ENERGETICS OF REPRODUCTION IN FEMALE KESTRELS

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ABSTRACT.—The breeding cycle of individual pairs of Eurasian Kestrels (*Falco tinnunculus*) started with an extension of male hunting time, followed by an increase in hunting yield. Both early- and late-breeding males hunted ca. 3 h/day, but had different hunting yields. In late-breeding males, increase in hunting yield was slower and started later in the season than in early males. Females stopped hunting during courtship and were fed by the males until the young were 10 days old. In the 2 weeks before laying, there was a 70-g rise in female body mass (64% was due to accumulation of body reserves; the remaining 36% was due to development of oviduct and eggs).

Experiments with lipophilic dyes showed that eggs developed in 9 days. Rapid growth of the follicles lasted 7 days; and the formation of egg membranes, albumen, and shell lasted 2 days. Total energetic content of an egg was 99.7 kJ, partitioned between yolk (65.0 kJ) and albumen (34.7 kJ). Daily costs of egg formation were similar for large and small clutches, but were extended at the maximum level for two more days for every extra egg laid.

During courtship and egg laying, late-breeding females had a 23–35% lower food intake and a 5% lower body mass than early breeders. Lower energy intake of late females corresponded with lower maintenance and thermoregulation costs. Late females had 33% lower body reserves than early females and were therefore less buffered against episodes of food shortage. Time of breeding for individual pairs seems to be regulated by proximate energetic limitations in the female combined with her declining body mass, and by the courtship strategy of the male. *Received 29 April 1988, accepted 10 April 1989.*

FOOD supply is a strong environmental determinant of onset of reproduction in birds. Field experiments performed with surplus food have, from the very first (Källander 1974), generally advanced laying in experimental vs. control birds (Davies and Lundberg 1985, Daan et al. 1988). In addition to its role as an important ultimate factor in the timing of avian reproduction (Lack 1968), food availability acts as a proximate factor. Several authors have considered food as a factor that limits the capacity of females to produce eggs (Perrins 1965, 1970; Lack 1968; Yom-Tov and Hilborn 1981). Others have emphasized that food availability may trigger reproductive behavior just as photoperiod, without involving energetic constraints on laying (Drent and Daan 1980, Daan et al. 1988). This distinction is important in the development of models of reproduction, where energetic constraints on egg production would severely affect the predictions. In order to establish whether or not energetic constraints operate, it is necessary to evaluate the energetic costs involved in the production of clutches of different size, as well as the rates at which energy can be obtained.

In a study on the temporal organization of behavior in the Eurasian Kestrel (*Falco tinnunculus*; Rijnsdorp et al. 1981, Daan and Aschoff 1982, Masman 1986, Dijkstra 1988, Meijer 1988), we analyzed the energetic costs of reproduction. Energy intake of free-living birds was compared with doubly labeled water measurements of energy turnover in captive birds. Female kestrels stop hunting completely during courtship until the young are 10 days old. The male provides the food for both the female and the brood. We studied male hunting behavior in association with female reproductive behavior. We present data on hunting time and hunting yields of males, number of prey delivered to females, and food intake by females during courtship, laying, and incubation. We analyzed the patterns of energy turnover in relation to the timing of egg laying and clutch size, and compared specifically pairs laying early or late, large or small clutches.

METHODS

We established energy intake by female kestrels during reproduction by dawn to dusk observations

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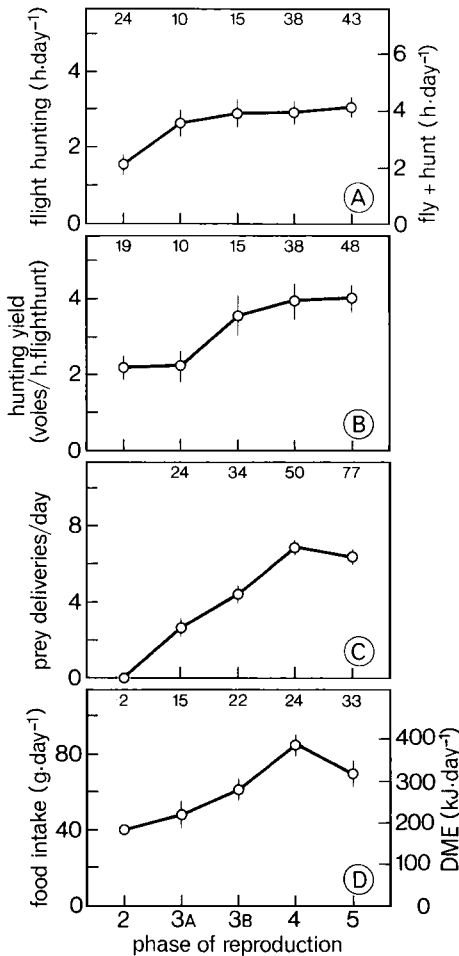
Fig. 1. Hunting time (A), hunting yield (B), prey deliveries to female (C), and female food intake (D) during the early phases of the reproductive cycle ($\bar{x}$ ± SE).

