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FEMALE CONDITION AND REPRODUCTION: EFFECTS OF FOOD MANIPULATION IN FREE-LIVING AND CAPTIVE KESTRELS

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1. INTRODUCTION

A seasonal decline of clutch size is characteristic for most single-brooded species of birds (Klomp 1970). This trend is probably adaptive in the sense that for early breeding pairs in a population the clutch size maximizing fitness is higher than for late breeding pairs. We have argued elsewhere (Daan *et al.* 1988) that such seasonal variation in optimal clutch size arises whenever the reproductive value of eggs declines with progressive laying date. Birds opting for late and small clutches are in poorer nutritional circumstances than those laying early large clutches. These circumstances may reflect both inter- and intra-individual variation in rates of energy acquisition for reproduction, determined by the foraging skills developed by individuals as well as by environmental heterogeneity in food abundance (territory quality). An increasing number of studies has shown experimentally that birds respond to food supplements by advancing their laying date and/or increasing their clutch size (reviewed by Davies & Lundberg 1985, Daan *et al.* 1988). The mechanism by which nutrition proximately controls these reproductive decisions remains unknown. Drent & Daan (1980) have theoretically distinguished two possible pathways in which food determines (a) the rate of energy storage in the body prior to breeding, which in turn affects both laying date and clutch size (the capital model), or (b) the rate of energy supply during

laying (the income model). For an operational distinction between these models, they suggested to experimentally supply late breeders with extra food: the income model would predict larger clutches than the - submaximal - control clutches laid at the same time, the capital model would predict no change. The opposite experiment - reducing food supply - is not generally feasible in natural conditions, but can readily be performed in birds showing normal reproductive behaviour in captive conditions. We have used both approaches to analyse the proximate role of food in reproductive decisions of the Kestrel.

Kestrels show a characteristic seasonal decline in clutch size, over a range of laying dates of about 70 days. The earliest breeders in NW-Europe start in late March with a clutch of six or seven eggs, the latest pairs lay three or four eggs in early June (Cavé 1968, O'Connor 1982, Dijkstra *et al.* 1982, Village 1986, Beukeboom *et al.* 1987). A causal role for food supply in determining both date and clutch was suggested by strong positive correlations with vole densities (Cavé 1968), as known indeed in many other raptors (Mebs 1964, Hagen 1969, Southern 1970, Lundberg 1981, Wijnandts 1984, Pietiäinen *et al.* 1986, Simmons *et al.* 1986, Korpimäki 1986a). We have shown elsewhere that vole indices and reproductive behaviour are both correlated with body mass of female Kestrels, whether studied during egg laying, incubation or rearing of the nestlings (Dijkstra 1988). Although predicted by the capital model, such correlations do not prove that female condition is indeed causally involved in determining laying date and clutch size in response to food supply. It is thus of interest to analyse the detailed pattern of female body mass change during surplus food experiments. We analyse these patterns along with the reproductive responses (date and clutch) in relation to four types of treatment: early and late feeding in free-living Kestrels and *ad libitum* fee-

ding and food rationing in captive pairs. For obvious reasons, our data on body mass are less complete for the field experiments than for those in captivity. Better condition of the earliest breeders would also be anticipated by those who argue that laying date and clutch size variation primarily represent genetic differentiation between individuals, which is also reflected in parameters associated with condition (Toft *et al.* 1984). It is therefore important to analyse at the outset how reproductive decisions vary within individuals and interindividually: from year to year, with age, and with variation in vole density indices.

2. METHODS

The study was performed in the Lauwersmeer (53°20' N, 6°16' E) and in the laboratory in Haren nearby. The field study area, its Kestrel population, and the general annual cycle of the Kestrel have been described by Masman *et al.* (1988). The determination of age (juveniles, yearlings and adults) and body mass of the Kestrels was described by Dijkstra *et al.* (1988). We have reduced each measurement of body mass to the morning value to account for systematic variation with time of day. Reproductive behaviour - laying date (*i.e.*, date of the first egg) and clutch size - was determined in regular checks of the nestboxes. In some cases clutches were found when already complete, and laying date was determined by backward calculation from the hatching date. We number dates starting with January 1st=1.

Two different surplus feeding experiments were carried out in the Lauwersmeer from 1978 till 1986: Early and Late Feeding. Early Feeding started at a time of year when sufficient Kestrels were present in the area, either paired or unpaired, to establish an experimental and a control group. From the start (day 57±21) each experimental pair was offered 60 g/bird/day dead white laboratory mice in its nestbox. The food was given every two days and the nestbox was checked each time to see if the food had actually been eaten. By direct observations and by finding white regurgitated pellets it was established that the local Kestrel pair which occupied the nestbox indeed consumed the food. Surplus feeding was stopped when the clutch was certainly completed, usually 12 or 14 days after the first egg had been laid. Late Feeding started in the beginning of May (day 121±2) and concerned only Kestrel pairs which had not yet started a clutch. Otherwise procedures were identical with those in Early Feeding.

Kestrel pairs have been held in captivity in rearing pens in Haren since 1982. Both wild caught and in captivity reared birds were used in breeding pairs. They were housed in separate outdoor cages (2x1.5x2 m), visually screened from each other and from the surroundings. Each cage was equipped with a nestbox (40x50x40 cm) with sand, three perches and a waterbath. Entrance to the cages was from a dark alley, from which observations through one-way screens could be made. All birds were fed daily in the afternoon with *ad libitum* rations of house mice or 1-day old cockerels, supplemented with a vitamin-mixture (Carnicon R). In 1983 (from 1 Jan to 27 Apr), in 1985 (from 14 Feb to 9 May), and in 1986 (from 1 Jan to 9 May) half of the pairs (n=3, 5 and 5, respectively) received reduced daily rations of food over a long period preceding the breeding

season. All birds were weighed at least once every week with a Pesola spring balance to the nearest gram.

