch size is independent of mechanism. Early, large clutches are bound to face a higher probability of spells of inclement weather, and it seems ultimately appropriate for such birds to retain larger body reserves than late breeding birds. Furthermore, late birds, breeding in poorer food circumstances, may gain time by putting up smaller reserves. By gaining time they may enhance both the (declining) fitness of their clutch (Daan & Dijkstra 1988, chapter 5) as well as avoid the conflict arising later in summer between offspring care and moult. We believe the costs and benefits of timing of reproduction in the annual cycle to be the crucial issue in reproductive strategies, and this theme will be pursued in a later article (Daan et al 1988b, chapter 7).

6. ACKNOWLEDGEMENTS

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Chapter 3

ENERGETIC LIMITATION OF AVIAN PARENTAL EFFORT: FIELD EXPERIMENTS IN THE KESTREL

Dirkjan Masman, Cor Dijkstra, Serge Daan & Ab Bult

1. SUMMARY

We studied the limiting factors for brood size in the kestrel, *Falco tinnunculus,* by measuring parental effort in natural broods of different size and parental response to manipulation of the food satiation of the brood. Parental effort was quantified as daily time spent in flight and daily energy expenditure, estimated using our Time-Energy Budget (TEB) model, from full-day observations. During nestling care kestrel males with different natural brood sizes (4 to 7 chicks) spent on average 4.75 h.day^{-1} in flight activity, independent of brood size, and expended on average 382 kJ.day^{-1}. Due to a higher flight-hunting yield (mammal prey caught per hour hunting), males with a larger natural brood were able to provision their brood with the same amount of food (mainly *Microtus arvalis*) per chick (62.6 g.day^{-1}.chick^{-1}), with the same effort. This provisioning rate was close to food intake rates of hand-raised chicks fed *at libitum* (66.8 g.day^{-1}.chick^{-1}).

Male kestrels strongly responded to food deprivation of the brood, especially in the older nestling phase. They increased the daily rate of food delivery to the nest by almost three times to 646.4 g.day^{-1}, by increasing their activity level from 4.46 to 8.41 h.day^{-1} in flight. The increased energy expenditure was sustained, in one case up to eleven days, by increasing the metabolizable energy intake up to the presumed maximum rate. Even under food stress about half of the available daylight was left unused for foraging, while the chicks were not satiated.

We conclude (1) that the mean daily energy expenditure of the male during nestling care - to which clutch size is apparently adjusted in anticipation - is well below the maximum they are able to sustain for a few days and (2) that the energy expenditure they are willing to sustain under extreme demand is not set by the available time for foraging or the available energy. Apparently there are costs, other than energy expenditure, involved in the increase of parental effort.

We finally consider generalisations about energetic limitations during parental care in altricial birds. From 32 published estimates of daily energy expenditure during parental care (DEE_{par}) in 30 different bird species we derived the equation: $DEE_{par} = 14.26\ Kg^{0.65}$ Watt. This relationship significantly differs in slope from the allometric equation for the maximum rate of energy assimilation (DME_{max}) provided by Kirkwood (1983): $DME_{max} = 19.82\ Kg^{0.72}$ Watt, such that in smaller species DEE_{par} about equals DME_{max}, while in the larger species DEE_{par} represents only about 60% of the predicted DME_{max}. This suggests, that when there is a limitation in parental effort set by the maximum sustainable energy intake, this is more likely to be reached in the smaller species. The allometric equation for DEE_{par} suggests that the relation between BMR and parental energy expenditure, is such that all bird parents work at a level somewhere between 3 and 4 times BMR.

2. INTRODUCTION

The number of offspring an individual produces per year is one of the major determinants of its total lifetime reproductive succes. Exploration of the limiting factors for brood size in altricial birds is important for understanding differences in reproductive behaviour between species and between individuals within species.

Two different penalties from raising large broods have been identified. Firstly, nestlings in larger broods may suffer from reduced chances of survival both in the nest and after fledging (Lack 1954). Secondly, increased parental work for the young may entail extra risks for the parents, and thereby threaten their prospects of future reproduction (Royama 1966; Charnov and Krebs 1974; Askenmo 1979). Thus, Drent and Daan (1980) have postulated that optimal parental care for nestlings is associated with daily energy expenditures at a level which represents the maximum sustained without deterioration of the parent's condition. They further suggested that this "optimal working capacity" (Royama 1966) involves a daily energy expenditure (DEE) for the parents bearing a constant relationship to a species' basal metabolic rate (BMR). This expenditure at about 4 times BMR, is somewhat less than estimates derived from maximal sustained energy consumption, converging at ca. 5 times BMR according to Kirkwood's allometric equation (Kirkwood 1983).

The data presented by Drent and Daan (1980) in support of their proposition were derived from five species, and were a mixture from studies in captivity and in the field, and of both experimentally enlarged and unmanipulated brood sizes. While the expression of parental effort in terms of DEE was an important step towards generalisation of reproductive strategies beyond more traditional assays of feeding rates (e.g. Hails and Bryant 1979; Cronmiller and Thompson 1980; Tinbergen 1981; Westerterp et al. 1982) the question whether parental energy expenditure is indeed submaximal still invites further experimentation.

Furthermore, submaximality of parental work would give rise to the question whether optimal work levels are equal for parents raising different numbers of nestlings. Unequal work levels might be expected on theoretical grounds from the trade-off between investment in current and future offspring (Trivers 1972). On the other hand, mechanisms adjusting broodsize to food and work conditions might lead to similar work levels in parents of different sized broods.

Our ongoing study on the seasonal cycle in behavioural energetics and proximate and ultimate control of reproductive behaviour in the Kestrel (*Falco tinnunculus*; Rijnsdorp et al. 1981; Daan and Aschoff 1982; Dijkstra et al. 1982; Masman et al. 1986, 1988a, 1988b; Masman and Klaassen 1987; Daan et al. 1988; Meijer 1988; Beukeboom et al. 1988) allows us to evaluate the consequences of variation in brood size for the parents. We shall discuss here the limiting factors for the rate of food provisioning by the parents. During nestling care, the time required for foraging is not a limiting factor since kestrels do not forage (flight-hunt) for more than 3 hours per day even though the daylight lasts ca. 17 hours (Masman et al. 1988b). There may however be energetic constraints. We have evaluated this possibility by studying the response to manipulations of nestling food demand.

In the kestrel, as in many raptors, the male is exclusively responsible for providing food to the female and nestlings from about two weeks before the first egg is laid until about two weeks after the eggs hatched. During the second half of the nestling phase the female cooperates with the male in provisioning food to the young, but the male is then still responsible for the major share of the energy flow to the nestlings. Therefore, the analysis of parental performance presented is concerned primarily with male kestrels feeding their broods.

3. METHODS

3.1. Brood size

In our study area, "Lauwersmeer" (53°20'N,6°21'E) in the Netherlands, kestrels breed mainly in nestboxes. During the reproductive season (March-August) we checked the nestboxes weekly to be able to determine laying date, clutch size, brood size and number of fledged young, for each kestrel pair. Clutch size declined from 5.98 eggs (n=50) in the beginning of the season (first half of April) to 3.67 (n=21) in the end of the season (first half of June) and averaged 5.27 (n=492; Beukeboom et al. 1988). A complete brood contains the same number of chicks as eggs were laid, in an incomplete brood eggs or chicks died.

3.2. Behavioural observations

Between 1977 and 1986 we made behavioural observations of male kestrels tending complete broods. The study area is a flat and open landscape and individual kestrels could be observed virtually continuously from dawn to dusk. For the analyses presented here we selected 32 complete observation days during nestling care, on the basis of two criteria: 1) budget time (from beginning to end of observation) exceeded 75% of the bird's "active day" (i.e. time from dawn civil twilight to dusk civil twilight - 0.71 h); 2) birds were in sight more than 75% of the budget time (Masman et al. 1988b). In the behavioural protocol we distinguished seven different states: directional flight, soaring, flight-hunting (wind hovering bouts alternating with short flight bouts), sitting perched, on the ground, sheltered or in a nestbox.

The yield during flight-hunting, the main foraging technique in summer (Masman et al 1988b), was calculated as the number of prey caught per hour flight-hunting. Daily food intake was also derived from the behavioural protocol and was based on an empirical relationship between prey mass and eating time (see Masman et al. 1986).

3.3 Daily energy expenditure

We calculated daily energy expenditure (E_t) using our Time Energy Budget (TEB) model, which previously has been validated by use of the Doubly Labeled Water (DLW) method (Masman et al 1988a). The reconstruction of E_t:

$$Et = B + T + A + H + S \qquad kJ.day^{-1}$$

was achieved by calculating the basal component (B), a mass specific and circadian phase specific value for energy expenditure under fasting thermoneutral conditions, measured in the laboratory. We augmented this basal level by addition of values for thermoregulation (T), activity (A), heat increment of feeding (H) and for the synthesis of tissues (S), based on local meteorological conditions, behaviour, food intake and individual condition respectively (see for details Masman et al. 1988a).

3.4 Food requirements of nestlings.

In addition to direct measurements of nestling food intake in the field, seven nestlings were handraised in the laboratory under *ad libitum* food conditions. Four kestrel chicks were taken from a captive brood (Meijer 1988), at an age of six days, and three chicks were taken from a wild brood at an age of seven days. Chicks were free to move and were held at a temperature of ca. 20°C. Food consisted of freezer stored Common voles (*Microtus arvalis*) trapped in the study area, thawed one day before, and given four times a day with four hour intervals between 08:00 and 20:00. Food was given until the chicks ignored the food and was weighed to the nearest 0.5 g. Total daily food intake per chick was recorded and is presented as the average for the seven chicks.

3.5 Experiments

Kestrels in our study area mainly breed in nestboxes. To be able to manipulate the food availability in the nest we mounted nestboxes against movable sheds, made an opening in the back and posted an observer behind the nestbox, in the shed. The whole operation of changing the position of the nestbox and opening the back was carried out step-wise over a period of several days during incubation or young nestling phase. The parents easily adapted to the new situation.

In all experiments we manipulated the energy demand in the nest without changing the brood size as experienced by the parents. The experiments differed in duration and type of manipulation:

I) Surplus food; between May 31 and June 17 1980 we carried out three feeding experiments in one nest. We recorded total prey delivery, body mass of nestlings and female, and food intake of the nestlings on control and experimental days. Female body mass and prey mass were determined using an electronical scale. We decreased the food demand by giving extra food (freshly killed laboratory mice) to the nestlings, such that food was available in the nest continuously. The extra food was easily accepted and was fed by the female to the nestlings (<10 days of age) or immediately eaten by the older nestlings (10-30 days).

II) Food deprivation for 1-3 days; between 1981 and 1985 12 food deprivation experiments were carried out with broods of different age (Table 1). We recorded parental behaviour, total food delivered to the nest, and body mass change of the nestlings. In broods younger than 10 days we increased the energy demand of the brood by rotating extra nestlings through the nest, of the same age but taken from other nests. Each time the parents delivered a prey and the nestlings had been fed, one or two nestlings were replaced by a hungry nestling. In this way the parents fed four more nestlings than their own brood size. In nests where the nestlings were old enough to take the food themselves (>10 days) we took away all prey as soon as it was delivered by one of the parents. In this way food intake of the nestlings was virtually zero during the day and begging behaviour of the nestlings increased notably. In the evening, when the parents had ceased hunting, the nestlings were fed by the observers.

III) Case study with prolonged food deprivation; between June 27 and July 12, 1985, one kestrel pair was observed in detail. We deprived the nestlings from food by taking away the food, every day for 11 days, starting at a nestling age of 19 days. At the end of each deprivation day the nestlings were again fed by the observers. The parents were observed for complete days every other day. Body mass of the parents was recorded daily with an electronic scale in the nestbox-entrance, connected to a paper chart recorder (Dijkstra et al. 1988a, chapter 2).

Statistical tests were two-tailed throughout unless stated otherwise.

4. RESULTS

4.1. Parents raising different numbers of nestlings.

During nestling care kestrel males spent on average 4.75 h.day^{-1} (s.d. = 1.55; n = 32) in flight activity (directional flight + flight-hunt, Fig. 1A), independent of the number of chicks in the brood (Spearman Rank correlation, $R_s = 0.16$; n = 32; $p > 0.2$). Using our TEB model we converted the time budgets in daily energy expenditure (E_t). There was again no correlation between E_t and broodsize ($R_s = 0.14$; n = 26; $p > 0.2$). The average E_t was estimated as 382 kJ.day^{-1} (s.d. = 74; n = 26; Fig. 1B). Since parental effort was independent of brood size either the returns during foraging, or the food provisioning rate per chick, must differ between males tending different number of chicks. The flight-hunting yield (prey.h flight-hunting^{-1}) was positively correlated with brood size (Fig. 1C; $R_s = 0.47$; n = 34; $p < 0.01$). By this relationship, a male with seven nestlings was able to obtain 59% more food with the same daily effort than males with only four nestlings. The number of prey deliveries to the nest per day gives only a rough estimate of food provisioning since prey mass is variable (Masman et al. 1986). Therefore, the amount

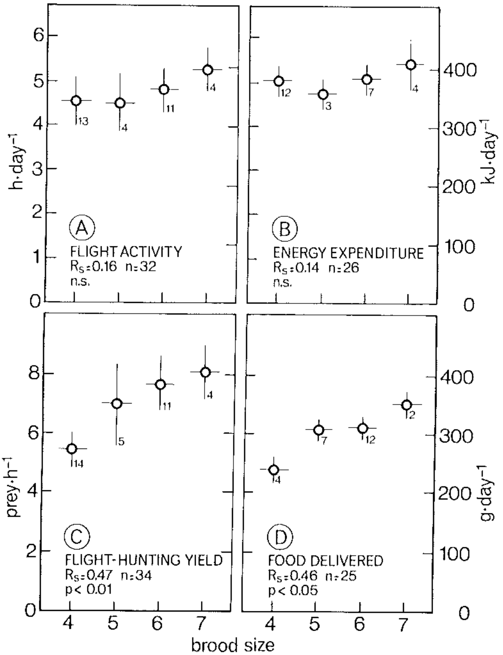

Figure 1. Performance of male kestrels tending complete (clutch size = brood size), unmanipulated broods of different size. A. Flight activity: daily time allocated to directional flight plus flight-hunting; B. Energy expenditure: daily energy expenditure estimated by TEB model, based on complete observation days where activity as well as food intake was recorded completely; C. Flight-hunting yield: mammal prey captured per hour flight-hunting based on days with at least one hour of flight-hunting observed; D. Food delivered: based on observations at close range behind the nestbox. Indicated are means and standard errors; numbers indicate sample size; correlations were tested with the Spearman Rank-test (one tailed).

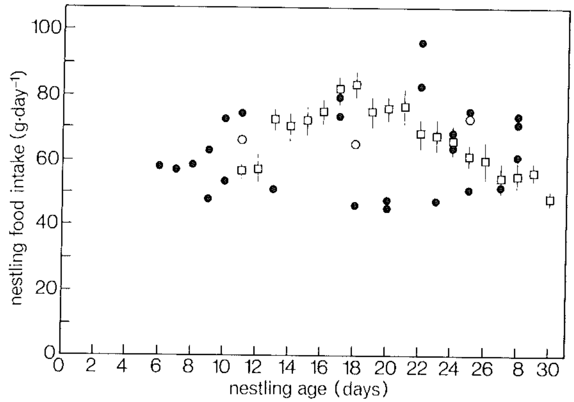

Figure 2. Nestling food intake as a function of nestling age on control days (closed symbols) and days with supplementary food (open dots) in free-living kestrels, and of *ad libitum* fed nestlings in the laboratory (open squares, indicating daily means ±1 s.e.m. for seven handraised chicks).

of food brought to the nestlings was quantified more accurately in a number of cases (25 observation days), where we mounted a nestbox against a shed and could observe the food brought from close range and weigh it. Total food brought by the male per day increased with brood size (Fig. 1D; $R_s = 0.46$; $n = 25$; $p < 0.05$). The amount of food brought per chick by the male parent decreased slightly with increasing brood size ($R_s = 0.42$; $n = 25$; $p < 0.05$). However, if we consider the total amount of food brought by both parents, including the female's share, this difference disappears ($R_s = 0.31$; $n = 25$; $p < 0.2$) and all broods were provisioned at an average rate of 62.6 $g.day^{-1}.chick^{-1}$ (s.d. = 13.5; $n = 25$).

Daily food intake of kestrel chicks in complete broods in the field varied considerably and was not correlated with nestling age from 6 days of age onwards (Fig. 2, closed symbols). Handraised chicks in the laboratory had an average daily food intake of 66.8 $g.day^{-1}$ (s.d. = 9.9; $n = 20$) which was not significantly different from the average intake in the field (62.6 $g.day^{-1}$; Mann-Whitney U-test; $p > 0.10$). However, food intake in the laboratory showed an increase from day 11 to 18 followed by a decrease over the rest of the nestling period until day 30, a trend not observed in the field (Fig. 2).

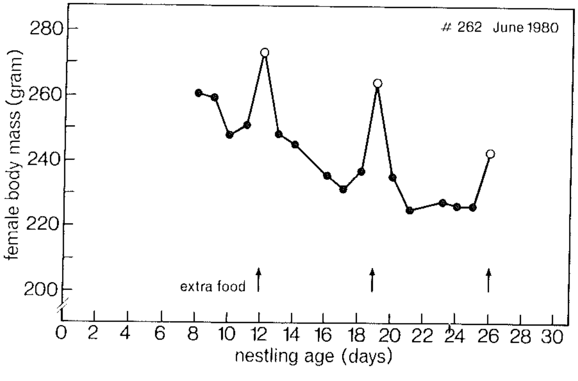

Figure 3. Body mass of female #262 during the nestling phase. Indicated are early morning post-apsorbtive weights on control days (closed symbols) and on mornings after days with supplementary food (open symbols).

4.2. Food deprivation

Before measuring the parental response on increased demand in the brood we evaluated the unmanipulated food provisioning rate by providing surplus food in one brood (experiments I). Total prey mass fed by the parents to the nestlings on control days averaged 63.6 g.day^{-1}.chick^{-1} (s.d.$=$14.0; $n=5$), of which the male provided the major share (93%). Nestling intake did not vary with age, which is in agreement with the larger data set (Fig. 2). On days when we increased the food satiation of the nest we fed on average 292.3 g freshly killed mice (s.d.$=$48.1; $n=3$) to the brood or 48.7 g.day^{-1}.chick^{-1}. On these days the male delivered an additional 19.3 g.day^{-1}.chick^{-1} (s.d.$=$6.7; $n=3$), bringing the total intake to 68.0 g.day^{-1}.chick^{-1} (open dots in Fig. 2).

The female did not participate in nestling food provisioning under these circumstances, but on the contrary, increased her daily food intake, which is reflected in her body mass (Fig. 3). Her body mass, recorded at the beginning of the active day, decreased from 260 g on May 31, eight days after egg hatching, to 226 g on June 16, with an average decrease on control days of -6.8 g.day^{-1} (s.d.$=$10.4; $n=13$). The fluctuations of female body mass were strongly affected by the experiments. On days when we gave additional food her mass increased with 22.0 g.day^{-1} (s.d.$=$5.0; $n=3$), and decreased again on the following day (Fig. 3).

We increased the demand in twelve broods (experiments II,Table 1). With broods younger than 10 days, male kestrels spent on average 4.61 h.day^{-1} (s.d.$=$0.36; $n=4$) in flight on control days. Males responded to extra nestlings with an increase (Mann Whitney U-test, $p<0.01$) to an average of 6.49 h.day^{-1} (s.d.$=$1.05; $n=5$) total flight (open triangles in Fig. 4). In the

Table 1. Food deprivation experiments in kestrel broods. Notes: 1) increase of brood energy demand by rotation of nestlings (see text); 2) deprivation by taking away the delivered food (see text); 3) female disappeared in early nestling phase, before the experiments.

Year	Male #	Female #	Clutch size	Brood size	Hatching date	Period of food deprivation
1981	397	366	5	5	May 28	June 4-5[1]; June 25[2]
1981	351	368	6	6	May 23	June 17[2]
1982	111	109	4	4	June 11	June 23-25[1]; June 7-9[2]
1982	454	450[3]	4	4	June 26	July 13[1]; July 21-22[2]
1983	562	577	7	7	May 20	May 31-June 1[1]; June 15-16[2]
1983	581	596	5	4	June 26	July 14-15[2]
1985	342	770	6	5	June 13	July 2-12[2]
1985	775	777	4	4	June 22	July 16-22[2]

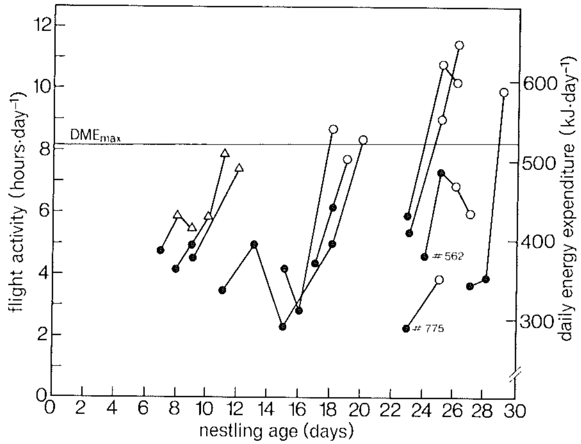

Figure 4. Effect of food deprivation of the nestlings on male activity, total flight per day. Days with food deprivation by rotation of nestlings (see text): triangles; by taking away the food: open circles; dots indicate control days. Lines connect days of one experiment. Daily energy expenditure (right axis) was estimated from the regression of CO_2 production (measured by Doubly Labeled Water; Masman and Klaassen 1987) on flight activity. Horizontal line indicates estimated daily maximal metabolizable energy intake (Kirkwood 1983). Two males (#562, #775) showed a deviant response (see text).

situation of older nestlings (>10 days) time spent in flight on control days (4.46 h.day^{-1}; s.d.$=1.42$; $n=13$) was similar (Mann Whitney U-test, $p>0.05$) to that in the early nestling phase. However, the response to food deprivation of older nestlings (8.41 h flight.d^{-1}; s.d.$=2.2$; $n=11$; open symbols in Fig. 4) was stronger (Mann Whitney U-test, $p<0.05$).The average response of male kestrels to experimental food shortage in the nest in the older nestling phase was estimated on the basis of kestrel flight costs (Masman and Klaassen 1987) as an increase in energy expenditure from 376 kJ.day^{-1} to 541 kJ.day^{-1} (Fig. 5A). Total food brought to the nest increased in correspondence with the increased activity (Fig. 5B). The total amount of food brought during food deprivation by the male (646.4 g.day^{-1}; s.d.$=276.7$; $n=16$) corresponds with 2728 kJ.day^{-1} metabolizable energy (Masman et al. 1986). This would be sufficient to cover the demand of about ten nestlings under normal conditions (see above), or the flight activity by an adult for more than the available daylight. Thus flight activity in response to nestling food deprivation is not directly limited by available time or energy.

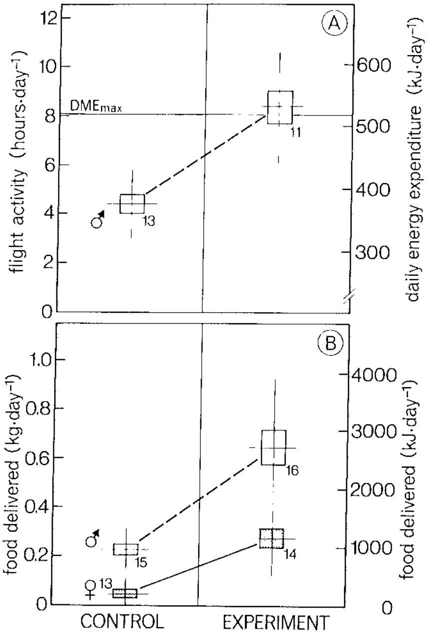

Figure 5. Summary of the effect of nestling food deprivation in the older nestling phase on flight activity in males (A) and food delivery rate in males and females (B). Indicated are the averages (horizontal lines), s.e.m. (boxes) and s.d. (vertical lines) for control days (left panels) and expertimental days (right panels). Numbers indicate sample size in days. Daily energy expenditure (right axes) and DME_{max} were estimated as in Fig. 4. The energetic equivalent of food deliveries was estimated as metabolizable energy for adults using conversion factors from Masman et al. (1986).

4.3 Case study of prolonged food deprivation

To see whether increased effort could be sustained, we studied the response of one kestrel pair to continuous food deprivation of the nestlings for eleven consecutive days. The male significantly (Mann Whitney U-test, $p<0.001$) increased his food delivery rate from 347 g.day^{-1} (s.d.$=54$; $n=4$) on control days to 788 g.day^{-1} (s.d.$=207$; $n=10$) on deprivation days. The female also increased her food delivery rate (Mann Whitney U-test, $p<0.01$) from 31 g.day^{-1} (s.d.$=43$; $n=4$) to 354 g.day^{-1} (s.d.$=212$; $n=10$; Fig. 6A). This response was essentially equal to that observed in the other experiments (Fig. 5).

Both parents increased their daily flight activity (Fig. 6B). This increase was partly due to a special situation. The territory of this pair included a dike causing updrafts in which the kestrels could flight-hunt by "hanging" motionless, a behaviour quite common in kestrels in a more hilly environment (Village 1983). The returns during "hanging" were relatively low. During flight-hunting on food deprivation days the yield averaged 6.78 voles.h^{-1} (s.d.$=1.30$; $n=5$ days) in the male and 6.35 voles.h^{-1} (s.d.$=0.08$; $n=4$ days) in the female, while the yield during "hanging" averaged 3.98 voles.h^{-1} (s.d.$=0.78$; $n=4$ days) and 3.80 (s.d.$=0.32$; $n=2$ days) in male and female respectively. We assume that the energetic costs of "hanging" were also very low, and similar to that during soaring (10% of flight costs; Masman et al. 1988a). The use of this low-cost low-profit hunting technique during increased food demand may indicate a general energy conserving policy of the parents. Nevertheless, in both parents daily energy expenditure increased (Mann Whitney U-test, for male $p<0.01$, female $p<0.05$) during food deprivation (Fig. 6C).