of focal birds in the Lauwersmeer (53°20'N, 6°16'E), The Netherlands. The area, kestrel population, and general methods are described by Rijnsdorp et al. (1981) and Masman et al. (1986; 1988a, b). Energy intake was estimated with the method of Masman et al. (1986), which involves prey mass estimates based on handling time and measurement of prey energy content and assimilation quotient in laboratory trials. For the present study, we used 96 full-day observations made in 1977–1986. On these days, the bird was observed >70% of the active day (i.e. civil day length − 0.71 h) and the bird was in sight for >70% of the observation time. Male hunting behavior and prey transfer to the female were based on 130 full observation days. We also report on the rate of energy expenditure by female kestrels breeding in captivity measured by doubly labeled water (DLW) turnover (Masman and Klaassen 1987).

We determined female body mass from trapped birds and with electronic balances mounted in the nestbox entrance. Analysis of body-mass data followed the procedures described by Dijkstra et al. (1988), which involve a standard correction for time of day, such that all data represent dawn weights. We distinguish four phases of the reproductive cycle. In Phase 2, male and female paired in winter or early spring. Phase 3 included courtship and male feeds female, and was separated into two parts: 3A (from 20 until 11 days before egg laying) and 3B (the last 10 days before laying). Phase 4 was laying, and Phase 5 was incubation and started 2 days before the last egg was laid. The other phases (1, 6–9; Masman et al. 1988b) are not relevant to the present paper. We analyzed data on male hunting time, hunting yield, rate of prey transfer to the female, and female food intake with respect to time of breeding. We divided the breeding population into three groups with different laying dates (Early: day 91 (1 April) to 110; Middle: day 111–130; and Late: day 131–150). Clutch sizes for the three date groups were 5.87 (±0.62), 5.15 (±0.73), and 4.29 (±0.91) eggs, respectively.

To investigate the temporal pattern of yolk deposition in the growing follicle, three captive females were given gelatin capsules of lipophilic dyes (Sudan Black B or IV Red) orally every 2 days before and during laying. These dyes bind to yolk lipoproteins and are deposited in the developing follicle in a discrete layer (Gilbert 1971, Teunis 1976) within a period of 24 h (Astheimer 1986). In 1985 one female was given a 50-mg capsule every 2 days from 14 days before egg laying until clutch completion; in 1986 the dose was reduced to 25 mg in two other laying females. After each egg was laid, it was removed, boiled for 15 min, and replaced by a dummy egg.

RESULTS

Female food intake.—To understand female energetics, it is appropriate to analyze first the behavior of the male, who provides female food. Males spent an average of 1.5 h/day in flight-hunt during winter, but they doubled this when they fed the female (Fig. 1A). The 3 h of hunting corresponded to 4 h of total flight, including flights to nestbox or female, and from one hunting area to the other. This is slightly less than the 4.6 h/day of total flight observed for males later in the breeding season when the young and the female are fed (Masman et al. 1988a). The hunting yield (number of prey caught per hour of hunt) increased from 2.2 in winter and early spring to 4.0 during incubation (Fig. 1B). The major increase occurred between early (2.3 prey/h) and late courtship (3.6 prey/h). The daily delivery of prey to the female increased
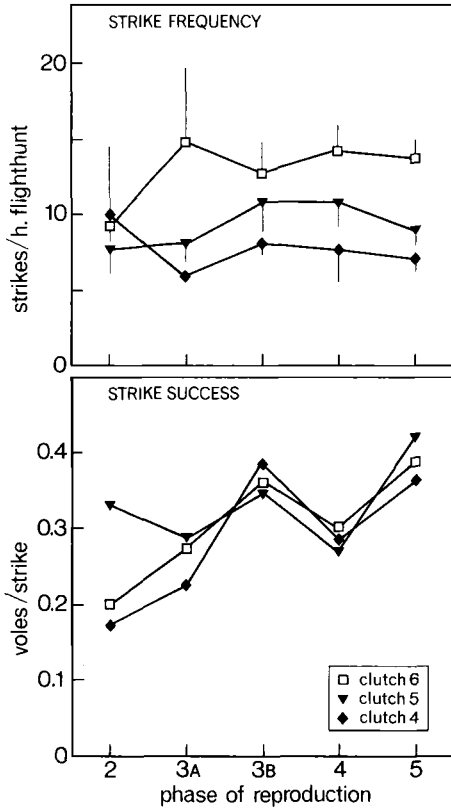
Fig. 2. Strike frequency (strikes/h flighthunt) and strike success (voles/strike) during the early phases of the reproductive cycle for males with 4, 5, and 6 eggs ($\bar{x} \pm$ SE).
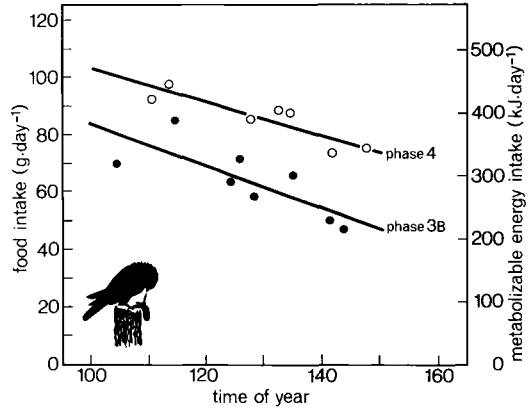