3. RESULTS

3.1. LAYING DATE AND CLUTCH SIZE

Year to year variations

As a basis for analyzing the effects of food additions in the wild and of food rationing in captivity we first analyse natural variations in laying date and clutch size in the Kestrel. The yearly means of clutch size and laying date vary in accordance with the general negative correlation between individual data. In the 16 years for which data were available from both Cavé's and our own study the mean laying date varied from day 106 (16 April 1965) to day 144 (24 May 1962, Fig. 1). As Cavé (1968) already observed, these variations in mean laying date are correlated with indices of vole abundance and with weather conditions during winter and early spring. In The Netherlands Kestrel laying dates are earlier following less severe winters - indexed by the Hellman number, *i.e.* the winter sum of all sub-zero mean daily air temperatures at the weather station in De Bilt - and at higher common vole densities (Table 1). In early years relatively large clutches were produced, in late years small clutches. All annual means of lay-

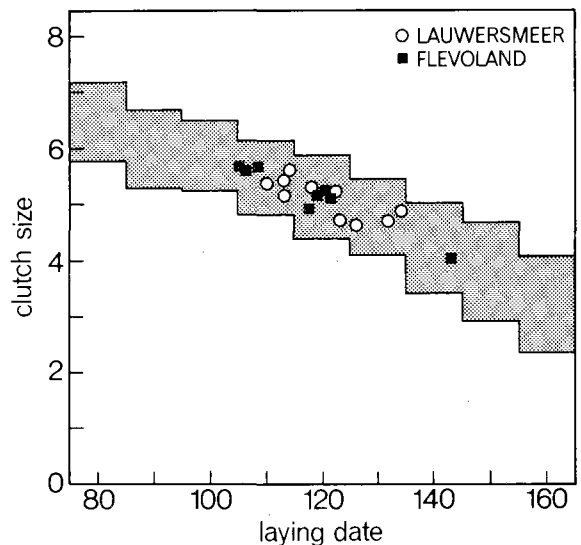


Fig. 1. Mean yearly clutch size as a function of laying date for the two study areas: Flevoland (squares) and Lauwersmeer (open dots). Shaded area represents mean \pm s.d. for all data (n=697, Beukeboom *et al.* 1988) in intervals of ten days.

Table 1. Average yearly laying dates and clutch sizes (\pm s.d.) in Flevoland and Lauwersmeer compared with vole index and winter temperature index (Hellman number, *i.e.* integrated subzero daily mean air temperatures at De Bilt in the preceding winter). Vole index: +: vole breakneck trap census in winter and spring above seasonal average; -: idem below average; ?: no census data available; (): high or low year based on data not strictly comparable with census. For the Lauwersmeer area there is a significant correlation between mean laying date and Hellman number h ($d=113+0.094xh$, $r=0.83$, $p<0.01$, $n=10$).

Area	Year	Laying date (1st egg)	Clutch size	n	Vole index	Hellman number
Flevoland	1960	107 \pm 15	5.62 \pm 0.95	95	+	42
	1961	118 \pm 12	4.95 \pm 0.80	97	+	25
	1962	144 \pm 10	4.03 \pm 0.98	29	-	83
	1963	122 \pm 12	5.24 \pm 0.91	42	-	346
	1964	109 \pm 10	5.60 \pm 0.66	73	+	109
	1965	106 \pm 14	5.61 \pm 0.86	61	?	60
	1985	121 \pm 11	5.24 \pm 0.70	41	?	194
	1986	122 \pm 11	5.11 \pm 0.84	54	?	149
Lauwersmeer	1977	114 \pm 14	5.42 \pm 0.90	19	(+)	19
	1978	127 \pm 15	4.59 \pm 0.94	17	(-)	44
	1979	133 \pm 12	4.67 \pm 0.78	12	(o)	206
	1980	115 \pm 11	5.53 \pm 0.70	19	(+)	47
	1981	111 \pm 13	5.35 \pm 0.94	26	o	40
	1982	124 \pm 14	4.69 \pm 1.01	26	-	127
	1983	120 \pm 17	5.30 \pm 0.95	33	+	24
	1984	114 \pm 12	5.14 \pm 0.88	29	+	36
	1985	135 \pm 12	4.83 \pm 0.84	12	-	194
	1986	123 \pm 11	5.25 \pm 0.91	20	+	149

ing date (d) and clutch size (c) were within one standard deviation from the 10-day interval means for all our data (approximated by $c=9.90-0.040xd$; $n=697$, based on data in Beukeboom *et al.* 1988).

With respect to the mechanism of the adaptive response to food and weather conditions, it is important to ask whether Kestrels laying at the same date differ in clutch size in early versus late years. For this analysis we divided the years into two groups: early years with a mean laying date before day 121 (May 1) and late years with a mean laying date after day 120. In late years no females started laying between day 75 and 95, against 56 females in early years, so that no comparisons can be made for very early clutches. In the other ten day intervals (Fig. 2), we did not observe any difference between the early and late years, except day 116-125, where clutches were slightly larger in early years (two tailed t -test, $p<0.05$). Thus with variations in winter food and temperature conditions Kestrel laying date-clutch size combinations shifted back and forth along an oblique trajectory.

Variation with age

One might presume that younger birds reproduce at a later date and lay fewer eggs than older birds - as is the case in the Mute Swan *Cygnus olor*

(Reynolds 1972) - and that variations in mean laying date and clutch size between years actually reflect changing proportions of adults and yearlings in the breeding population. However, yearling females initiate clutches over the whole season as do adult females, and in none of the ten-day intervals a difference between yearling and adult

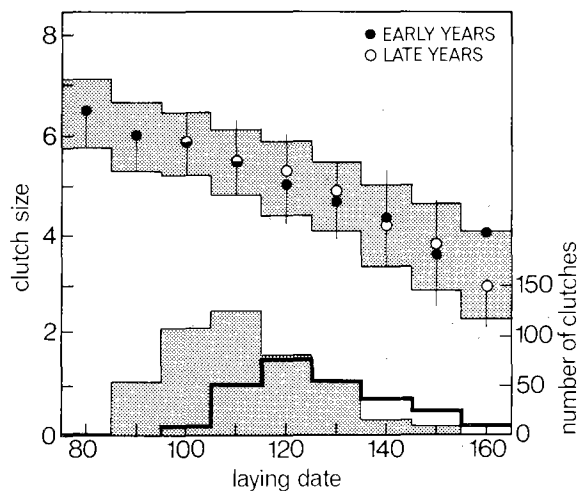


Fig. 2. Number of clutches initiated and mean clutch size (\pm s.d.) in early (dots, mean laying date before day 121) and in late years (open circles). Shaded area as in Fig. 1.