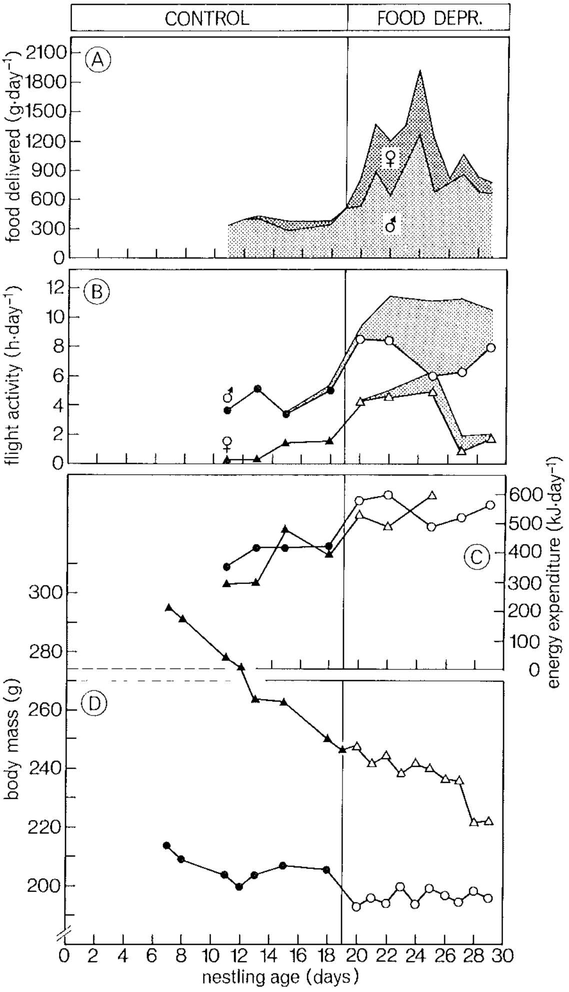

Figure 6. Case study (Pair 28, 1985) of the effect of long term food deprivation of a brood (5 nestlings) on: A. Total food delivered per day; B. Flight activity (male: circles, female: triangles; on control days (closed) and food deprived days (open), supplemented with the time spent "hanging" (see text), indicated by shading); C. Daily energy expenditure, estimated as in Fig. 1; D. Parental body mass.

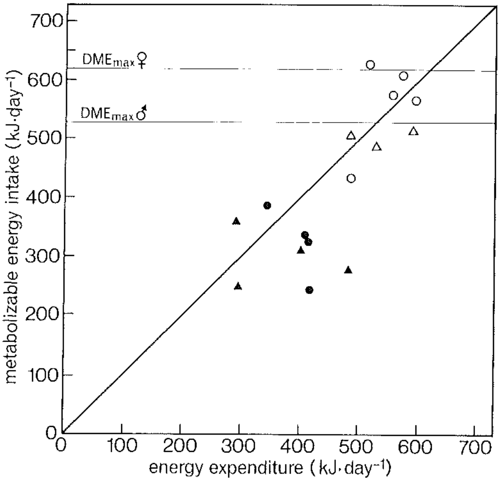

Fig.7 Daily energy balance in the male (circles) and female (triangles) of the case study presented in Fig. 6, on control days (closed) and experimental days (open). Line indicates equality of DME and DEE estimated as in Fig. 1. Horizontal lines indicate the estimated DME_{max} for male (lower) and female (upper) derived from Kirkwood's (1983) equation.

In the female body mass decreased during nestling care (Fig. 6D), following the general pattern in female kestrels in our population (Dijkstra et al. 1988a, chapter 2). Daily female body mass decrease was not stronger during food deprivation (Mann Whitney U-test, $p>0.05$). The male, however, only lost mass at the beginning of the experiment, but stabilized in mass during the food deprivation period at an average of 196.4 g (s.d.$=2.8$; $n=10$; Fig. 6D). This indicates that for the male the energy expenditure and metabolizable energy intake were, on average, in balance during the period of increased activity.

Both male and female increased their energy intake with increased energy expenditure, in response to our manipulation (Fig. 7). Thus this male spent on average 38% more energy during the food deprivation experiment, delivered 2.3 times more food to the nest, and, nevertheless retained energy balance for these ten days. For this male of 196.4 g (average during food deprivation) Kirkwood's (1983) allometric equation for homeotherms would predict a maximum rate of metabolizable energy intake ($DME_{max}=$ 1713 $Kg^{0.72}$ $kJ.day^{-1}$) of 531 $kJ.day^{-1}$. This level, indicated in Fig. 7, is slightly less than the observed daily metabolizable energy intake during our experiment, suggesting that the male was performing close to an energetically sustainable maximum.

5. DISCUSSION

5.1. Parental effort in different natural brood sizes.

Kestrel male parental effort was independent of brood size in complete broods, where brood size equaled clutch size (Fig. 1), and showed no relation with the age of the brood from six days of age onwards (Fig. 4). Food provisioning by both parents was such that daily food intake per chick was also independent of brood size, and was moreover similar to that of *ad libitum* fed chicks in the laboratory. However, nestling mortality due to starvation occurs regularly in kestrels, indicating that food provisioning is not always adequate (Daan et al. 1988b). In this study we observed large daily variations in nestling food provisioning in the field. During the early and late nestling phase chicks in the field tended to have a somewhat higher intake than in the laboratory. These observations suggest that on some days the parents compensate for a food shortage caused by unfavourable weather conditions or by a natural high food demand halfway the nestling phase as observed in the laboratory. The temporary accumulation of reserves by the female during high food availability, as observed during our surplus food experiment, can also be seen as a functional response in this respect. The extra energy store will facilitate her to refrain from food intake during poor conditions. We emphasize that by analysing parental performance in complete broods we probably biased our sample towards parents of good quality in hunting skills and habitat choice. Furthermore we compared parental food provisioning rate with food intake of laboratory raised nestlings wich will have had relatively low thermoregulatory requirements.

We conclude that clutch size in different kestrels seems to be adjusted to the daily amount of food the males are able to provide to their brood with the same effort. In this way the daily food intake per chick is sufficient and similar in different sized broods. The total amount of food delivered to the nest seems to be set by the males' hunting yield, at a more or less constant level of male daily energy expenditure. The hunting yield, which was shown to be positively correlated with brood size, does not vary with different experimental levels of brood demand (Masman et al. 1988b). Thus hunting yield seems to be set by either male- or territory-quality or by both. This raises intriguing questions concerning the proximate regulation of clutch size in the kestrel which are beyond the scope of this paper and are discussed elsewhere (Meijer 1988; Beukeboom et al. 1988).

5.2. Energetic limitation of kestrel parental effort.

Our food deprivation experiments revealed that male kestrels strongly respond to food shortage in the nest, especially in the older nestling phase. By increasing their activity level they on average increased the daily rate of food delivery to the nest by almost three times. Thereby daily energy expenditure increased considerably and was sustained, in one case up to eleven days, by increasing the metabolizable energy intake correspondingly. Even under considerable food stress about half of the available daylight was left unused for foraging, while the chicks were not satiated, due to the continuous removal of food delivered.

Two males in the older nestling phase responded differently from the others (Fig. 4). In spite of an extreme hunger situation in its brood of seven nestlings, one male (#562 in Fig. 4) spent only slightly more time in total flight than on control days. This male had a body mass of 168 g just before and 164 g after the experiment which is extremely low (mean for males in older nestling phase: 193 g; s.d.=11; n=28; Dijkstra et al. 1988a, chapter 2). We surmise that a lack of body reserves prevented this bird from raising its parental effort significantly. The second male (#775 in Fig. 4) reached activity levels during nestling food deprivation similar to the normal control level. This male had a very high hunting yield (9.47 prey.h^{-1}, s.d.=0.81; n=3) and his prey delivery rate during nestling food deprivation thereby reached the same level as that of other experimental males.

We conclude (1) that the mean daily energy expenditure accepted by the male during nestling care - to which clutch size is apparently adjusted in anticipation - is well below the maximum they are able to sustain for a few days and (2) that the maximum energy expenditure they are willing to sustain under extreme high nestling demand is not set by the available time for foraging or the available energy in the environment. Two questions have to be considered: 1) What limits the effort of the parent during food deprivation of the nestlings ? and 2) Why don't parents normally work at the maximum rate they accept during food deprivation experiments, to increase the number of offspring raised?

During food deprivation of the nestlings the male in our long-term experiment increased metabolizable energy intake up to the level of the increased energy expenditure and thus retained energy balance. This suggests that a kestrel male is able to be in energy balance at levels of expenditure far above what they normally perform. On average the birds operate well below what is presumably their maximum. During food shortage in the brood they increased activity up to this sustainable maximum. This observation suggests that there are costs, other than energy expenditure, involved in the increase of parental effort.

In addition to direct energetical consequences, parental effort may entail costs in terms of future survival. Local survival in Pied Flycatcher males (*Ficedula hypoleuca*, Askenmo 1979) and Blue Tit females (*Parus caeruleus*, Nur 1984) has been demonstrated to be reduced in parents of experimentally enlarged broods. The probability of having a second clutch in the same season is reduced in Great Tit females (*Parus major*) after experimental brood enlargements (Tinbergen 1987; Smith et al. 1987). In the kestrel local survival of parents tending enlarged broods is also reduced compared to control broods, for both males and females as will be discussed in the next chapter (Dijkstra et al. 1988b). Whether energy expenditure during nestling care is directly causally related to overwinter survival remains to be established. Clearly however, raising enlarged broods may reduce future reproductive success, and this may be an explanation for submaximal parental effort and submaximal clutches.

5.3. Interspecific comparison of parental effort

We finally consider the possibility of making generalisations about existing energetic limitations during parental care in birds and their relationship with BMR, as postulated by Drent and Daan (1980). The literature so far provides 32 estimates of daily energy expenditure during parental care in 30 different bird species, all measured with singly or doubly labeled water. This allows us to derive an allometric relationship for parental effort (Table 2; Fig. 8), and compare this with the maximum of daily metabolizable energy intake as predicted by Kirkwood (1983):

$$DME_{max} = 19.82 \ Kg^{0.72} \quad Watt \qquad (1)$$

The linear regression of log-transformed daily energy expenditure on body mass (Kg) for all available studies yielded the equation for parental daily energy expenditure (DEE_{par}):

$$DEE_{par} = 14.26 \ Kg^{0.65} \quad Watt \qquad (2)$$

($r=0.983$; $n=32$; $p<0.001$). The two regressions of DME_{max} (eq.1) and DEE_{par} (eq.2) on body mass have a different slope ($t=-2.49$; $p<0.02$) such that in a 25 g bird DEE_{par} is estimated as 94% of the predicted DME_{max} and in a 10 Kg bird DEE_{par} is only about 61% of DME_{max}. Thus it seems that the larger species have a performance further below their predicted physiological maximum than the smaller species. Various functional explanations are appealing, such as the hypothesis that larger species on average have a longer lifespan and might therefore be more conservative in energy expenditure rate. Working near their maximal sustainable level might reduce their survival and it would be more advantageous for longer lived species not to risk future reproduction. However we have to keep in mind that Kirkwoods' (1983) equation gives only a crude impression of the actual metabolic capacity of a particular species. The equation is based on birds as well as mammals and actual maxima in DME for the different bird species presented in Fig. 8 have not been measured yet.

To be able to express DEE_{par} in multiples of basal metabolic rate (BMR), using Aschoff and Pohl's (1970) allometric equations for the inactive phase of the daily cycle, we calculated the allometric equations of DEE_{par} for passerines and non-passerines separately. For passerines (mean mass$=28.6$ g; s.d.$=17.8$; $n=13$; range: 12.6-77.5) the allometric equation for DEE_{par} is:

$$DEE_{par} = 10.12 \ Kg^{0.57} \quad Watt \qquad (3)$$

($r=0.790$; $n=13$; $p<0.002$). For the average passerine in our sample (28.6 g) this equation

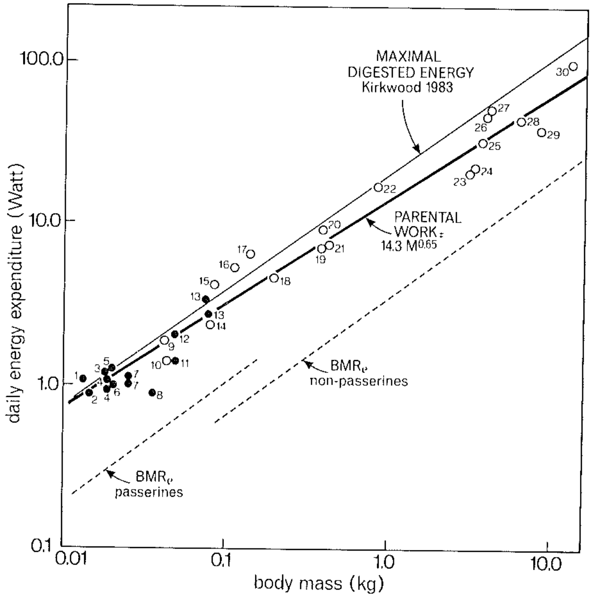

Figure 8. Daily energy expenditure during parental care in birds, measured by isotopically labeled water. Closed symbols: passerines; open symbols: non-passerines; numbers refer to Table 2. Solid line indicates linear regression of log DEE_{par} on log body mass: $DEE_{par} = 14.26\ Kg^{0.65}$ Watt. Dashed line indicates DME_{max} estimated from Kirkwood (1983); stippled lines indicate BMR for passerines and non-passerines in the inactive phase of their daily cycle from Aschoff and Pohl (1970).

estimates a DEE_{par} of 1.33 Watt, or 3.2 times BMR. For non-passerines (mean mass = 2529 g; s.d. = 3507.0; n = 19; range 42-13000 g) parental effort is estimated by:

$$DEE_{par} = 14.73\ Kg^{0.62} \quad \text{Watt} \qquad (4)$$

($r = 0.975$; $n = 19$; $p < 0.002$). For the average non-passerine in our sample (2529 g) DEE_{par} is estimated as 26.18 Watt, or 3.7 times BMR.

The comparison, presented here, suggests that the relation between BMR and the observed parental energy expenditure, is such that parents work at a level somewhere between 3 and 4 times BMR. Another interspecific analysis of parental effort, estimated by TEB methods, revealed a daily energy expenditure of 2.9 BMR (Dolnik 1987). There is considerable variation in DEE_{par} between species of about the same body mass. This has also been recognized for the BMR in species of about the same mass, partly related to latitude (Weathers 1979) and life style (Kersten and Piersma, 1987). A more detailed analysis of the relation between BMR and DEE, measured in the same species, is deferred to a future article (S. Daan, L. Groenewold & D. Masman, in prep.).

We thus remain in the dark as to whether parental energy expenditure is optimized at a level somehow associated with basal metabolic rate, determined by the maximal sustainable energy intake or that all three parameters are related in a predictable way. Further comparative analyses and determination of the maximum in daily energy assimilation in a number of species are needed to help to refine hypotheses. Experimental studies of parental response to the nestling food situation, as presented here for the kestrel, should bring us closer to the nature of parental strategies.

Table 2. Daily energy expenditure in birds during parental care, measured by labeled water.

#	Species	Body mass kg	DEE kJ.day^{-1}	Reference
1	Riparia riparia	0.0126	92.5	Turner 1983
2	Hirundo tahitica	0.0141	76.6	Bryant et al 1984
3	Parus major	0.0177	101.1	J.M. Tinbergen unpublished
4	Delichon urbica	0.0178	80.8	Hails & Bryant 1979
		0.0182	94.5	Bryant & Westerterp 1980
5	Hirundo rustica	0.0190	107.8	Turner 1983
6	Passerculus sandwichensis	0.0193	86.8	Williams 1987
7	Oenanthe oenanthe	0.0243	86.8	J. Moreno unpublished
		0.0243	95.3	P. Tatner unpublished
8	Merops viridis	0.0338	77.4	Bryant et al 1984
9	Oceanites oceanites	0.0420	165.3	Obst et al 1987
10	Oceanodroma leucorhoa	0.0428	122.8	Ricklefs et al 1986
11	Mimus polyglottos	0.0476	121.0	Utter 1971 in Nagy 1986
12	Progne subis	0.0477	174.4	Utter and LeFebre 1973
13	Sturnus vulgaris	0.0740	301.0	Ricklefs & Williams 1984
		0.0775	232.9	Westerterp & Drent 1985
14	Ceryle rudis	0.0770	201.9	Reyer & Westerterp 1985
15	Aethia pusilla	0.0835	357.9	Roby & Ricklefs 1986
16	Pelecanoides georgicus	0.1092	463.5	Roby & Ricklefs 1986
17	Pelecanoides urinatrix exul	0.1365	556.6	Roby & Ricklefs 1986
18	Falco tinnunculus	0.1923	391.5	Masman et al 1988a
19	Puffinus pacificus	0.3840	613.7	Ellis 1984
20	Rissa tridactyla	0.3860	794.0	Gabrielsen et al 1987
21	Cepphus grylle	0.4200	640.2	Roby & Ricklefs 1986
22	Uria lomvia	0.8340	1475.2	Roby & Ricklefs 1986
23	Diomedea immutabilis	3.0690	1447.0	Nagy 1987
24	Spheniscus demersus	3.1700	1945.0	Nagy et al 1984
25	Eudyptes chrysolophus	3.6000	2830.4	Davids et al 1983
26	Pygoscelis adeliae	3.8680	4002.0	Nagy 1987
27	Macronectes giganteus	4.0440	4443.0	Nagy 1987
28	Pygoscelis papua	6.2000	3803.3	Davids et al 1983
29	Diomedea exulans	8.4000	3320.0	Adams et al 1986
30	Aptenodytes patagonica	13.0000	6851.4	Kooyman et al 1982

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Chapter 4

BROOD MANIPULATIONS IN THE KESTREL: EFFECTS ON OFFSPRING AND PARENT SURVIVAL

C.Dijkstra, A.Bult, S.Bijlsma & T.Meijer.

1. SUMMARY

Brood reductions and enlargements were carried out in kestrel nests to evaluate the consequences of raising different numbers of nestlings for both the offspring and the parents. Brood enlargements caused increased daily hunting activity of the parents, reduced growth rate of the nestlings, increased nestling mortality, enhanced weight loss in the female parent and reduced probability of local survival of the parents. Brood reductions caused reduced parental hunting activity, increased food intake by the nestlings, and increased local survival of the parents. A review of the literature on brood enlargements is presented, showing that parents were able to raise more young than their natural broods in 27 out of 38 altricial bird species investigated. Negative effects of brood enlargements on parental survival or future reproduction were established in 6 out of 10 species investigated. The results are consistent with the theory that parental work for the offspring entails an inherent reduction in future reproductive output and that natural broods, by being smaller than the maximum number of nestlings that can be raised, maximize the total reproductive output.

2. INTRODUCTION

Lack (1948) suggested that clutch size in birds is evolved in such a way that it matches the maximal number of offspring that can be raised, and through natural selection the most common clutch size is also the most productive in the population. In contrast with this proposition several studies have shown the largest clutch size to be more productive than the most common (Cavé 1968, Perrins 1965, Perrins and Moss 1975). Lack's hypothesis was extended by postulating a variable optimal clutch size, dependent on individual differences in habitat quality or condition of the bird (Drent and Daan 1980, Högstedt 1980). In other words individual birds phenotypically adjust clutch size to their own situation. Furthermore Williams (1966) proposed a possible trade-off between current parental effort and future reproductive output. This trade-off would result in a lower optimal cluch size than expected when only the current breeding attempt were taken into account (Charnov & Krebs 1974). Individuals reproducing submaximally, i.e., laying relatively small clutches, might enhance their own chances of survival and thereby increase their total fitness. A number of brood manipulation experiments have been carried out to test whether the clutch size laid equals the most productive broodsize (for review, see Lessels 1986). The majority of these studies did not support Lack's hypothesis since enlarged broods were more productive than natural broods. In most studies productivity was measured in terms of numbers fledged (e.g. Hegner & Wingfield 1987, Tarburton 1987) or the number of offspring alive after three months (Nur 1984b). Ideally, survival of the juveniles till reproductive age should be taken into account to test the hypothesis thoroughly. Few studies investigated effects of brood manipulation on adult survival (Askenmo 1979) and on future adult reproductive output, either within the same year in multiple breeders (Finke 1987, Tinbergen 1987) or in subsequent years (Røskaft 1985). Parental effort in food provisioning to manipulated broods was estimated in some of these studies through the rate of food deliveries to the nestlings. The feeding rate is only a crude estimate of parental effort since variations in habitat quality or foraging efficiency affect parental energy expenditure. We have undertaken a study in the European Kestrel, attempting to cover the effects on offspring prospects and on parental effort and survival as complete as possible.

In the European Kestrel the largest clutch size is the most productive in terms of surviving offspring till reproductive age (Daan and Dijkstra 1988, chapter 5). Energy expenditure of kestrel male parents in complete broods, i.e. without preceeding mortality, did not vary with respect to brood size (Masman et al 1988a, chapter 3), and hunting yield, in terms of voles caught per hour flight-hunting, was positively correlated with brood size. Thus the kestrel presents a situation where clutch size seems adjusted to the individual food availability, such that at the time of highest parental effort the parents of broods of different sizes are able to feed their broods with the same effort. Nestling food deprivation experiments in the kestrel showed that energy expenditure of the parents was considerably increased in response to enhanced food demand from the brood. The amount of food brought to the nest was about twice as much as under natural conditions in these short-term experiments, which lasted two to ten days (Masman et al 1988a). These results strongly suggest that kestrels produce fewer young than they are actually able to raise if working to peak performance although it is uncertain whether increased parental energy expenditure could be maintained throughout the nestling and fledgling stage. It is therefore of interest to analyse the consequences of artificial brood size changes on both parental behaviour and on survival. We manipulated brood sizes in such a way that the experimental broods contained two young more (enlargements) or two young less (reductions) than the original clutch size and assessed growth and survival of the nestlings as well as local survival of the juveniles till reproductive age. Also parental effort and energy expenditure for manipulated broods was investigated and adult body mass during the experiment was recorded. In subsequent breeding seasons we established local adult survival and reproductive performance.

3. METHODS

The data presented here were obtained in two different areas in the Netherlands: the Lauwersmeer polder and Flevoland. For a description of the areas we refer to Joenje (1977) and Cavé (1968). In both areas nestboxes were mounted on poles or against buildings and were regularly checked during the breeding season (Dijkstra et al 1988, chapter 5). Kestrel pairs were caught during the breeding season using the *bal-chatri* in the field (Cavé 1968), or a net for catching them in the nestbox. The breeding population was marked individually by colour rings in Flevoland and by wingtags (Village 1982) in the Lauwersmeer area.

Manipulations of brood sizes were done in Flevoland in 1985 and 1986. Experiments in the Lauwersmeer took place in 1986 and 1987. The experiments started when the nestlings were five to ten days old. Brood size was changed in such a way that the number of nestlings was either two more (enlarged broods) or two less (reduced broods) than the original clutch size. In the control broods the brood size matched original clutch size. In these clutches failure to hatch was compensated by addition of chicks of appropriate age but the brood but the nests were otherwise unmanipulated. All broods were randomly placed in one of the three groups irrespective of preceeding egg mortality. Experimental brood sizes of 72 broods, (i.e. 25 enlarged, 25 reduced and 22 controls) used for nestling growth analyses are shown in Figure 1 as a function of laying date of the first egg of the clutch. The experimental broods were a representative sample of all nests with respect to laying date and clutch size. The nestboxes were checked at intervals of two to five days until the young

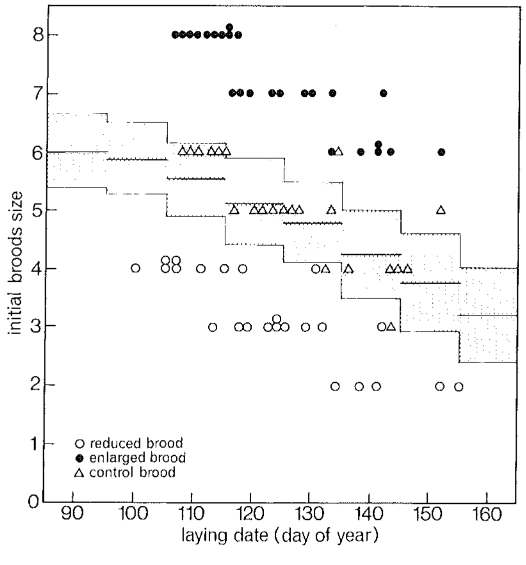

Figure 1. Distributions of experimental brood sizes after brood manipulations and laying dates (of the first egg of the clutch). Reduced broods: two young less than original clutch size. Enlarged broods : two young more. Horizontal bars and shaded areas indicate mean clutch size ± s.d. per ten day interval of laying dates,(Daan & Dijkstra 1988).

fledged at about thirty days of age. Nestlings were marked individually with flexible rubber rings and as soon as possible with aluminium rings from the Bird Ringing Centre (Heteren). Body mass was taken to the nearest gram using Pesola spring balances. Winglength was measured and time of day recorded since body mass of nestlings of all ages was highly dependent on time of day (section 4.1). Occasionally prey was found stored in the nestbox. Such prey were identified and weighed. After fledging a number of juveniles could be caught by *bal-chatri* and weighed while still being fed by the parents. Recognition of the broods during the postfledging phase was possible by marking the fledglings with colour dyes and with the aid of the wing-tagged parents.

Parental effort in the experimental broods was investigated by continuous observation of a selected sample of individual kestrels throughout their daily activity period, from ca 0.5 hrs. before sunrise till 0.5 hrs. after sunset. These data were obtained in 1986 in the Lauwersmeer area. Only those days when the kestrels were in sight for more than 75% of the observation time were used for time and energy budget analyses. For a detailed description of the behavioural protocol we refer to Masman et al (1988b). Parental energy expenditure was estimated using data on basal metabolic rate, flight and perching costs, temperature regulation and heat increment of feeding, established for the kestrel (Masman et al 1988c). Food provisioning of the nestlings was determined by mounting electronic balances at the bottom or in the entrance of the nestbox. Prey mass as well as the parent's mass could be measured when the bird entered the nestbox with prey and left without.

Duration of parental care after the young had fledged was established by making behavioural protocols of the parents every other day after the fledglings left the nestbox. The daily observation period for establishing parental care of fledglings started at ± 6 a.m. since feeding frequency was the highest from 7 till 12 a.m., and was continued until at least one prey delivery to the young was seen. When no prey transfers were recorded for 8 hours, providing weather conditions were favourable and the parents had been in sight nearly continuously, we assumed they had stopped feeding the young.

Local survival of the parents of experimental and control broods was determined by establishing the whole breeding population a year later. This was done by recording the tagged individuals (previous breeders) during next year's breeding season and by catching the untagged birds (local juveniles and immigrants of all ages). Pairs of which the complete clutch failed to hatch as well as cases of polygamy were excluded from survival analyses. Statistical tests were two-tailed, unless stated otherwise.

4. RESULTS

4.1 Parental effort and food provisioning.

Male parents from enlarged broods in the Lauwersmeer in 1986 spent on average 1.2 h.day^{-1} (27%) more time in flight and flight-hunting than the controls (table 1). Males from reduced broods hunted on average 0.8 h.day^{-1} (17%) less than control males but this difference was not statistically significant. Daily flight time of males with enlarged broods was 2.0 hrs (50%) longer compared with those having a reduced brood ($p<0.05$). Consequently, male daily energy expenditure, determined by the time-energy budget model of Masman et. al. (1988c), was significantly higher in the enlarged broods compared with both the controls and

Table 1. Parental effort, hunting yield and nestling food intake in a subsample of experimental broods. Means ± st.dev. (n,N) = (nr. of observation days, Nr. of broods). Mann Whitney U-test one-tailed; hunting yield: two-tailed. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Reduced	Control	Enlarged	level of sign		
	R	C	E	R-C	C-E	RE
Original clutch size	5.0± 1.0 (3)	5.1± 0.8 (8)	5.3± 1.0 (4)	ns	ns	ns
Experimental brood size	2.7± 0.6 (3)	5.1± 0.8 (8)	7.3± 1.0 (4)			
Male flight hrs/day	3.8± 2.2 (7,3)	4.6± 1.6 (27,8)	5.8± 1.4 (10,4)	ns	*	*
Male energy expenditure kJ/day	363.7±99.5 (7,3)	388.3±77.8 (25,7)	459.3±74.5 (10,4)	ns	*	*
Male hunting yield prey/hr.hunt	6.4± 1.6 (7,3)	6.4± 2.7 (29,8)	7.3± 1.4 (11,4)	ns	ns	ns
Female flight hrs/day	0.3± 0.3 (4,2)	1.8± 1.3 (5,3)	2.3± 1.4 (14,4)	*	ns	**
Food intake per brood g/day	205.4±78.1 (8,3)	325.3±82.3 (24,8)	486.4±63.1 (14,4)	***	***	***
Food intake per nestling g/day	81.5±23.7 (8,3)	61.4±11.6 (24,8)	65.8± 8.3 (14,4)	**	ns	*

the brood reductions. The females in the three groups showed the same trends in flight activity as the males, although in all cases they did less flying than the males. Hunting by females with reduced broods ceased almost completely.