Fig. 3. Food intake (g/day) and metabolizable energy intake (kJ/day) of females during late courtship (phase 3B, linear regression: $y = 156 - (0.73 \cdot d)$, $r = -0.80$, $P < 0.01$) and laying (4: $y = 161 - (0.59 \cdot d)$, $r = -0.89$, $P < 0.01$), plotted against day (d) of year.

from 2.7 in early courtship to 6.9 during laying, followed by a slight drop to 6.4 during incubation (Fig. 1C). Mean mass of delivered prey decreased, from 14.06 g (± 2.11, $n = 22$) during late courtship to 12.45 g (± 2.35, $n = 23$) during laying and 9.83 g (± 2.80, $n = 32$) during incubation. This decrease was due to a higher percentage of young voles and shrews later in the season (see also Masman et al. 1986). More precise estimates of food consumed include food caught by the female herself before laying. During early courtship females still caught 33% of their own food (49.3 g), but this fell to 5% in late courtship. Laying females consumed 84.7 g/day and incubating females 71.2 g/day (Fig. 1D). When food intake was converted to daily metabolizable energy intake (DME), there was a peak DME of 388 kJ in laying females. This assumed 69.8% water in voles, 21.35 kJ/g dry mass for the months March through May, and an assimilation quotient of 0.71 (Masman 1986).

There was no systematic variation in male hunting time among the early, middle, and late laying groups. The hunting yield (strike frequency × strike success) started in all three groups at a level of 2.1–2.3 voles/h hunting, but increased earlier and faster in the Early Group. During incubation, the yield for the Early Group had increased to 5.5 (± 2.8, $n = 16$), and for the Late Group to 3.4 (± 2.1, $n = 7$). Strike frequency did not vary systematically over the breeding season (Fig. 2: upper), but was higher in early pairs with large clutches. The mean strike frequency for males with clutches of six eggs was 13.3 (± 5.7, $n = 54$ days) and for males with clutches of four eggs it was 7.5 (± 3.6, $n = 26$). Strike success increased from 0.26 during winter and early courtship to 0.40 during incubation, and was surprisingly similar for the three clutch size groups during all the phases investigated (Fig. 2: lower).

Energy intake by kestrels varied daily (Masman et al. 1986). We obtained more precise estimates of mean intake rates by combining two or more successive observation days per individual. We did this for eight females during late courtship (20 days) and for seven females during egg laying (19 days). There was an 88–112 kJ/day increase in food intake of individuals from late courtship to laying, and a significant seasonal decrease in food intake between individuals in the same phase (Fig. 3). Food intake in late females was 65% and 77% below that of early females during late courtship and laying, respectively.
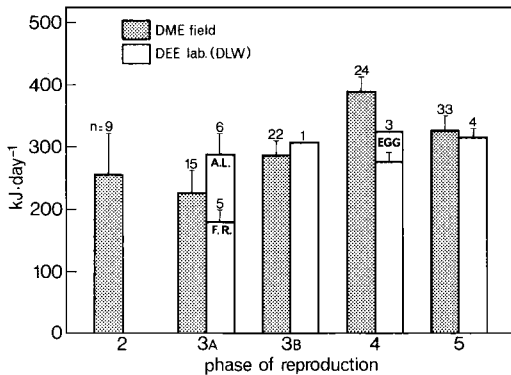
Fig. 4. Comparison between field data for daily metabolizable energy (DME) and laboratory data for daily energy expenditure (DEE, measured with DLW) of female kestrels in the early phases of the reproductive cycle. DEE in captivity was measured under food rationed (F.R.) and food *ad libitum* (A.L.) conditions during early courtship (Phase 3A).