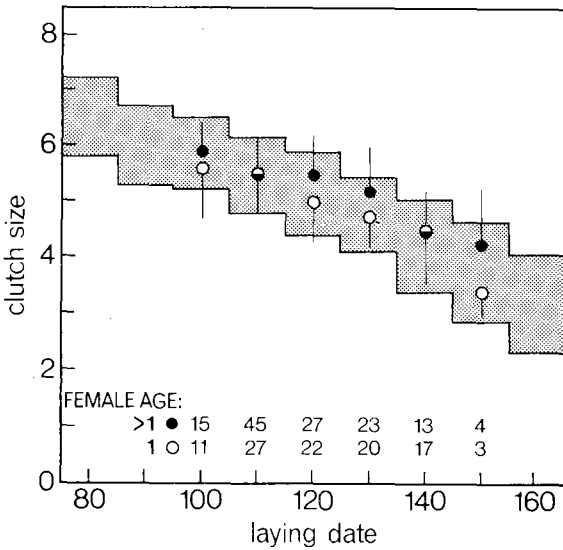


Fig. 3. Mean clutch size (\pm s.d.) of juvenile (open circles) and adult (dots) females as a function of laying date. Shaded area as in Fig. 1.

females was found (Fig. 3). The regression of clutch size (c) on laying date (d) is indistinguishable between the two age groups ($c=9.1-0.033xd$ for yearlings, and $c=9.1-0.031xd$ for adults). There is thus no evidence for age as a primary factor deter-

mining both clutch size and laying date.

Intra-individual variation

The next question to be addressed is whether the distributions of clutch size and laying date come about by consistent interindividual variations: some individuals always laying early and large clutches and others tending to produce late and small clutches. This problem is traditionally approached by calculating 'repeatabilities' which are thought to reflect degrees of genetic fixation of the behaviour (Van Noordwijk *et al.* 1981). In contrast with the usual interpretation, repeatability may come about by any phenotypic response mechanism, just as well as by genetic determination. Kestrels have for instance a strong site fidelity. Breeding in the same territory will tend to expose individuals to situations which are more similar than expected with random redistribution and hence may elicit greater than chance intra-individual correspondence between clutch size and date in consecutive years. Be this as it may, repeatabilities in the Kestrel are not significantly different from zero: 0.19 (n=54) for clutch size and 0.00 (n=58) for laying date, respectively. This result suggests that we may treat multiple observations of the same individuals as essentially independent.

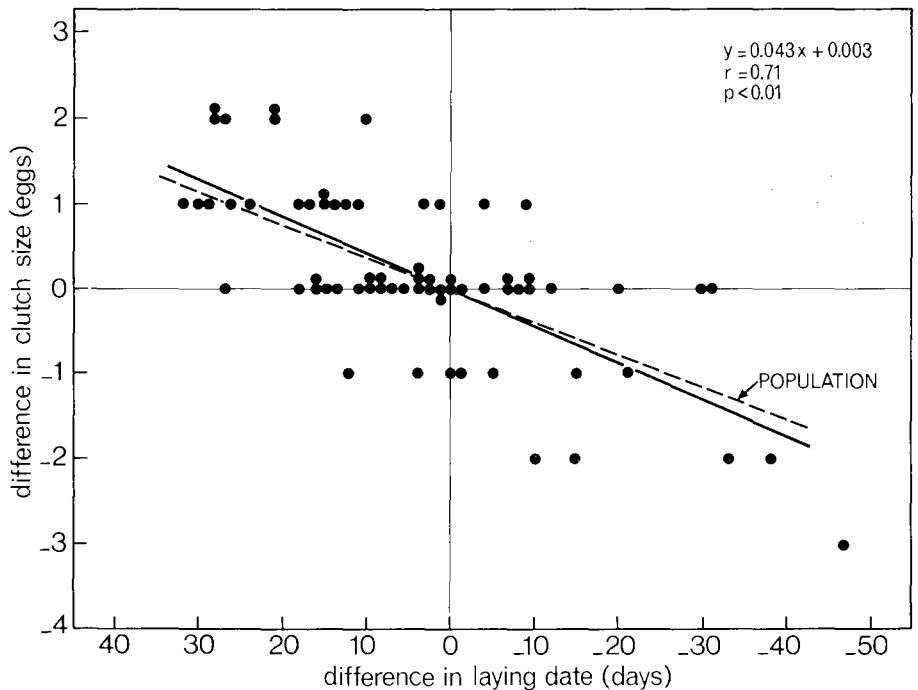


Fig. 4. Relation between the shift in laying date and in clutch size for individual females, breeding in two successive years. Dashed line is the regression of clutch size on laying date for the whole population, with slope (0.040) through the origin.

A more powerful analysis addresses the simultaneous year-to-year variability in both laying date and clutch size. Data of individual females which reproduced in more than one year showed a change in laying date associated with a change in the number of eggs, which corresponded closely to the overall seasonal decline (Fig. 4). Females which laid earlier in year x than in year $x-1$ tended to produce a larger clutch, those which laid later to produce a smaller clutch. Changes in laying date from year to year were up to 50 days and the maximum change in number of eggs between two years was three. The mean difference in clutch size with laying date difference was one egg per 23 days. Differences in laying date of the same female between years may have been caused by many factors: changing vole densities, change of partner or territory or both, or chance variations in arrival time in spring. The important result is that all such variations in date resulted in an associated change in clutch size, and that hence the relation between clutch size and laying date reflect intra-individual variations in phenotypic response, and not merely variation between genetically different individuals.

Thus in all of these comparisons, between different areas (Lauwersmeer and Flevoland), between early and late years, between juvenile and adult females and intra-individually in consecutive years, there was a consistent combination of laying date and clutch size. For a better understanding of

this relationship we now turn to the experimental food manipulations both in the field and in the laboratory.

3.2. FOOD EXPERIMENTS: EFFECTS ON REPRODUCTION

Early Feeding

During five years (1978, '79, '80, '85 and '86) half of the Kestrel pairs that were in the Lauwersmeer at the end of the winter received surplus food every two days. Visual observations confirmed that during the feeding experiment the males decreased their daily hunting time. Some males stopped hunting completely, so that the pair lived exclusively on the mice we offered. The effects of surplus food on reproduction for the first three years have been published by Dijkstra *et al.* (1982). The analysis of all data together show that the experiment resulted in a significant 10 day advance in laying date of the pairs which received surplus food (Table 2, Fig. 5). However, the date effect was dependent on the natural food situation. In years with high vole density there was no difference between mean laying date of the experimental and control group. In years with low vole density experimental clutches were advanced on average by 21 days relative to controls. This suggests that only in low vole years natural food abundance may have been low enough in control pairs to postpone their laying date relative to the experimental pairs. Mean

Table 2. Mean (\pm s.d.) laying date (A: day of the year) and clutch size (B) of control and experimental pairs (n) in the Early and Late Feeding experiment. The Early experiment is divided in low and high vole years (– and + in Table 1). * = three females in this group did not lay eggs. Differences between experimental pairs, control pairs and expected clutch sizes tested by Wilcoxon's signed-ranked test, two tailed.