Male flight-hunting yield, expressed as the number of voles caught per hour hunting, did not differ significantly between the groups. This suggests that a relaxed or increased food demand of the nestlings did not affect parental hunting yield. There is a positive correlation between brood size and hunting yield in the control situation as we have established elsewhere (Masman et al 1988a, chapter 3), and observations on enlarged and reduced broods were not quite evenly distributed with respect to original brood size. In order to measure the effect of the experimental manipulation itself on hunting yield, the expected yield based on original brood size was assigned to every kestrel observed. Experimental yields did not differ from expected yields, neither in the reduced broods (Mann Whitney U-test, ns.) nor in the enlarged broods. The difference between observed and expected yields also showed no relation with type of experiment (reduced vs. enlarged, ns).

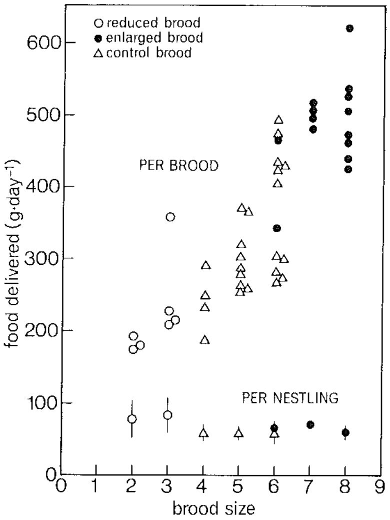

Figure 2. Daily amount of food (g) delivered by the parents to the experimental broods. Per brood: Each symbol indicates one observation day. Per nestling : Means ± s.d.

Different parental effort with equal hunting yield resulted in different amounts of food brought to the nest (Table 1, Fig.2). The parents brought more food to the enlarged broods and less to the reduced ones, compared with the controls. Food intake per nestling was the same for controls and enlarged broods, but was significantly higher in reduced broods.

In addition to daily parental effort, the duration of parental care after fledging is a major factor in determining total energy expenditure of the adults during reproduction. Duration of parental care in kestrels breeding late in the season is significantly curtailed compared with early breeders. No additional effect of brood manipulations could be established since fledglings from both enlarged and reduced broods became independent at about the age expected for the time of year (Fig. 3).

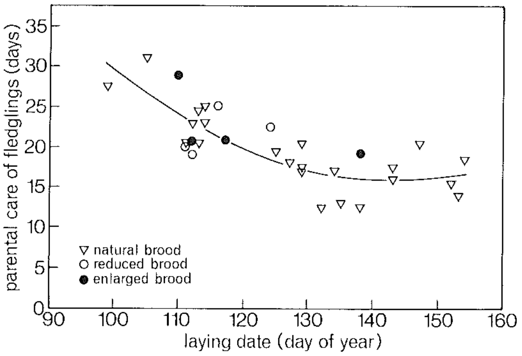

Figure 3. Duration (days) of parental food provisioning of the young after fledging in natural broods and manipulated broods, as a function of laying date of the first egg of the clutch. Each symbol indicates one brood. Line is the quadratic regression fitted by least squares.

4.2 Nestling growth and survival.

Growth of those nestlings surviving till fledging in unmanipulated broods is shown in fig. 4. Variation in body mass in the course of the day was ruled out by calculating mass increase during the day as a function of age and converting all body mass data to 12 a.m. Both sexes weighed about 16 grams at hatching and reached peak weights around 24 days of age. Females were growing faster and reached higher peak weights than males. Bodymass decreased in the final days before fledging. This trend continued during the fledgling period and both sexes attained minimum bodymass around the age of independence. The age of independence varied among broods from ca 44 till ca 62 days, depending on time of year (Fig.3). Growth of the primaries showed a different pattern from body mass (Fig. 4b). At fledging wing length was only 75 % of the ultimate length. The flight feathers were fully grown at an age of approximately 50 days, 20 days after fledging. Variation in duration of parental care indicates that some parents stopped feeding the young even before their flight feathers were fully grown, especially those breeding late in the season (Figs. 3,4).

Growth of chicks in the manipulated broods was analysed by calculating individual body mass increase per day between the first measurement after age 9 days, i.e. at the start of the experiment, and the last measurement before age 20 days. Since the rate of increase in wing length in natural broods was approximately constant from age 10 till 24 (Fig 4b) we used this interval in the analyses of wing length growth in the experimental broods.

Growth rates of body mass as well as wing length in nestlings which survived till fledging were significantly lower in enlarged broods compared with reduced broods as well as controls, both for males and females (Table 2). The differences between reduced and

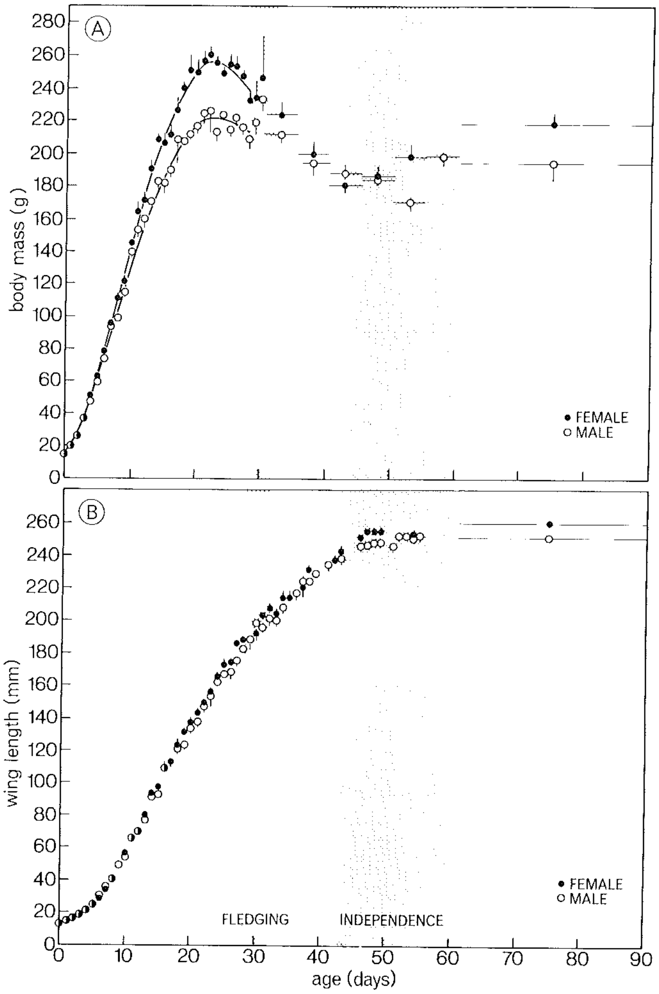

Figure 4. Mean body mass (A), and wing length (B), of male and female nestlings from natural broods as a function of age and of birds recaptured after fledging. Means (g) ± s.e.m. The curves in body mass indicate the five day running means of body mass for males and females in the nestling period.

control broods were not significant although body mass increase tended to be faster in reduced broods. Since individual growth rates of nestlings within broods are probably not independent, the mean growth rate per brood was also calculated for both sexes. This analysis showed the same trends. To test whether the reduced growth in enlarged broods was due to some individuals within the brood or the result of slower development of the whole brood, variance in growth rates within broods was calculated for all nests (Table 2). The differences in variance between the experimental groups were not statistically significant.

Table 2. Nestling growth in manipulated broods. Individual body mass increase (gr/day) was calculated from the first measurement after age 10(days) and the last before age 20 (Fig.4). Winglength: age 10-24. Means ± sd(n). Mann Whitney U-test, one-tailed. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Reduced R	Control C	Enlarged E	statistics R-C	 C-E	 R-E
Males	**body mass increase (g/day)**					
individual	9.6± 2.7(27)	8.4± 2.7(39)	6.2± 3.5(79)	ns	***	***
per brood	9.5± 2.8(17)	8.4± 2.6(15)	5.9± 2.7(25)	ns	**	***
var.within broods	1.7± 1.7(7)	3.1± 3.4(12)	4.6± 5.5(20)	ns	ns	ns
Females	**body mass increase (g/day)**					
individual	10.8± 2.9(29)	9.8± 3.7(39)	8.3± 4.0(62)	ns	ns	**
per brood	10.5± 2.5(15)	10.1± 2.9(19)	6.9± 4.6(23)	ns	**	**
var.within broods	1.8± 2.9(11)	6.0±11.9(14)	3.9± 5.6(17)	ns	ns	ns
Males	**winglength increase (mm/day)**					
individual	7.3± 0.4(35)	7.2± 0.5(49)	6.9± 0.6(79)	ns	***	***
per brood	7.2± 0.3(20)	7.2± 0.4(19)	6.9± 0.5(25)	ns	*	**
var.within broods	0.05±0.04(10)	0.1± 0.2(15)	0.13± 0.2(20)	ns	ns	ns
Females	**winglength increase (mm/day)**					
individual	7.5± 0.4(36)	7.5± 0.4(47)	7.3± 0.6(62)	ns	*	*
per brood	7.5± 0.3(21)	7.5± 0.3(20)	7.1± 0.7(23)	ns	*	*
var.within broods	0.06±0.06(12)	0.07±0.06(19)	0.12± 0.2(17)	ns	ns	ns

This does not support the idea that the reduced growth rate of the enlarged broods was due to more uneven distribution of food over the brood.

The body mass increase was far from linear after age 20 and even became negative shortly before fledging in the natural broods. We therefore calculated relative mass of the experimental nestlings for this age class. Expected mass for every day of age was determined by taking the 5-day running mean of nestling weight in natural broods (Fig.4a). The same method was used for analyses of winglength during the last ten days before fledging. Body mass before fledging in enlarged broods was significantly lower than in reduced broods, whereas mean relative wing length did not differ between the groups (table 3). After fledging, only a fraction of the juveniles could be recaptured and no differences in body mass between the groups could be established in the females. The males from reduced

Table 3. Relative body mass and wing length of nestlings from experimental broods during the last ten days before fledging (age 21-30 days), expressed as percentage of the values obtained in natural broods in this age class. Mean ± s.d. Levels of significance as in Table 2. Mann Whitney U test, one-tailed.

	Reduced R	Control C	Enlarged E	statistics R-C	 C-E	 R-E
Males		**body mass**				
individual	103.44±7.15(34)	101.92±8.35(54)	98.94±8.44(69)	ns	*	**
per brood	102.70±6.93(19)	100.95±7.90(21)	97.97±7.31(23)	ns	ns	*
Females						
individual	101.26±9.30(34)	99.10±7.52(48)	98.07±7.48(57)	*	ns	**
per brood	101.28±8.74(20)	99.80±5.62(21)	96.41±7.27(22)	ns	ns	**
Males		**winglength**				
individual	97.89±3.57(34)	98.63±4.39(54)	97.95±4.56(69)	ns	ns	ns
per brood	98.03±2.44(19)	98.93±3.36(21)	96.88±3.93(23)	ns	ns	ns
Females						
individual	98.82±4.48(34)	98.85±4.63(48)	97.93±4.04(57)	ns	ns	ns
per brood	99.11±3.95(20)	98.51±3.59(21)	96.81±4.60(22)	ns	ns	*

Table 4. Body mass of male and female fledglings from manipulated broods. Means (g) ± sd. Age groups: 31-40 and 41-50 days, during parental care. Age group 51-90, at independence. Mann Whitney U-test, one-tailed. * p<0.05, ** p<0.001.

Age	Reduced R	Control C	Enlarged E	level of sign R-C	 C-E	 R-E
		Females				
31-40	238.4±12.4(11)	224.0±20.7(14)	232.5±11.7(23)	ns	ns	ns
41-50	222.9±14.0(3)	-------	217.7±23.4(14)			ns
51-90	187.7 (1)	206.0±19.6(6)	197.9±17.9(4)	ns	ns	ns
		Males				
31-40	216.7±13.9(12)	186.3±25.2(10)	199.2±28.8(33)	***	ns	*
41-50	206.3±20.6(3)	192.3± 9.90(6)	190.1±20.2(11)	ns	ns	ns
51-90	188.7±13.7(9)	180.5±10.6(9)	187.1±12.2(8)	*	ns	ns

broods were significantly heavier than the controls in age class 31 to 40 days (table 4). Since both sexes from enlarged broods did not differ in mass from the other groups during the fledgling period, initial arrears in growth before fledging were possibly made up by then.

Nestling mortality was significantly higher in the enlarged broods whereas reduced and control broods both showed the same low mortality rates (table 5). In spite of increased mortality in the enlarged broods the brood sizes at fledging were still larger than in the other groups. This must have resulted in prolonged increased nestling food demand till after fledging in the enlarged broods.

Out of 575 juvenile kestrels fledged from all broods in this study, 42 were caught alive in the study area after one year. Hence local survival amounted to 7.3%. Survival estimates based on ring analyses showed a mean survival during the first year of 36.6% in natural broods and local survival obviously underestimates overall survival due to the dispersion of juvenile kestrels (Daan & Dijkstra 1988). Analyses of local survival after fledging till the next breeding season of juveniles from experimental broods showed no relation with brood manipulations (logistic regression, $t=0.22$ ns.).

Table 5. Nestling survival and brood size at fledging in reduced, control and enlarged broods. Means ±sd. Mann Whitney U test, one tailed * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Reduced R	Control C	Enlarged E	level of sign R-C	C-E	R-E
nr.broods	25	22	25			
orig.clutch size	5.2± 0.8	5.0± 0.9	5.2± 0.8	ns	ns	ns
experimental brood size	3.2± 0.8	5.0± 0.9	7.2± 0.8			
broodsize at fledging	3.1± 0.8	4.9± 0.9	5.7± 1.9	***	*	***
survival (%) nestlings	98.0±10.0	98.5± 0.9	80.6±26.5	ns	***	***

4.3 Adult body mass and survival.

Mean body mass of adult male and female kestrels raising experimental broods is shown in fig.5 as a function of nestling age. Before the broods were manipulated mean adult body mass did not differ significantly between the groups, neither in the males nor in the females (Mann Whitney U-test, ns.in all cases), although females with complete broods happened on average to be lighter than the other females at the onset (fig 5, nestling age 0-10 days). During the nestling period the females showed a decrease in body mass. Females raising reduced broods were consistently heavier than those with enlarged broods: In the first ten days after the onset of the experiment (age 11-20, MWU-test $p<0.05$), during the last ten days before fledging (age 21-30, MWU-test $p<0.05$), and during the fledgling period (age 31-50, MWU-test $p<0.05$). Females of enlarged broods lost weight more rapidly than those with reduced broods (ANCOVA, $F_{1,69}=5.91$ $p<0.05$). The rate of decrease in body mass of females raising complete broods was intermediate and did not differ from females with either reduced (ANCOVA, $F_{1,48}=2.37$ ns.) or enlarged broods (ANCOVA, $F_{1,69}=0.75$ ns.) The males showed no significant change in body mass in the course of the nestling period and no effect of brood manipulations on body mass can be seen in figure 5.

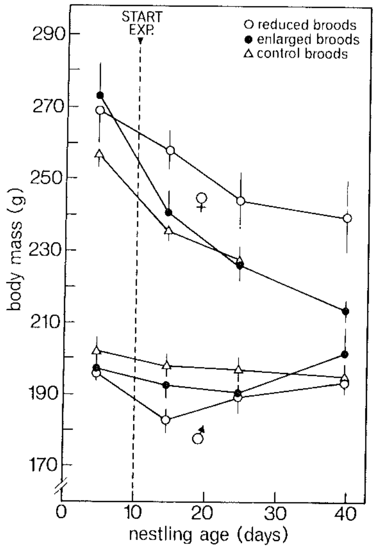

Figure 5. Mean body mass (g) ± s.e.m. of male and female parents of experimental broods during the nestling stage, per ten day interval of nestling age. Dashed line indicates the start of the experiments.

By monitoring tagged kestrels and capturing untagged individuals during the next breeding season, local survival of kestrel parents with manipulated broods could be established (Fig.6). Mean local survival of parents raising enlarged broods was approximately 15% lower than in those raising complete broods, and 23% lower than in parents from reduced broods (table 6). These trends were the same in both sexes, although female survival rates

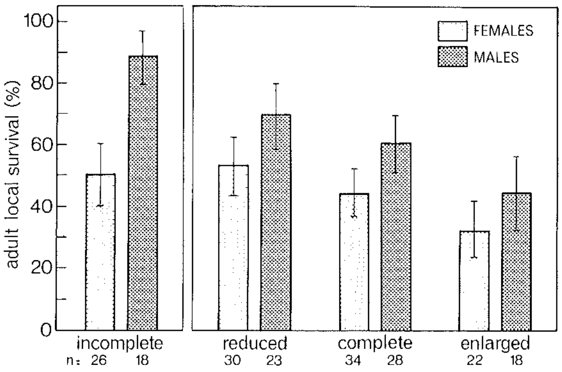

Figure 6. Local survival till the next breeding season of kestrel parents after brood manipulation. Means ± s.e.m. Survival of those parents who raised a reduced brood due to egg mortality (natural brood reductions) is shown in the left panel.

were lower than in males. The effect on adult survival was not significant for either of the sexes seperately. Both sexes combined showed a significant correlation of local survival with type of experiment (table 4). Survival of those parents which had an incomplete brood due to egg mortality (natural brood reductions) is also shown in figure 6. Survival of these parents was not statistically different from the experimentally reduced broods (females $\chi^2=0.06$, males $\chi^2=2.2$, both ns.). When we included the natural brood reductions in the experimentally reduced group, the effect of "brood manipulations" was statistically significant on male survival was established (table 6). The sexes combined again showed a pronounced effect of deviations from the complete brood size on adult local survival ($p<0.01$).

Table 6. Local adult survival after brood manipulations. Number of individuals in parentheses. p values indicate significance of logistic regression on brood manipulations. p1: excluding natural brood reductions; p2: natural brood reductions included with reduced group.

Category	Males	Females	Both
Enlarged	0.444 (18)	0.318 (22)	0.375 (40)
Complete	0.607 (28)	0.441 (34)	0.516 (62)
Reduced	0.696 (23)	0.533 (30)	0.604 (53)
Natural br.reduction	0.889 (18)	0.500 (26)	0.659 (44)
p1	>0.1	>0.1	<0.05
p2	<0.02	>0.1	<0.01

5. DISCUSSION

Brood size manipulations in altricial birds have become a popular tool in avian reproductive ecology, ever since Von Haartman (1954) did the first experiments of this kind in the Pied Flycatcher (see Table 7). They are designed to evaluate the consequences for parameters associated with individual fitness of raising more or fewer young than the natural brood size. The approach is based on the assumption that the parents of the manipulated broods are "fooled" by the experiment and accept the extra nestlings as their own. In order to derive conclusions on the relation between brood size and fitness from such experiments it is necessary to evaluate the effects on both the brood and the parents. The analysis of repercussions on the parents is usually more difficult, and started much later (Harris 1970) than studies on the broods. In our study in the kestrel, we have attempted to cover influences on the prospects of both nestlings and parents. We realize that the proximate control of egg laying in the kestrel involves a close association between clutch size and laying date, probably based on a largely endogenous temporal programme (Meijer et al 1988a,b). Since variations in clutch size and laying date are presumably adaptive to the nutritional circumstances of individual pairs (Daan & Dijkstra 1988, chapter 5), they are likely to affect the results of experimental manipulations. Our data set is not large enough to differentiate between broods at different dates. Additional experimentation will be required to specifically study the effects of date per se on fitness. In any case, our experimental nests were representative for the natural distribution of clutch sizes and laying dates (Figure 1).

The consequences of the manipulations for the nestlings may be summarized as follows: Surviving nestlings from enlarged broods initially showed lower growth rates than both complete broods and reduced broods (table 2). Shortly before fledging body mass was still relatively low in the enlarged broods whereas wing length was the same as in the other groups (table 3). After fledging no effect of brood manipulation on fledgling body mass could be established. Increased nestling mortality in enlarged broods (table 5) resulting in relaxed competition for food among survivors possibly caused compensation of initial arrears in physical development. Brood size at fledging was still larger in the enlarged broods in spite of increased mortality (table 5). Duration of parental care showed no relation with type of experiment. Survival of the offspring from independence till reproductive age can not be exactly established. Due to a large fraction of the birds dispersing from the study area, local survival underestimates true survival rates till maturation. The experiments did not cause significant effects on local survival. Hence we must conclude that kestrel parents, under the conditions of the experiment, were able to raise more offspring surviving till reproductive age than they do under natural conditions.

With respect to the offspring, the kestrel results are in line with the conclusions from the literature. Most studies have reported increased nestling mortality and/or reduced condition (usually body mass) in enlarged broods (Table 7). However, the majority of studies also demonstrated that altricial birds are usually able to raise more nestlings than the number they opted for themselves. Although reduced condition of fledglings in enlarged broods

Table 7. Summary of brood enlargement experiments in altricial birds. Fitness components analysed: N_f = Number of fledglings; M_f = Body mass of fledglings; S_o = Survival of nestlings till fledging; S_f = Survival of fledglings till autumn or next breeding season; M_p = Body mass of parents; S_p = Survival of parents; B_p = Future breeding performance of parents. Positive, negative and zero effects are indicated by +, - and 0, respectively.

A. NON-PASSERES

Order / species	offspring				parents			Author
	N_f	M_f	S_o	S_f	M_p	S_p	B_p	
Procellariiformes								
Diomedea immutabilis	-		-					Rice & Kenyon (1962)
Oceanodroma castro	-		-					Harris (1969)
Oceanodroma leucorrhoa	0	-	-					Huntington, in Lack (1966)
Puffinus puffinus	-	-	-		0			Harris (1966)
Puffinus tenuirostris	0	-	-					Norman & Gottish (1969)
Pelecaniformes								
Sula sula	-		-					Nelson (1966)
Sula bassana	+		-					Nelson (1964)
Sula capensis	+	-			0			Jarvis (1974)
Falconiformes								
Accipiter rufiventris		-	-					Simmons (1986)
Falco tinnunculus	+	-	-	0	-	-	0	this study
Charadriiformes								
Stercorarius longicaudus	+		0					Andersson (1976)
Larus argentatus	+	0	0					Haymes & Morris (1977)
Larus glaucescens	+	-						Ward (1973)
Larus glaucescens	+		0					Vermeer (1963)
Larus fuscus	+	0	0					Harris & Plumb (1965)
Rissa tridactyla	+	-	0					Coulson, in Lack (1966)
Creagrus furcatus	+	0	0		0	0		Harris (1970)
Fratercula arctica	+		-					Corkhill (1973)
Fratercula arctica	-		-					Nettleship (1972)
Cepphus grylle	+	0	0					Asbirk (1979)
Alca torda	+	-	-					Lloyd (1977)
Alca torda	+	-	-					Plumb (1965)
Columbiformes								
Columba palumbus	+	-	-	0				Murton et al (1974)
Caprimulgiformes								
Apus apus	-		-					Perrins (1964)
Aerodramus spodiopygius	0	-	-					Tarburton (1987)

B. PASSERES

Order / species	offspring				parents			Author
	N_f	M_f	S_o	S_f	M_p	S_p	B_p	
Passeriformes								
Delichon urbica	+	0	0					Bryant (1975)
Delichon urbica	+	-	-					Bryant & Westerterp (1983)
Iridoprocne bicolor	+	-	0	0	0	0		DeSteven (1980)
Troglodytes aedon	+	0	0		0		0	Finke et al (1987)
Ficedula hypoleuca	0	-	-		-	-		Askenmo (1977, 1979)
Ficedula hypoleuca	+	-	0	0				Von Haartman (1954)
Turdus pilaris	+	0	0					Slagsvold (1982)
Parus major			-				-	Smith et al (1987)
Parus major	+	-	-		0		-	Tinbergen (1987)
Parus major	+		-			0		Lindèn (unpublished)
Parus caeruleus	+		0	0	-	-		Nur (1984a,b)
Plectrophenax nivalis	+	0	-		-			Hussell (1972)
Agelaius phoeniceus	+	-	-					Cronmiller, Thompson (1980)
Pyrrhula pyrrhula	-		-	-				Newton, in Lack (1966)
Passer domesticus	+	-	-					Schifferli (1978)
Passer domesticus	+	-	0		0	0	-	Hegnes & Wingfield (1987)
Quelea quelea	0	0	-					Ward (1965)
Sturnus vulgaris	+	-						Crossner (1977)
Sturnus cinerareus	+		-					Kuroda (1959)
Pica pica	-	0	-					Högstedt (1980)
Corvus corone	+	0	-					Loman (1980)
Corvus frugilegus	+					0	-	Rφskaft (1985)

suggests that such increase might be offset by reduced prospects for the offspring, effects on fledgling survival have been documented only in the Bullfinch (Newton in Lack 1966) and then only in local survival till autumn, which may well reflect differential dispersal.

Turning now to the parents, the kestrels showed clearly increased daily hunting effort to nourish the enlarged broods, and energy expenditure was increased correspondingly. Yields per hour hunting were the same in all groups. This confirms our conclusions from nestling food deprivation experiments (Masman et al 1988, chapter 3). Females with reduced broods almost completely stopped hunting. Body mass decrease in this group averaged 30 g during the nestling phase which is the same as in *ad lib* fed females breeding in captivity (Dijkstra et al 1988, chapter 2), in contrast with an average weight loss of 60 g in females with enlarged broods (fig.5). This result supports the notion that female raptors build up fat reserves functioning as a buffer for nestling food provisioning during periods of food shortage (Wijnandts 1984). Males did not show differences in body mass in relation with brood manipulations (fig.5). They probably attain low body reserve levels during the nestling phase independent of variations in nestling food demand.

Local adult survival was negatively correlated with the change in brood size (fig 6, table

6). Parents from reduced broods survived best, and their survival rates were 23% higher than in parents with enlarged broods. Female kestrels had lower local survival rates than males. This is true both in experimentally manipulated and natural broods, and presumably reflects sex differences in dispersal rather than in survival. Survival analyses based on ring recoveries of all nestlings ringed in the Netherlands from 1967 till 1986, compared with local survival in our study area from 1979 till 1987, indicated that 16 to 42% (depending on age) of the natural breeding population disappeared due to dispersion (Daan & Dijkstra 1988, chapter 5). For an analysis of ring recoveries of the manipulated parents (1985-1987) insufficient data have so far accumulated. Thus, although local survival reflects only one aspect of the future reproductive prospects of the parents, the results suggest that there may be rather important repercussions for the parents of raising more young than they "intended" to. The behavioural analysis suggests that reduced survival in parents of enlarged broods may be related to increased activity and energy expenditure in providing food for the young. The daily time spent in flight hunt, a major determinant of daily energy expenditure (Masman & Klaassen 1987) was affected in both sexes. Although kestrels can compensate, within limits, for increased work loads by raising energy intake (Masman et al 1988), we surmise that the increased energy turnover in the brood enlargements is involved in the reduction in survival.