We compared energy intake with DLW turnover for females that bred in captivity. From courtship until the nestling period, captive females had only minor differences in behavior and body mass compared with free-living birds (Dijkstra et al. 1988). The DLW method measures the energy expenditure (E_d), but does not account for energy deposited in the form of body reserves or egg material (D). D was added to E_d, to obtain an estimate of daily energy expenditure (DEE). DME determined from field observations on food intake and DEE determined by the DLW method on captive kestrels were similar (Fig. 4). In early courtship the DEE of captive females varied from 178 kJ (food rationed) to 287 kJ (food *ad libitum*). Free-living females, which experience both extremes due to weather and feeding conditions (see also Village 1983a), had an intermediate DME (226 kJ, $n = 15$). One difference between the two methods appeared during laying. Three captive females laid their first egg on 15, 15, and 17 May. The corresponding DME value for this period in the field was 374 kJ (Fig. 3). We calculated the deposited energy (D) for these laying females as $(50.2 + 50.2 + 17.3)/3 = 39.2$ kJ/day (see below). The difference between the DME and $E_d + D$ in the laying phase was still $374 - (273 + 39) = 62$ kJ. Two factors were responsible for this difference. First, 2 of the 3 DLW measurements were made during the first 2 days of the laying period, when incubation behavior was almost absent, in contrast to later on during

laying (Beukeboom et al. 1988). Second, increased water turnover during egg formation (Skadhauge 1981) leads to an underestimation of energy expenditure by the DLW method.

Overall, early males (with large clutches) hunted as hard as late males, made more strikes, and caught more voles. The hunting yield of the early males increased more rapidly than late males, and early males fed their females more and earlier in the breeding season. Thus, male hunting yield had a major influence on female reproduction.

Egg development.—Colored rings appeared in the yolk 11.5–9.5 days before the egg was laid ($n = 16$). Ring diameter was 17.8% (± 10.1, $n = 5$) of the yolk of a fully developed egg (diameter $= 20.83$ mm, $n = 6$), and corresponded to 0.6% of the total yolk volume. One captive kestrel, examined on 3 March (1 month before first eggs are normally laid), had follicles with a diameter of 3.0–4.0 mm, on average 16.8% of the total diameter. Similar values for the diameter of follicles prior to the rapid growth phase are reported in House Sparrows (*Passer domesticus*), 24% (Pinowska 1979); Pied Flycatchers (*Ficedula hypoleuca*), 28% (Ojanen 1983); Lesser Blackbacked Gulls (*Larus fuscus*), 14% (Houston et al. 1983); and Eurasian Rooks (*Corvus frugilegus*), 14% (Lincoln et al. 1980). We defined 9 days before laying the first egg as the start of the final growth phase, with an initial yolk diameter of 20%. No colored layers were deposited in the yolk <2 days before any eggs were laid, which indicated that ovulation had occurred and the ovum was in the oviduct. We estimated yolk mass deposition as 9% on day -9, and 15% on the 6 following days. Linear growth of the follicles during most of the rapid growth phase has been reported in the Black-headed Gull (*Larus ridibundus*; Weidmann 1956), the American Kestrel (*Falco sparverius*; Porter and Wiemeijer 1972), the Wood Duck (*Aix sponsa*; Drobney 1980), and a number of seabird species (Grau 1984). The egg albumen, the shell membranes, and the shell must be made during the last 2 days before laying (see Porter and Wiemeijer 1972). We assumed that on both days 50% of the albumen accumulated and that the shell was formed on the last day. Because kestrels lay 1 egg every 2 days, the second follicle enters the final growth phase on day -7, and the third on day -5, etc. Consequently, a female deposits material in up to 4–5 eggs simultaneously. The resorption of follicles begins ca. 4 days before

the last egg is laid (Beukeboom et al. 1988) and a female who lays 5 eggs, develops 7 follicles (see also Houston et al. 1983). Her sixth and seventh follicle enter the rapid growth phase on days 1 and 3, after which resorption starts (day 4; Fig. 5). We calculated the mass changes due to egg formation in a female laying 5 eggs (Table 1). By the last day before laying the first egg, the bird produced 19.5 g of egg material and accumulated another 12 g that day. Prior to laying, her mass had increased by 31.5 g because of the developing eggs.

The mean mass of 6 freshly laid eggs was 21.5 g ($\pm$1.8); this was divided among shell (2.1 g $\pm$ 0.2), albumen (14.8 g $\pm$ 1.5), and yolk (4.6 g $\pm$ 0.4). The caloric content of fresh albumen was 2.34 kJ/g and of yolk 14.29 kJ/g. Water content for yolk was 56.7% and for albumen 89.3%. The total albumen contained 34.66 kJ and the yolk 65.04 kJ, for a total of 99.70 kJ/egg. We estimated energy deposition for one egg at 5.9 kJ on day -9 and 9.8 kJ/day for the next 6 days, after which ovulation occurs. During the last 2 days, 17.3 kJ/day of albumen was added. For a clutch of 5 eggs, the daily energy deposited increases from 5.9 kJ on day -9 to 53.0 kJ on day -1, after which it gradually decreases to zero (day 8), the day the fifth egg is laid (Fig. 5). Assuming an efficiency of tissue production of 70% (Ricklefs 1974, Walsberg 1983), we estimated the daily costs. The daily peak energy needed to form a clutch of five eggs fluctuated on the last 2 days before laying between 68 and 76 kJ. This level was the same for clutches of six or seven eggs, because no more than five eggs are growing simultaneously (Fig. 5). During laying, the mean daily cost of egg formation for a female laying 6 eggs was 14.8% higher than for a female laying four eggs (63.5 vs. 55.3 kJ). The peak energy requirement for egg formation (72 kJ/day) represents 19% of the daily energy intake (388 kJ).

