Re-examination of the capital and income dichotomy in breeding birds

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During egg-formation, energy and protein are deposited in the developing eggs but are, at the same time, needed by the laying female herself. This has been largely overlooked in the discussion on income and capital breeders (Drent & Daan 1980, Thomas 1988). We discuss data on exogenous versus endogenous energy and nutrients used during egg-formation for 12 well-studied species ranging from the Adelie Penguin *Pygoscelis adelie* (3400 g) to the Blue Tit *Parus caeruleus* (11 g) and calculate which part of the *total* energy and nutrient requirements (of clutch and laying female) originates from direct food intake and/or from body reserves. Because energy and nutrients are also needed by the laying female, some large species breeding in cold regions deposit sufficient reserve that they can fast completely during egg-formation (like the Adelie Penguin) and even throughout incubation (like the Eider *Somateria mollissima*). However, almost all smaller species must forage for most of their energy and nutrients during the egg-formation period. For the large species, energy and protein of the clutch represent 30% and 70%, respectively, of the total requirements of laying females, much more than in small species like passerines (4% and 40%). Therefore, the requirements for the clutch are much greater in larger than in smaller species, and egg-production is much more limited by protein than by energy. The effects of food supplementation on timing of laying (moderate advance), on number of eggs laid (not more, when corrected for date) and on egg size (not larger) of income and capital breeders/layers are discussed. It seems that neither the start of egg-laying nor the number or quality of eggs are directly related to the energetics of the laying female.

During the breeding season, a female bird has to make important decisions: such as when to start (laying date) and to stop laying, thus determining the clutch size. Both laying date and clutch size have profound consequences for the number of surviving offspring. Many studies, such as the work of Perrins on the Great Tit *Parus major* (Perrins 1965) and the Manx Shearwater *Puffinus puffinus* (Perrins 1966), have clearly shown that, especially in single-brooded species, the early clutches produce the greatest number of surviving offspring. Therefore, females should start egg-laying as early as possible. However, if egg-laying is energetically costly, timing of breeding may be constrained by the ability to obtain sufficient food (Perrins 1970). We discuss the effect of food intake and female body reserves on the timing of breeding and on clutch size.

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Reynolds (1972) was the first to present a model relating the gain in female mass prior to the breeding season to laying date and clutch size. Drent and Daan (1980) elaborated this idea and presented two models: in the 'capital model', females use body condition relative to a changing threshold (as in Reynolds model) whereas in the 'income model' females use the rate of change in body condition relative to fixed thresholds. Furthermore, they suggested feeding experiments that could discriminate between the two models. Later, Thomas (1988) suggested that there is a continuum extending between 'capital breeders' with total reliance upon stored reserves (e.g. *Anserinae*) and 'income breeders' with no reserves yet forming eggs immediately from ingested nutrients (e.g. *Tetraoninae*).

Using published data, we discuss in detail the use of endogenous versus exogenous energy and nutrient reserves (especially lipids and proteins) during egg-formation, for a number of well-documented bird

species of different size: Adelie Penguin *Pygoscelis adeliae*, Lesser Snow Goose *Chen caerulescens caerulescens*, Eider *Somateria mollissima*, Mallard *Anas platyrhynchos*, Willow Grouse *Lagopus lagopus*, American Coot *Fulica americana*, Kestrel *Falco tinnunculus*, Starling *Sturnus vulgaris*, Pied Flycatcher *Ficedula hypoleuca*, Red-billed Quelea *Quelea quelea*, Zebra Finch *Taeniopygia guttata* and Blue Tit *Parus caeruleus*.

Besides lipids and proteins, calcium is important for egg-formation (Perrins 1996). Calcium intake increases 10–15-fold from the non-laying to the laying period, both in domestic fowl (Simkiss 1961, 1975) and the Great Tit (Graveland 1995). For more information on calcium metabolism and egg-shell formation, we refer to these publications.

Lipids and protein are not only needed for egg formation itself, but also as an energy substrate and for nitrogen metabolism during the period of egg-formation, respectively. Therefore, it is essential to look at the *total* fat and protein requirements of the laying female. Chickens, for example, deposit about 2 g of protein in the egg for each gram of protein used for nitrogen metabolism (Scott *et al.* 1976). Robbins (1981) showed that for five groups of birds (passerines, galliformes, ducks, shorebirds, gulls and terns with mean body mass between 25 and 947 g), the protein costs of egg production were twice as high (201 ± 30%, $n = 5$ groups) as the protein costs in the non-laying period. Robbins estimated the non-laying protein costs as $2.68W^{0.75}$ g dry protein/day (W = weight in kg), at maintenance level (1.7 × basal metabolic rate BMR; see Ricklefs 1974).