Effects of brood enlargements on parental prospects have been documented so far in only eleven studies (table 7). Effects on the parents' condition during brood raising have more frequently been looked at, and two out of eight studies report reduced body mass following brood enlargement. The kestrel results are in agreement with those of Hussell (1972) in the Snow bunting, where the sexes differed. However, body mass may be equivocal in this respect, and the absence of any conditional response does not preclude long term impacts on future reproduction. Such impacts have now been documented for five species. In the Pied Flycatcher (Askenmo 1979) and the Kestrel, there were effects on parental local survival rates. In the House Sparrow (Hegner 1987), Great Tit (Tinbergen 1987; Smith 1987) and Rook (Roskaft 1985), the effects were on rates of future reproduction of those parents surviving. Effects on survival are further probable in the Blue Tit (Nur 1984), although the design of these experiments, where the smallest natural broods were the most likely to be enlarged, leaves room for other interpretations. A further two studies (Harris 1970, DeSteven 1980) did not demonstrate long-term effects on parental survival (Table 7).

Thus, while the ability of altricial birds to raise additional young beyond the natural brood size, albeit at the expense of increased brood mortality, has been amply documented, the repercussions of raising enlarged broods for the parents have been shown convincingly in only few cases. We further remain in the dark as to which aspects of parental care are causally involved in such repercussions. Our experience with the kestrels suggest that neither time nor food was in short supply, and increased energy expenditure in the males, who have the major share in food provisioning, can be made up for by increased intake. Yet, the increased energy turnover, at levels probably approaching the maximum sustainable (Masman et al 1988, chapter 2), may have resulted in reduced adult survival till the next breeding season. This trade off between parental effort and survival will be incorporated when we evaluate the ultimate regulation of clutch size and laying date which we present elsewhere (Daan et al. 1988, chapter 7).

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Chapter 5

DATE OF BIRTH AND REPRODUCTIVE VALUE OF KESTREL EGGS: ON THE SIGNIFICANCE OF EARLY BREEDING

Serge Daan and Cor Dijkstra.

1. SUMMARY

Fisher's (1930) concept of **reproductive value** was applied to estimate the relative fitness of Kestrel eggs in the Netherlands. Clutch size in two study areas varied with laying date within years, and with prey density and mean laying date between years. Survival of eggs till fledging varied with laying date within years, not between years. Annual clutch size variations led to major 3-4 year cycles in nestlings ringed in association with the vole cycle. Age specific survival was analyzed by ML estimation from ring recovery data over 20 years. Both juvenile (age 0) and adult survival varied in association with vole density data and with mean date of ringing. Juvenile survival (till age 1) was associated with date of ringing within years as well as with mean ringing date between years. Adult survival (age 1 till age 2) varied only with the mean ringing date in the year of birth, probably by the cyclic nature of the food supply. Probability of breeding of surviving yearlings was sharply suppressed in late born birds. Due to the declining probabilities of survival from egg till fledging, from fledging till age 1, the reproductive value of eggs declined progressively with laying date.

2. INTRODUCTION

Annual rhythms in animals are tuned to seasonal cycles in the environment. With predictable variations in food, daylength, and temperature, birds in the temperate zone face the decisions when to breed, when to moult, when to migrate. Such decisions have profound effects on the rate of gene propagation. To understand the evolutionary basis of annual rhythms we need eventually to define the problem of optimal timing in terms of maximization of evolutionary fitness (Williams & Nichols 1984), and empirically estimate its parameters.

While the consequences of early or late breeding or moult in nature can rarely be assessed in terms of a bird's chance of survival till next breeding, we can at least in some species evaluate the impact of birthdate on the offspring. It was Lack (1947/48, 1966, 1968) who first advocated exploiting natural variation in reproductive behaviour within populations for this purpose. This variation is partly due to individual optimization in response to varying conditions instead of to genetic heterogeneity (Williams 1966, Greenlaw 1978, Drent & Daan 1980), but that needs not detract from the potential offered by species with a large variation in birth dates. Assaying juvenile survival in the egg and nestling stages has long been popular among ornithologists, and pertinent data are available for many species. However, the number of fledglings raised by a pair is an insufficient measure of its reproductive success. What we need to know is how many of those born at different dates participate in the next reproductive generation and how soon. Variations in this probability will be mainly related to two factors: mortality during the prereproductive phase of life and for those surviving, the chance of breeding when attaining maturity.

Variations with birthdate in the survival after fledging have been reported for several avian species. They consistently demonstrate a decline in the later fledged young. As an indicator of survival, the percent recovered in the study area after a few (2-6) months is commonly used (*Columbus palumbus*: Murton 1961; *Puffinus puffinus*: Perrins 1966; *Parus major*: Perrins 1965,1970; *Ficedula hypoleuca*: Von Haartman 1967). This may indeed cover the main episode of survival variation with birthdate, but it excludes mortality during the first winter as well as survival of migrating birds. Cavé (1968) went a step further as he used ring recoveries of the kestrel, *Falco tinnunculus*, to estimate survival till reproductive age. He found that for late born fledglings the probability of being alive after May of their second calendar year was smaller than for early fledglings. This is the more intriguing since food conditions (common vole densities) gradually improved during the season. There are, however, profound year to year variations in food supply as well as in mean birthdate, and this must have repercussions for both reproduction and survival. Since Cavé's (1968) work, the total number of kestrel ring recoveries has increased sixfold. Hence we are now in a position to analyse the relation between birthday (i.e., the date at which an egg is laid) and survival till reproductive age in more quantitative detail, and solve some of the ambiguities still present in the data set from the 1960's. In addition to the ring analyses we have collected field data in a kestrel population which allow us to estimate for those birds surviving the dependence of the probability to participate in breeding on their date of birth.

Reproductive value

To estimate the expected rate of gene propagation by individuals born at different times in the breeding season we use Fisher's "reproductive value". This measure was introduced as a population parameter representing the present value of future offspring for individuals of different age relative to the value at the time of birth:

$$V_t = (\lambda^t/l_t) \sum_{x=t}^{\infty} \lambda^{-x} * l_x * b_x \qquad (1)$$

where V_t = reproductive value at age t; λ (= e^r) = innate rate of population increase; l_x = probability of survival till age x; b_x = expected number of eggs produced at age x (Fisher 1958). In this notation V_o = 1 at the time of birth, since l_o = 1 and $\Sigma \ \lambda^{-x} * l_x * b_x = 1$ for a population with stable age composition.

We shall demonstrate that l_x and b_x are critically dependent on the "date of birth" of the egg, defined as the ten day interval (i) in which the clutch was initiated. Thus, while V_t has usually been treated as a population parameter (with V_o = 1 per definition, or V_o = 2 if only female offspring are considered, as by Fisher 1958, Fig.2), we can extend its meaning to differentiate between eggs laid at different i:

$$V_o(i) = \sum_{x=o}^{\infty} \lambda^{-x} * l_x(i) * b_x(i) \qquad (2)$$

Other authors (e.g., Pianka 1974,1978, Pianka & Parker 1975, Millar & Zammuto 1983; Curio & Regelmann 1982) have redefined reproductive value by omitting the λ^{-x} term from equation (2). This may be convenient when is difficult to estimate, but it leads to the equivalence of reproductive value and lifetime reproductive output and ignores the fact that reproducing early in life promotes gene propagation rate more than reproduction late in life. λ^{-x} Is the appropriate weighing factor for reproduction at different ages (Charlesworth & Giesel 1972, Charlesworth & Leon 1976, Roughgarden 1979). λ Itself has been succesfully used as a population measure of fitness in the development of optimal life history theory (Schaffer 1974, Ricklefs 1983). However, λ is solely defined as a population parameter, and can not be extended to subgroups in the population for which the assumption of stable age distribution may not hold.

$V_0(i)$ represents the expected rate of propagation of parental genes via an egg produced at date i irrespective of the extent to which variance in i is genetic. For a full evaluation of parental reproductive strategy, $V_0(i)$ is an insufficient measure, since the residual adult reproductive value as affected by reproductive decisions has to be considered as well (Fisher 1958, Trivers 1972). This is beyond the scope of the present analysis. A complete theoretical model for the optimization of clutch size and laying date with empirically estimated parameters for the European kestrel is therefore deferred to a future article (Daan et al, 1988, chapter 7).

3. METHODS

For the analysis of $V_0(i)$, it is necessary to estimate the probability $l_x(i)$ of survival till age x (x = 1, ...) of eggs laid at different times of year (i). This is the product of survival in the nest (S_0) and of the probabilities of survival of fledglings till age 1, from age 1 till age 2, from age 2 till age 3, etcetera:

$$l_x = S_0 \prod_{y=1}^{x} S_y \qquad (3)$$

where S_y = probability of survival from age y-1 till age y.

Survival in egg and nestling stage (S_0):

Data were collected in the Lauwersmeer (53°.20' N 6°.17' E) in the Netherlands (see Rijnsdorp et al. 1981) during the years 1977-1987. We maintained from 19 (in 1977) to 47 nestboxes (in 1987) on ca. 3 m. poles (Cavé 1968) in this area, and in most years the majority of these, varying from 16 (1977) to 40 (1983) boxes, were used by kestrel pairs for breeding. Nestboxes were checked in at most fortnightly intervals, usually allowing us to determine clutch initiation dates within 2 days, assuming an interval of 2 days between consecutive eggs (Beukeboom et al 1987). Clutch initiations (date of first egg) were expressed as day of the year (100 = April 10; 150 = May 30) and used as a reference date for the whole clutch. Data were pooled in 10-day intervals (day 86-95, 96-105, etc.). Fates of 230 clutches in the Lauwersmeer were analysed excluding those where either parents or clutches were experimentally manipulated (Dijkstra et al. 1982; Masman et al. 1988; Daan et al. 1988). In addition, A.J.Cavé kindly put his data (352 clutches) from Flevoland in the years 1960-65 (Cavé 1968) at our disposal. A further 122 clutches were studied by us in Flevoland in the years 1985-87. Nestlings were ringed between 10 and 20 days of age, both in Cavé's (1968) and in our study.

We calculated the probability of survival till fledging, $S_0(i)$ of eggs in clutches initiated in the 10-day date interval i (i = 80, 90, 100.....,150) as

$$S_0(i) = F(i)/N(i) \qquad (4)$$

where F(i) is the total number of fledglings produced in clutches initiated in the interval i-4 to i + 5, together containing N(i) eggs.

Survival of fledglings and adults (S_x):

Through the courtesy of the Dutch Bird Ringing Centre (Heteren), we could analyse survival patterns of kestrels ringed as nestlings. Between 1911 and 1.1.1987 47559 kestrels have been ringed in the Netherlands and a total number of 8189 recoveries has accumulated. Of the recovered birds, 7142 (87.2%) were ringed as nestlings. We discarded 3142 recoveries on various grounds: ringing or recovery date inaccurately reported (297); death due to shooting or pollution (1435); wingtag sightings (28); only ring or ringed leg found (56); condition in which found unknown (90); dead explicitly for more than one week (856); birds trapped alive (240); handraised and experimentally displaced birds (140). This leaves a total data base of 5047 recoveries for survival analysis. These include 460 birds found sick and mostly brought to bird revalidation centres. We have treated these birds as though they had been found freshly dead.

The highest recorded age was 14.6 years and only 0.18% of all recoveries was made after 11 years of age. We thus assume (for life table analysis) that recovery records were virtually complete on 1.6.1987 for all birds ringed up till 1976 inclusive. 2121 Recoveries in the data base (50.3%) concern birds ringed as nestlings before 1977. For age specific survival analysis we chose June 1 as the boundary date between age groups. This date distinguishes roughly between those birds which died certainly before they had a chance to reproduce and those which may have reproduced. There is some justification in two facts: the mean date of hatching was 5 June in the Lauwersmeer (Masman et al. 1988a). Death of one parent before hatching will inevitably lead to loss of the whole clutch; death of a parent after hatching of the eggs at least in two cases in the Lauwersmeer (at ages 17 and 20 days of the nestlings) did not lead to loss of the brood. Reduced mortality during the breeding season (figure 7) makes the analysis insensitive anyway to the precise choice of a boundary date.

For the analysis of age specific survival we have employed both the lifetable method (Lack 1951, applied already to kestrels by Schifferli 1964) and a Maximum Likelihood (ML) estimation (Seber 1973; applied to kestrels by Noer & Secher 1983). The lifetable method was used for birds recovered after ringing as nestlings between 1911 and 1978 (see table 1a).

Table 1. Age specific survival rates (S_x) of the kestrel based on different methods. a) Life table of 2121 nestlings ringed from 1911 till 1976 inclusive, and recovered freshly dead before 1.6.1987. Age=0 for recoveries before June 1 of the year after birth, age=1 for the next year till June 1, etcetera. b) Maximum Likelihood estimates of S_x, based on annual recoveries from 20 cohorts, totalling 38193 nestlings ringed from 1967 till 1986 inclusive. c) Local survival of nestlings and adult birds of known age in the study areas Lauwersmeer and Flevoland.

Age	a. Life Table			b. ML estimate		c. Local survival	
	Recovered	S_x	$\prod_{y=1}^{\infty} S_y$	S_x	$\prod_{y=1}^{\infty} S_y$	S_x	$\prod_{y=1}^{\infty} S_y$
0	1050	-	1.000	-	1.000	-	1.000
1	451	0.505	0.505	0.366	0.366	0.096	0.096
2	215	0.579	0.292	0.633	0.220	0.372	0.036
3	131	0.653	0.191	0.698	0.150	0.470	0.017
4	92	0.677	0.129	0.721	0.111	0.603	0.010
5	57	0.664	0.086	0.697	0.079		0.006
6	46	0.687	0.059	0.704	0.051		0.004
7	37	0.632	0.037		0.036		0.002
8	19	0.532	0.020		0.025		0.001
9	9	0.538	0.011		0.017		0.001
10	8		0.006		0.012		0.000
11	3		0.003		0.009		0.000
12	1		0.002		0.006		0.000
13	1		0.001		0.004		0.000
14	1		0.000		0.003		0.000

This method has recently been the subject of severe criticism (Lakhani and Newton 1983; Anderson et al 1985; Lakhani 1987). Therefore we estimated age specific survival rates also by the ML-method, using the SURVIV software routines kindly provided by dr. G.C. White (White 1983). This program allowed us to estimate survival and reporting probabilities separately for years with high, medium and low vole densities (see below) during the winter. We restricted the ML analysis to the cohorts ringed in the years 1967-1986, when the numbers of nestlings ringed consistently exceeded 300. The data base on nestlings ringed and recovered freshly dead is presented in table 2. The ML-estimation procedure yielded reporting probabilities of 0.099 for juveniles (age 0) and of 0.143 for adults (see section 3). Age specific survival rates computed as the average for high, medium and low vole years (fig. 5.) are shown in table 1b. The fraction surviving till age x is generally overestimated by the lifetable method for the younger age classes, underestimated for the older age classes. This is due to the lower reporting rate of age 0 birds, which is not taken into account in the life table.

Table 2. Basic ring recovery data used for the ML estimation of reporting rates and age specific survival. cat = estimated category of vole densities during the winter based on local peak and trough years (see text). Ringed = number of nestlings ringed during the summer in the Netherlands. Sum 1911/73 = total numbers of kestrels recovered among nestlings ringed in years for which recoveries are complete. C_k = correction factor derived for recoveries > age 1 for recent years with incomplete recoveries.

year	cat	ringed	recovered freshly dead at age:													
			0	1	2	3	4	5	6	7	8	9	10	11	12	>12
1967	III	485	15	32	6	5	0	2	2	1	0	0	0	1	0	0
1968	I	639	41	8	2	0	1	3	0	2	1	2	0	0	0	0
1969	II	312	16	3	4	3	2	1	0	0	0	2	0	0	0	0
1970	II	543	21	4	18	3	2	4	1	0	2	2	1	0	0	0
1971	III	1237	33	65	15	8	14	3	5	6	0	0	0	0	0	0
1972	I	1798	157	24	5	12	4	7	7	2	0	1	2	1	0	0
1973	II	1150	70	16	17	9	4	6	0	1	0	1	0	0	0	1
1974	III	2135	96	88	23	24	34	7	6	7	4	0	2	1	0	
1975	I	2680	174	22	15	18	5	3	4	6	0	1	0	0		
1976	II	2592	166	57	52	19	11	9	10	2	4	0	0			
1977	II	3700	244	106	30	8	18	15	4	1	4	1				
1978	I	2486	215	19	7	7	6	1	6	1	0					
1979	II	1920	127	17	11	13	4	2	2	1						
1980	III	2567	99	108	25	17	19	8	3							
1981	I	3052	239	37	16	19	9	4								
1982	II	2274	165	19	23	2	5									
1983	III	2317	123	56	18	7										
1984	I	2484	194	28	9											
1985	II	2030	162	23												
1986	III	1792	91													
sum	1911/73:		646	292	127	72	45	38	28	25	11	8	6	2	1	1
C_k:			---	---	2.87	1.83	1.49	1.29	1.17	1.09	1.05	1.03	1.01	1.01	1.00	1.00

A third estimate for age-specific survival comes from birds ringed in our study areas. This local survival (table 1c) clearly underestimates ML survival rates due to dispersion of the birds - particularly nestlings - from the study area. Thus the ML method provides the closest approximation to age-specific survival rates. Lakhani (1987) has proposed to employ recoveries of birds ringed as yearlings to test the assumption of constant adult reporting rates. However not enough data are available on kestrels ringed as yearlings to carry out this test.

In order to estimate survival rates for different subgroups of the population, viz. those born at different dates, it is not possible to use the ML-method, since the Euring-data bank does not provide access to the numbers of nestlings ringed at different dates. Therefore we adopted a modified life-table method. We have investigated survival in the first two years of life for subgroups of the population, making use of the reporting rates established by the ML method. If m_x represents for any cohort investigated the number of birds recovered freshly dead at age x, then $M_o = m_o/0.099$ estimates the number dying as juveniles and $M_x = m_x/0.143$ the number dying in any age class $x > 0$. The number alive at age 2 (A_2) is estimated by

$$A_2 = \sum_{x=2}^{\infty} m_x \; / \; 0.143 \qquad (5),$$

for any cohort for which recoveries are complete. These are the cohorts 1911-1973 inclusive. For cohorts from the years 1974-1980 at least 7 age classes are recovered completely, and here A_2 can be estimated by using a correction term:

$$A_2 = C_k . \sum_{x=2}^{k} m_x \; / \; 0.143 \qquad (6).$$

In the complete data set 1911/73 we calculated C_k (the fraction of recoveries made in the first k age classes) to have the following values: $C_6 = 1.177$, $C_7 = 1.089$, $C_8 = 1.054$, $C_9 = 1.031$, $C_{10} = 1.013$, $C_{11} = 1.008$, $C_{12} = 1.005$ (see table 2). These values were applied for the cohorts 1980, 79, 78, 77, 76, 75, 74, respectively. Survival in the first two years of population subgroups born at different times of year can thus be established as:

$$S_1 = (M_1 + A_2) \; / \; (M_o + M_1 + A_2) \quad \text{and}$$
$$S_2 = A_2 \; / \; (M_1 + A_2) \qquad (7)$$

Fertility of birds at age x (b_x)

The expected number of eggs produced by an individual bird reaching age x equals the probability of breeding at that age (P_x) times the expected number of eggs produced per breeding pair (E_x):

$$b_x(i) = P_x(i).\; E_x(i) \qquad (8)$$

$b_x(i)$ appeared to be independent of the age of parents, and, likewise, no significant differences for parents born at different dates were found. In estimating $b_x(i)$ we have used the average clutch size for yearlings (4.91 eggs, s.d. 0.78, n=163) and for adult females (5.33 eggs, s.d. 0.731, n=292). These averages were significantly different (Anova $F_{1,454} = 24.39$; $p < 0.0001$), while there was no significant dependence of clutch size on age after age 1. $P_1(i)$ in equation (8) was estimated from annual surveys of the whole breeding population in the Lauwersmeer, in which the identity of all pairs was established by using numbered rings, color bands and wingtags. For each birthday interval, the number (L(i)) expected to be aliv e as yearlings in the summers of 1979-1987 in the area (i.e. within 10 km from the ringing site) was calculated on the basis of nestlings fledged in the Lauwersmeer in 1978-1986, and taking mortality and emigration into account. The number actually breeding as yearlings in the area was $B_1(i)$, and the ratio

$$P_1 = B_1(i) \;/\; L_1(i) \tag{9}$$

was used as an approximation of the probability of breeding as yearlings. We further assumed that $P_x = 1$ for all $x > 1$. There is no evidence for or against the assumption that adult kestrels will indeed always breed. Our justification for this assumption is in the consideration that $P_1 = 1$ was already reached among early born yearlings, and that it does not seem reasonable to presume that these same birds have reduced chances to breed when reaching ages > 1, or that birthday dependence of P_x would persist beyond age 1.

Table 3. Reproduction and nest survival (S_o) in different years in the study areas Lauwersmeer (L) and Flevoland (F). S_o is the fraction of eggs surviving till fledging. Voles = index of vole abundance during the breeding season in Flevoland (1), and Lauwersmeer (2).

Area	Year	Voles	Laying date			Clutch size			S_o
			mean	s.d.	n	mean	s.d.	n	
F	1960	peak[1]	107.4	14.9	97	5.65	0.96	12	0.644
F	1961		118.1	12.1	96	4.94	0.79	96	0.738
F	1962	trough[1]	142.4	11.6	30	4.03	0.96	30	0.533
F	1963		121.9	11.6	42	5.24	0.91	42	0.809
F	1964	peak[1]	110.0	10.7	30	5.50	0.63	30	0.748
F	1965		103.4	11.2	59	5.69	0.80	58	0.536
F	1985	trough[2]	120.6	11.4	56	5.23	0.73	47	0.740
F	1986	peak[2]	120.3	12.0	59	5.24	0.85	50	0.672
F	1987		113.4	9.8	78	5.37	1.04	68	0.773
L	1977	peak[2]	113.4	14.6	19	5.42	0.90	19	0.621
L	1978	trough[2]	127.8	14.8	17	4.59	0.94	17	0.692
L	1979	trough[2]	130.8	12.4	13	4.67	0.78	12	0.625
L	1980	peak[2]	114.4	11.2	21	5.53	0.70	19	0.752
L	1981		109.3	12.8	28	5.14	1.13	29	0.691
L	1982	trough[2]	122.7	14.7	23	4.91	0.68	22	0.740
L	1983	peak[2]	119.0	16.4	36	5.44	0.87	29	0.480
L	1984		115.3	13.8	33	5.00	1.00	21	0.388
L	1985	trough[2]	132.7	10.2	15	5.00	0.82	13	0.630
L	1986	peak[2]	122.9	10.7	22	5.15	1.09	20	0.770
L	1987		128.5	16.5	34	4.84	0.88	32	0.520

Innate rate of population increase (λ)

V_0 as defined in equation (1) equals expected lifetime reproductive output per egg when $\lambda = 1$ is substituted. Lifetime reproductive output is obviously not the relevant parameter here since eggs produced at an early age contribute more to reproductive value (rate of penetration of genes in future generation). The weighting factor λ^{-x} to be applied should depend on the average reproductive behaviour in the population. Under the assumption that over the long time span (1911- 1986) over which the data were assembled, the Dutch kestrel population has approximately maintained a stable age composition, we can estimate λ from the Lotka-Euler equation, valid for the population as a whole:

$$1 = \sum_{x=o}^{\infty} \lambda^{-x} . l_x . b_x \tag{10}$$

l_x and b_x were derived as described above without taking birthday into account, and λ was then computed by numerical approximation.

Vole density fluctuations

In the analysis of various reproduction and survival parameters it is of importance to take year-to-year variations, associated with density fluctuations in the common vole (*Microtus arvalis*), the primary food in the kestrel in the Netherlands, into account. There are no longterm quantitative data available on vole densities in the whole country. However, three studies allow us to roughly reconstruct in which years local peaks and troughs in local vole populations occurred in the past 27 years. These data, stemming from Flevoland 1960-65 (Cavé 1968), Achterhoek 1967-1977 (De Bruijn 1979) and Lauwersmeer 1976-1987 (Dijkstra et al 1988) are summarized in Table 3 and 4. There is no evidence that these peaks and troughs are more than local phenomena, except for the episode 1978-1981 when a regular census of vole burrows established the synchronous occurrence of extremely high vole densities all over the Netherlands (Buker 1984). For the analysis of reproductive parameters in association with vole peak and trough years we are on comparatively safe ground, since the vole indices were obtained in the same local areas as the kestrel data. For the analysis of postfledging and adult survival from one year till the next we have tentatively classed the winters from 1960 till 1987 in three categories, also indicated in Tables 2 and 4.

I Either the previous or the next year was a local trough, the other not a peak year;
II Either the previous or the next year was a local trough, the other a peak year;
III Either the previous or the next year was a local peak, the other not a trough year.

4. YEAR-TO-YEAR VARIATIONS IN REPRODUCTION AND SURVIVAL

Before turning to the effects of birthday we have to analyse year to year variations in several of the parameters evaluated. Kestrels show considerable annual differences in reproductive output. This has long been known in raptors and there is ample evidence documenting that reproduction in vole predators is strongly affected by long-term cycles in

Table 4. Annual mean date of ringing (D) and survival through the next winter of fledgling kestrels (S_1) and yearlings (S_2). Voles = winter category of vole abundance as in table 2.

Year	D	Voles	S_1	S_2
1960	162.0	III	0.521	0.786
1961	168.7	I	0.330	0.432
1962	188.1	I	0.316	0.531
1963	170.8	III	0.489	0.667
1964	162.5	III	0.517	0.722
1965	164.3	II	0.267	0.265
1966	177.0	III	0.335	0.650
1967	170.0	III	0.698	0.375
1968	164.1	I	0.243	0.360
1969	172.1	II	0.394	0.579
1970	175.7	II	0.550	0.800
1971	162.4	III	0.709	0.892
1972	163.2	I	0.223	0.440
1973	177.4	II	0.352	0.631
1974	163.8	III	0.586	0.709
1975	173.2	I	0.228	0.552
1976	171.2	II	0.408	0.704
1977	167.5	II	0.350	0.655
1978	177.0	I	0.135	0.441
1979	180.2	II	0.224	0.608
1980	171.4	III	0.579	0.679

the density of their prey (e.g.,Mebs 1964, Cavé 1968, Hagen 1969, Linkola & Myllymäki 1969, Wijnandts 1984). In the numbers of nestlings ringed per year such fluctuations are superimposed on long-term changes due to changes in raptor population density and ringing activity. If we eliminate long term trends by expressing the number ringed in the Netherlands as a fraction of its 5-pt running mean, a clear 3-4 year cycle emerges in both the kestrel and the long-eared owl (Fig. 1A). This cycle appears to run in synchrony with local peaks in vole density. In spite of the local nature of the vole data, the production of both kestrel ànd long-eared owl nestlings in the whole country was clearly associated with these peaks, suggesting that the latter may indeed have been representative of countrywide vole abundances. Peak numbers of nestlings ringed often occurred in the year of the peak ànd the subsequent year, in the kestrel as well as in the long-eared owl.