Female body mass.—Interindividual variation in energy balance of breeding females will be reflected in their body mass. In all phases (Table 2), body mass declined with later laying dates (see also Dijkstra et al. 1988 and Village 1983b). The difference between the early and late breeding group varied between 15 and 27 g and was smallest just before and during laying. The same body-mass changes in relation to breeding were found within individuals as shown in four free-living and one captive female (Fig. 6).

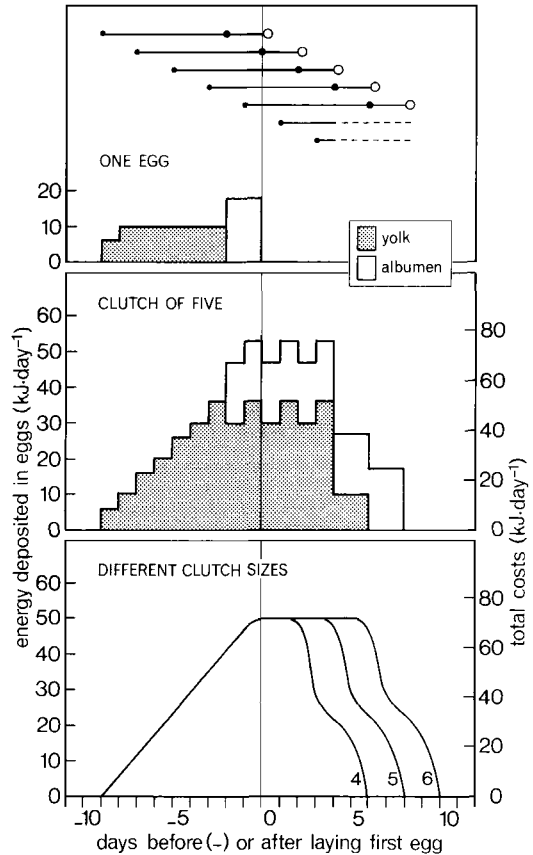Body mass was low during early courtship ($\bar{x}$

Fig. 5. Energy deposited and total costs (kJ/day) allocated to yolk and albumen, for one egg (upper), for a clutch of 5 eggs (middle), and for different clutch sizes (lower). The horizontal lines in upper panel represent the formation of a clutch of five eggs (per text).

= 234.2 g, Table 2) and increased by 45.1 g during the next 10 days. The observed weight gain included reproductive organs, egg yolk, and body reserves (surplus weight above that required for reproductive organs and eggs). We estimated each component separately. The nonovulatory ovary and oviduct were estimated as 6% of adult weight (Ricklefs 1974). We assumed that ovary and oviduct each account for 50% of this, or $0.5 \times 0.06 \times 234.2 = 7.2$ g. The ovary is functional long before the eggs are laid. Various authors have shown in raptors (including the Eurasian Kestrel [Cavé 1968]), that a slow development of the follicles occurs during autumn and winter (Lincoln et al. 1980, Lundberg 1981, Hirons et al. 1984). The oviduct in birds develops during the last period before egg lay-

TABLE 1. Weight changes due to egg formation in a female Eurasian Kestrel producing a clutch of 5 eggs.

	\-9	\-8	\-7	\-6	\-5	\-4	\-3	\-2	\-1	0	1	2	3	4	5	6	7	8
								Days in relation to laying first egg (day 0)										
Amount of yolk and albumen deposited per egg (g)																		
Egg 1	0.4	0.7	0.7	0.7	0.7	0.7	0.7	7.4	7.4									
2			0.4	0.7	0.7	0.7	0.7	0.7	0.7	7.4	7.4							
3					0.4	0.7	0.7	0.7	0.7	0.7	0.7	7.4	7.4					
4							0.4	0.7	0.7	0.7	0.7	0.7	0.7	7.4	7.4			
5									0.4	0.7	0.7	0.7	0.7	0.7	0.7	7.4	7.4	
6											0.4	0.7	0.7	resorbed				
7													0.4	resorbed				
Total grams deposited																		
Yolk	0.4	0.7	1.1	1.4	1.8	2.1	2.5	2.1	2.5	2.1	2.5	2.1	2.5	0.7	0.7			
Albumen								7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	7.4	
Shell									2.1		2.1		2.1		2.1		2.1	
Cumulative weight change																		
Body mass (g)	0.4	1.1	2.2	3.6	5.4	7.5	10.0	19.5	31.5	19.5	31.5	19.5	31.5	18.1	28.3	14.2	23.7	
Egg mass ($\bar{x}$)									−21.5		−21.5		−21.5		−21.5		−21.5	
Total									10.0		10.0		10.0		6.8		2.2	

