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

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1. 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 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 1982, Daan & Dijkstra 1988). 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.* 1988a) we use these descriptive data as a background to evaluate the results of experimental food manipulation.

2. 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 (1978).

2.1. 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, 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 placed in a wooden case underneath the nest. Male and female of a pair could be easily distinguished by their weight difference, and multiple weights could be obtained throughout the daylight period.

2.2. COMMON VOLE CENSUS

In order to evaluate food conditions, densities of the common vole, 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 m 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.

3. RESULTS

3.1. 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.

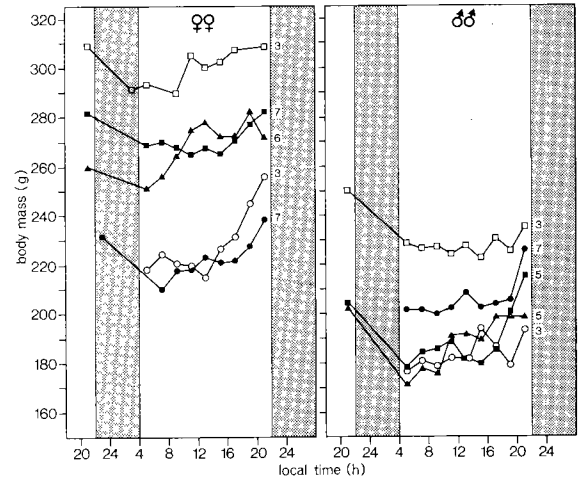


Fig. 1. Examples of body mass recordings of female (left panel) and male Kestrels (right panel) on electronic balances mounted in the entrance of nest boxes. Shaded areas indicate approximate time of darkness. Numbers indicate phase of the breeding cycle.

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 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

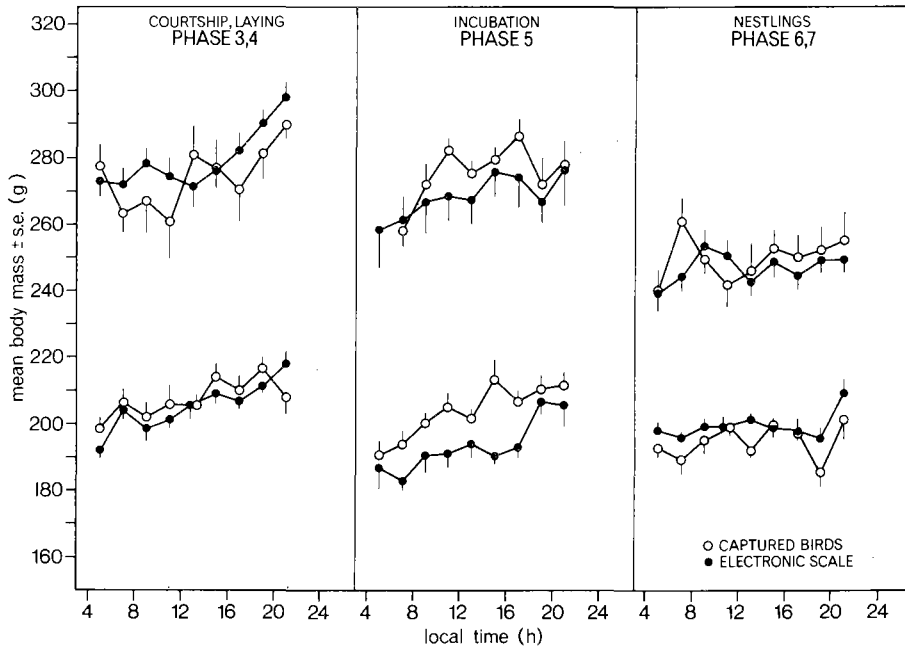


Fig. 2. Variations over the daylight period in mean body mass of all free-living birds recorded by electronic scales in the field (solid symbols) and of those captured and weighed on spring balances. Upper curves: females; lower curves: males.

again shown as a function of time of day in Fig. 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 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 significantly improve the fit. We used the equations from Table 1, to correct for time of day