Fluctuations opposite to those in nestling numbers ringed are seen in the numbers of kestrels and long-eared owls recovered per year (Fig. 1B). In peak vole years, when many nestlings were ringed, few birds were recovered. This implies that survival rates in such years were high. Apparently, vole cycles not only exert their influence on reproductive output but also on survival. In analysing survival rates we have therefore to take variations

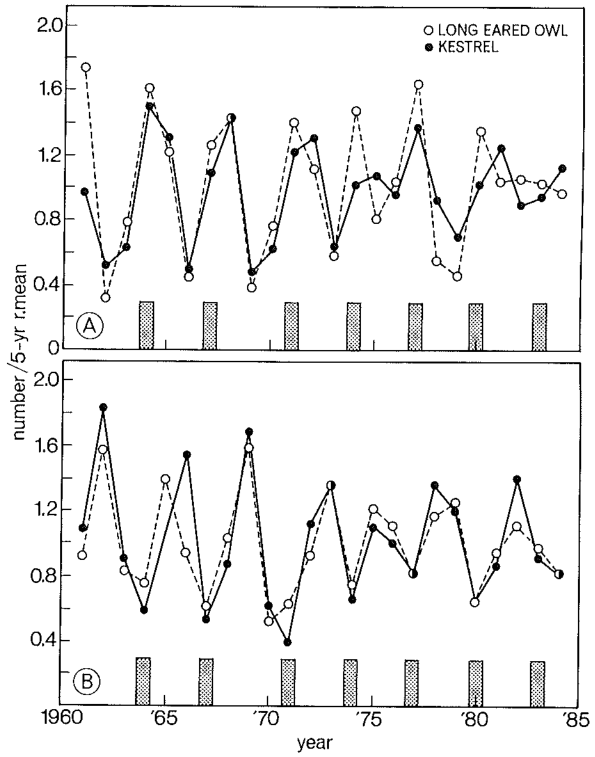

Figure 1. Annual variations in numbers of kestrels and Long-eared Owls ringed as nestlings in the Netherlands (A) and numbers of Dutch birds recovered (B). Data are expressed as a fraction of the 5-year running mean to reduce long-term trends. Data from Vogeltrekstation, Heteren. Local peak densities of common voles indicated by dark bars.

with calendar year into account; this point is taken up later.

A further argument for the assumption that local year-to-year variations are representative for variations on the larger geographical scale of the whole of the Netherlands stems from a comparison of mean yearly ringing dates of recovered birds, ringed as nestlings and mean laying dates in our study areas Flevoland and Lauwersmeer (Fig 2). The significantly positive slope of the regression ($b=1.35$ ± s.e. 0.15) is somewhat steeper than 1, perhaps indicating that the earliest and latest broods were underrepresented in the ringed sample. Obviously, kestrel breeding was late in vole trough years and this trend was not restricted to the study areas but occurred countrywide. Neither mean laying date in the study areas, nor mean ringing date (countrywide) distinguish between peak vole years and "other years". For some of the "other years" there is evidence that the vole density crashed in the course of the breeding season. 1981 and 1984 were such "crash years"

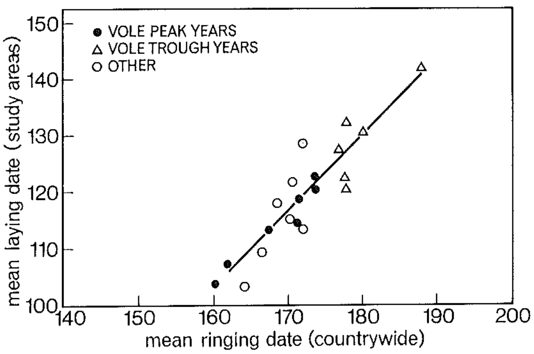

Figure 2. Relationship between annual mean ringing date of nestling kestrels in the Netherlands and local mean laying date in Flevoland and Lauwersmeer. Line indicates linear regression.

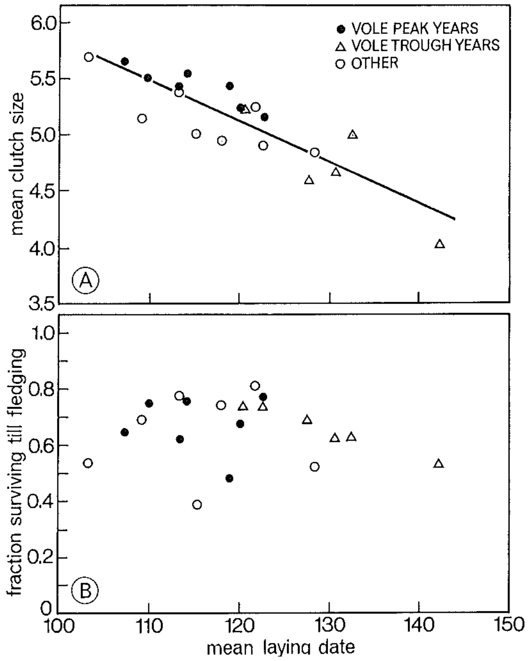

Figure 3. Relationship of annual mean laying date with clutch size (A), and fraction of eggs surviving till fledging (B), in years caracterized by different vole abundance. The line in A shows the linear regression $c = 9.49 - 0.03d$ ($r^2 = 0.747$; $p<0.001$). S_0 was not significantly related to d($r^2 = 0.012$; $p> 0.1$).

(Dijkstra et al 1988), during which very few birds initiated clutches in the later part of the breeding season (May), such that the mean laying date was no later than during peak years.

We analysed the consequences of vole density as well as date of laying for reproduction and survival. Table 3 shows the basic data on mean date of laying, mean clutch size and fractions of eggs surviving till fledging. Mean annual clutch size varied from 4.03 to 5.69 and

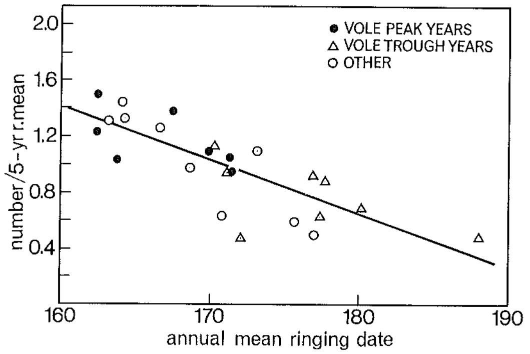

Figure 4. Relationship between the relative number of kestrel nestlings ringed per year and the annual mean ringing date. Line shows linear regression.

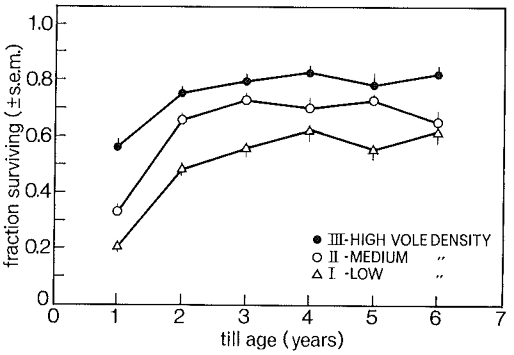

Figure 5. Maximum likelihood estimates of age-specific annual survival rates (June 1 - May 31) in winters pooled in three vole density categories, based on the data in table 2.

was clearly negatively correlated with mean laying date (Figure 3A), as demonstrated already by Cavé (1968) and Village (1986). This trend was associated with vole density indices (Table 3). For survival of eggs till fledging (S_0) no significant trend with either mean laying date or with vole density indices could be established (Fig 3B). This again confirms the conclusions drawn by Cavé (1968).

The increased production of nestlings in years with early ringing (and laying) dates (Figure 4) as associated with vole density peaks can thus not be attributed to greater survival in the nest but must be due primarily to increased clutch sizes in such years in addition to larger numbers breeding. In vole peak years it is conceivable that the opportunities for young birds to breed for the first time are more favourable than at other stages of the vole cycle.

Annual survival rates of juveniles and adults were estimated using the ML estimation on the basis of 1302 nestlings ringed from 1967 till 1987 inclusive and recovered freshly dead, as explained under Methods. Reporting rates were estimated separately for juveniles and adults, and were 0.099 (s.e.m. 0.004) and 0.143 (s.e.m. 0.011), respectively. Age specific survival rates in the three year categories are shown in Figure 5. It is remarkable how the rather rough

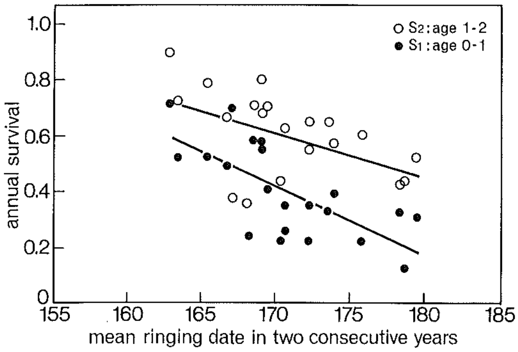

Figure 6. Correlation between kestrel survival and bi-annual mean ringing date. Abscissa: Average of two annual mean ringing dates, of kestrel nestlings ringed in year x and year x + 1. Ordinate: Annual survival percentage from year x till year x + 1 of kestrels born in year x (S_1) and of those born in year x - 1.

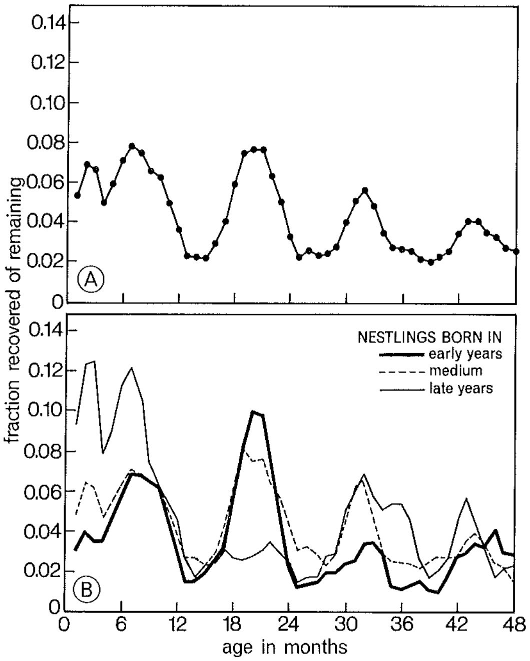

Figure 7. Monthly recovery rates of kestrels (ringed as nestlings in the Netherlands 1960-1980), plotted as a function of age and time of year. Each point represents the fraction of birds recovered freshly dead during a 3-month span of those recovered during and after this span. A. All birds. B. Birds born in Early, Middle and Late years.

categorization of years on the basis of local vole data from two small areas turn out to differentiate between survival patterns countrywide. This again attests to the probability of synchronicity of fluctuations in vole abundance over large areas, and to their impact on kestrel survival. Within each year category, juvenile survival (S_1), was considerably lower than adult survival, while further increments in survival rates from age 2 till 6 were minor at best.

Since survival rates thus are associated with the vole data available, and since annual date of ringing (used here as indicative for mean date of reproduction) is associated with local vole densities (Fig 4), it is appropriate to investigate whether annual mean ringing dates are predictive for survival. This is indeed the case, as shown in Figure 6. There is a significant tendency of reduced survival in years when reproduction is late. This phenomenon holds not only for the nestlings themselves which are ringed, but also for the age 1 birds around in such years (Table 4). In the analysis of survival of individuals as a function of date of birth this annual variation has obviously to be taken into account.

On the basis of mean ringing date we have for further analysis pooled the different years 1960-1987 into three groups: Early years (mean ringing date < 165), Medium years ($165 <$ mean date < 175) and Late years (> 175). This distinction allows us to investigate the time of year at which the difference in mortality rates between years comes about. Figure 7A plots per month of life the number recovered freshly dead in that month as a fraction of all remaining recoveries from the beginning of that month onwards ("mortality"). Since reporting rates may vary with season and were therefore not taken into account this measure does not estimate mortality precisely. However, the differences per month between Early, Medium and Late years are not explicable by different reporting rates. Figure 7B suggests therefore that mortality of nestlings is especially enhanced in the first summer and autumn after fledging in late years. By late winter the mortality rates are no longer distinguishable between the three groups. Birds reaching the second winter seem to suffer less mortality when fledged in a late year.

5. SEASONAL VARIATIONS IN CLUTCH SIZE AND SURVIVAL

The average clutch size declined with the progression of laying date (Table 5), a trend observed consistently in many bird species (Klomp 1970), and described earlier for the kestrel (Cavé 1968, O'Connor 1982, Village 1986, Beukeboom et al 1988). For 762 first clutches we calculated the regression of clutch size (c) on laying date (d, day of the year) and mean laying date for the year and area (D):

$$c = 9.62 - 0.0388 \text{ (s.e.m. } 0.0022).d + 0.0012 \text{ (s.e.m. } 0.0038).D. \qquad (11)$$

The coefficient of d was significantly different from zero ($p<0.0001$), the coefficient of D was not ($p>0.1$). Partial correlation coefficients (controlling for the other variable) were -0.545 for c and d, and 0.012 for c and D. Thus, for any given date the sizes of clutches laid in early, medium or late breeding years are indistinguishable. The difference in distribution of laying dates between those years, however, gives rise to annual mean clutch size differences (Table 5). We shall consider the fate of eggs laid at different dates in terms of their probability of survival till fledging and till reproduction.

Table 5. Clutch size variation with laying date in years with early, medium and late breeding. Means ± s.e. (n clutches).

laying date	years			total
	early	medium	late	
76- 85	6.50±0.71(2)	-	-	6.50±0.71(2)
86- 95	6.04±0.68(48)	5.80±0.45(5)	-	6.02±0.66(53)
96-105	5.84±0.81(86)	5.86±0.64(29)	6.00±0.00(2)	5.85±0.76(117)
106-115	5.48±0.87(91)	5.52±0.56(100)	5.41±0.80(17)	5.49±0.73(208)
116-125	5.12±0.76(48)	5.13±0.79(105)	5.17±0.72(12)	5.13±0.77(105)
126-135	4.94±0.92(34)	4.73±0.71(66)	4.76±0.77(21)	4.79±0.78(121)
136-145	4.67±1.03(6)	4.32±0.57(22)	4.18±0.74(27)	4.29±0.71(55)
146-155	3.00±0.00(2)	3.67±0.98(12)	3.95±0.65(22)	3.81±0.79(36)
155-165	-	3.50±0.71(2)	3.00±1.00(3)	3.20±0.84(5)
Total:	5.53±0.92(317)	5.13±0.85(341)	4.57±0.95(104)	5.22±0.95(762)

Survival till fledging (S_0)

Among 3684 eggs produced in the study areas there was a gradual decay in S_0, from 0.846 to 0.409, for eggs laid at progressive dates of the year (Table 6). This variation was associated with a trend towards smaller clutches laid later in the year and with reduced nest survival in small clutches. Both trends were statistically distinguishable from zero as shown by logistic regression (SX program, NH Analytical Software) of S_0 on clutch size (c) and laying date (d) ($p<0.002$). Furthermore, the annual mean laying date (D) contributed to the variance and S_0 is predictable by the multiple logistic regression:

$$\mathrm{Ln}\ \frac{S_0}{(1-S_0)} = -\ 0.321\ +\ 0.102\ *\ c\ -\ 0.0072\ *\ d\ +\ 0.012\ *\ D \qquad (12)$$

In the combined equation, all three coefficients were significantly different from zero at the 5% level. Mean laying date D alone was not significantly correlated with S_0 (see also Figure 3B). Also, in equation (11), the coefficient of D is positive, while the coefficient of d is negative, Therefore, the effect of laying date on nest survival is a within-year effect, which is not due to differences between years.

Due to the close association between clutch size and laying date it is not possible to firmly establish which of the two is the primary independent variable associated with S_0. We have partitioned the nest mortality ($1-S_0$) into mortality due to complete nest failures and mortality of offspring in nests with at least 1 fledgling ("other mortality", B in Table 6). This partitioning does not identify causes of mortality. Yet the distinction is useful in view of the striking seasonal changes in the incidence of both types of mortality. Mortality by complete

Table 6. Nest survival (100^*S_o) for different laying dates and clutch sizes. The numbers of eggs on which each percentage is based appears in parentheses. The column and row indicated by A show the percentage of all eggs lost in nests where no fledglings were produced. B is the difference between 100 % and ($A + S_o$), i.e., the mortality in successfull nests (with at least one fledgling).

Laying date interval	Clutch size 3	4	5	6	7	8	Total	A	B
76- 85	-------	-------	-------	83(6)	86(7)	-----	84.6(13)	0.0	15.4
86- 95	-------	100(4)	86(35)	65(216)	71(56)	75(8)	69.0(319)	7.5	23.5
96-105	-------	60(20)	61(90)	66(438)	61(98)	-----	64.7(646)	15.5	19.8
106-115	33(3)	66(56)	72(365)	69(588)	86(42)	-----	70.7(1054)	11.4	17.9
116-125	25(12)	60(88)	69(360)	69(252)	79(14)	-----	67.4(726)	14.3	18.3
126-135	0(3)	65(160)	63(260)	55(96)	71(7)	-----	62.0(526)	21.9	16.2
136-145	67(12)	58(96)	73(110)	0(6)	-------	-----	64.3(224)	23.2	12.5
146-155	28(18)	53(96)	82(40)	-------	-------	-----	57.8(154)	20.8	21.4
156-165	67(6)	31(16)	-------	-------	-------	-----	40.9(22)	36.4	22.7
Total:	38.9 (54)	60.1 (536)	69.4 (1260)	66.8 (1602)	70.5 (224)	75.0 (8)	66.5(3684)	14.8	18.7
A	44.4	21.6	14.7	13.5	6.2	0.0	14.8		
B	16.7	18.3	15.9	19.7	23.2	25.0	18.7		

nest failure increased gradually from 0 to 36.4% with progression of laying date, while 'other mortality' remained stable around the average of 18.7% (Table 6). The seasonal decrease in S_o is thus completely due to increased frequency of nest failure. In contrast, both nest failure and other mortality were correlated with clutch size, albeit with opposite sign. Nest failure affected 44.4% of the 3-egg clutches and only 6.2% of the 7-egg clutches. Other mortality rose with increasing clutch size. It is probable that nest competition among eggs (warmth) and/or nestlings (food) increases mortality without brood loss among larger broods, whereas nest failure, involving parental desertion, occurs typically in association with poorer food conditions as prevail among pairs producing small and late clutches. However, it is not excluded that also reduced hatchability of late clutches might reflect the reduced hatchebility of late-laid eggs, as found in artificial incubation in *Falco sparverius* (Bird & Lagüe 1982).

Survival till reproductive age (S_1 and S_2)

Survival of ringed kestrel nestlings till age 1 (June 1 of their second calendar year), estimated by equation (7) was negatively correlated with laying date i (Table 7). This effect is partly due to variation between years in both mean date of ringing and survival of the nestlings ringed. Multiple regression showed significant coefficients of both yeargroup G (1=Early, 2=Middle, 3=Late) and ringing date interval (d)

$$S_1 = 0.900 - 0.021 \text{ (s.e.m. } 0.008) \; d - 0.097 \text{ (s.e.m. } 0.018) \; G \qquad (13)$$

Correlation coefficients of S_1 with G and d were -0.833 ($n=17$, $p<0.001$) and -0.579 ($p<0.01$) respectively. The partial correlation of S_1 and d, after controlling for G was -0.556 ($p<0.025$). Hence also within years with the same ringing date distribution there was a tendency towards reduced survival till age 1 with increasing date of birth.

Table 7. Postfledging survival in relation to date of birth: Fractions recovered freshly dead at ages 0 (S1) and 1 (S2), corrected for reporting rates, of kestrels ringed as nestlings 1960-1980 and subsequently recovered. Date of birth (approximately) = date of ringing-50.

Date of birth	S1				S2
	Early	Years: Middle	Late	Total	Total
86- 95	0.442	-----	-----	0.381	0.436
96-105	0.468	0.428	-----	0.442	0.470
106-115	0.507	0.394	0.239	0.423	0.560
116-125	0.463	0.427	0.270	0.397	0.554
126-135	0.503	0.389	0.247	0.346	0.587
136-145	0.316	0.258	0.218	0.246	0.525
146-155	-----	0.349	0.134	0.243	0.622
Total:	0.468	0.393	0.241	0.379	0.547

Table 7 also lists survival from age 1 till age 2 (S_2) for different dates of birth. Interestingly, S_2 increased towards later birthdates. Statistical analysis revealed that this trend is due to variation between years: S_2 was significantly correlated only with G ($r=0.754$, $p<0.001$), not with d ($r=0.215$ n.s.).

Thus, survival after fledging is subject to some peculiar relations with birthday. In years of late breeding, the probability of survival was low, but for those birds surviving till age 1, the probability of surviving till age 2 increased (see also Figure 7B). This reversal of fortunes may be due both to the cyclic nature of the main food supply and to changes in population density of the kestrels. Following low vole years with high kestrel mortality we should expect improvements due both to increasing prey numbers and to reduced predator populations. In vole peak years, with reduced mortality, and perhaps relaxed selection, subsequent mortality may be increased when predator competition is high and a vole crash likely to occur.

From an analysis of the distances travelled by birds recovered in their first winter (Table 8) it appears that late born birds had a greater tendency to move far away (median distance 56 km), whereas early birds tended to stay closer to the nest area (median distance 18 km). This difference disappeared in the next summer (Table 8) which may suggest that late born birds tended to return closer to the natal area. On average, 26.7% of recoveries in the summer of age 1 were made within 10 km from the place of birth and 83.1% were within 100 km.

Table 8. Median distances from place of ringing as nestling (a) and fractions found within 10 km (b) among kestrels found freshly dead in their first, second and subsequent summers (April through September) and in their first and subsequent winters (October through March). p indicates significance of difference between distributions for different ringing dates (Kruskal-Wallis one-way analysis of variance).

Ringing dates	<156			156-175			>175			
	a	b	N	a	b	N	a	b	N	p
Summer age 0	7	62	45	15	35	231	36	31	203	<0.001
Winter age 0	18	23	43	28.5	23	166	56	11	123	<0.001
Summer age 1	23	17	35	15	28	107	35.5	17	54	n.s.
Winter age≥1	25	19	117	22	24	428	33.5	18	204	n.s.
Summer age≥2	12	36	28	13	35	133	19	29	69	n.s.
	km	%		km	%		km	%		

There is further evidence from birthday distributions of birds trapped alive in their first winter in the Lauwersmeer (Table 9) that early born kestrels are at an advantage compared to late birds. Table 9 shows that early born young are overrepresented, as a consequence of both differential mortality and migration.

In summary, late born nestlings suffer higher mortality than early born birds particularly in late summer and early autumn. Those surviving apparently have an increased tendency to leave the natal area, and this may well be related to a reduced ability to compete with early born rivals in the autumn conflicts about territorial establishment.

There are various possible causes for increased tendencies to leave the natal area and for increased mortality in late fledglings. There is evidence from behavioural observation that later fledglings become independent and have to obtain their own food at a younger age than early born juveniles (Dijkstra et al 1988, chapter 4). After independence, hunting skills in the young kestrels need to be developed, and one may expect that succes during territorial skirmishes in autumn is better for early than for late birds.

Table 9. Relative frequencies of birthday among fledglings ringed in the Lauwersmeer (1978-1983) and among juvenile birds resident in the same area in their first winter (October through March): Early born birds are overrepresented among winter residents ($\chi^2_4 = 17.81$; $p < 0.005$).

Date of birth	Fledglings		Resident juveniles	
	n	%	n	%
86- 95	10	15.0	15	36.6
96-105	74			
106-115	167	29.9	13	31.7
116-125	117	20.9	6	14.6
126-135	91	16.3	5	12.2
136-145	69	17.9	2	4.9
146-155	31			

Participation in breeding (P_1)

In addition to S_0 and S_1 , the probability for survivors till age 1 to enter the breeding population is birthday dependent. This is deduced from the fact that in the Lauwersmeer early born kestrels were overrepresented among yearling breeders, not only with respect to nestlings produced in the area, but also with respect to the nestlings estimated to survive till age 1 (Figure 8).

We have used these data to obtain a quantitative estimate of the probability for surviving yearlings to participate in reproduction (Table 10). This analysis was based on the number of nestlings born at different dates in the Lauwersmeer in nine years (1978-86), and on the breeding pairs which were identified in the whole area in the years 1979-87. Table 10 lists the total numbers ringed per laying date and the expected numbers surviving. 39 Birds born before day 115 were expected to survive as yearlings in the area and 38 were found breeding. In contrast, 21 was the expected number within 10 km surviving from the birds born after day 125, and only 5 were found breeding. Presumably, birthday is a major determinant of the chances for breeding at age 1, and we have estimated the corresponding probabilities in Table 10, column F. These estimates reflect solely the variation in breeding probability for kestrel yearlings which remain in the vicinity of their natal area. It is not excluded that this

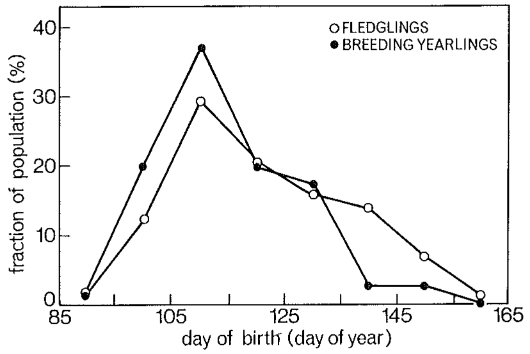

Figure 8. Relative frequencies of birthdays of kestrels in the Lauwersmeer. (a) among 559 nestlings ringed 1978-83; (b) among 231.3 yearlings estimated to have survived from these, of which 52 with the same birthday distribution are expected to be in the area in their first summer. (c) Among 46 locally born yearlings breeding in the Lauwersmeer 1979-84.

subgroup (estimated at 26.7%) is not representative for all yearlings, or that the Lauwersmeer birds are not representative for the whole population. Such possible deviations cannot be investigated presently. There are no a priori reasons to suspect that birthday dependence in the probability of breeding by yearlings is different for birds moving more than 10 km from the natal area, or for birds born outside the Lauwersmeer. We therefore have applied the estimates obtained in the calculation of the number of yearling breeders per egg for different birthdays. The full reconstruction of nestling fractions surviving till fledging, till one year old and of those breeding in year 1 is shown in Figure 9.

Table 10. Estimation of the probability of breeding for yearling kestrels with different dates of birth. Columns: A. 10-day interval of laying dates. B. Number of fledglings ringed in the Lauwersmeer 1978-86. C. Number of fledglings expected to survive till age 1 (= column B * S1 from table 7). D. Number of surviving yearlings expected to be present within 10 km from the place of birth (= column C * 0.267). E. Observed yearling breeders from birthdate intervals in the natal area 1979-87. F. Probability of breeding (column E / D). Early born birds are overrepresented among 1st year breeders after accounting for the differences in survival ($^{2}_{4}$ = 11.74; $p < 0.025$).