ing (Drobney 1980, Walsberg 1983). Hutchison and Bendor (1968) measured an increase in oviduct mass in Common Canaries (*Serinus canaria*) from the moment the rapid follicle growth started. We assumed that the period of oviduct development occurs from 9 until 2 days before laying the first egg. Five days before laying, the oviduct would then account for 4.5 g, the yolk for 3.6 g, and the body reserves for 45.1 − (4.5 + 3.6) = 37.0 g. From 5 days before the first egg until 5 days after, there was a further increase in body mass (Table 2). This is attributed partly to oviduct completion (2.7 g) and accumulation of egg material (14.5 g; i.e. the difference between day −5 and day +5, Table 1). The remainder of the mass increase (7.5 g) represents body reserves. After laying, there is probably a rapid regression of oviduct and ovary (cf. Krapu 1981, Houston et al. 1983, Ojanen 1983, Ricklefs and Hussell 1984). In the kestrel this would decrease body mass 14.4 g (ovary and oviduct) and 18.1 g (egg material, Table 1). The total predicted weight loss of 32.5 g is slightly exceeded by the observed difference between laying and incubation (36.2 g, Table 2). We believe that the energy from reduction of reproductive tissue is not generally retained in further body reserves.

DISCUSSION

Variation in body mass.—Body mass changes from 2 weeks before laying to 2 weeks after laying for females laying 5 eggs (Fig. 7). Approximately 44.5 g of body reserves were deposited, which were then retained during incubation (see Village 1983b). With an energy equivalent of 19.2 kJ/g (Masman et al. 1988a),

TABLE 2. Body mass (g) of free-living Eurasian Kestrels in the early phases of the reproductive cycle; 40–21 days before laying (Phase 2), early courtship (3A), late courtship (3B), laying (4), and incubation (5).

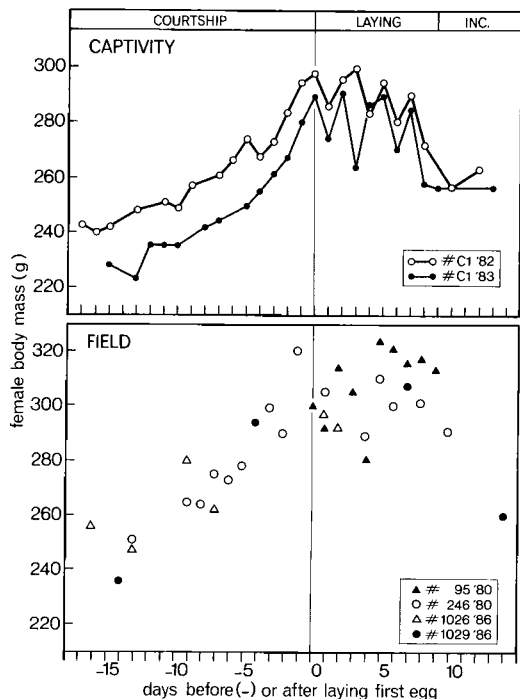|	Groups			
	Early	Middle	Late	All
Phase	91–110[a]	111–113	131–150	91–150
2	249.4 ± 15 (15)[b]	230.8 ± 22 (21)	227.3 ± 28 (8)	236.4 ± 23 (44)
3A	249.0 ± 19 (7)	240.7 ± 19 (15)	222.4 ± 17 (17)	234.2 ± 21 (39)
3B	295.3 ± 21 (4)	280.6 ± 24 (22)	269.0 ± 22 (9)	279.3 ± 24 (35)
4	309.0 ± 16 (6)	305.5 ± 20 (22)	293.7 ± 20 (6)	304.0 ± 19 (34)
5	272.1 ± 30 (27)	271.1 ± 28 (45)	257.0 ± 22 (24)	267.8 ± 27 (96)

[a] Laying date.
[b] $\bar{x}$ ± SD (n).

Fig. 6. Variation in body mass (g) from 2 weeks before until 2 weeks after laying of first egg; 1 captive female laying 4 eggs in 2 successive years (upper), and 4 free-living females (lower).
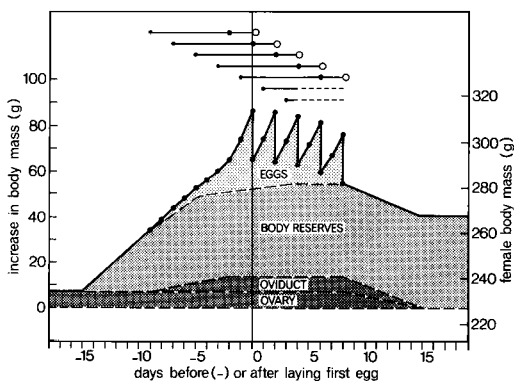