Table 1. Regressions of body mass (g) on hour of the day during daylight (t, Middle 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	***

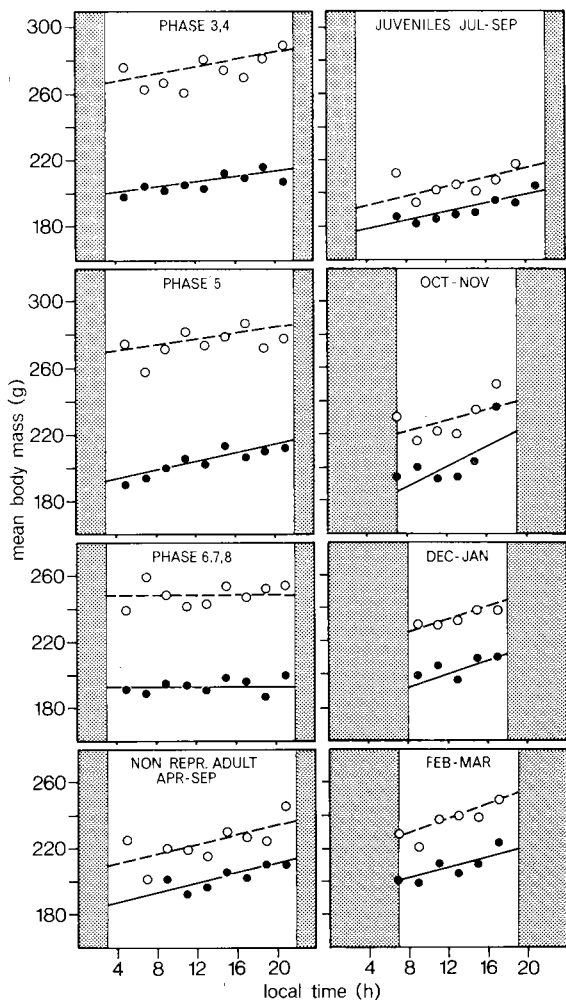


Fig. 3. Mean body mass of captured free-living Kestrels in two-hourly intervals of the daylight period in different phases of the annual cycle. Open symbols: females; solid symbols: males. Lines show linear regressions (see Table 1).

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. Morning weights were used in all further calculations.

3.2. 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 female body mass

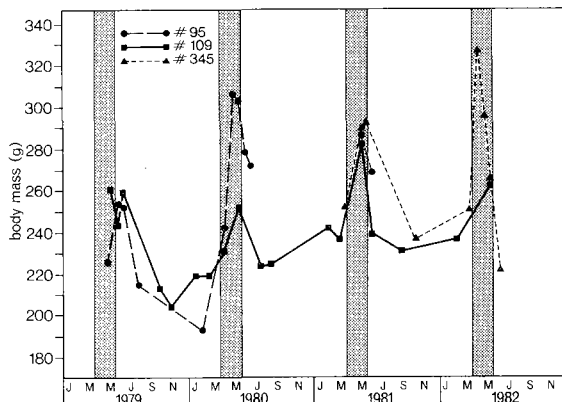


Fig. 4. Examples of body mass measurements taken in three individual free-living female Kestrels captured repeatedly in the course of three years. Shaded areas indicate the breeding season.

data, pooled per 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

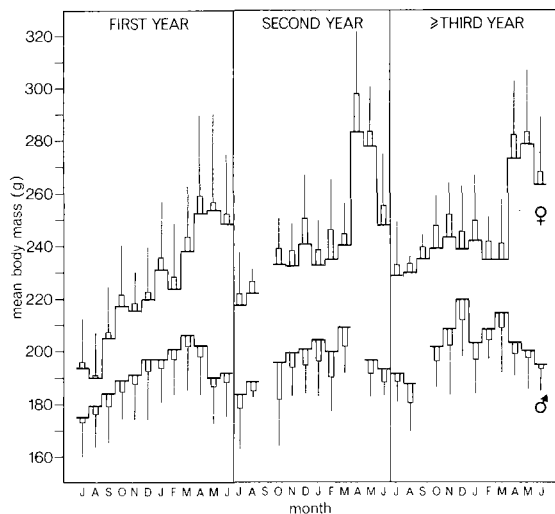


Fig. 5. Mean body mass per month of known-age wild caught Kestrels as a function of age in their first and second year of life, and as a function of time of year in older birds. Rectangles indicate 1 s.e.m., lines 1 s.d.