We calculate the *total* energy and protein requirements of the laying female needed for the clutch and her own metabolism, and then calculate which part originates from her own reserves and/or from her food intake. Where possible, data will be presented for females laying different clutch sizes and for individuals laying early or late in the season.

METHODS

Energy and protein requirements of the laying female

Measurements of the daily energy expenditure (DEE) and/or metabolizable energy intake (DME) of free-living females during the egg-formation period are scarce. DEE of captive Galliformes was measured at a level of 1.7 × BMR with an additional 1.1 × BMR for sustained egg production (King 1973). The energy

deposited in the eggs is not measured in the DEE. For captive laying Zebra Finches, housed indoors in small cages, Houston *et al.*(1995) measured a daily seed intake of 2.85 g/bird, corresponding with a DME of 2.0 × BMR (or DEE of 1.7 × BMR; see Table 1). The DME of captive female Great Tits during laying, housed outdoors in small aviaries, was 90 kJ, or 2.8 × BMR (Graveland 1995). From field observations of male prey deliveries to female Kestrels, the DME of the laying female was estimated as 388 kJ (Meijer *et al.* 1989) representing 2.8 × BMR (or DEE of 2.3 × BMR; see Table 1).

Bryant and Westerterp (1980) tried to measure DEE in House Martins *Delichon urbica* with the doubly-labelled water method, but females interrupted laying. Similar measurements in Swallows *Hirundo rustica* showed that energy expenditure of females did not differ significantly between the egg-formation, incubation and nestling periods. Field metabolic rate was measured at 104–112 kJ/day, representing 2.9–3.1 × BMR (Ward 1996). Walsberg (1983) estimated the DEE of 42 different species (all but one between 3 and 1200 g) in the *non-breeding* phase at a level of $13.05W^{0.605}$ kJ/day (W in g), equivalent to almost 3 × BMR for species with body mass up to 1 kg. We therefore take an energy expenditure level of 3 × BMR for small *free-living* birds (less than 1 kg) during egg-formation. For large species, energy levels seem far below 3 × BMR. This agrees with the difference in slopes between Walsberg's DEE (0.605) (Walsberg 1983) and Aschoff and Pohl's BMR estimation (0.722–0.724) (Aschoff and Pohl 1970) in relation to body mass.

The rates of fat loss for the fasting Penguin, Lesser Snow Goose and Eider (see Results) indicate that an energy expenditure level between 1.5–2.0 × BMR is more realistic. For species above 1 kg, we therefore take an energy expenditure level of 1.7 × BMR. When not measured for individual species, BMR levels are taken from Aschoff and Pohl (1970): i.e. for non-passerines 330 $W^{0.722}$ kJ/day and for passerines 542 $W^{0.724}$ kJ/day (W in kg).

The DEE level influences the amount of protein needed by the female herself. Robbins (1981) estimated the nitrogen intake at maintenance level (of 1.7 × BMR). A higher DEE consequently increases nitrogen intake.

In fasting birds, the estimated minimum endogenous loss would be 0.60 $W^{0.75}$ g dry protein/day (Robbins 1981). However, estimated losses of 1.4 and 1.1 g dry protein/day for the fasting, incubating Snow Goose and laying Eider are much lower than the measured loss of 2.3 g (Ankney & MacInnes 1978) and 8.2 g

(Parker & Holm 1990), respectively. The estimated 6.5 g dry protein lost per day by the fasting Adelie Penguin (Astheimer & Grau 1985) is also much higher than Robbins' estimation (1.8 g) and almost equals protein maintenance costs in non-fasting birds (8.3 g). We therefore use Robbins' protein costs of $2.68W^{0.75}$ g dry protein/day. It is possible that females' protein requirements are depressed temporarily during laying, to spare protein for the eggs. However, data are lacking, and protein sparing was not taken into account.

Energy and protein content of the eggs

For 11 of the 12 species discussed, data on egg mass and on energy and protein content of the eggs were taken from the literature cited. For Lesser SnowGoose eggs, Williams *et al.* (1993) calculated egg-protein and lipid as if they were Canada Goose *Branta canadensis* eggs.