	Early Feeding		Late Feeding	
	Vole abundance		all years	all years
	high	low		
A control	112 \pm 8(18)	126 \pm 13(18)	119 \pm 13(36)	138 \pm 7(19)*
experiment	115 \pm 5(5)	105 \pm 11(8)	109 \pm 10(13)	132 \pm 6(14)
p	>0.1	<0.001	<0.01	<0.05
B control	5.7 \pm 0.6(17)	4.9 \pm 1.1(17)	5.3 \pm 1.0(34)	4.4 \pm 0.8(19)
experiment	5.6 \pm 0.9(5)	5.5 \pm 0.5(6)	5.5 \pm 0.7(11)	4.8 \pm 0.7(13)
p	>0.1	>0.1	>0.1	<0.05
expected clutch size experimental birds	5.3	5.7	5.5	4.6
experim. vs expected clutch size p	>0.1	>0.1	>0.1	>0.1

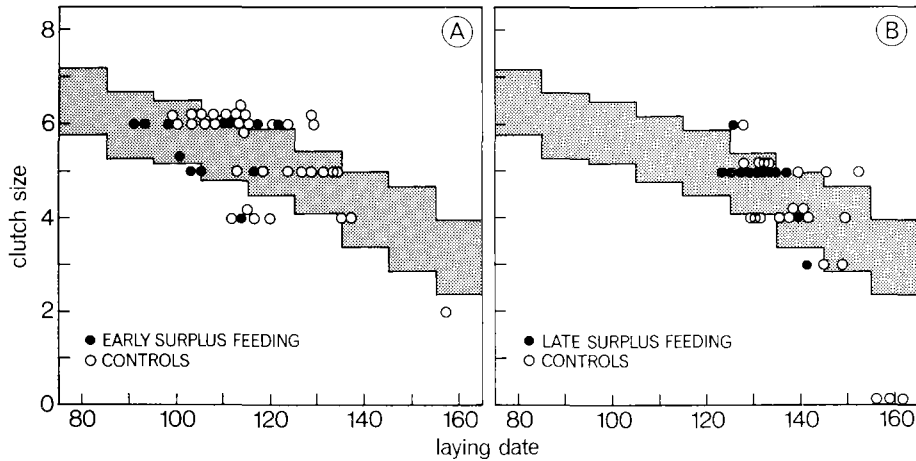


Fig. 5. Clutch size and laying date for free-living pairs receiving surplus food (dots) in the Early (A) and Late (B) Feeding experiment, compared with control birds (open circles). Shaded area as in Fig. 1.

clutch sizes differed between experimental and control group as expected on the basis of laying date, although these differences were insufficient for statistical significance (Table 2).

Late Feeding

During the intervening years 1981, '82 and '83 we carried out a feeding experiment in the second half of the season, to address the question whether in late pairs the small clutch is itself due to restricted food supply, independent of laying date. Beginning in the first days of May surplus food was offered to half of the pairs which had not yet started laying at that time. There was a significant advance of 6 days in mean laying date in the experimental females relative to controls (Table 2). No differences were found between years with high and low vole densities. In the control group three females did not lay. The females with extra food laid on average 0.4 eggs more than the controls, excluding the non-breeders ($p < 0.05$). We compared the clutch sizes of the experimental group with the clutch expected at the same time of year. Again the clutch size followed the expected pattern without significant deviations (Table 2). However, if we compare mean clutch sizes of the experimental groups in Early and Late Feeding, there is a clear difference: late fed birds having smaller clutches (Table 2; MWU., $p < 0.02$). Since both groups received the same daily amount of surplus food - about as much as they would eat - this result supports the interpretation that excess food during egg laying does not cause the female to lay

extra eggs beyond those she would lay otherwise at that time of year (Fig. 5).

Food restriction

A third experiment was carried out with Kestrel pairs in captivity in 1983, '85 and '86. One group was fed continuously *ad lib.* with mice (80 g/day/pair) or chickens (150 g/day/pair), the other group was food rationed to ca 50 g/day/pair during late winter and early spring. The control group started laying between days 98 and 142. The experimental females did not lay as long as food restriction lasted. After restoring *ad lib.* feeding in early May, on average 16 days (± 11 ; $n=9$) elapsed until the first egg was laid. The experimental birds laid clutches smaller than the *ad lib.* birds (4.6 and 5.0 eggs respectively). Both groups laid on average as many eggs as expected for the time of year (Fig. 6).

3.3. FOOD EXPERIMENTS: EFFECTS ON FEMALE BODY MASS

Early Feeding

Females receiving extra food long in advance of the laying season, increased rapidly in body mass. Within a week such females weighed between 263-269 g, while unfed controls were on average 237-242 g (Fig. 7, Table 3). We compared body mass of the experimental group with other females which in the course of the years laid in the same period as the experimental ones, *i.e.* before day 125 (Fig. 5A). As Fig. 7 shows, there was initially

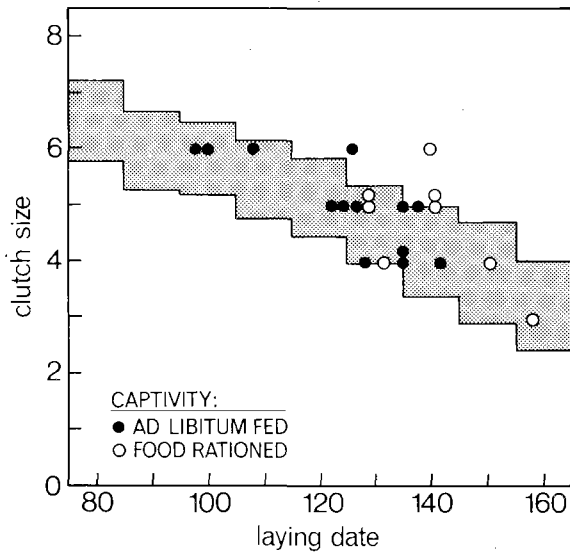


Fig. 6. Clutch size and laying date for captive pairs fed *ad libitum* (dots) compared with birds that were food rationed till early May (open circles). Shaded area as in Fig. 1.

a consistent 20-30 g difference between experimentally fed and unfed birds. With the approach of laying, mass differences between the groups gradually vanished. During the last 10 days of courtship and during laying there were no significant mass differences. After termination of the surplus feeding both groups had virtually the same mass for the next two months.