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

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

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 than 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 than the breeding birds (section 3.4).

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 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.

3.3. 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 plot-

Table 3. Regressions of body mass (g) on winglength (w, in cm) 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			Males		
		Mass	Sign	n	Mass	Sign	n
Juveniles	Jul/Sep	- 68 + 1.0 w	***	(245)	- 12 + 0.8 w	***	(179)
Juveniles	Oct/Mar	205 + 0.1 w	-	(92)	- 83 + 1.1 w	**	(84)
Adults	Oct/Mar	217 + 0.1 w	-	(114)	- 19 + 0.9 w	**	(102)
All	3/4	- 11 + 1.1 w	-	(46)	116 + 0.4 w	-	(38)
All	5	-102 + 1.5 w	***	(114)	83 + 0.5 w	-	(65)
All	6/7/8	188 + 0.2 w	-	(60)	144 + 0.2 w	-	(42)
All	non-rep	205 + 0.0 w	-	(56)	2 + 0.7 w	*	(61)

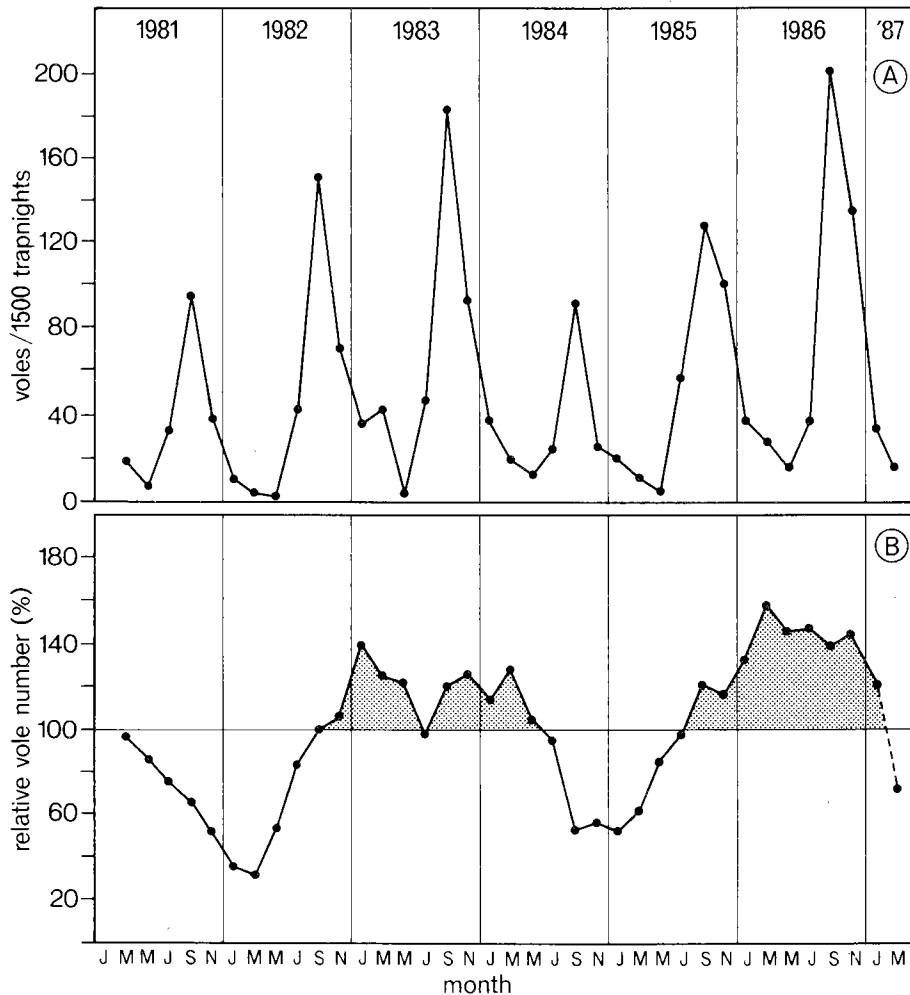


Fig. 6. A. Number of common voles trapped per 1500 trapnights in a standard bi-monthly trapping census in the Lauwersmeer over a six-year period. B. Vole numbers expressed relative to the mean (100%) of all values obtained in the same month over six years.

ted 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 (Hooogenboom *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). 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

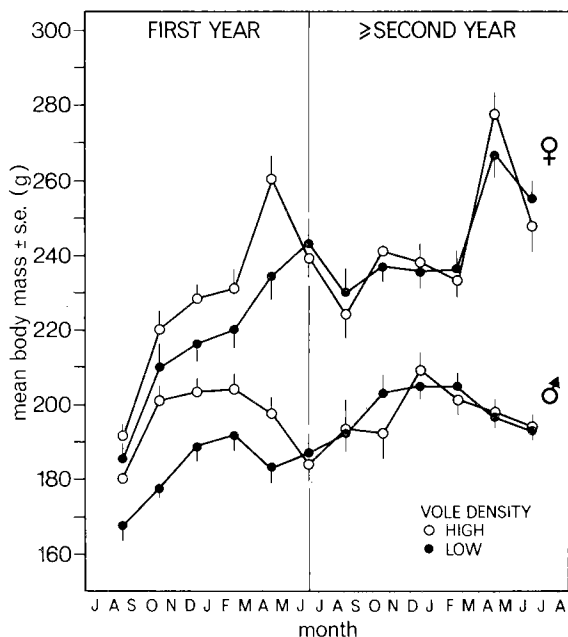


Fig. 7. Two-monthly mean values for body mass of male and female Kestrels trapped as juveniles or adults in months with high and with low common vole densities.

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 below).

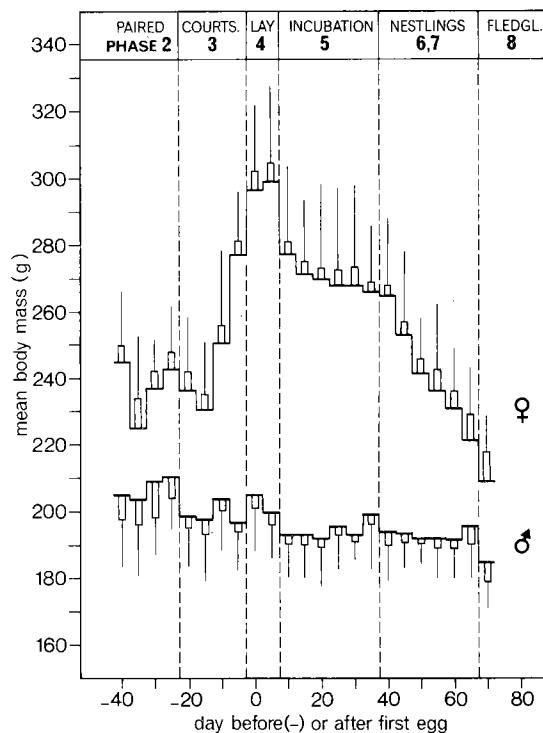


Fig. 8. Mean body mass per five days relative to the laying date of the first egg for breeding male and female Kestrels trapped or recorded in the field. Rectangles: 1 s.e.m.; lines: 1 s.d.