A	B	C	D	E	F
86-95	7	2.7 }	12.6	12	0.95
96-105	101	44.6 }			
106-115	234	99.0	26.4	26	0.98
116-125	174	69.1	18.4	11	0.60
126-135	123	42.6	11.4	4	0.35
136-145	97	23.9 }	9.6	1	0.10
146-155	41	10.0 }			
156-165	9	2.2 }			
Total:	786	294.1	78.5	54	0.69

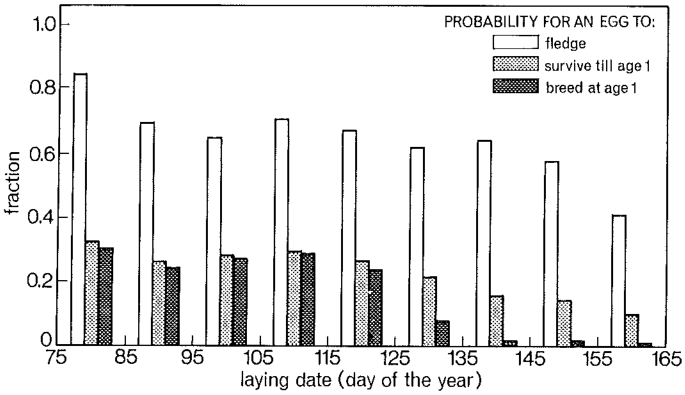

Figure 9. Proportions of kestrel eggs from different birthdays surviving till fledging, till June 1 of the next year (age 1), and participating in the next reproductive generation.

Reconstruction of egg reproductive value (V_o)

On the assumption that the kestrel populations we have studied are characterized by a stable age distribution in the long run, we may use equation (10) to estimate the weighting factor λ^{-x}. For this calculation, we have used the l_x-values in Table 1b. b_1 was estimated using equation (8), with $P_1 = 0.69$ (Table 10) and $E_1 = 4.91$, hence $b_1 = 3.388$, and b_x $(x > 1) = 5.33$. Numerical approximation of equation 10 then yields $\lambda = 1.19$.

Table 11. Birthday dependence of life history parameters and reproductive value of kestrel eggs. S_o = fraction of eggs surviving till fledging; S_1 = fraction of fledglings surviving till age 1; S_2 = fraction of yearlings surviving till age 2; P_1 = probability of breeding of yearlings; N = expected lifetime reproductive output in eggs per egg. V_o = reproductive value of eggs (* = 1.0 for the population by definition).

Laying date	S_o	S_1	S_2	P_1	N	V_o
76-85	0.846	0.381	0.436	0.95	1.97	1.28
86-95	0.690	0.381	0.436	0.95	1.60	1.05
96-105	0.647	0.442	0.470	0.95	1.83	1.18
106-115	0.707	0.423	0.560	0.98	2.17	1.38
116-125	0.674	0.397	0.554	0.60	1.68	1.02
126-135	0.620	0.349	0.587	0.35	1.27	0.74
136-145	0.643	0.246	0.525	0.10	0.76	0.42
146-155	0.578	0.243	0.622	0.10	0.78	0.43
156-165	0.409	0.243	0.622	0.10	0.56	0.31
population:	0.665	0.379	0.547	0.69	1.62	1.00*

Above we have identified four parameters involved in egg reproductive value which are dependent on birthday i : $S_0(i)$, $S_1(i)$, $S_2(i)$, $P_1(i)$ (Table 11). For S_x ($x > 2$) and for P_x ($x > 1$), we have assumed independence of birthday, i.e. that for birds surviving till age 2 further survival and chances of breeding were no longer distinguishable for those born early or late. For S_x ($x > 2$) the ML estimates of age-specific survival (Table 1) were used, for P_x ($x > 1$) a value of 1 (see methods). The resulting values of $V_0(i)$ are presented in Table 11. Evidently, eggs produced before day 115 have a higher reproductive value, those after day 125 a lower V_0 than the average egg ($V_0 = 1$). The reproductive value of kestrel eggs deteriorates rapidly with the progress of the breeding season (Figure 10).

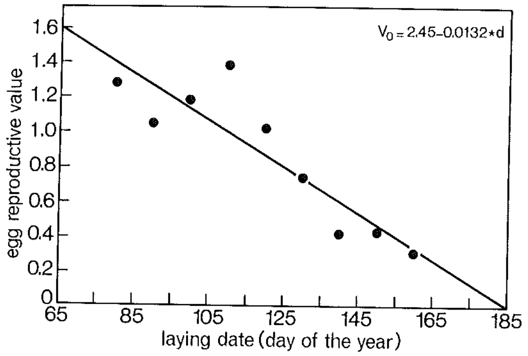

Figure 10. Variations in relative fitness with date of birth in kestrel eggs.

6. DISCUSSION: PARENTAL STRATEGIES IN REPRODUCTIVE TIMING

The reproductive value of eggs, as derived from an analysis of birthday specific rates of survival and reproduction decreased significantly with progress of laying date in the European kestrel. We have identified three negative contributions of date of birth to this correlation:

Firstly, the survival in the nest (S_0) was reduced with progressive date of birth. The reduction was mainly due to increased failure of whole nests. This confirms the conclusions of Cavé (1968) and Village (1986) for the kestrel, and corresponds closely to the reduced success of late clutches in other bird species raising single broods per year (Sparrowhawk, Newton & Marquiss 1984, review Klomp 1970). Decline in nest survival (S_0) presumably reflected interindividual variation in food supply within years, rather than general variations between years. Given the clear annual differences in clutch size associated with mean laying date and with food conditions, this implies that the Kestrels were able to adequately adjust their clutch size to the local food situation.

Secondly, survival till age 1 (S_1) declined progressively with birthday. This was due to variation both between years and to variation between individuals in the same year (Table 7). This is understandable since local variations between territories of birth must play a smaller role in survival after than before fledging. Reduced S_1 of late fledglings was mainly effected by increased mortality in late summer of age 0. This is associated with a reduction of post-fledging parental care for late-born offspring (Dijkstra et al 1988,chapter 4), while the development of hunting skills after independence will start earlier in the early born and hence put them at a competitive advantage over later young. Reduced survival in late born fledglings has been postulated as the cause of reduced recruitment to the study population in other bird species (see introduction) and is probably general for single brooded birds (Daan et al 1988a).

Thirdly, the probability of breeding at age 1 (P_1) appeared reduced for surviving late born young, even after accounting for the higher losses in the nest and at age 0. It is likely that late born juveniles had less chance to develop during their first winter the behavioural and conditional preparations required for breeding. During winter they tended to disperse further from the natal area than the early born although in the summer of age 1 proportions of early, medium and late young within 10 km from the place of birth were indistinguishable. Reduced probability of breeding contributed dramatically to the reduction in fitness with progression of birthday. Probability of breeding is a difficult parameter to reliably assess in the field, and our data on this aspect should be considered preliminary, awaiting further analysis for the two sexes separately. We are not aware of comparable data in the literature. A study on Blue herons (*Ardea cinerea*) has demonstrated that the advancement of reproductive timing in urban populations led to an increase in instances of breeding as yearlings (Blok pers.comm.). Thus age of first breeding, a major determinant of the innate rate of increase and hence of genetic fitness (Ricklefs 1980), is potentially more generally dependent on birthday. In species where this is true, a strong selection pressure on annual reproductive timing may be expected.

Reduction in both S_0 and S_1 occurred in spite of a general improvement of the food supply throughout the summer. The dominant food of kestrels in the Netherlands, and in our study area in particular is the common vole *Microtus arvalis*. Voles reproduce throughout the summer and reach peak densities in September-October, long past the date when the last pair of kestrels has attempted to breed (Hoogenboom et al. 1984, Masman et al. 1988). This situation contrasts with Lack's generalization that avian reproductive cycles have ultimately evolved by the benefits of synchronizing maximal food demand with maximal food availability. Previous attempts to reconcile the higher reproductive successes of the earliest breeding birds with Lack's theory, have involved an energetic bottleneck during egg production, whereby most females in the population are unable to produce a clutch in time for the food peak (Perrins 1970, Lack 1966). The kestrel data suggest that all birds reproduce during the increase, rather than during the decrease phase of food supply. Apparently there is a premium on breeding early in this phase: The reproductive value of eggs laid by the earliest pairs is highest in the population. Moreover, parents breeding early still have a chance of relaying if they happen to loose their first clutch, later ones do not (see chapter 7).

A major problem in the functional interpretation of such patterns obtained from population analysis is the uncertainty if all the options observed in the population are really open to each individual. However, annual variations in food supply are reflected in intra-individual variations in reproductive timing and experimental manipulation of food supply is known to elicit reproductive adjustment (Drent & Daan 1980, Dijkstra et al. 1982, Meijer et al 1988). We therefore suggest that such adjustments as observed in laying date and in clutch size are regarded as strategic decisions. Such decisions may contribute to an optimal compromise between tendencies to breed as early as possible to maximize V_0 per egg on the one hand and to breed as late as possible to benefit from the increased food supply on the other. Such an individual compromise would cause the late pairs to accelerate reproduction at the expense of clutch size and thereby lead to the observed seasonal decline in clutch size (Table 5). A full optimization model for clutch size and laying date is deferred to a subsequent article (Daan et al. 1988, chapter 7). Here it suffices to conclude that the principle of breeding early may be an important ultimate aspect of reproductive timing, in addition to synchronization with the food availability peak (Lack 1966) and to synchronization with conspecifics (Fraser Darling 1938). It may well provide the basic principle underlying the general seasonal decline in clutch size in single-brooded species, well known in birds (Klomp 1970), but probably widespread among temperate zone vertebrates.

7. ACKNOWLEDGEMENTS

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Chapter 6

ADAPTIVE SEASONAL VARIATION IN THE SEX RATIO OF KESTREL BROODS

Cor Dijkstra, Serge Daan, Joop B. Buker

1. SUMMARY

The sex ratio (% males) in broods of European Kestrels, Falco tinnunculus, declined with progressive date of birth. This decline enhanced the broods' reproductive prospects since the probability of breeding as yearling declined with birth date for male offspring, not for females. The sex ratio bias of the brood was produced by non-random sex segregation at meiosis: by altering the within-clutch sequence of sexes (first male then female eggs in early clutches, the reverse in late clutches) laying kestrels assigned the sex with the better long-term reproductive prospects to the initial eggs of their clutch, which suffer least mortality in the nest.

2. INTRODUCTION

Natural selection should favour variable offspring sex ratios when the relative fitnesses of daughters and sons vary in the population (Trivers & Willard 1973; Werren & Charnov 1978; Charnov 1982). Fitness maximization theory further predicts that sex ratio variations should occur primarily in sexually dimorphic species, where a surplus of the smaller and cheaper to raise sex is expected (Fisher 1930, Clutton-Brock et al 1985). Variable sex differences in fitness have rarely been documented in vertebrates (Clutton-Brock & Iason 1986) and adaptive sex ratio variation remains to be established in birds (Clutton-Brock 1985). We have therefore studied sex ratios among offspring of the sexually dimorphic European Kestrel (Falco tinnunculus), and analysed the data with reference to the probabilities of survival and breeding as they vary for the sexes with laying date and with sequence in the clutch.

3. METHODS

Kestrel nestlings can be sexed in the nest after external development of the tail cover feathers, around the age of 20 days. The juvenile plumage of male kestrels resembles that of females (Village et al 1980), except that their tail coverts are greyish instead of brown and have narrow, pointed crossbars. In a national dutch ringing scheme during 1980-1986, 15 bird ringers collected one tail covert from each of 3765 ringed nestlings, together with information on laying date, clutch and brood size. From these feathers, we determined sex for each nestling. Sex determination was verified 193 birds recaptured as adults after their first moult, and proved to be correct in 191 cases. One male and one female had been assigned the wrong sex. This indicates sufficient accuracy for the analysis of sex ratio variations.

Variations with date of birth in the probability of breeding as yearlings for males and females were assessed by comparing the distributions of date of birth of yearling breeders in our study area Lauwersmeer (see Dijkstra et al 1988a) with those in the population of nestlings fledged.

Finally, we assayed sex ratio variations as depending on the laying sequence in a sample of 265 eggs in the study areas Lauwersmeer and Flevoland. This was done by visiting nests at least every two days during the laying phase and marking each new egg (kestrels lay eggs in two-day intervals; Beukeboom et al 1988). Frequent visits around hatching allowed us to identify the egg from which each nestling hatched, and its sex was determined around three weeks later on the basis of tail covert colour.

4. RESULTS

Sex ratios, defined as the fraction male birds, among 2620 nestlings from 684 nests of known clutch size and date (laying date of the first egg ± 3 days) declined with progressive laying date (Table 1). The relationship can be described by the linear regression $S = 0.815 - 0.00249 * d$ (S = sex ratio; d = day of the year; $r = 0.965$; $p < 0.002$). Since the linear regression does not take different sample sizes for the different laying dates into account, the trend can also be tested for significance using Kendall's τ_b (SPSS package; Snedecor & Cochran 1967, p.195). This yielded $\tau_b = 0.045$ ($p < 0.01$). Further regressions and τ_b-values are indicated in the tables and figure legends. Simultaneously with the seasonal trend in sex ratio, sex ratio declined with the wellknown (Cavé 1968) decline in clutch size (table 1). This trend could not be verified statistically for clutches produced within the same 10-day laying date intervals. Sharper declines of sex ratio with progressive laying date and reducing clutch size were observed in a subsample of 1192 nestlings from 236 nests where no mortality had occurred and where all nestlings were sexed ('complete broods'), although in this smaller sample the levels of significance were higher. The overall sex ratio was not different from parity.

To establish the consequences of the seasonal sex bias for fitness, it would be necessary to evaluate the dependence of reproductive value (Fisher 1930) of male and female eggs on their date of birth. Until now, not enough data has accumulated on male and female survival to establish their reproductive value, although we have calculated reproductive value of kestrel eggs for the sexes together (Daan & Dijkstra 1988). However, a major component of fitness is the probability for offspring to breed as yearlings. This reflects both juvenile

Table 1. Sex ratios in % males among nestlings (number in parentheses) in 684 broods of known clutch size and laying date of the first egg (day of the year), and in a subsample of 236 complete broods, i.e. nests without mortality.

clutch	laying date							complete
size	<106	106-115	116-125	126-135	136-145	>145	total	broods
7	68(28)	50(24)	67(12)	(0)	(0)	(0)	60.9(64)	65.7(35)
6	54(124)	56(479)	50(306)	54(110)	33(9)	75(4)	53.8(1032)	53.5(432)
5	58(19)	47(224)	52(419)	51(365)	38(74)	53(17)	50.3(1118)	50.4(500)
4	(0)	40(25)	54(65)	49(110)	51(123)	33(39)	48.9(362)	46.9(196)
2/3	(0)	0(2)	20(5)	33(3)	52(27)	57(7)	45.5(44)	44.8(29)
total	56.7 (171)	52.9 (754)	51.7 (807)	51.5 (588)	46.4 (233)	43.3 (67)	51.6 (2620)	-----
compl. broods	58.4 (89)	51.6 (347)	50.8 (364)	52.5 (244)	48.3 (120)	32.1 (28)	-----	51.3 (1192)

Regressions and significances of associations:

Sex ratio (M) and laying date (d):
All broods: $M=0.815-0.00249.d$ ($r=-0.965$; $p<0.002$); $\tau_b=0.037$ ($p<0.02$)
Complete br.: $M=0.988-0.00399.d$ ($r=-0.839$; $p<0.05$); $\tau_b=0.036$ ($p<0.1$)

Sex ratio and clutch size (c):
All broods: $M=0.339+0.03585.c$ ($r=+0.965$; $p<0.01$); $\tau_b=0.045$ ($p<0.01$)
Complete br.: $M=0.281+0.04831.c$ ($r=+0.931$; $p<0.05$); $\tau_b=0.058$ ($p<0.02$)

survival and maturation. We compared the frequency distributions of birthdate (i.e., laying date for the clutch from which they were raised) for male and female kestrels breeding as yearlings in 1981 through 1986 in the Lauwersmeer, and for those fledged a year before (years 1980/85). These distributions (Figure 1) differed significantly in the males, not in the females. Males born early in the year are more likely to breed the following year than males born late. Late broods are typically produced in poor food circumstances, and suffer higher mortality both before and after fledging (Cavé 1968), partly due to a reduced period of nourishing by the parents (Dijkstra et al 1988b). If late born males survive, they tend to skip the first breeding season. For females, entering male-defended territories either in autumn or spring, date of birth is apparently unimportant for their chance to breed if surviving till age 1. This interpretation is supported by the different age distribution of males and females in the breeding population: 32.4% of the breeding males (n = 179) and 46.2% of the breeding females (n = 184) in 1981/86 were yearlings (χ^2 = 7.21; p < 0.01).

The shift from male bias in early nests to female bias in late nests may be due to either a change in primary sex ratio (of the eggs) or survival in the nest or both. The seasonal

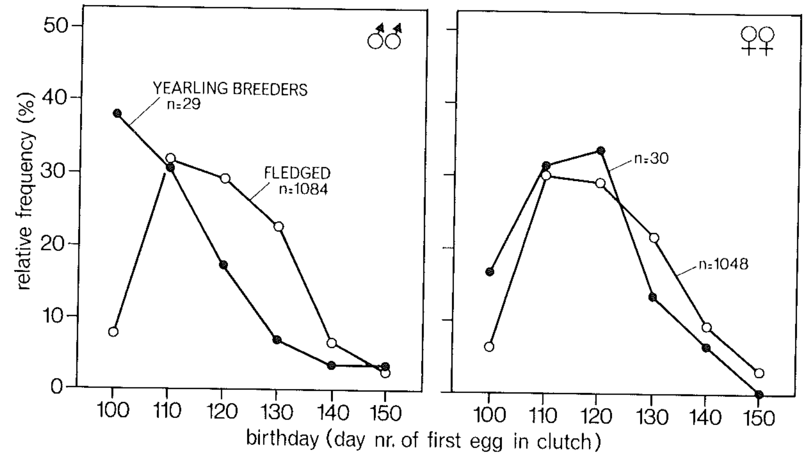

Figure 1. Relative frequencies of birthdays (10-day interval containing initiation date of the clutch from which an individual was raised) among breeding yearling kestrels in the Lauwersmeer (years 1981/85) and among nestlings fledged the year before (1980/85). Significance of the difference between distributions: males: $X^2 = 10.92$ ($p < 0.005$); females: $X^2 = 2.73$ (not sign.).

trend in complete broods does not distinguish between these possibilities since these also may be biased by differential survival (Fiala 1980). Since nestling mortality mainly affects the last born young, which hatch from the last laid eggs in a clutch (the fraction fledging is correlated with laying/hatching order: $r = -0.89$, $n = 95$, $p < 0.01$), we investigated sex ratio variations with laying sequence in a sample of 265 eggs. Sex ratio declined sharply with the sequence of laying in early clutches and increased with the sequence in late clutches (Table 2). Consequently, sex ratios of nestlings hatched from eggs ranked 1-3 of a clutch declined with progressive laying date, while sex ratios of nesltings from egg 4-7 increased (Figure 2). If differential survival of nestlings were the main cause of the seasonal decline in % males, we would expect no seasonal decline in eggs 1-2, which suffered no mortality and some seasonal decline in eggs 5-7 where mortality was 7.0%. The opposite is true. Nestling mortality was too small to explain the sequence bias: eggs ranked 1-2 hatched twice as many males early than late in the season ($p < 0.002$). Egg mortality was higher (15%) than nestling mortality in this study. However, even if we assume that all eggs of ranks 1-2 that did not hatch in early nests ($n = 7$) have been females, and that all those that did not hatch in late nests ($n = 14$) have been males, a seasonal decline from 56% to 47% males remains. These data argue strongly against differential mortality as the cause of sex ratio bias. The data thus indicate that the sequence dependence of the sex ratio at hatching reflects systematic variations in the primary sex ratio of the eggs as laid.

Table 2. Sex ratios in % males among 265 nestlings (number in parentheses) hatched from eggs of different rank in the laying sequence, in early nests (initiated before day 116) and late nests (after day 115).

Season	Egg rank in clutch 1-2	 3-4	 5-7
early nests	66.7 (39)	53.8 (39)	43.2 (37)
late nests	34.5 (58)	55.6 (63)	65.5 (29)
difference early-late	$p < 0.002$	not sign.	$p < 0.05$

Significances of associations between sex ratio and egg rank (tested by Kendall's τ_b: $p < 0.05$ ($\tau_b = 0.181$, early nests); $p < 0.002$, ($\tau_b = -0.232$, late nests).

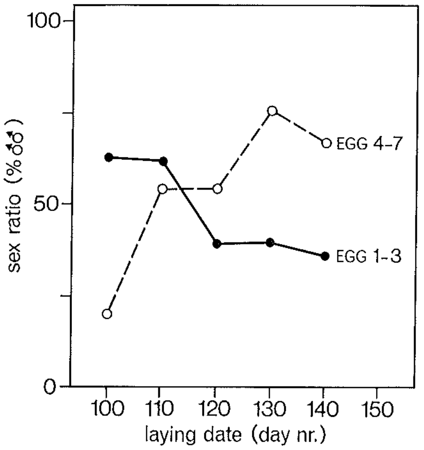

Figure 2. Seasonal change in sex ratio of 265 kestrel eggs of known laying order within the clutch (88 clutches). Symbols indicate nestlings from eggs 1-3 (association of eggs and date significant at $p<0.005$; $\tau_b = 0.189$) and from eggs 4-7 ($p < 0.01$; $\tau_b = -0.198$).

5. DISCUSSION

The overall sex ratio in the nestling population was not significantly different from 0.5, in spite of the pronounced sexual size dimorphism (Dijkstra et al 1988a) of the kestrel. The same is true for the even more sexually dimorphic Sparrowhawk (Newton 1979). These facts does not lend support to the view that size difference between the sexes by itself should lead to a biased sex ratio.

On the other hand, the female kestrel apparently has a means of influencing sex of the eggs she lays in an adaptive manner. Nests produced early had an excess of males, late nests an excess of females. Early born males appeared to have a major fitness advantage (in terms of the probability of breeding as yearling) over late born males, and hence the profitability of producing male offspring declined with the progression of laying date. This result supports the general proposition of Trivers & Willard (1973) that sex ratio variation is expected when the profitabilities of raising sons or daughters vary between individuals.

Seasonal dependence of secondary sex ratio, in the reverse direction, has been reported for the Common Grackle (Howe 1977), while a decline in sex ratio with egg sequence is known in Ring-billed Gulls (Ryder 1980) and Lesser Snow Geese (Ankney 1982; although not confirmed in a larger sample of this species: Cooke & Harmsen 1983). In none of these cases the adaptive significance of the pattern is known. While the fitness of eggs declines with progressive laying date in many bird species (Daan et al 1988), a steeper decline in male than in female eggs appears crucial for the adaptive advantage of a seasonal decline in sex ratio. We anticipate that other species may have a steeper decline of fitness in female than male eggs. Such species should have evolved a seasonal increase in sex ratio, as observed in the Common Grackle (Howe 1977).

The production of male biased early broods and of female biased late broods by the kestrel apparently involves the control of the sequence of sexes within a clutch. Assigning the sex with the lesser prospects preferentially to the later eggs in a follicular hierarchy would enhance the deviant sex ratio, since follicles 4-7 are occasionally resorbed (Beukeboom et al 1988), and, if laid, suffer higher mortality as nestlings. The opportunity to vary sex ratio with laying sequence is open to the female since in birds the female is the heterogametic sex. Sex of the zygote is determined by segregation of chromosomes just prior to ovulation (Romanoff 1960). Female sex determination may generally benefit birds by allowing maternal control over the sex of the zygote before fertilization, since birds lack the mammalian opportunity for corrective sex ratio adjustments during embryonic development (Trivers & Willard 1973).

6. Acknowledgements

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Chapter 7

FAMILY PLANNING IN THE KESTREL: AN EVALUATION OF THE ULTIMATE CONTROL OF REPRODUCTIVE TACTICS

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1. SUMMARY

The theory that individual birds maximize their fitness by the two major decisions in reproduction concerning date (when to start laying eggs) and clutch size (when to stop laying eggs) is empirically approached in the Kestrel by quantifying Fisher's Reproductive Value for both the clutch (V_c) and the parents (V_p).

V_c was found to decrease monotonically with laying date (d) due to significant correlations between d and the components F (probability of nest success), S_f (probability for an egg to survive till fledging in a successfull nest), S_1 (probability to survive from fledging till age 1), S_2 (survival age 1 till age 2), and P_1 (probability of breeding at age 1). V_c increased monotonically with clutch size (c) due to significant correlations with c of the same components.

V_p declined almost negligibly with laying date due to significant correlations between d (laying date) and F, P_r (probability of a repeat clutch following nest failure), and L_p (probability of local survival of the parents following breeding). V_p increased monotonically with clutch size due to significant correlations between c and the components L_p, and b_p (clutch size in the year following breeding).

In experiments where brood size at day 10 after hatching was increased or reduced, V_c increased with increasing experimental brood size, while V_p simultaneously decreased. Total reproductive value ($V = V_c + V_p$) remained unaffected by the experiments. This result suggests that a rather broad range of clutch sizes maximizes total reproductive value, as far as detectable by the data.

While the yield of kestrel hunting, and hence the number of young raisable with constant parental effort, increased with the spring increase in vole population density, reproductive value of the clutches decreased. On the assumption that the latter tendency reflects the consequences for individual pairs of shifting laying date, the combination of c and d maximizing V could be worked out. 47 - 73 % of all clutches observed obeyed the maximization criteria, which, however, depended strongly on the method of computation. Qualitatively, any method predicts a seasonal decrease in the optimal clutch size when the environment improves while reproductive value declines with progressive date. Preliminary results from an experimental approach to test the above assumption using the release of juvenile kestrels reared in captivity under artificial light schedules are presented.

2. INTRODUCTION

Two major decisions face a reproducing bird: When to start laying eggs, and how many eggs to lay. Both laying date and clutch size often have profound consequences for the number of surviving offspring. Drent & Daan (1980) have proposed that natural variation in both properties would largely reflect phenotypic tuning to individual nutritional circumstances rather than genetic variability which would soon be counteracted by strong selection pressure. This proposition reconciles Lack's (e.g., 1948) notion of optimization of breeding behaviour with the fact that often the earliest and largest clutches produce more surviving offspring than the average nest in the population (Perrins 1965, Cavé 1968). Individual optimization may explain why in many single-brooded birds there is a seasonal decline in average clutch size (Daan et al 1988). However, it remains to be established if observed variation in these reproductive parameters really reflects variation in the optimal solutions.