Late Feeding

Body mass data for this experiment are less complete than for Early Feeding for two reasons. Weighing scales in the entrance of the nestboxes to weigh the birds without disturbing them were still in a pilot stage when the experiment was done. Furthermore, birds started laying within one or two weeks after the start of the experiment, so that we obtained no body mass data for the remaining courtship phase and only two weighings during laying. Immediately after laying all birds were weighed however, and at this stage they were significantly heavier than unfed controls (one tailed t-test, $p < 0.05$). After termination of the surplus feeding there was a striking drop in body mass of the experimental females, so that the difference with the controls disappeared (Fig. 7B, Table 3). Experimental females had a mean body mass during laying (day 0-9 after the first egg) and during early incubation (day 10-19) which was not distinguishable from female body mass in the Early Feeding experiment. In spite of this similarity in body mass experimental females in the Late Feeding experiment laid 23 days later and produced a significantly smaller clutch (4.8 versus 5.5 eggs, Table 2).

Food restriction

The experiment in captivity allows documentation of female body mass in greater detail than the

Table 3. Mean body mass of control and experimental females for four 10-day intervals before and six intervals after the first egg (= day 0). Bold face indicates data obtained during the period of surplus food. If more than one weight was taken from a female in an interval her average weight was used. p-values for difference between experimental and control birds obtained by t-test (one tailed).

Interval		-40	-30	-20	-10	0	10	20	30	40	50
		-31	-21	-11	- 1	9	19	29	39	49	59
Early Feeding	mean	269	263	278	293	306	280	270	264	254	252
	sd	30	25	21	13	26	32	31	22	17	18
	n	4	4	5	5	6	9	7	6	7	4
Early controls	mean	237	242	247	288	301	279	273	274	260	241
	sd	23	22	18	21	24	24	28	20	22	23
	n	14	16	17	20	25	96	63	64	48	21
	p	<0.01	<0.05	<0.01	ns	ns	ns	ns	ns	ns	ns
Late Feeding	mean	219	242	211	—	300	280	254	264	236	—
	sd	11	—	24	—	25	17	26	16	—	—
	n	2	1	4	—	2	11	5	7	1	—
Late controls	mean	219	237	225	267	280	263	258	255	244	232
	sd	27	18	18	23	25	26	23	21	22	22
	n	6	8	22	15	18	46	33	32	14	11
	p	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns

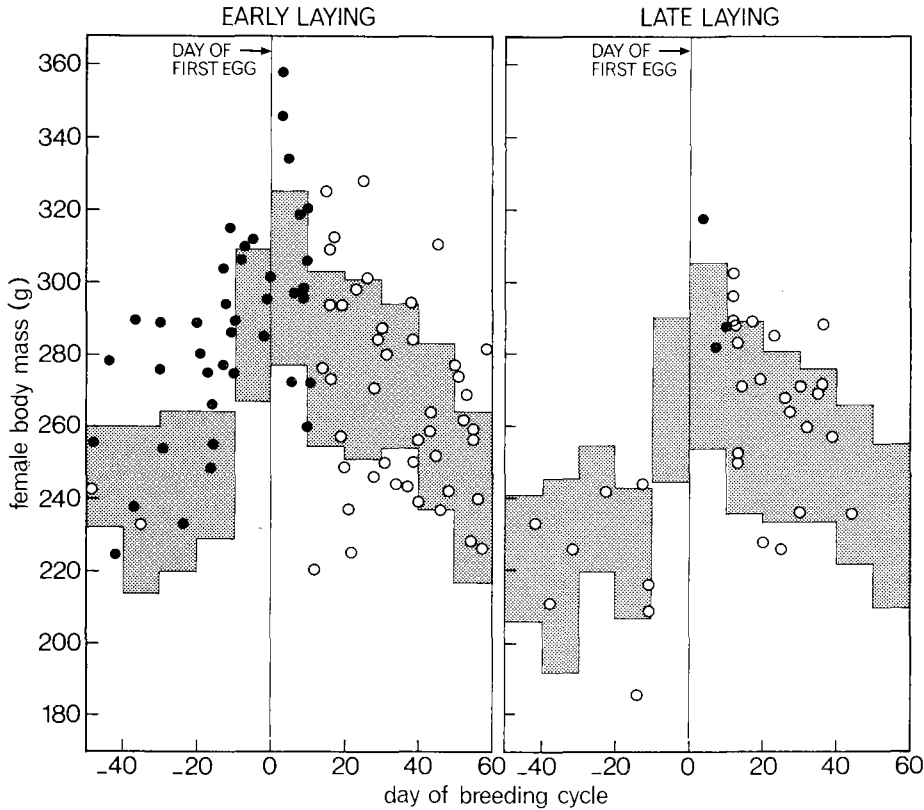


Fig. 7. Body mass of experimental females of the Early and Late Feeding experiment, during (dots) and after (open circles) the feeding period, compared with body mass of control birds laying in the same period (shaded area: mean \pm s.d. for that 10-day interval).

field experiments. In Fig. 8 we plotted the means (\pm s.d.) of body mass in three groups of birds: A. *ad lib.* fed Kestrels which spontaneously started laying in early April (mean day 101, $n=3$, Fig. 6), D. *ad lib.* fed birds which laid around mid May (mean day 131, $n=13$), and G. experimental birds for which food restriction was terminated on average around May 5 and which laid in late May (mean day 141, $n=9$). Clearly, group G retained low body mass all through the food restriction period, but restored their mass immediately upon termination of food restriction, gaining on average 99 g in 16 days. During egg laying, their body mass (mean 303 g) was not distinguishable from that of group D (mean 304 g), which also laid the same average number of eggs (means 5.0 versus 4.6 eggs, $p>0.05$). Interestingly, body mass during laying was again not different from the early laying group A (mean 308 g), all of which produced 6 eggs. During courtship, weights of the early fed birds in the field resembled strongly those of the females in captivity, which received *ad lib.* food (Table 3, Fig. 8).

Thus the field and laboratory experiments lead to the same conclusions: a. surplus food caused an advance in laying, while food restriction delayed laying; b. late breeding females made smaller clutches, even when brought into good condition by extra food; c. the natural pattern of laying date-clutch size combinations was unchanged by the experimental manipulations.