Most of the protein is deposited in the developing eggs during the second half of the egg-formation period when the albumen is built up (in fact it is the laying period itself), whereas energy or fat are deposited in the eggs more equally over the whole egg-formation period (see Figs 3, 4). In our calculations, we integrated lipid and protein requirements of the clutch over the laying period only (as did Ricklefs 1974 and Walsberg 1983).

Conversion of body lipids and protein into eggs is taken as 100%. Energy content of the oviduct and the (non-ovulating) ovary are so low compared with other aspects of reproduction (see Walsberg 1983) that they were not taken into account.

RESULTS

For various species, we discuss in detail the total energy and nutrient requirements of the laying female, allocated to the clutch and to her own metabolism, in decreasing order of their body mass.

Adelie Penguin

Adelie Penguins required 19–24 days to produce each egg, and egg-formation started when the females were still at sea. They arrived in the breeding colony ten days before laying the first egg. Normally, these penguins laid two eggs, with a three-day interval, but 56% of the females laid a third egg after the first and/ or second egg was removed, which means that three follicles develop successively. Astheimer and Grau (1985) observed two types of yolk in the eggs, probably originating directly from food intake at sea

(orange-pigmented inner layers) or from body reserves (more homogeneous layers toward the periphery). There was a three-day interval between the *a* and *b* egg (and again between the *b* and *c* egg), and a 5.7-day interval between yolk completion and laying (Astheimer & Grau 1985). Following clutch completion, the male took over incubation first, the female departed from the rookery, ending the 12-day fast. An estimated 70 g of body mass was lost daily, representing a total energy expenditure of 1659 × 12 = 19 908 kJ (Astheimer & Grau 1985). Of the energy content of the clutch, 75% (or 1024 kJ) was deposited after the female had arrived at the rookery (Astheimer & Grau 1985), but this represents only 4% of her total energy requirements during laying. The same holds for protein. Overall, the Adelie Penguin stops feeding almost two weeks before laying starts and almost all energy (96%) and nutrients (99%) for the laying female and her clutch come from endogenous reserves (Table 1).

Lesser Snow Goose

By examining the body reserves and the ovaries of Lesser Snow Geese breeding in the Arctic, Ankney and MacInnes (1978) reported that the female's clutch size was determined by the size of her nutrient reserves. Drent and Daan (1980) treated the Snow Goose as a classic representative of the capital model. The large body mass differences before laying (from 2400 to 3300 g) correlated with the number of developing follicles (potential clutch size). After arrival on the breeding grounds, laying started almost immediately. At the onset of incubation, regardless of the putative clutch size, females had more or less the same mass (2530 g). Late in the incubation period, females weighed on average 1710 g. Carcass composition studies showed that females had lost (over this 20-day incubation period) large amounts of fat (315 g) and protein (46 g dry) (Ankney & MacInnes 1978).

Careful examination of the data before and after laying (Fig. 1) shows that only about 14% (three-egg clutch) to 55% (six-egg clutch) of the egg protein can originate from endogenous stores. However, according to Robbins (1981), a female Snow Goose would need an additional 6.0 g dry protein/day for protein metabolism at 1.7 × BMR. In this case, endogenous protein would only cover 10–39% of the *total* protein needs (Table 1).

The measured decrease in fat levels of a female Lesser Snow Goose, with a DEE of 1.7 × BMR, only accounts for 46% (for a female with three eggs) to 70%

Table 1. Summary of reproductive data, particularly the protein and lipid energy requirements for the laying female and her clutch.

General characteristics

	Body mass (g)	No. of eggs	Egg mass (g)	Egg mass/ body mass (%)	Clutch mass/ body mass (%)	Egg interval (h)	Laying period (days)
Adelie Penguin	3400	2	119	3.5	7	72	3
Lesser Snow Goose	2950	3–6	125	4.2	13–25	33	4–8
Eider	2163	4.6	104	4.8	22	24	6.7[a]
Mallard	1300	8–11	52	4.0	332–44	24	8–11
Willow Grouse	615	10	22	3.6	36	42	17.5
American Coot	500	8.3	30	6.0	50	24	8.3
Kestrel	300	5	21	7.0	35	48	9
Starling	90	5	7	7.8	39	24	5
Red-billed Quelea	22[c]	3	2[c]	9.1	27	24	3
Pied Flycatcher	16	6	1.7	10.4	62	24	6
Zebra Finch	15	4	1	6.5	26	24	4
Blue Tit	11	11	1.2	10.9	120	24	11