Optimization analysis requires that we quantify the consequences for fitness of different combinations of clutch size (c) and laying date (d). Fitness, i.e., the (expected) rate of gene propagation in future generations, can theoretically be divided into two components: a contribution via the current reproductive attempt and a contribution via expected future reproduction. Any enhancement of current reproductive output by parental efforts in raising the young has been postulated to reduce the future reproductive output (Fisher 1930) or "residual reproductive value" (Williams 1966). For such reduction in future reproduction the term "parental investment" was coined by Trivers (1972). Indeed, experimental evidence from

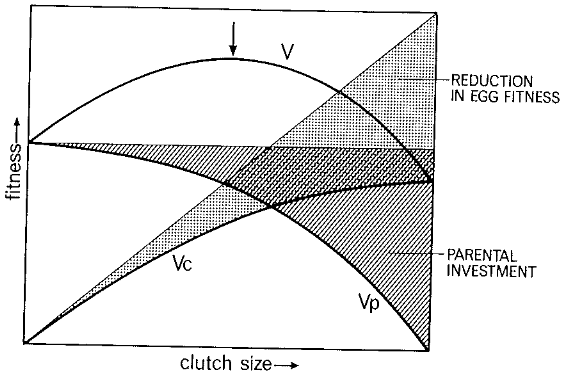

Figure 1. General scheme of clutch size optimization theories. With increasing clutch size, clutch fitness (V_c) increases, but not proportionally. Expected future reproductive output is progressively reduced (V_p). Total fitness (V) is maximized where $dV_c/dc = - dV_p/dc$.

brood enlargement experiments has recently begun to show reductions in parental survival (Askenmo 1979) and future reproductive potential (Røskaft 1985, Tinbergen 1987, Tinbergen et al 1987). The current views on clutch size optimization (Charnov & Krebs 1974, Stearns 1976), based on parental investment, are schematically summarized in Figure 1. Current reproductive output increases with increasing clutch size, although results from brood manipulations generally indicate that the increase is not linear: brood enlargements enhance mortality in the nest (review in Dijkstra et al 1988). Expected future reproductive output decreases with increasing clutch size, probably as a consequence of increasing parental efforts. The reduction, indicated by shading in figure 1, is Trivers' parental investment.

In solving the optimal solutions for clutch size, it is important that the two contributions to fitness are expressed in the same currency. This currency, the expected rate of gene propagation in the population, is derived from by Fishers (1930) definition of Reproductive Value:

$$V_t = (\lambda^t/l_t) \cdot \sum_{x=t}^{\infty} \lambda^{-x} \cdot l_x \cdot b_x \qquad (1),$$

where V_t = reproductive value at age t; $\lambda(= e^r)$ = innate rate of (population) increase; l_x = probability of survival from age 0 till age x; b_x = expected number of eggs produced at age x (Charlesworth and Giesel 1972). In this notation, the reproductive value V_c of a clutch of c eggs equals:

$$V_c = c.V_O = c.\ 0.5. \sum_{x=0}^{\infty} \lambda^{-x} \cdot l_x.b_x \qquad (2),$$

where V_O = the reproductive value of one egg. The factor 0.5 is introduced to account for the fact that offspring share half of their genome with each of the parents. Equivalently, one may regard it as the average fraction of female eggs in each clutch, and consider V_p and V_c for the female parent and offspring only. The parent reproductive value V_p equals:

$$V_p = \sum_{x=t}^{\infty} \lambda^{-(x-t)}.\ b_x \cdot l_x \ / \ l_t \qquad (3)$$

Maximization of total reproductive value by clutch size occurs when:

$$d\ V_c(c)/dc = -\ d\ V_p(c)/dc \qquad (4)$$

This theory is not at all new. Its formalization in terms of reproductive value of eggs and parents, however, allows us to investigate the proposition of varying optima in avian populations, at least when it is possible to estimate V_c and V_p.

In the European kestrel, we have obtained evidence on components of clutch reproductive value and their variations with clutch size and laying date (Daan & Dijkstra 1988). This analysis was based on the production of fledglings in 704 clutches in two study areas, on birthdate- and age-specific annual survival of 38193 nestlings ringed in the Netherlands, and on local estimations of the probability of breeding. It demonstrated a clear decline in reproductive value of eggs with progressive date of laying.

The variation of egg reproductive value was intimately associated with the nutritional situation as reflected in local vole density (Daan & Dijkstra 1988) and in the yield of hunting in parents provisioning their offspring (Meijer et al 1988). Clearly, the variance between nests does not reflect how varying c and d by individual parents would affect their reproductive value. However, we can estimate the effects of alternative clutch sizes from brood manipulation experiments and their consequences for individual nestling and adult survival (Dijkstra et al 1988). Effects on individual families from alternative laying dates can presently not be deduced from experimentation, but may at least partly be inferred from seasonal changes in the yield of hunting and hence in the number of offspring that can be raised with constant effort. It is therefore now appropriate to present the full analysis for V_c and V_p as dependent on clutch and date, and to attempt to evaluate the proposition of individual maximization of $V = V_c + V_p$

2. Clutch reproductive value V_c

The reproductive value V_0 of one egg can be rewritten from equation (2) as:

$$V_0 = S_0.S_1.\lambda^{-1}.b_1 + S_0.S_1.S_2.\lambda^{-2}.b_2 + S_0.S_1.S_2.\sum_{x=3}^{\infty} \lambda^{-x}.b_x.\prod_{y=3}^{x} S_y \qquad (5),$$

where the three terms represent the expected number of eggs produced at age 1, at age 2, and after age 2. Notations in equation (5) are as follows: S_0 = probability for an egg to survive in the nest till fledging; S_1 = probability for a fledgling to survive till age 1 (defined as June 1 of the year following birth); S_x = probability of birds alive at age (x-1) to survive till age x; b_x = expected number of zygotes produced at age x.

Several of the variables in equation (5) were estimated earlier for the kestrel study population (Daan & Dijkstra 1988): $S_3=0.698$; $S_4=0.721$; $S_5=0.697$; $S_x(x>5)=0.704$; $\lambda = 1.19$; $b_x(x>1) = 5.33$. The following variables were found to systematically vary with date (d): S_0, S_1, S_2, and b_1. There is a tight correlation between natural clutch sizes (c) and laying dates (d), described by the equation:

$$c = 9.604 - 0.0374 * d \tag{6}$$

(d = first egg date, day of the year; s.e. of coefficient of $d = 0.0016$; $n=815$; $r = 0.619$; $p<0.0001$). This correlation generally precludes a simultaneous analysis of the separate contributions of c and d to the variance in various fitness components. Since there are biological reasons why clutch size may be causally involved in some, and laying date in other components, we present the whole analysis for c and d separately. We approximated the relationships either by second order least squares linear regression, and in the case of probabilities by second order maximum likelihood logistic regression, using SX software (NH Analytical Software Corp.). Quadratic terms (c^2 and d^2) were omitted when they did not contribute significantly to the relationships.

Dependence of V_O on laying date.

The probability for an egg to survive till fledging (S_O) can conveniently be considered the product of the probability of a nest to succeed (F), i.e. to produce at least one fledgling, and the conditional probability of an egg in a successful nest to produce a fledgling (S_f):

$$S_O = F \,.\, S_f \tag{7}.$$

The probability of success (F) was significantly correlated with laying date, as established by logistic regression:

$$\ln(F/(1-F)) = 4.229 - 0.0217.d \tag{8}$$

($n = 687$ first clutches; $t = -3.26$; $p<0.002$). Hence the probability of producing at least one fledgling decreased with progressive laying date. The probability of survival till fledging for eggs in successful nests (S_f) was also significantly correlated with d, but here the quadratic term added significantly to the explained variance:

$$\ln(S_f/(1-S_f)) = -3.405 + 0.0802.d - 0.000338.d^2 \tag{9}$$

($n = 577$ successfull first clutches; coefficient of d: $t = 2.29$, $p<0.05$; coefficient of d^2: $t=-2.28$, $p<0.05$). Survival of fledglings till age 1 (S_1) was analysed from ring recoveries, using Maximum Likelihood approximation to reporting and mortality rates simultaneously (see Daan & Dijkstra 1988 for a description of data set and method, and White 1983 for the computer program SURVIV used). Equation (10) is the least squares regression fitted to the date-specific survival rates presented in table 7 of Daan & Dijkstra (1988):

$$S_1 = 0.737 - 0.00319.d \tag{10}$$

($n = 7$ 10-day date intervals, $r = -0.843$; $p<0.02$) Survival from year 1 till year 2 was positively correlated with "date of birth" of the kestrels, and this relationship is approximated by:

$$S_2 = 0.238 + 0.00248.d \tag{11}$$

($n = 7$; $r = 0.825$; $p<0.05$), fitted to the data in table 7 of Daan & Dijkstra (1988). Finally, the expected number of eggs produced by birds surviving till age 1 (b_1) equals:

$$b_1 = P_1 \,.\, E_1 \tag{12},$$

where $E_1 = 4.91$ eggs, being the average clutch size of yearling females (s.d. $= 0.78$; $n = 163$), and the probability P_1 of breeding as yearling is approximated by:

$$\ln(P_1/(1-P_1)) = 16.48 - 0.1302 \,.\, d \tag{13},$$

($n = 8$ 10-day intervals; $t = -4.29$; $p<0.01$), based on Daan & Dijkstra (1988, table 10). Equations (7) through (13), when combined with equation (5), specify the reproductive value of clutches in terms of the laying date (d).

Dependence of V_0 on clutch size.

The relationships of the components F and S_f with clutch size could be determined directly by regression analysis of individual nests:

$$\ln(F/(1-F)) = -0.422 + 0.404 \,.\, c \tag{14}$$

($n = 687$; $t = 3.52$; $p<0.001$), and

$$\ln(S_f/(1-S_f)) = -1.324 + 1.037.c - 0.1003.c^2 \tag{15}$$

($n = 577$; coefficient of c: $t = 2.25$; $p < 0.05$; coefficient of c^2: $t = -2.34$; $p < 0.02$). To estimate the relationships with clutch size of the probabilities S_1, S_2, and P_1, we replaced estimate the relationships with clutch size of the probabilities S_1, S_2, and P_1, we replaced the 10-day laying date interval in the original data of Daan & Dijkstra (1988, tables 7, 10) by the corresponding average clutch sizes (ibidem, table 5), and calculated the regressions:

$$S_1 = -0.0995 + 0.0899 \,.\, c \qquad (16)$$

$(n = 7;\ r = 0.894;\ p < 0.01)$;

$$S_2 = 0.8542 - 0.0629 \,.\, c \qquad (17)$$

$(n = 7;\ r = -0.786;\ p < 0.05)$; and

$$\ln(P_1/(1-P_1)) = -16.92 + 3.471 \,.\, c \qquad (18)$$

$(n = 8;\ t = 4.15;\ p < 0.01)$. Again, equations (14) through (18) can be incorporated in equation (5) to obtain the egg reproductive value as predicted by clutch size. Figure 2 presents the resulting reproductive values as depending on both date (figure 2A) and clutch size (figure 2B).

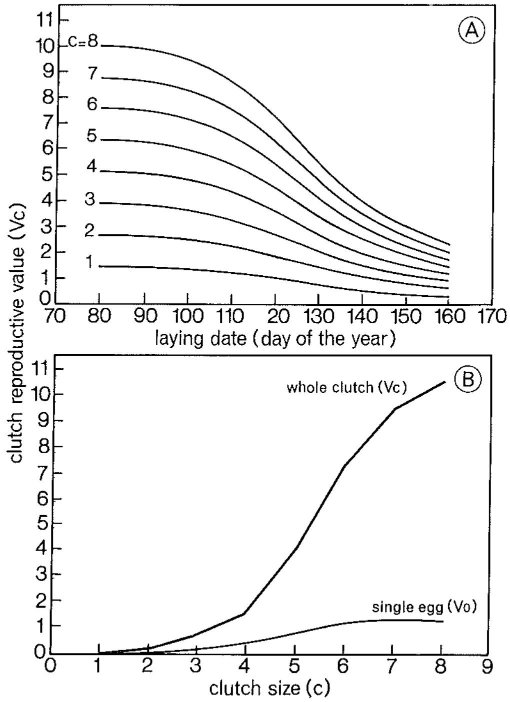

Figure 2. Clutch reproductive value ($c.V_o$) as a function of laying date for different numbers of eggs (A) and as a function of clutch size (B).

4. PARENT REPRODUCTIVE VALUE (V_p)

The reproductive value V_p of a parent bird who has just initiated a breeding attempt can be rewritten from equation (3) as:

$$V_p = P_O.E_r + S_p.\lambda^{-1}.b_p + S_p.\sum_{x=2}^{\infty} \lambda^{-x}.b_x.S_a^{x-1} \qquad (19).$$

The three terms in equation (19) represent the numbers of eggs expected to be laid in the same year in subsequent clutches, in the next year and in all years afterwards. The European kestrel makes no second clutches in our area after successfully raising a first clutch (although it may do so under artificial photoperiodic conditions, see Meijer 1988). Hence P_O, the probability of a second breeding attempt equals the probability of nest failure (1-F) times the probability of a repeat clutch after nest failure P_r. E_r is the expected number of eggs in repeat clutches. S_p in equation (19) indicates the probability for parents surviving till next year following a breeding attempt, and b_p is the expected number of eggs produced next year. S_a is the general expected rate of annual survival of adults, and was estimated from the age specific survival estimation (Daan & Dijkstra 1988, table 1), after weighting for age distribution, to equal 0.681. The components P_O = (1-F) * P_r, E_r, S_p, and b_p, were again analysed for significant relationships with date and clutch separately.

Dependence of V_p on laying date.

The probability of nest failure (1-F) as depending on laying date is given by equation (8). The probability of producing a repeat clutch following nest failure (P_r) was logistically regressed on laying date:

$$\ln(P_r/(1-P_r)) = 4.126 - 0.0551 \; . \; d \qquad (20)$$

($n = 124$ failed breeding attempts; $t = -2.40$; $p < 0.02$). No significant relationship was found between the clutch size of repeat clutches (E_r) and laying date of the first clutch. Hence we estimate E_r by its grand average $E_r = 4.33$ (s.d. $= 0.84$; $n = 18$). True probabilities of survival following breeding can not be estimated directly. The only reliable survival estimate is based on general analysis of ring recovery patterns in birds of which the individual breeding behaviour is unknown. However, we can make use of local survival in the study area of adult birds following breeding, under the assumption that local survival bears a constant relationship to real survival. This relationship was estimated by calculating local adult survival (S_l) in the breeding population for 9 different years (1978/87) and comparing this with the

Maximum Likelihood estimates of adult survival (S_a) in those years, as predicted by vole density characteristics (see Daan & Dijkstra 1988). The resulting relationship, depicted in Figure 3, is described by the equation:

$$S_P = 0.4843 + 0.4286 \cdot S_I \tag{21}$$

(n = 9 years; r = 0.793; p < 0.02). Local survival of adult breeders in the study areas was always less than the country-wide survival based on ring recoveries. This is not surprising,

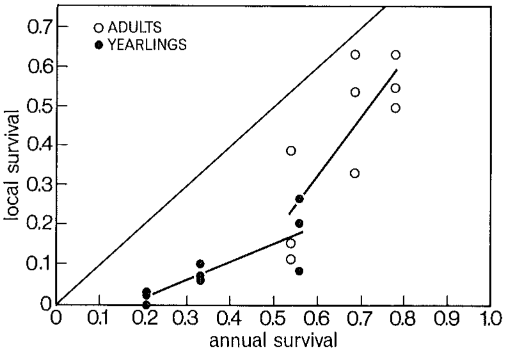

Figure 3. Local survival (fractions per year) in the study area Lauwersmeer in nine years (1978/87) of adult and juvenile (age 0) kestrels, plotted against general annual survival estimates based on maximum likelihood approximation in annual recoveries of birds reported freshly dead in the Netherlands.

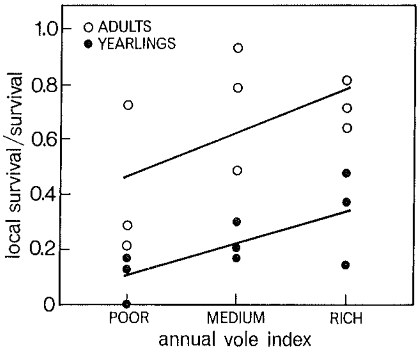

Figure 4. Ratios between local and real survival of adult and juvenile kestrels in nine years (1978/87) characterized by poor, medium and rich vole densities in winter.

since any tendency towards dispersal would reduce local, not general survival rates. The ratio of local over general survival increased significantly with increasing vole density category (Figure 4). This phenomenon may have various interpretations: it is likely that dispersal tendencies increase with deterioration of the food supply. Alternatively, since vole indices were based upon trapping census in the study area Lauwersmeer, the amplitude of vole fluctuations might be less for larger and perhaps not fully synchronous areas outside the study area. This could potentially lead to more extreme variations in kestrel mortality in the study area than countrywide. Local survival of fledgling kestrels follows the same patterns as in the adults (Figures 3,4), albeit at a lower level. This is consistent with both interpretations, since first year birds are known both to suffer higher mortality (Daan & Dijkstra 1988), and to migrate more (Cavé 1968). At any rate, the fact that variations in winter food supply seem somehow involved precludes the use of equation (21) to estimate general survival S_p for situations where variations in local survival are due to other factors such as reproductive behaviour. We therefore apply a single overall estimate for adult survival of:

$$S_p = 1.474 \cdot S_l \qquad (22)$$

The dependence of S_l on date of laying could be analysed on the basis of annually repeated captures and individual colour ring and wingtag sightings by which the whole breeding population in the study area was identified each year. Locally surviving parents include those birds observed in the next breeding season as non-breeders and those reported from the study area after that season. The relationship established by logistic regression:

$$\ln(S_l/(1-S_l)) = 1.4105 - 0.01305 \cdot d \qquad (23)$$

($n = 225$ males and females; $t = -1.83$; $p < 0.10$) was statistically not significant. We therefore used the overall rate of local survival of breeding birds instead of equation (23): $S_l = 0.462$. This yielded in equation (22) a value for general survival of $S_p = 0.682$, essentially equivalent to the average adult survival S_a used earlier. A final fitness component investigated, the expected number of eggs produced in the year following a breeding attempt was not significantly related to laying date ($n = 147$ males and females; $r = 0.000$), and hence was estimated by the grand average of non-yearling clutches (5.33; s.d. = 0.731; $n = 292$).

Dependence of V_p on clutch size.

The probability of nest failure (1-F) as dependent on clutch size is given by equation (15). The probability of producing a repeat clutch following nest failure was $P_r = 0.102$ ($n = 127$), and was not significantly related to size of the first clutch. Also the size of the repeat clutches (mean 4.33; s.d. 0.84; $n = 18$) was not predictable on the basis of the size of the first clutch. A parental fitness component which did vary with clutch size was local survival:

$$\ln(S_l/(1-S_l)) = -2.558 + 0.4641 \cdot c \qquad (24)$$

($n = 225$; $t = 3.74$; $p < 0.001$). This is presumably related to the fact that both clutch size and adult survival, c.q. tendency not to disperse, are positively affected by high vole densities. Equation (24) can be combined with equation (22) to generate the dependence of parent survival on clutch size. A further component is the clutch size produced by locally surviving parents the next year:

$$b_{p} = 4.34 + 0.213 \; . \; c \qquad (25)$$

($n = 147$ males and females; $r = 0.207$; $p < 0.02$). This rather weak relationship is caused by slightly different but positive correlations for males ($n = 82$; $r = 0.167$; $p > 0.1$) and females ($n = 65$; $r = 0.245$; $p < 0.05$) separately. These small correlation coefficients in the kestrel attest to the high degree of intraindividual variation involved in the population variation in clutch size (see also Meijer et al 1988). It is of interest here to report also the year-to-year correlation for laying date, although of no concern for the calculation of parental reproductive value. This was $r = 0.301$ ($n = 161$ males and females; $p < 0.0005$). In contrast to clutch size, the intraindividual year-to-year correlation of laying dates was larger in males ($n = 87$; $r = 0.333$; $p < 0.002$) than in females ($n = 74$; $r = 0.254$; $p < 0.05$).

In Figure 5, we have plotted parental reproductive value V_p, as derived from equations (19) through (25) against both laying date (Figure 5A) and clutch size (Figure 5B). Total reproductive value as a function of c and d is shown in figure 8.

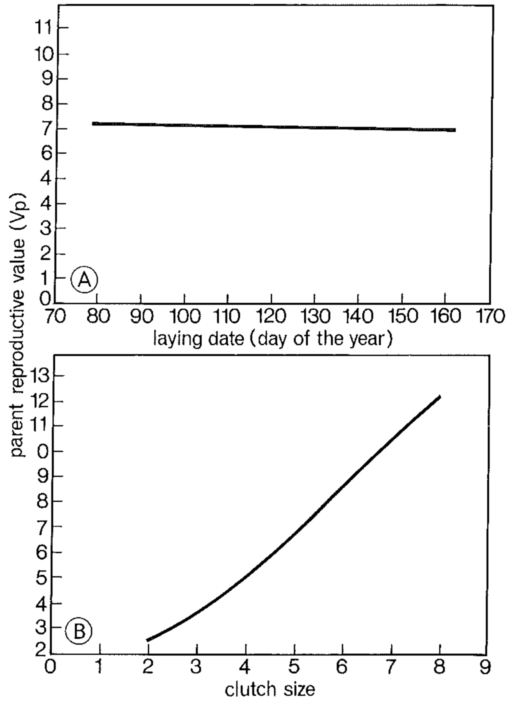

Figure 5. Parent reproductive value (V_p) as a function of laying date (A) and as a function of clutch size (B).

5. BROOD SIZE MANIPULATION EXPERIMENTS

What emerges clearly from the previous analysis (Figures 2A, 5A) is that total reproductive value through current and future reproduction increases monotonically with clutch size. It is of course unlikely that this relationship holds for individual parents: there is no accepted theory supporting the idea that a parent raises its future reproductive output by increasing its current clutch size. However, the analysis of reproductive value presented above allows us to evaluate the brood manipulation experiments in the kestrel (Dijkstra et al 1988). These addressed the question of intraindividual effects on fitness. We can now ask: Does the reduction in V_p in enlarged broods outweigh the gain in V_c and does the reduction in V_c in reduced broods outweigh the increase in V_p ? It is only by translating the effects on the brood and the parent in the same currency of reproductive value that the problem of individual maximization of fitness by varying clutch size can be properly attacked.

The brood manipulations started around day 10 after hatching. In reduced broods one or two (mean 1.74) nestlings were taken from the nest. In enlarged broods nestlings (mean number 2.51) were added, such that the total brood exceeded the original clutch size. Control broods were not manipulated. The computational data for the evaluation of V_c and V_p in the reduced, control and enlarged broods are summarized in Table 1.

Table 1. Computation of reproductive values in experimentally reduced, unchanged and enlarged kestrel broods (Lauwersmeer and Flevoland, 1985/1987).

Brood:	Reduced	Control	Enlarged
number of broods:	28	54	20
mean clutch size:	5.25	5.19	5.40
mean brood size (age 10 days):	4.53	4.20	4.83
mean change in brood size:	-1.74	0.00	2.51
mean nr. fledged:	2.60	3.95	5.84
fledglings corrected*:	2.49	4.14	5.51
V of fledgling:	1.55	1.55	1.55
Brood reproductive value:	3.85	6.40	8.52
Clutch reproductive value V_c**:	2.52	4.20	5.59
Parents:			
Number of males and females:	49	85	35
Parent local survival S_l:	0.653	0.588	0.429
Parent reproductive value V_p:	9.88	8.89	6.49
Total:			
Reproductive value V:	12.40	13.09	12.08

* correction factor: (4.14+brood size change)/(experimental brood size)

** corrected for the difference between reproductive values in control broods and of eggs in a clutch of five.

No effects on local survival of the fledglings could be established, although nestlings in enlarged broods had significantly reduced body mass in the final days before fledging, which points to a deterioration in condition (Dijkstra et al 1988). Hence we assigned the same reproductive value to all fledglings produced. Their number was corrected for the slight differences in initial brood sizes in the three groups, while their reproductive value was scaled down by a factor 0.66 (4.2, V_c of a clutch of 5 eggs, from figure 2b, divided by 6.40, Vf of the fledglings in the control group), to account for the fact that the experiments were done in a successful subgroup of all clutches, viz. those which had a substantial number of nestlings in the nest at the time the experiments started, and thus were implicitly (and unavoidably) selected for high V_c. The only significant effects on the parents were on local survival, not on clutch sizes produced by locally surviving parents in the next year (Dijkstra et al 1988). Hence the estimated V_p declines proportionally with S_1.

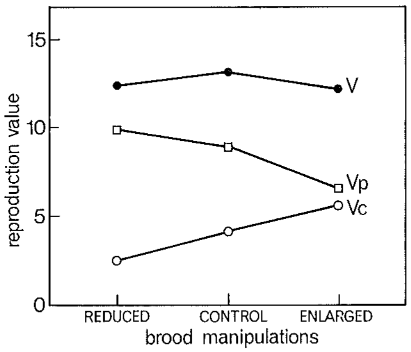

Figure 6. Reproductive value of brood (V_c) and parent (V_p) in experimentally reduced and enlarged and control broods, and their sum (V).

V_c and V_p and their sum V from table 1 are plotted in Figure 6. Clearly, clutch reproductive value increased with brood size across the experimental groups, although not in proportion with the brood sizes. Also, parent reproductive value declined as a consequence of brood enlargement and increased as a consequence of brood reduction. Both effects are compatible with the general theory displayed in figure 1. However, the negative effects on the parents and the positive effects on the offspring seem to virtually balance each other. We can not interpret the slight excess in V of the control nests as evidence for the proposition that both brood reduction and brood enlargement reduce total reproductive value. In fact, if we apply slightly different criteria restricting the three experimental groups to nests where at most one egg or nestling had disappeared before day 10, the reproductive values are indistinguishable (Reduced: V = 11.94; Control: V = 11.90; Enlarged: V = 12.16). The data at best do not refute the notion that clutch sizes chosen by individual birds maximize reproductive value with respect to smaller or larger clutches.

There are various interpretations of this result. One is that the experiments, restricted as they were to only a limited portion (from age 10 days till independence of the nestlings) of the whole breeding period, may not have caused sufficient effects on offspring and parents to generate the deviations from reproductive value which might have occurred, had clutch size been altered by the parents themselves. This interpretation implicitly assumes that the bottleneck in reproduction occurred before the start of the experiment, i.e., during incubation and in the early nestling phase. This is unattractive since we know that both food demands of the offspring and energy expenditure of the parents peak after the early nestling phase (Masman et al 1988).

Another interpretation is that there are long term effects of brood size on future reproduction by both parents and offspring which went undetected in our data set. The potential for such effects is suggested by the reduced clutch size in rooks (*Corvus frugilegus*) which had raised experimentally enlarged broods in the previous year (Rφskaft 1985), and for the offspring by the finding that kestrel nestlings in enlarged broods fledged at a lower average body mass than in control broods (Dijkstra et al 1988). If such effects show up in a larger data base, they may well reduce the total reproductive value for enlarged broods. Potential drawbacks from brood reductions are less easy to envisage, unless we have somehow overestimated the positive effects of brood reduction on parental survival. The relationship between local survival and real survival rates is an elusive one, and a slight decrease in the tendency to disperse in parents of reduced broods might erroneously have led to an increased survival estimate. Be this all as it may, the analysis presently suggests that there is no sharply defined clutch size maximizing an individual pair's total reproductive value. The optimal solutions must cover a rather broad range of clutch sizes.

6. MAXIMIZATION OF REPRODUCTIVE VALUE BY CLUTCH SIZE AND DATE ?

We shall now take this problem one step further by including laying date in the evaluation. In our kestrel population, V_P varied negligibly with date of laying (Figure 5A). This is compatible with the virtually clutch- and date-independent level of energy expenditure of parent birds (Masman et al 1988). However, the clutch component of fitness, as estimated by V_C, decayed with the progress of season (Figure 2A). Meanwhile, food availability, the prime ultimate factor determining reproductive output, increased simultaneously. This is reflected in the general spring increase in vole populations when their reproduction starts, and in the hunting yield of kestrels, i.e., the number of voles obtained per hour of flight-hunt (Masman et al 1988). This increase would allow individual birds to raise more nestlings with the same effort if they would delay the date of breeding.