4. DISCUSSION

Individual response norms determine population variability

The available data show that body mass, laying date and clutch size are closely associated with each other as well as with food abundance. Particularly good evidence is available for Kestrels (Cavé 1968, O'Connor 1982, Dijkstra *et al.* 1982, 1988, Village 1986, Beukeboom *et al.* 1988, this paper Fig. 1 and Table 1) and other raptors such as the Buzzard *Buteo buteo* (Mebs 1964), Tawny Owl *Strix aluco* (Southern 1970), Ural Owl *Strix uralensis* (Lundberg 1981, Pietiäinen *et al.* 1986),

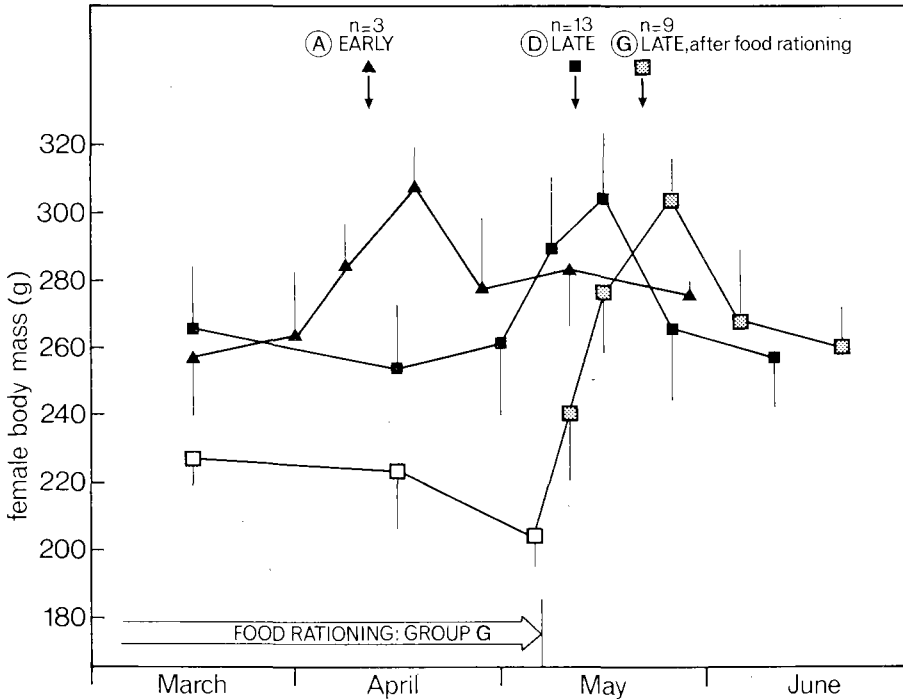


Fig. 8. Changes of female body mass (mean \pm s.d.) during the courtship, laying and incubation period for three groups in captivity: early layers (A), late layers (D) and birds that were food rationed till early May (G). Mean laying dates indicated with arrows.

Tengmalm's Owl *Aegolius funereus* (Korpimäki 1986a), and Northern Harrier *Circus cyaneus* (Simmons *et al.* 1986). We have suggested elsewhere that these associations reflect an adaptive avian reproductive response system (Daan *et al.* 1988). The experiments and measurements reported here allow us to analyse to what extent the correlations reflect causal mechanisms in this response system.

Important in this analysis is the notion that the variations in reproductive behaviour in the population reflect intra-individual phenotypic variability. Kestrels can lay eggs over a period of seventy days, from late March till early June. The variations observed are not simply age-dependent (Fig. 3). In consecutive years individual Kestrels shift their laying date back and forth, while at the same time changing their clutch size (Fig. 4). The relationship between clutch size and laying date in the population reflects the relationship within individuals. As different years vary in their food and weather characteristics, average laying date and average clutch size vary in tune with this individual response system (Fig. 1).

Food availability causes laying date-clutch size variations

While there is abundant correlative evidence for the association between food abundance on the one hand and avian laying dates and clutch sizes on the other, a causal role of food availability can only be established experimentally. That food is indeed causally involved in the Kestrels, emerges in the first place from the Early Feeding experiment. This started about 50 days before the first egg was laid. There was on average a 10 day advance in laying date for fed birds compared with their controls (Table 2). However there was a large effect of the actual food supply in the field. In years with high vole abundance fed and unfed birds laid almost on the same day, but in years with low vole abundance there was a three week difference. So it seems that only in poor vole years reduced food supply caused a delay in the moment of laying, and that the start of the breeding season by the earliest birds in rich vole years is restricted largely by some other proximate factor, possibly daylength. That even in rich vole years some clutches are initiated in May may be due to pairs in suboptimal habitats,

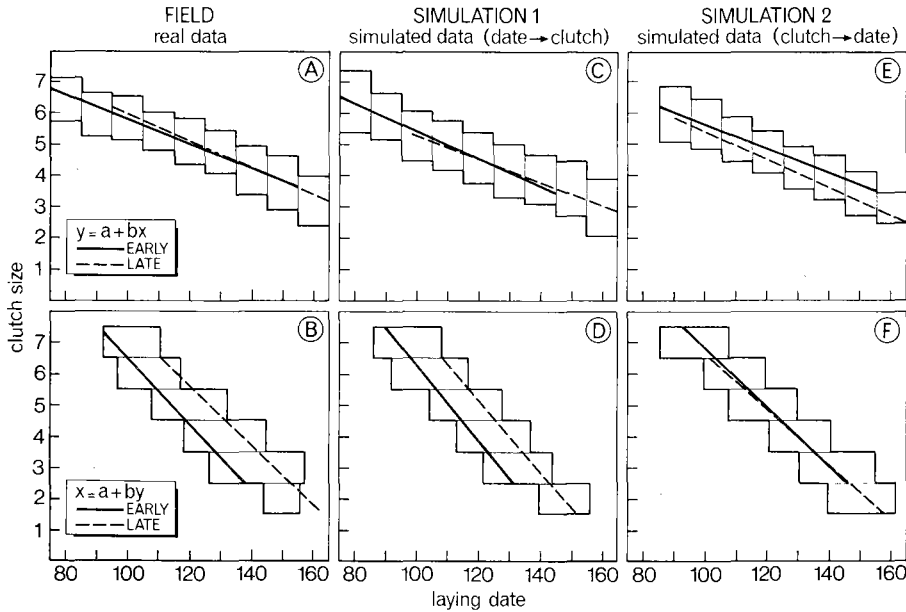


Fig. 9. Comparison between field (A,B) and simulated data (C,D,E,F) in early and late years for two different situations; laying date determines clutch size (upper panel) and clutch size determines laying date (lower panel).

some of which did not arrive in the area until late in the year. Our results agree with other feeding experiments, to which seven out of eight multiple-brooded passerine species responded with a significant advance in laying date: Great Tit *Parus major* (Källander 1973), Willow & Crested Tits *P. montanus* and *P. cristatus* (Von Brömsson & Jansson 1980), Song Sparrow *Melospiza melodia* (Smith *et al.* 1980), Red-winged Blackbird *Agelaius phoeniceus* (Ewald & Rowher 1982), Starling *Sturnus vulgaris* (Karlsson & Källander 1983) and Dunnock *Prunella modularis* (Davies & Lundberg 1985). Only the Robin *Erithacus rubecula* (Harper 1984, cited in Davies & Lundberg 1985) did not react to extra food. Among four single-brooded species only the Carrion Crow *Corvus corone* (Yom-Tov 1974) showed a significant advance in laying (4.8 days), while the Magpie *Pica pica* (Högstedt 1981, Hochachka & Boag 1987), the Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1981) and the Osprey *Pandion haliaetus* (Poole 1985) all showed a slight but insignificant advance. We surmise that the success of surplus feeding experiments may generally depend on the natural food supply in the territories where food is added.