Fig. 7. Reconstruction of female body mass from 2 weeks before until 2 weeks after laying of the first egg; divided between ovary and oviduct, body reserves, and egg material.

these reserves represent an energy store of 44.5 × 19.2 = 854 kJ, equivalent to the metabolizable energy content of ca. 12 voles. Egg formation occurred after most of the reserves were accumulated. This implies that a female first improves her condition, then she begins formation of eggs (and probably of oviduct). These reserves could serve to buffer the female from interrupted food supply during laying and incubation, when unfavorable conditions prevent the male from hunting efficiently. Females which forgo this increase in condition could lay 6 days earlier at a lower body mass. We once observed a laying female with a body mass of 260 g (laying date 10 May 1986); she stopped laying after the first egg. Her male had a low strike success (0.22 ± 0.04, n = 162) and worked unusually hard (5.84 ± 0.95 h/day) just before and after the first egg was laid.

The difference in body mass between early (309.0 g) and late (293.7 g) females was primarily a difference in body reserves, because "reproductive tissue" is equal for both. If we assume that the body mass 15 days before laying (Table 2) represents a female with an ovary of 7.2 g and negligible reserves, then the early female had a body reserve of 44.5 + (309.0 − 304.0) = 49.5 g and a late female of 44.5 + (293.7 − 304.0) = 33.2 g. The early female had 49% more body reserves than the late female and was better buffered against periodic food shortage during the breeding season. This is consistent with the fact that desertion of eggs or young occurs mostly in late-breeding females (Cavé 1968, Newton and Marquiss 1984, Village 1986, Dijkstra 1988).

Variation in energy intake and expenditure.— There was a difference in food intake between late courtship and laying (Fig. 3), which corresponded to a difference in DME of 88–112 kJ. The extra energy was required to compensate for the higher maintenance costs of the laying female. The average body mass difference (ca. 25 g) between the two phases (Table 2) produced an estimated 45.4 kJ/day rise in the maintenance costs (24.7 g × 1.83 kJ·day^{-1}·g^{-1}, see Masman 1986). Incubation behavior increased gradually during laying, from 0 on the day of the first egg to 100% 2 days before the last egg (Beukeboom et al. 1988). We estimated incubation costs during laying as 50% of the costs measured with DLW during full incubation (146 kJ/day, n = 9). Energy was needed for the formation of body reserves, oviduct, and eggs. A female that laid 5 eggs would need 60.8 kJ/day for egg formation during laying compared with 34.7 kJ/day in the 10 preceding days (see Table 3 and Fig. 5). Oviduct development during late courtship would require 65.2 kJ (Walsberg 1983). Body reserves deposited during late courtship and laying were estimated to average 18.1 and
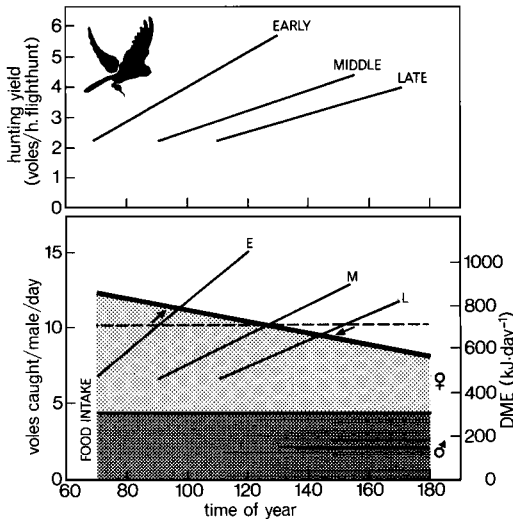
Fig. 8. Upper: increase in hunting yield with progression of the season of Early (regression line: $y = 0.056 \times d - 1.64$), Middle ($y = 0.033 \times d - 0.69$) and Late males ($y = 0.027 \times d - 0.70$). Lower: development of daily food provisioning by the males (indicated by E, M, and L lines), taking into account 3 h of hunting per day. For male and female food intake during laying see text.

TABLE 3. Difference in female energy requirements (kJ/day) between late courtship and laying.

	Late courtship	Laying
Extra maintenance energy		45.4
Incubation		73.0
Egg production	34.7	60.8
Oviduct development	6.5	
Body reserves	50.1	17.2
Total	91.3	196.4

3.7 g (Fig. 7). With an energetic equivalent of 19.2 kJ/g (Masman et al. 1988a), and a production efficiency of 0.7 (Ricklefs 1974, Walsberg 1983), a female would require 501 kJ for the 10 days of late courtship (50.1 kJ/day) and 103 kJ for the 6 days of laying (17.2 kJ/day). The total difference in energy expenditure between late courtship and laying in free-living kestrels was estimated as 105.1 kJ/day (Table 3), and approximates the difference in energy intake (88–112 kJ/day).