Protein

	Maintenance (g/day)	Laying period (g)	Clutch (g)	Total (g)	Clutch/ total (%)	Lost (g)	Endogenous (%)
Adelie Penguin	6.7	19.2	24	43.2	56	?	96
Lesser Snow Goose	6.0	24–48	56–112	80–160	70	8–62	10–39
Eider	4.8	32	57	89	64	112.7	100
Mallard	3.3	26–36	50–69	76–105	65	4	4–5
Willow Grouse	1.9	33.3	22.0	55.3	40	?	?
American Coot	1.6	23.4	32.4	55.8	57	1.6	2.9
Kestrel	1.1	13.3	12.6	25.9	46	0	0
Starling	0.44	3.88	3.50	7.38	47	0	0
Red-billed Quelea	0.15	0.81	0.75	1.56	50	0.16[d]	10
Pied Flycatcher	0.12	1.3	1.3	2.6	50	0	0
Zebra Finch	0.12	0.46	0.54	1.00	46	0.52[e]	26
Blue Tit	0.09	1.77	0.90	2.67	33	0	0

Lipid

	1 × BMR (kJ)	Mass-specific BMR (kJ/g)	Fat (g/day)	DEE (×BMR)	Laying period (g fat)	Clutch (g)	Total (g)	Clutch/ total (%)	Lost (g)	Endogenous (%)
Adelie Penguin	798	0.23	21	1.7	107	20	127	16	?	99
Lesser Snow Goose	721	0.24	19	1.7	129–258	49–98	178–356	28	82–250	46–70
Eider	576	0.27	15.1	1.7	173.0	66.2	239.0	28	261.5	100
Mallard	399	0.31	10.5	1.7	143–196	45–64	188–260	24	12–116	6–45
Willow Grouse	232	0.37	6.1	1.7	181.5	40.0	221.5	18	?	?
American Coot	200	0.40	5.3	3.0	132	21	153	14	12	7.8
Kestrel	138	0.46	3.6	2.3[b]	75.4	10.5	85.9	12	0	0
Starling	94.8	1.05	2.5	3.0	37.5	1.9	39.4	4.8	0	0
Red-billed Quelea	34.2	1.55	0.91	3.0	8.15	0.30	8.45	3.6	0.52[d]	6.2
Pied Flycatcher	27.2	1.70	0.72	3.0	12.9	0.6	13.5	4.6	0.7	5.2
Zebra Finch	26.6	1.72	0.68	1.7[b]	4.24	0.23	4.47	5.3	0.9[e]	10
Blue Tit	20.7	1.88	0.55	3.0	18.2	0.7	18.9	3.7	0	0