Laying date determines clutch size, independent of food

The next question is: does food act on both

parameters independently? This is first clarified with a set of simulations. We know that for any particular laying date there is no difference between clutches produced in early and in late years (Fig. 2). Also, the linear regressions of clutch on date are indistinguishable for early and late years (Fig. 9A). If, on the other hand we would compare the average dates for clutches of any particular size, we would find that in late years the same clutches appear on average 13.3 days later. Accordingly, the regressions of laying date on clutch size are clearly different for early and late years (Fig. 9B). Two computer simulations were set up of 500 combinations of laying date and clutch size. In the first simulation it was assumed that laying date determines the clutch size. Within an early and a late laying group, 500 dates were drawn randomly from the observed distributions of laying date and then clutch size drawn randomly from the distribution around the overall regression ($c = 9.9 - 0.04xd$). In the second simulation the opposite assumption was made: clutch size (or some factor associated with it) determines the laying date. Here clutch sizes were drawn at random within a large and a small clutch size group, and then the corresponding dates drawn from the observed distribution around the regression $d = 175 - 11.1xc$. In both simulations two regressions were then calculated in the distributions generated: the regression of clutch size on laying

date and of laying date on clutch size. Simulation 1 gave results (Fig. 9C,D) which corresponded exactly to the real data (Fig. 9A,B). Simulation 2 gave results which strongly diverge from the real data (Fig. 9E,F). The simulations support the contention that it is the date of laying which determines the clutch size, and not vice versa. Proof for the causal role of laying date in determining clutch size comes again from experimental rather than correlative or simulation analysis. Both Late Feeding in the field and *ad lib.* feeding following rationed food supply in captivity showed that late laying kestrels produced submaximal clutches even when provided with as much food as they would eat during laying (Fig. 5B). Kestrels in the Late Feeding experiment received extra food from May 1 onwards and responded immediately to the extra food: they started laying after 12 days on average, but laid the expected number of eggs for the time of year. Those in captivity seemed to start immediately after the food restriction period (*i.e.* when *ad lib.* feeding was restored) with the formation of eggs as they laid on average within 16 days. Five females began laying within twelve or thirteen days, which is two or three days more than the total time required for the completion of egg formation (Meijer *et al.* 1988). Again their clutches were as expected for the time of year (Fig. 6). The Late Feeding experiment, suggested by Drent & Daan (1980) to distinguish between their capital and income models of date-clutch regulation, thus forces us to reject the income model which supposed independent effects of food on clutch and date. On the basis of surplus feeding experiments in the Sparrowhawk, Newton & Marquiss (1981) and Newton (1986) have suggested that food addition increased clutch size in this species independently of laying date. However, clutches of fed birds were only $0.346 (\pm 0.799, n=13, n.s.)$ eggs larger than mean clutches (Newton 1976) of unfed birds laying at the same date in the experimental area. Of all food experiments carried out to day (see also Daan *et al.* 1988) only the Song Sparrow has shown date-independent effects on clutch size, although this result is complicated by a density effect (Arcese & Smith 1988).

Laying date determines clutch size, independent of female condition

As shown by Dijkstra *et al.* (1988) female Kes-

tre body mass declines as a function of her laying date. This decline was observable in all phases of the reproductive cycle. The heaviest females laid the earliest and largest clutches. There is similar evidence for other raptors: Sparrowhawk (Newton & Marquiss 1984), Ural Owl (Pietiäinen *et al.* 1986), and Tengmalm's Owl (Korpimäki 1986b).

In Mallards and geese there is a positive correlation between the female's lipid reserve and the number of eggs laid, suggesting that clutch size is determined by stored lipids (Ankney & Mac Innes 1978, Krapu 1981). The decline in clutch size as the season progresses, appears to be related to exhaustion of lipid reserves. In these birds with precocial young, eggs are relatively large and during laying there is a large drop in weight, almost exactly corresponding to the total weight of the clutch. This holds also for the Mute Swan (Reynolds 1972, J. Beekman pers. comm.). In the altricial birds, like the Sparrowhawk, Ural Owl and Kestrel, the decrease in weight during laying is much smaller and only a weak correlation is found between body reserves and clutch size. For the Kestrel the mean clutch weighs $5 \times 21 = 105$ g while the difference between laying and incubation mass averages only 36 g and represents the loss of egg material and the regression of ovary and oviduct (Meijer *et al.* 1988). For the Sparrowhawk the weight difference is even smaller; 20 g for a total clutch of 180 g, although birds which produced late and small clutches had a greater weight loss (Newton & Marquiss 1984).

The Pied Flycatcher *Ficedula hypoleuca* (Silverin 1981), the Starling (Ricklefs & Husell 1984) and House Sparrow *Passer domesticus* (Pinowska 1979) resemble these other altricial species mentioned. In two other passerine species, the Red-billed Quelea *Quelea quelea* (Jones & Ward 1976) and the Grey-backed Cameroptera *Cameroptera brevicaudata* (Fogden & Fogden 1979), the build up of protein reserves seems to be the proximate factor controlling the onset of breeding. The decline in protein reserves during the laying phase is again small in relation to the total amount needed for the formation of a clutch (15 and 13% respectively), and it is unlikely that the condition of the female controls clutch size (Fogden & Fogden 1979). Thus, the available literature suggests a broad variation in the contribution of body reserves toward clutch size determination. Several

authors have suggested similar models to account for the seasonal associations between body mass, laying date and clutch size (Reynolds 1972, Drent & Daan 1980, Newton & Marquiss 1984). We can now use our experimental data to analyse whether female condition in Kestrels is indeed causally involved in determining clutch size independent of laying date. Fig. 10 summarizes the data on body mass, clutch size and laying date in our various experimental and control groups. The seasonal decline in body mass in unmanipulated Kestrels is reflected in the difference in body mass between groups C and F during both laying and incubation. The three late experimental groups (D and G in captivity, E in the field) exceeded group F in body mass, and were not statistically distinguishable from the early layers (group A, B and C). Nevertheless, they laid submaximal clutches, as

expected at the time of year. Thus, while all the available evidence points to close associations between body mass and reproduction, the experiments show that body mass in Kestrels is not causally involved in determining the small clutches of late breeders.