3.4. 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

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

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

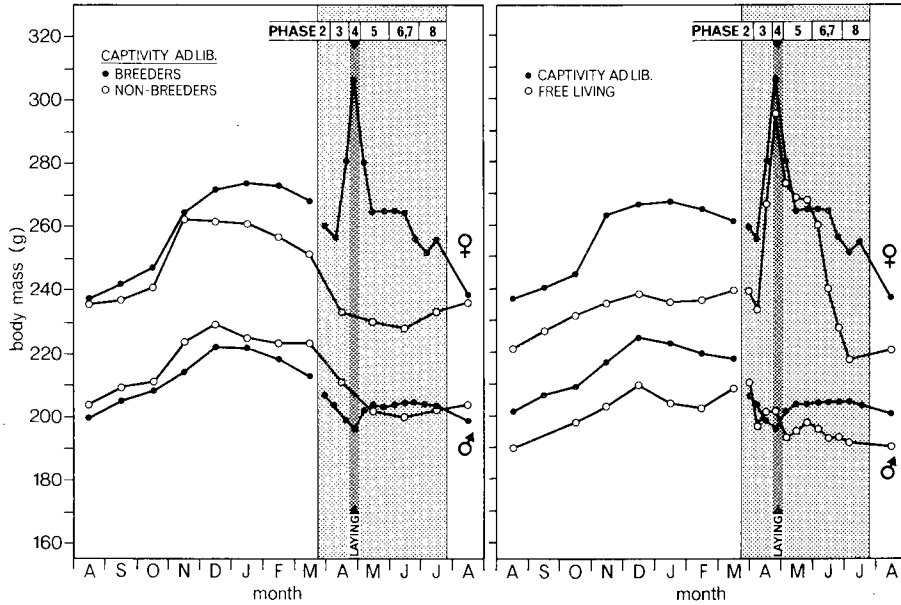


Fig. 9. Comparison of mean body mass of breeding and non-breeding Kestrels in captivity fed *ad lib.* (left panel). Comparison of mean body mass in captive birds and in free-living breeding Kestrels in the course of the year (right panel).

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). 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. Kestrels in captivity weighed considerably more than free-living birds (Fig. 9). 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). It is therefore of interest to analyse body

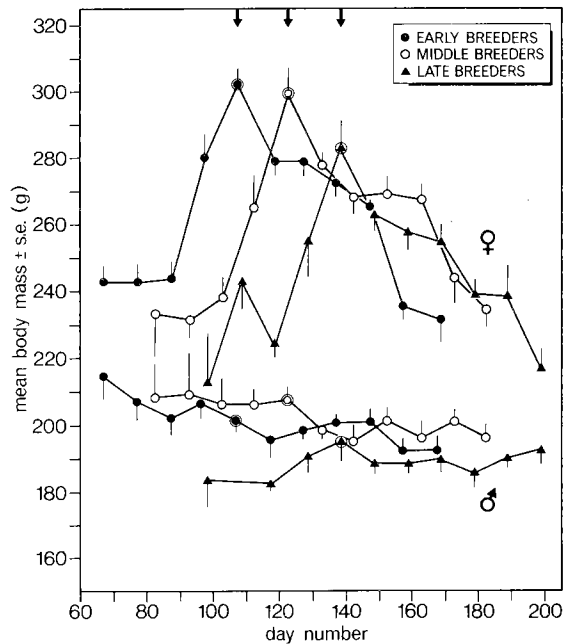


Fig. 10. Mean body mass per ten day interval in early, middle and late breeding free-living Kestrels, based on both captured and electronically recorded birds. Data are plotted relative to the mean laying date (arrows).

Table 5. Mean body mass (g)± s.d. (n) of incubating 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)	131.1 ± 14.0 (51)	4.57 ± 0.98 (51)
Crash	270.9 ± 20.9 (61)	110.0 ± 11.9 (61)	5.43 ± 0.74 (57)

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 persistently above mean) *low vole years* (persistently below mean) and *vole crash years* (switch from high to low occurred during the reproductive season).

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.