Body mass, body mass of laying female; No. of eggs, number of eggs in the clutch; egg mass/body mass, egg mass as a percentage of female body mass; clutch mass/body mass, clutch mass as a percentage of female body mass. Protein, given as g dry protein: maintenance, normal requirements for the female per day at 1.7 × BMR (see Robbins 1981); laying period, normal requirements for the female over the laying period; clutch, the protein of the clutch; total, total protein demands of the laying female; clutch/total, the clutch protein as a percentage of the total protein demand; lost, protein lost from endogenous reserves; endogenous, the percentage of total protein covered by these endogenous losses. Lipid: 1 × BMR, the energy equivalent of 1 × BMR; mass-specific BMR, the mass-specific basal metabolic rate (kJ/g body mass); fat, the equivalent of 1 BMR in g fat/day; DEE, the DEE level of the laying female (multiples of BMR); laying peroid, the energy demand (as g fat) over the laying period. Further calculations as for protein. [a]Also 2.1 incubation days. [b]See Methods. [c]Meijer unpubl. data. [d]Lost over 6 days. [e]Lost over 8 days.
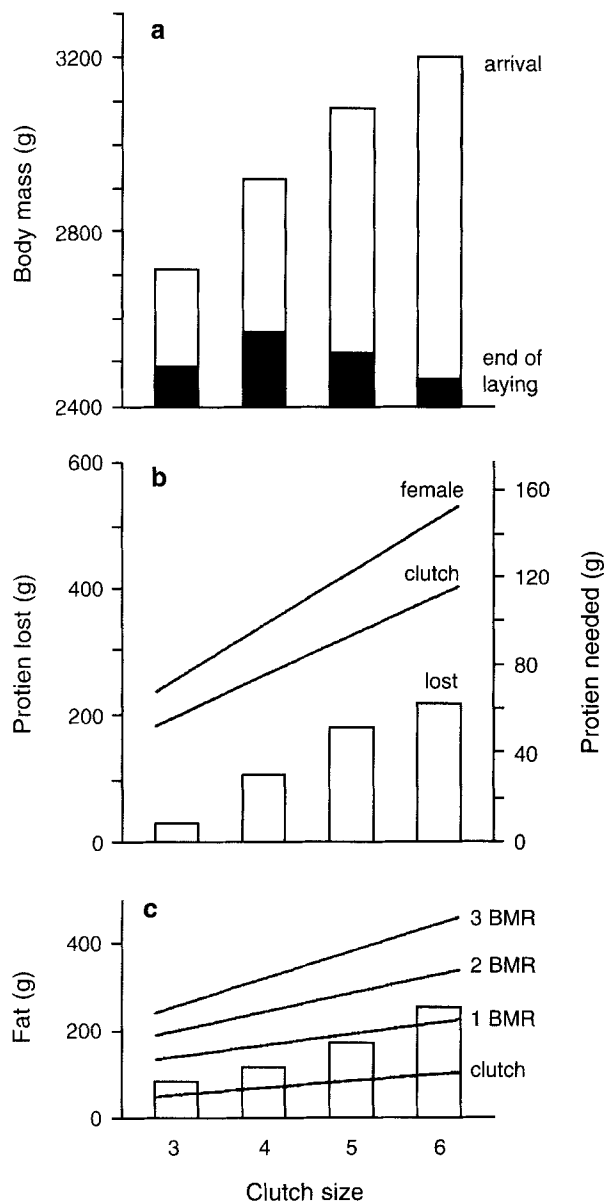
Figure 1. Summary of reproductive data for female Lesser Snow Geese laying clutches of three to six eggs. (a) Body mass data of females arriving at the breeding grounds, and at the end of laying. Open bars represent the mass loss from arrival until end of laying. (b) Loss of body protein (bars) compared with the protein needed for 3–6 eggs (lower line) and the female herself (upper line). (c) Loss of body fat (bars) compared with the fat needed for eggs (lower line) and for the different levels of DEE (1–3 BMR, upper lines).

(with six eggs) of the fat needed for living and yolk formation (Table 1). So, egg-formation in this species seems almost impossible without substantial amounts of dietary protein and fat (Fig. 1). Support comes from Cooke *et al.* (1995), who mentioned the importance of exogenous nutrients, both during laying and incubation. Females arrived 11 ± 1.7 days before laying (range 7–13 days, *n* = 10 years), actively fed upon arrival on plant stolons, rhizomes and other overwintering storage plant organs. Some incubating females left the nest for up to 3 hours/day for foraging (see also Ganter & Cooke 1996). In the Greater Snow Goose *Chen caerulescens atlantica* studied in northern Canada by Choiniere and Gauthier (1995), rapid follicular growth also started after arrival on the breeding grounds, females foraged intensively before laying and their fat reserves even *increased* during the egg-formation period.

Eider

Female Eiders, breeding in the high Arctic, fed heavily near nesting islands before laying (Parker & Holm 1990), increasing body mass by approximately 20% above winter level. Females then fasted completely during laying and incubation, losing 29 and 17% of the prelaying mass, respectively (or 33.8 and 34.6% of the total prelaying energy). Carcass analysis showed that during laying, female eiders lost 112.7 g of protein (Parker & Holm 1990), of which 57 g must have been allocated to the clutch (Table 1). During the same period of 6–7 days, for the last two days of which females already incubated, 261.5 g of fat disappeared (Parker & Holm 1990), of which the clutch contained 66.2 g (Table 1).

Using indirect calorimetry, Gabrielsen *et al.* (1991) measured the energy expenditure of incubating Eiders (mean body mass of 1571 g). The DEE, at mean ambient temperature of about 2°C (slightly below Eider lower critical temperature of 6–7°C) was 490 kJ, equivalent to only 1.1 × BMR. Incubation costs of arctic breeding species like the Eider and the Snow Goose seem to be extremely low. The Lesser Snow Goose, incubating in a similar cold environment, lost 16 g of fat and 2.3 g of protein per day (Ankney & MacInnes 1978), which represents a DEE of 653 kJ or only 1.3 × BMR (when the female does not leave the nest to forage).