The data presented here for laying date and clutch size in Kestrels in combination with detailed information concerning body mass of the females do support neither the income model (rate of energy supply during laying determines the clutch size) nor the capital model (condition of the female determines the clutch size) of Drent & Daan (1980).

In support of their general theory, we have established the causal chain: food \rightarrow laying date \rightarrow clutch size. Female condition depends on food but does not immediately control clutch size in the Kestrel. Whether condition determines laying date is still open to investigation. If it does, the body reserve level which triggers reproduction is higher early in the year than late in the year - in accordance with the capital model (Reynolds 1972, Drent & Daan 1980, Newton & Marquiss 1984). The distinction between rate of food intake (income) and body reserves (capital) as triggers for the onset of reproduction requires a detailed analysis of the energetics of female birds (Meijer *et al.* 1988).

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6. SUMMARY

Experiments on free-living and captive Kestrels were set up to investigate the effect of food and condition on laying date and clutch size, and to distinguish between the income and capital models of Drent & Daan (1980).

Kestrels showed the same seasonal decrease in clutch size in different areas (Flevoland and Lauwersmeer) and in different years (early and late). Juveniles and adults had the same distribution of laying dates and laid the same number of eggs in any particular date interval. The seasonal decline in clutch size found between individuals was also found within individuals, breeding in different years. Feeding experiments in the field,

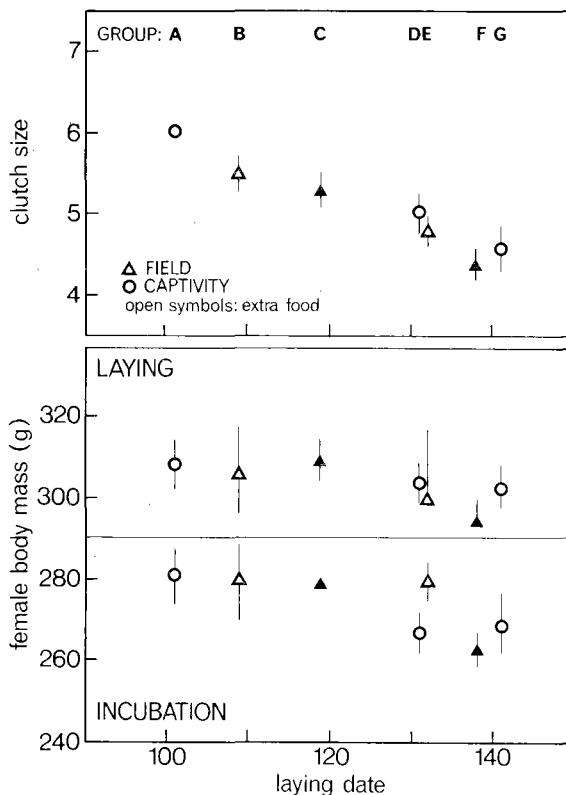


Fig. 10. Mean clutch size and mean body mass (\pm s.e., during laying and early incubation) of free-living females in the Early and Late Feeding experiment (group B + E, and group C + F: controls), and of captive females (laying early: group A, late: D and after food rationing: G)

early and late in the breeding season, advanced the mean date of laying by 10 and 6 days respectively, compared with controls. However, the advance depended on the actual food situation: in low vole years experimental birds laid three weeks earlier than controls, in high vole years experimental and control birds had no significant difference in laying date. The advance in laying date was associated with a change in the number of eggs, and clutch size did not deviate from the expected size for the date. Food experiments in the laboratory supported these findings: food supply had a direct effect on the date of laying but not on the number of eggs.

Body mass of laying females with surplus food was higher than in their controls (specially of late breeders) and did not vary with date over two months, still late surplus fed breeders laid smaller clutches. The data do support neither the income model (rate of energy supply during laying determines clutch size) nor the capital model (condition of the laying female determines clutch size). We propose that food availability determines the laying date and the number of eggs is determined by date itself. Whether body mass as an indicator of condition is causally involved in determining laying date or is merely correlated with food supply can not presently be established.

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8. SAMENVATTING

Aan vrijlevende en in gevangenschap gehouden Torenvalken werd het effect van voedsel en conditie op legdatum en legselgrootte onderzocht, tegen de achtergrond van het income (voedselopname tijdens de leg bepaalt de legselgrootte) en capital model (conditie van het leggende vrouwtje bepaalt het aantal eieren) van Drent & Daan (1980).

Een afnemende seizoenstrend in legselgrootte werd gevonden in verschillende gebieden (Flevoland en Lauwersmeer), in verschillende jaren (vroeg en late) en bij vrouwtjes met verschillende leeftijden (juvenile en adulte). Deze trend bestond ook binnen dezelfde individuen, broedend in verschillende jaren.

Bij voedselexperimenten in het veld – vroeg en laat in het broedseizoen – legden valken resp. 10 en 6 dagen eerder dan niet bijgevoerde paren. De verschuiving in legdatum was afhankelijk van het actuele voedselaanbod. In jaren met veel veldmuizen was er geen verschil in legdatum tussen controle en experimentele paren, in jaren met weinig muizen legden de bijgevoerde valken 3 weken eerder. Verandering in legdatum ging gepaard met een verandering in legselgrootte, maar deze verschilde niet van de verwachte legselgrootte voor die datum. Voedselexperimenten bij paren in gevangenschap hadden een effect op de legdatum, niet op het aantal eieren dat gelegd werd. Gedurende april en mei was er geen verschil in leggewicht tussen bijgevoerde vrouwtjes in het veld en *ad libitum* gevoerde vrouwtjes in gevangenschap. Laat bijgevoerde vrouwtjes waren tijdens de leg zwaarder dan hun controles, maar maakten ook een kleiner legsel. Deze resultaten ondersteunen noch het income model noch het capital model. We veronderstellen dat voedselaanbod bij Torenvalken de legdatum bepaalt en dat het aantal eieren bepaald wordt door de datum zelf. Onduidelijk is nog of lichaamsgewicht – als indicator van conditie – oorzakelijk betrokken is bij de bepaling van de legdatum of slechts gecorreleerd is met voedselaanbod.