To include this effect in a general maximization model it is necessary to obtain an accurate quantitative estimate of the rise in food availability. Vole trapping indices are insufficient for this purpose since vole trappability varies with season (Hoogenboom et al 1984), and the density of voles, even when reliably estimated, would not be the only factor determining their availability to predators. We chose to use a general measure based on prolonged dawn-to-dusk observations of focal birds as carried out by our team in the years 1976-1986 in the Lauwersmeer area (Masman et al 1988). This measure is the "flight yield" (Y), i.e., the number of vole equivalents captured (1 bird equals energetically 2.0 voles as a rule of thumb; Masman et al 1988a, appendix) divided by the number of hours spent in flight-hunt and directional flight. 131 Series of 1 to 7 consecutive full observation days were available for male kestrels in the breeding season. We discarded 40 of these which contained less than 5 hours of total flight and therefore gave less reliable estimates of Y. The remaining 91 series, together based on 4089.6 hours of observation, in which 985.3 hours of flight + hunt occurred, are plotted in Figure 7A. The linear regression through these values (weighted for hours of flight + hunt) was:

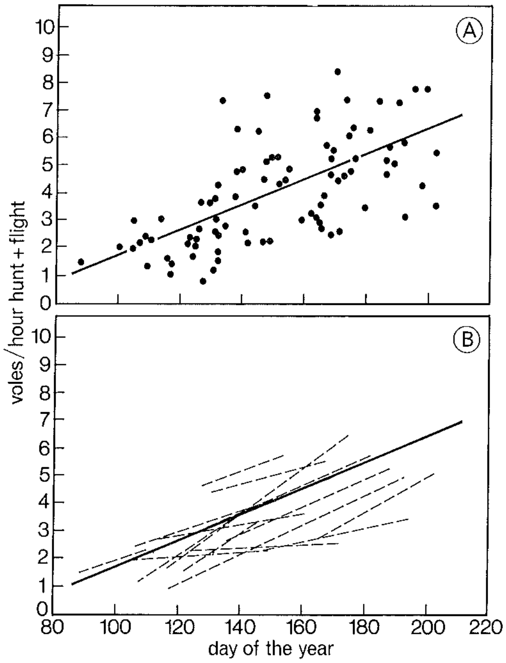

Figure 7. Seasonal change in the yield (Y) of flight-hunt + directional flight. A. In 91 series of 1-7 day dawn-to-dusk observations of focal male birds. B. Linear regressions of Y on date d in 16 individual birds. The linear regression of Y on d based on the data in Figure 7A is shown as a solid line in both panels.

$$Y = -2.998 + 0.0470 \,.\, d \qquad (26)$$

(s.e. of slope 0.0056; $r = 0.664$; $t = 8.39$; $n = 91$; $p < 0.0001$). Clearly, there is considerable variance around the regression. This is partly due to individual birds being in different food situations. For sixteen birds, repeated series of observations, spread out over at least 20 days, are available, and individual regressions of Y on d could be calculated. These regressions are shown in figure 7b. Their slopes ranged from 0.0053 to 0.0840 voles/hr.day, around a mean of 0.0440 (s.e.m. 0.0059). This is significantly different from zero ($p<0.001$), but not from the slope 0.0470 in equation (26). We therefore trust the latter value to be a reliable estimator of the average rate of increase in food availability to the individual hunting kestrel in the breeding season. This slope is smaller than the value of 0.069 prey/hr.day presented in a preliminary analysis (Daan et al 1988), which was based on a smaller data set, less rigorously screened for minimally 5 hours of flight per observation series, and moreover related prey captures to hunting hours only (excluding directional flight).

The next question is how this rate of increase in food availability translates to an increase in the number of nestlings a pair is able to feed with constant effort. From previous analysis, we know that male kestrels in the nestling phase spend on average 4.75 hours/day (s.d. 1.55; n = 32) in flighthunt + flight, independent of their natural brood size (Masman et al 1988). Female kestrels refrain from hunting and hardly fly during the early nestling stage (phase 6, 0-10 days after hatching). When the nestlings are between 10 and 30 days of age (phase 7), female daily flight can be estimated as 1.8 hours (s.d. 1.3; n=5; Dijkstra et al 1988, table 1). These values do not represent the maximal sustainable daily effort, but approach an upper limit of energy expenditure, which is similar for the males and the (heavier and thereby energetically more expensive) females, and beyond which extra work has negative repercussions (Masman et al 1988). Averaged over the nestling period (phase 6 + 7), this points to a combined daily flight time for the parents of 4.75 + 1.8 . 20/30 = 5.95 hours/day. The seasonal increase in flight yield would hence lead to an increase in daily prey returns of 0.0470 . 5.95 = 0.280 vole equivalents/day^2. Nestling requirements can be estimated at 3.89 voles/day (Masman et al 1988, appendix). Hence the seasonal rate of increase of energy to kestrel parents works out at 0.280/3.89 = 0.072 nestling rations per day. This implies that a delay in breeding of 1/0.072 = 14 days would allow a kestrel pair to raise one extra nestling with the same effort per day.

We now make the (tenuous) assumption that for individual pairs the reproductive values of eggs and parents would decline with progressive laying date according to the relationship established for the population (figures 2A and 5A). If this assumption holds then the brood sizes maximizing total reproductive value V(c,d) under constant parental effort would obey the condition:

$$V\ (c-1,\ d-14)\ <\ V\ (c,d)\ >\ V\ (c+1,\ d+14) \qquad (27)$$

In a series of graphs representing the V-values of different clutches as a function of date d, this maximization criterion can easily be found by locating where the horizontal distance between graphs for consecutive c attains the value 14 days (cf. Drent & Daan 1980). This is done in figure 8A and 8B for two estimates of V(c,d). Figure 8A presents the curves for V as the addition of the curves established in figure 2A for clutch reproductive value and the one in figure 5A for parent reproductive value. Figure 8B is the addition of parent reproductive value with c * (2.45 - 0.0132 . d), being the linear approximation to declining egg reproductive values (Daan & Dijkstra 1988). The two sets of curves are based on essentially the same data, but calculated in a slightly different manner: In the analysis presented here, we estimated each significant contribution of date to V by a linear or logistic equation, and their eventual multiplication of course introduced strong nonlinearity (Figure 8A). In the earlier analysis of egg reproductive value, point estimates per ten-day interval were derived, and then approximated by linear regression (Figure 8B).

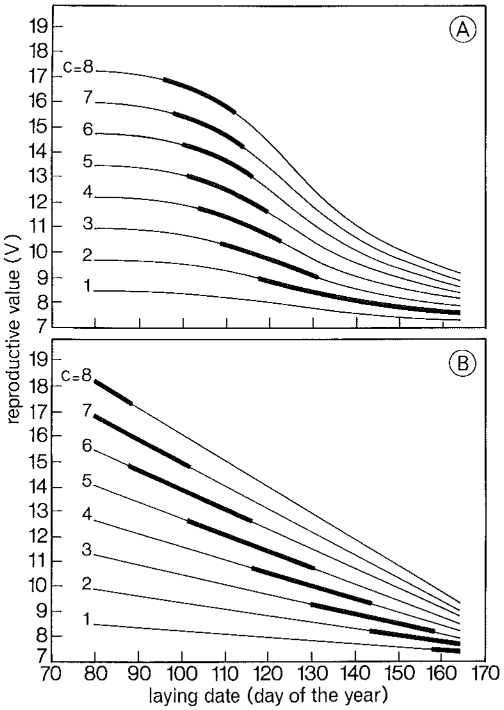

Figure 8. Total reproductive value (V) as a function of laying date for clutches of different size: A. based on equations 2 to 23 in this article. B. based on the linear regression to 10-day interval estimates of egg reproductive value in Daan & Dijkstra (1988). For each clutch size, the sections obeying the maximization criteria (equation 27) are marked.

The "nonlinear" and "linear" methods of calculation yielded maximization criteria which differ considerably. They have in common a clear decrease in clutch sizes maximizing reproductive value with the progress of season, as postulated by Drent & Daan (1980). The range of laying dates for each clutch size obeying the criteria is indicated in figure 9A and 9B, together with the central tendencies in 797 observed clutches. Among these, 47% obeyed the "nonlinear" maximization criteria, whereas 73% obeyed the "linear" maximization criteria. This is considerably more than when laying dates and clutches with the same distributions would have been randomly assigned to each other (42 % and 52 % for the "nonlinear" and the "linear" criteria respectively). However, a major proportion of the nests did not obey the criteria. The best fit was obtained by the linear criteria (Figure 9B). Interestingly, these criteria are dependent only on the day when V_o reaches the value 0 (i.e. the laying date after which prospects for eggs are predicted to be nil). In the equation obtained this was day 186 (July 5), ca three weeks after the latest clutch ever observed in the population. This is important since the precise definition of reproductive value thereby has little effect on the predictions. For instance, if λ is changed from 1.19 to 1, to set reproductive value equal to expected lifetime reproductive output, the linear regression of V_o on laying date becomes:

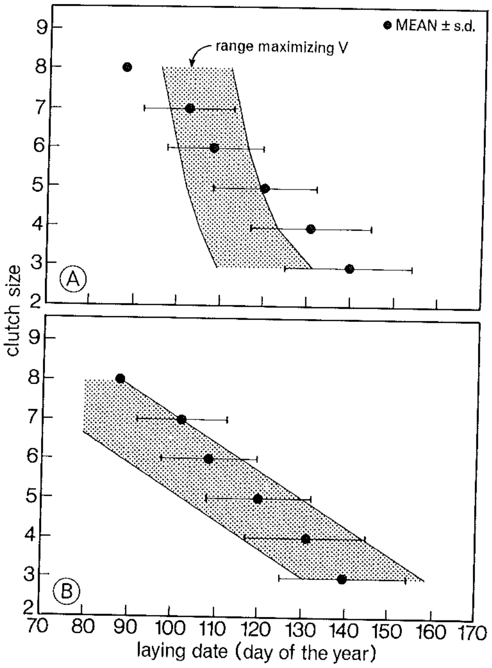

Figure 9. Ranges of clutch size-laying date combinations maximizing total reproductive value, based on the "nonlinear" (A) and "linear" measures (B) in figure 8. In both cases the ranges are compared with the laying date distributions of 797 clutches observed.

$$V_o = 3.62 - 0.0185 \cdot d \qquad (28)$$

which yields $V_o = 0$ for $d = 196$, so that the predictions shift ten days to the right, but remain otherwise unaffected.

Thus, while the maximization criteria for reproductive value are robust in the sense that they are not extremely sensitive to whether the population is expanding ($\lambda > 1$), stable ($\lambda = 1$) or shrinking ($\lambda < 1$), they appear rather sensitive to the computational method. Using the straightforward calculation of reproductive values per ten-day interval yielded somewhat wider maximization criteria then the approach using fitting of functions to each component of fitness, and thereby also a better fit with the observed data.

7. PERSPECTIVE

The conclusion from the analysis in the previous section must be that the precise form of the predicted combinations of clutch size and laying date depends rather heavily on the computational method. This restricts the potential of the descriptive data to evaluate the proposition that kestrels adjust their reproductive decisions to the expected food availability. It is important to note however that any decline in egg reproductive value, computed in whatever manner, yields a decline in clutch sizes maximizing total reproductive value, and that this predicted decline covers the observed ranges of clutch sizes and laying dates. Thus the data are consistent with the general proposition of a simultaneous optimalization of date and egg number.

It is possible that the theory is applicable more generally to other single-brooded bird species, most of which show a similar seasonal decline in clutch size as the kestrel (Klomp 1970), and for some of which a decline in egg fitness components has been found (Daan et al 1988). However, there are aspects of the kestrel-vole system which make the theory particularly appealing for this system. Common voles are the dominant prey species of kestrels in our area throughout the year, and the vole abundance in spring has predictive value for the food availability two months later when most kestrels raise their nestlings. At least the male, who hunts during the courtship phase to provision his partner, thereby has access to information about how many nestlings he will be able to raise. Obviously, it is the female who "decides" on the number of eggs she lays. However, there is circumstantial evidence that the male suddenly raises its food supply to the female in spring and, by allowing her to start egg production, determines the laying date (Meijer et al 1988). Natural selection has equipped the female kestrel with a system which adjusts clutch size to her date of laying, independent of food supply and body reserves (Meijer et al 1988). Hence the male, who does most of the food provisioning to the nest, is able to adjust the brood size in advance to his predicted food situation later on.

Our model for the maximization of reproductive value clearly predicts that several clutch sizes, not only one, obey the maximization criteria, even at the same laying date (figure 9). Observed clutches were to a considerable extent outside this range. It is not excluded that kestrels take other parameters of the food situation into account, apart from the average change in hunting yield. There is for instance the intriguing possibility that they may respond to the reproductive condition of their prey in early spring as a predictor for the vole availability in the nestling phase. This suggestion invites further experimentation on the proximate causation of reproduction (Meijer et al 1988). On the ultimate side of the reproductive coin, the immediate challenge for further analysis is to test the basic assumption that the decline in egg reproductive value in the population is caused by date of birth itself rather than by some variable merely correlated with it, such as the quality of parents and/or territory. Such a test can only be carried out by experimentally affecting date of birth. Exchange of eggs between nests at different stages of incubation is one approach, presently used in Herring gulls (Spaans pers.comm.), Flycatchers (Tinbergen pers.comm.), and Coots (Cavé, pers.comm.). Another possibility is offered by the photoperiodic response of birds. We have recently initiated a study using young kestrels born and raised by their parents at different dates, triggered by artificial daylengths (Meijer 1988). These birds were taken away from their parents at an age of circa 45 days, corresponding with the age of independence in nature (Dijkstra et al 1988). They were then kept for circa 15 days in an outdoor aviary to obtain experience in capturing and subsisting on live laboratory mice. After banding and colour marking they were released in the Lauwersmeer study area, and their fates recorded as far as known. Figure 10 shows a preliminary analysis of frequencies of recaptures and of dead recoveries before the next breeding season. The results suggest that chances of survival may be reduced in juveniles born earlier (< day 50) and later (> day 150) than the normal breeding season, and hence that date itself may have some effect on the prospects for fledglings. However, it remains to be established in larger data sets whether also experimentally induced variations within the natural range of laying dates would exert the

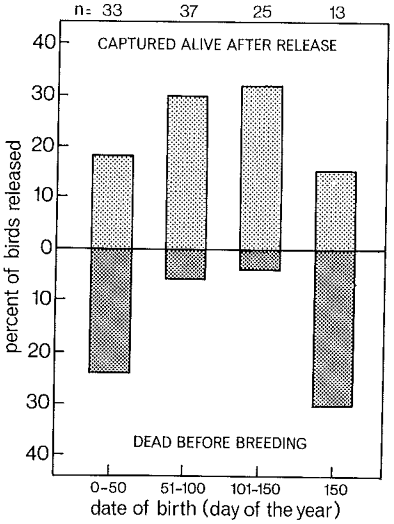

Figure 10. Fate of 108 kestrels reared by their parents in captivity under various photoperiodic conditions and released in the Lauwersmeer study area around 60 days after hatching. Date of birth is the day of the year at which the first egg of the clutch was laid.

same effects as observed in the population.

The use of total reproductive value developed in this article has shown how different components of fitness, as affected by reproductive decisions, may be combined in the one currency which natural selection deals with: the rate of gene propagation in future generations. In evaluating brood size experiments in the kestrel, this application has shown that the positive effects of larger clutch size on clutch reproductive value balance the negative effects on parent reproductive value, and hence there is no sharply defined clutch size which maximizes individual fitness. The application to the combined laying date-clutch size decisions yielded a decline in the clutch size maximizing total reproductive value with progressive date. However, the precise form of the predicted decline depends strongly on the computational method, and rests on the untested assumption that the progressive reduction in reproductive value with date of birth holds up for individual birds. The proposition that individual birds maximize their fitness by the adjustment of clutch size and laying date in anticipation to the local energy supply thereby remains untested and appears to require even more extensive experimentation and detailed survival analysis than we originally anticipated.

8. Acknowledgements

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Dankwoord

Nadat in de herfst van 1976 voor de eerste keer in de Lauwersmeerpolder een derdejaars cursus aan veldmuizen en het jaaggedrag van Torenvalken was opgezet, kon niemand voorzien dat dit onderzoek uiteindelijk zou uitgroeien tot een uitgebreid project dat nu, twaalf jaar later, heeft geresulteerd in drie dissertaties. In de allereerste plaats is Serge Daan verantwoordelijk geweest voor de opbouw van het Torenvalk project, voor de begeleiding van de promovendi en van de vele tientallen studenten die hebben geparticipeerd. Door zijn intense betrokkenheid en sterke persoonlijkheid heeft hij het Torenvalk project gemaakt tot wat het is, namelijk een produkt van jarenlang teamwork, waarin de verzamelde gegevens werden beschouwd als gemeenschappelijke bron, waaruit iedereen voor zijn of haar deelonderzoek kon putten. Ook ik heb vanaf 1977 intensief en met veel genoegen met hem samengewerkt. Dit proefschrift was niet nu, waarschijnlijk nooit, en zeker niet in de huidige vorm tot stand gekomen, als Serge niet voortdurend de vaart erin had gehouden. Zijn kreatieve denken, rationele aanpak en enorme doorzettingsvermogen waren en zijn voor mij een voorbeeld waarvan ik veel heb kunnen leren.

De andere drie mensen die zowel voor mij persoonlijk als met betrekking tot het onderzoek een centrale rol hebben gespeeld, waren Adriaan Rijnsdorp, Dirkjan Masman en Theo Meijer. Met Adriaan startte ik in 1977 mijn eerste doktoraal onderwerp aan Torenvalken in de Lauwersmeer. Met hem deel ik de unieke ervaring van het voor de eerste keer volgen en protokoleren van een individuele vrijlevende Torenvalk, van 's ochtends voor zonsopgang tot 's avonds na het invliegen op de slaapplaats. Dit was des te spannender omdat we ons realiseerden dat dergelijke observaties slechts bij zeer weinig soorten mogelijk zijn, terwijl een komplete beschrijving van het gedrag onder natuurlijke omstandigheden in verschillende fasen van de jaarcyclus een ideale basis vormt voor gedragsoecologisch en ook populatiebiologisch onderzoek. Met Adriaan en Lourens Vuursteen werden de eerste bijvoer experimenten uitgevoerd, die resulteerden in een aanzienlijke vervroeging van de legdatum van de valken, waarmee de eerste stap was gezet op weg naar de ontrafeling van het verband tussen voedsel en reproduktie.

Daarna raakte Dirkjan Masman bij het onderzoek betrokken, eerst als cursist, toen als doktoraal student, vervolgens als promovendus en de laatste tijd als wetenschappelijk medewerker. De tijdens zijn promotieonderzoek uitgevoerde hongerexperimenten, opgenomen in Hoofdstuk 3, waaruit bleek dat Torenvalk ouders minimaal twee tot drie dagen in staat zijn om veel meer voedsel voor de jongen te verzamelen dan ze van nature doen, waren de direkte aanleiding tot de broedsel manipulaties die vanaf 1985 werden opgezet. Ook werd dankbaar gebruik gemaakt van de energetische kosten metingen, die door hem werden uitgevoerd. De jarenlange samenwerking met hem was en is voor mij een groot genoegen. Het werken in een team gaat niet iedereen even gemakkelijk af, maar is Dirkjan op het lijf geschreven.

Vanaf de "officiele" start van het promotie onderzoek in 1984 was Theo Meijer degene met wie ik met veel plezier heb samengewerkt. Aan het identificeren van de broedpopulatie, de broedselmanipulaties en de tijdsbestedings waarnemingen heeft hij een grote bijdrage geleverd. Verder werden de gewichten van valken in gevangenschap door hem verzameld, en kon de overleving en vestiging van op verschillende data losgelaten jonge Torenvalken alleen worden onderzocht dankzij de meer dan 100 jongen die hij had "voortgebracht" in de kolonie op het lab. Zijn gedisciplineerde manier van werken was voor mij een belangrijke steun.

Rudi Drent volgde het onderzoek kritisch en zijn ideeen over individuele optimalisatie van de voortplanting stonden centraal in dit project. Ook zijn kritiek op eerdere versies van de hoofdstukken kwam de tekst van dit proefschrift ten goede.

Ton Cavé wil ik speciaal bedanken voor het loyaal beschikbaar stellen van de door hem verzamelde gegevens over legdata, legselgroottes, gewichten van de valken en de veldmuizen vangsten. Zijn proefschrift "The breeding of the Kestrel in the reclaimed area Oostelijk Flevoland" vormde de solide basis voor het huidige onderzoek. Zijn kritiek op de tekst was erg waardevol en verder was hij , samen met Ab Perdeck, behulpzaam bij een deel van de statistiek.

Joost Tinbergen was nauw betrokken bij het tot stand komen van het laatste hoofdstuk. Zijn inzicht en ervaring op het gebied van de ultimate regulatie van de reproduktie waren een belangrijke ondersteuning tijdens de laatste hectische fase van dit onderzoek.

Naast bovengenoemde personen waren er tientallen studenten die in de loop der jaren hun bijdrage hebben geleverd aan het Torenvalk project. Ik beperk mij hier noodgedwongen tot het bedanken van diegenen die het meest direkt waren betrokken bij de totstandkoming van dit proefschrift: Sjef van Esch nam de eerste analyses van de ringterugmeldingen voor zijn rekening. Fred de Haas was verantwoordelijk voor de opzet van het veldmuis vangprogramma. Willy Schulte, Theo Vulink, Marten Scheepstra en Johan Vochteloo voerden de eerste hongerexperimenten uit. Nico Beemster zette zich meerdere seizoenen in om, als de anderen op vakantie gingen, de ouderlijke verzorging van de uitgevlogen jongen vast te stellen. Marijke Gordijn had gedurende de eerste jaren van de veldmuiscensus een belangrijk aandeel in de uitvoering, en later bij het uitwerken van de resultaten. Inge Hoogenboom bracht vele dagen door in de keet, achter de nestkast, tijdens de elf-daagse honger experimenten, en zorgde verder voor de broodnodige orde in het veldlab. getuige de nu nog aanwezige briefjes met "huisregels". Bert Toxopeus was degene die als eerste, de later zo belangrijk gebleken methode van de vleugelmerkjes toepaste in de Lauwersmeer. Karin Kiekenbos registreerde de voedselopname en de groei van nestjongen onder *ad lib.* voedsel condities in het laboratorium. Leo Beukeboom verzorgde vele nestkastkontroles tijdens de legperiode, rond het uitkomen van de eieren en vlak voor het uitvliegen van de jongen, om de relatie tussen eivolgorde en het geslacht van de jongen vast te stellen. Ook deed hij in 1985 de eerste broedselmanipulaties in de Flevopolders, en registreerde de jongengroei. Deze experimenten werden het jaar daarna voortgezet door Simon Bijlsma, terwijl Ab Bult, Ruud Foppen, Mark Jalink en Janny Swavink dezelfde experimenten in de Lauwersmeer uitvoerden, gecombineerd met waarnemingen aan de tijdsbesteding, prooiaanvoer en gewichten van de ouders. Ab Bult was het jaar daarna opnieuw present om de overleving van de ouders van de gemanipuleerde broedsels vast te stellen, terwijl hij ook Kees Vos assisteerde bij zijn onderwerp aan overleving en groei van de jongen. Ruud Foppen, Simon Bijlsma en Ab Bult waren verder direkt betrokken bij de uitwerking van de gegevens gepresenteerd in de Hoofdstukken 2 en 4. Ina van de Beld en Johan Krol waren met veel enthousiasme op allerlei manieren behulpzaam, zowel bij de kastkontroles, de gedragsobservaties als bij de muizencensus waren zij frekwent betrokken. Ook verzorgde Ina de invoer van de meer dan 3000 gewichten en broedresultaten van de valken in de computer. Zonder de enthousiaste inzet van al deze mensen, en daarnaast van de vele cursisten was dit onderzoek niet mogelijk geweest.

Behalve de genoemde studenten zijn er nog velen op de een of andere manier bij het project betrokken geweest. Vanaf 1982 werd het landelijk ringprogramma opgezet, om de jongen op grote schaal te sexen en na verloop van jaren de overleving van de geslachten afzonderlijk te kunnen analyseren. Behalve het Vogeltrekstation, in de persoon van Rinse Wassenaar, die ook het uitgebreide databestand van ringterugmeldingen beschikbaar stelde, verleenden de volgende ringers hun medewerking aan dit programma: J. Buker, L. Buurma, J. Doevendans, H. Esselink en de Werkgroep Roofvogels Noord en Oost-Nederland, de Ringgroep Franeker, J. de Jong, J.W. Lensink, W. Lok, P.J. Maeghs, F. Versluys, D. Westra, J.E. Winkelman en M. Zijlstra. Joop Buker had een belangrijk aandeel in de opzet en de uitvoering van dit project, en samen met hem werd aan de hand van de verzamelde stuitveertjes het geslacht van de jongen bepaald.

Ook de samenwerking met de Rijksdienst voor de IJsselmeerpolders (RIJP) was van groot belang voor het slagen van het onderzoek. Het waren vooral Wiebe de Vries, Sietse Keuning en zijn mensen en Menno Zijlstra die ons op allerlei manieren van dienst zijn geweest. Niet alleen voor de vergunningen maar ook voor technische hulp en materieel konden wij altijd een beroep op hen doen. Menno Zijlstra zorgde bovendien voor een stageplaats bij de RIJP voor de studenten die in de Flevopolder werkten en hielp daar regelmatig mee met het veldwerk. Ook de jachtopzieners Schuldink en Onderdijk wil ik bedanken voor de prettige samenwerking vanaf de allereerste nestkastkontroles die Serge en ik achter in de laadbak van hun auto meemaakten.

Ook het personeel in Haren was onmisbaar voor het slagen van dit project. Allereerst waren er de dierverzorgers Barend de Graaf, Sjoerd Veenstra, Gerard Bakker, Bram de Haan en Auke Meinema. Jan Nijboer was verantwoordelijk voor de technische ondersteuning, maakte verschillende vangmiddelen en repareerde de meest uiteenlopende dingen. Jan Koenes en zijn mensen timmerden de nestkasten voor de valken en de electronici, met name Wim Beukema en

Edzo Paap ontwikkelden de weegapparatuur. Henk Visser, Arnold Leenders en in een eerder stadium de heer Eggen waren verantwoordelijk voor de administratieve beslommeringen. Leon Steijvers verzorgde de computer programmatuur en Gea Breider was behulpzaam bij de tekstverwerking. Dick Visser tekende de figuren en maakte ook de omslag van dit proefschrift op de van hem bekende vakkundige wijze. Al het technisch en administratief personeel en de dierverzorgers wil ik bedanken voor de loyale medewerking tijdens de uitvoering van het onderzoek en de totstandkoming van dit proefschrift.

Tenslotte ben ik de meeste dank verschuldigd aan Margriet die voortdurend met de lasten en veel te weinig met de lusten van het onderzoek werd geconfronteerd.