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 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

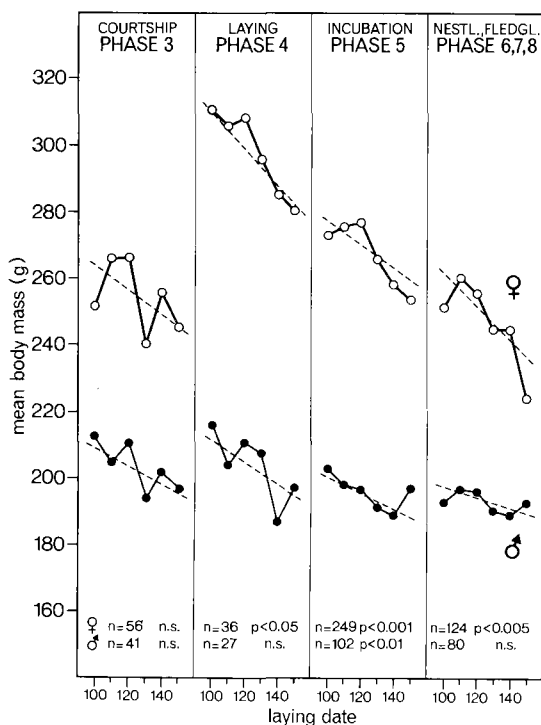


Fig. 11. Mean body mass of free-living Kestrels during the major phases of reproduction per ten day interval of laying dates. Dashed lines show individual linear regressions for females (upper) and males (lower). p-values indicate significance levels for the difference between regression slopes and zero.

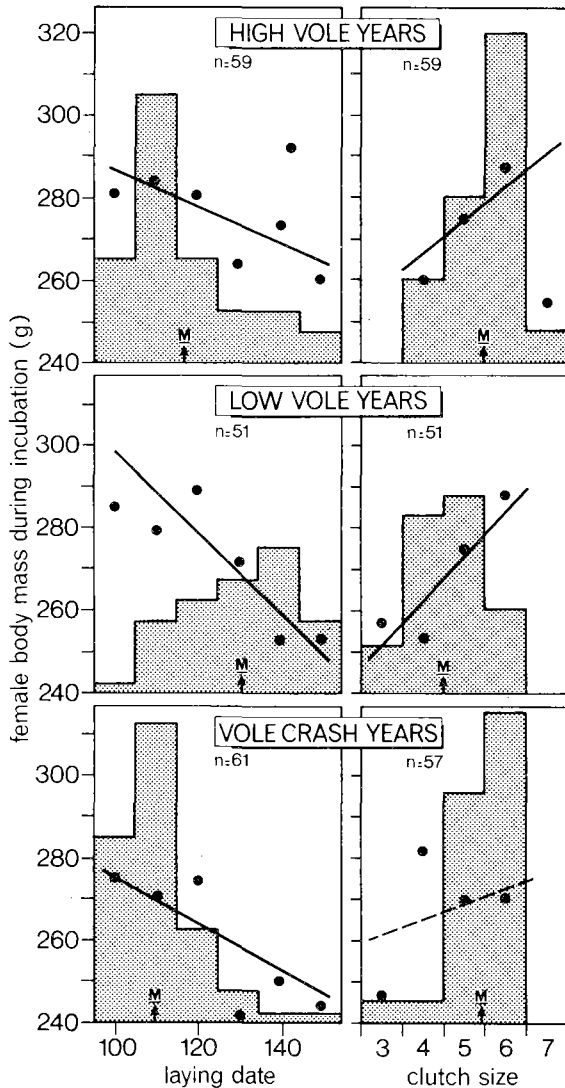


Fig. 12. Mean body mass (dots) per ten day interval of laying dates (left panels) and per clutch size (right panels) in high vole years (upper), low vole years (middle) and vole crash years (lower). Lines indicate linear regressions through individual data points (Table 6). Histograms show the distribution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

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 main-

tain 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 (Fig. 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 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.