The decrease in female food intake with progressive laying date during late courtship and laying (Fig. 3) corresponded with the decline in female body mass (Table 2 and Dijkstra et al. 1988). An early female (laying at day 100) received 29 g/day more food during late courtship and 24 g/day more during laying than a late female (day 140). This amounts to differences of 133 and 110 kJ in DME. The extra intake of early females compensated for their higher maintenance and thermoregulation costs. The average body-mass difference between early and late females was 26 g (late courtship) and 15 g (laying, Table 2). This was equivalent to differences in energy expenditure of 47.6 and 27.5 kJ/day, respectively. Costs associated with body-

mass increase were similar from 15 to 5 days before laying for early and late females, but were slightly higher for late females in the following 10 days (Table 2). Thermoregulation costs were estimated roughly from mean daily temperature and energy consumption data (Masman 1986). Early females spent 66.8 kJ/day while late females spent 30.7 kJ/day. A third contribution to higher energy expenditure in early females is the formation of more eggs (8.2 kJ/day during laying; Fig. 5). A fourth factor, increased incubation costs for early females due to colder weather (ca. 5°C lower, Masman 1986) and due to larger clutches, could not be estimated accurately. Presumably, the higher energy intake of early-breeding females was due to their higher maintenance and thermoregulation costs.

Food as a trigger or limiting factor for reproduction.—For most of the breeding season, the male hunted for the whole family. Both early and late males hunted for ca. 3.0 h/day during courtship, laying, and incubation. There was a large difference in numbers of voles caught, due to differences in strike frequency. Strike frequency probably reflects vole abundance, which could be expected to be higher in territories of early pairs. Strike success increased during the breeding season and was the same for males with different clutch sizes (Fig. 2). Strike success probably increased because of vole reproductive activity (Masman et al. 1988a). Conceivably, prey reproduction might trigger the reproduction of the predator.

Hunting yield rose earlier and faster among early males. Hunting yield per phase was determined at each time of year for the three laying date groups (Fig. 8: upper). From these regression lines, we calculated the number of voles the males were able to catch in 3 h of flight-hunting for each of the three groups (lines E, M and L in Fig. 8: lower). This total catch

must be shared by male and female. During egg laying, males consumed 67.1 g/day ($\pm$32.2, n = 22) or 279 kJ DME and showed no seasonal trend. However, the energy intake of laying females decreased during the season (Fig. 3), and the total energy required by the pair also decreased (heavy line in Fig. 8: lower). The intersections of these lines mark the days on which the average males were able to catch enough food in 3 h/day of hunting to feed their mates during egg laying. These dates are 97 (Early), 125 (Mid), and 143 (Late). A late female would have to wait until 164 (13 June) for the same food intake at laying as an early female. In the 10 yr of study, we never observed clutches initiated so late. Apparently, early birds delayed, and late birds advanced, laying relative to the food situation at which middle birds lay (Fig. 8).

Presumably, the reproductive cycle is triggered by male behavior. The early male does not work longer than the late male, but has a higher strike frequency and therefore a higher hunting yield. Hunting yield starts to increase earlier in the season and at a faster rate. This is probably due to a higher vole abundance in his territory and an earlier reproduction of these voles. He can feed his mate earlier in the year and bring her more food. Early and late females are related by the rates of provisioning by their respective mates. The food intake of females determines when they start forming body reserves, oviduct, and eggs, and thus when they lay. Late females lay with a 30–40% lower food intake (also found in laying Ospreys, *Pandion haliaetus*; Poole 1985), and with 33% lower body reserves. Late females begin egg formation at a point where an early female still would wait for several days. The greater body mass of the early-laying female, and the higher thermoregulation costs, will postpone the moment the male is capable of compensating her energetic needs. This also delays laying, because this triggers the formation of body reserves and eggs, both in early and late females.

Late females produce small clutches even when their body-mass and energy intake is raised to those of early females (Meijer et al. 1988). We found no hormonal differences in spring between free-living female breeders or between captive females with different food availabilities (Meijer and Schwabl 1989). Clutch size seems to be independent of female age, food intake, and condition (Meijer et al. 1988), and is determined by the laying date. Clutch size may follow an endogenous rhythm that is phase-locked to the reproductive cycle (Meijer 1989). For the male, the 3 h of hunting that determine the food supply to the pair is hard to interpret as an energetic constraint, because males work longer later in the nestling phase (Masman et al. 1988a). Presently we are inclined to attribute the seasonal decline in clutch size to a set of factors that involves both the hunting strategy of the male and the intrinsic reproductive value of the offspring, which declines steeply with date (Dijkstra 1988). Males employed a combination of increased hunting yield and a limited number of prey deliveries to the female early in the breeding season, which gave them the possibility later to feed the whole family with 4–5 h of work and not exceed energetic limits (Masman et al. 1988a, Dijkstra 1988). The change in male behavior determines the initiation of female preparations for reproduction in response to food availability. Female body reserves, precise laying date, and clutch size are adjusted to the time of year when the male begins to provision her.

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