4. 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

Table 6. Linear regressions of female body mass (W in g) during incubation on laying date (d) 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	$W = -0.50 d + 336.1 (59)^*$	High/Low : slope : $F_{1,106} = 1.86$ n.s. intercept : $F_{1,107} = 0.003$ n.s.
Low	$W = -0.89 d + 386.6 (51)^{***}$	
Crash	$W = -0.55 d + 332.5 (61)^{**}$	High + Low/Crash : slope $F_{1,167} = 0.20$ n.s. intercept : $F_{1,168} = 9.66^{**}$
High	$W = 8.68 c + 230.2 (59)^*$	High/Low : slope : $F_{1,106} = 0.16$ n.s. intercept : $F_{1,107} = 0.01$ n.s.
Low	$W = 10.62 c + 219.8 (51)^{***}$	
Crash	$W = 3.90 c + 248.9 (57)$ n.s.	High + Low/Crash : slope : $F_{1,163} = 1.81$ n.s. intercept : $F_{1,164} = 3.30$ n.s.

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, 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 in-

cubation 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). 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

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			Partial correlation coefficients		
	Clutch	Date	Year	Clutch	Date	Year
Mass	0.408****	-0.488****	0.203*	0.124	-0.236*	0.033
Clutch		-0.754****	0.475****		-0.631****	0.219*
Date			0.463****			-0.184*

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.

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, Hiron *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 *c.* 70 g increase during the last 20 days before egg laying (Fig. 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 *c.* 2 g/day. 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 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 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) 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).

5. ACKNOWLEDGEMENTS

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6. 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 c. 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 than 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.

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8. SAMENVATTING

Variaties in lichaamsgewicht van de Torenvalk werden geanalyseerd in relatie tot leeftijd, voedselaanbod en voortplanting. Alle gewichten werden gecorrigeerd voor de tijd van de dag, aangezien er een significante toename van het lichaamsgewicht optrad in de loop van de dag. Eerstejaars individuen waren lichter dan adulte valken, vooral in jaren met een laag aanbod van veldmuizen. Zowel mannetjes als vrouwtjes waren 's winters zwaarder dan 's zomers. Vrouwtjes die aan de voortplanting deelnamen, wogen het zwaarst tijdens de leg en de broedfase, terwijl niet-broeders een relatief laag gewicht handhaafden gedurende de gehele reproductie periode. *Ad lib.* gevoerde valken in gevangenschap vertoonden eenzelfde verschil in gewicht tussen broedende en niet-broedende vrouwtjes. Dit wijst op een verschillende gewichtsnorm voor broeders en niet-broeders. Vrouwtjes vertoonden een snelle toename in gewicht in de laatste twee weken voorafgaand aan de eileg. Tijdens het broeden was het gewicht konstant en ongeveer 30 g lager dan het piekgewicht tijdens de leg. Na het uitkomen van de eieren nam het gewicht van de vrouwtjes snel af en aan het einde van de nestjongenperiode wogen ze 50 g (20%) minder dan tijdens het broeden.

De mannetjes vertoonden een geleidelijke geringe afname in gewicht van ongeveer 10 g over de gehele voortplantingsperiode. *Ad lib.* gevoerde Torenvalken in gevangenschap vertoonden hetzelfde patroon in lichaamsgewicht in de loop van het jaar, maar waren zwaarder dan vrijlevende individuen, behalve tijdens de leg (beide sexen) en tijdens de broedfase (alleen vrouwtjes). Vrouwtjes die laat in het seizoen eieren legden, produceerden kleinere legfels en wogen minder zwaar dan vroege broeders gedurende de gehele reproductie periode en dezelfde trend in lichaamsgewicht trad op bij mannetjes. Vrouwtjes legden eerder in het seizoen in goede veldmuizen jaren en waren zwaarder tijdens het broeden dan in jaren met een laag veldmuizen aanbod. Door middel van covariantie analyse werd aangetoond dat het verband tussen legdatum en lichaamsgewicht gelijk is in goede en slechte veldmuizen jaren, en dus variatie binnen jaren weergeeft, waarschijnlijk gerelateerd aan individuele verschillen in voedselaanbod. Het aanleggen van minder lichaamsreserves door laat leggende vrouwtjes stelt hen in staat tijd te winnen en de legdatum te vervroegen, terwijl vroeg in het voorjaar leggende vrouwtjes voordeel zouden kunnen hebben van meer reserves als buffer tegen ongunstige weersomstandigheden.