Mallard

Clutch size of Mallards decreased during the breeding season (April–June) and correlated with the laying female's carcass lipid reserves (Krapu 1981). Early-laying females carried 116 g of fat, i.e. almost twice the amount needed for the total clutch, whereas late-laying females carried only 12 g (only 26% of the
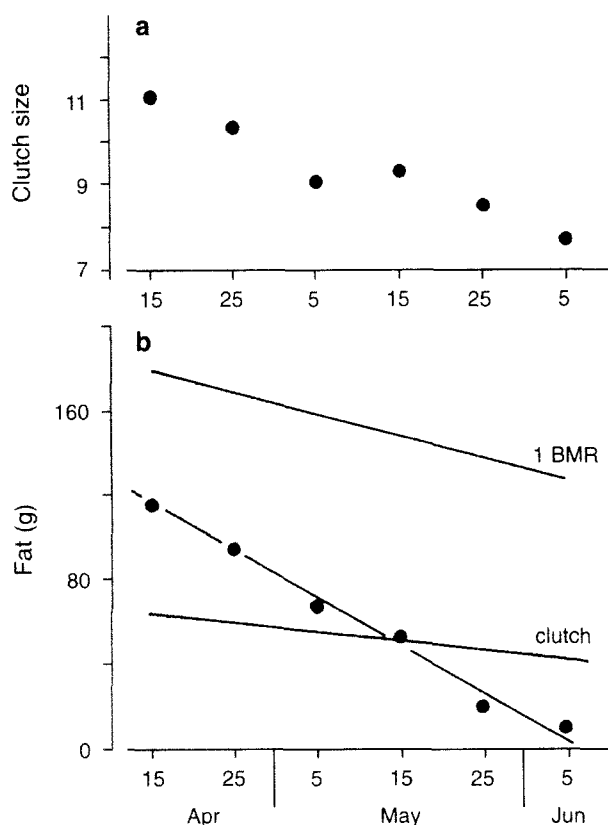
Figure 2. Seasonal decrease in (a) clutch size of Mallards and (b) body fat of laying females (●) compared with the fat needed for the clutch and the equivalent of 1 BMR (upper line).

clutch fat; Fig. 2). The energy expended over the laying period of 8–11 days is equivalent to 143–196 g fat, and the clutch contains another 45–64 g of fat (Table 1). Therefore, the fat store of early-laying females represents only 45% of the total fat demands. Late-laying females, laying eight eggs, need a total of 188 g fat, of which only 12 g (6%) could be endogenous (Table 1).

The percentage of the total protein requirements that is endogenous is even smaller. A clutch of 8–11 eggs contains 50–69 g of dry protein, whereas a significant (wet) mass loss could be detected only in the gizzard (from 34 to 22 g, corresponding to less than 4 g of dry protein) (Krapu 1981). Furthermore, 26–36 g of dry protein is needed for nitrogen metabolism during the 8–11 laying days (Table 1). Krapu concluded that laying was timed to coincide with access to protein-rich food, and that stored lipids moderated clutch size through their influence on female capacity to secure protein needs. Our calculations show that female Mallards rely heavily on exogenous nutrients

and energy during egg-formation, especially late-laying ones.

Willow Ptarmigan

On the continuum from capital to income breeders, the *Tetraoninae* represent those breeders with the lowest body reserves, for grouse species less than 2% of their body mass (Thomas 1988). This contrasts with the literature data, which are all presented from a more 'capital' viewpoint. Gonadal recrudescence of the Willow Ptarmigan begins in early May. In the spring of 1978 and 1980, just before laying, carcass analysis revealed that mean neutral fat content of females increased up to 2.8% (range 1.3–3.3%) and 5.1% (range 3.9–6.0%), respectively (Thomas 1982). If females diverted all of their neutral fat into the yolk, the maximum number of mature ova that the reserves could produce was three or four in 1978, and eight in 1980 (Thomas 1982). Furthermore, depletion of muscle protein would allocate protein for 7–8 eggs (Thomas 1982). Unfortunately, body mass data after laying are lacking, as are data for changes in the protein and fat levels of laying ptarmigan. Similar sets of incomplete data exist for the related Spruce Grouse *Dendragapus canadensis* (Naylor & Bendell 1989), captive Red Grouse *Lagopus lagopus scoticus* (Savory 1975) and for captive Ruffed Grouse *Bonsa umbellus* (Beckerton & Middleton 1982). However, all these data show that a substantial part of clutch energy and protein could originate from endogenous reserves, and do not support the classification of *Tetranoninae* as extreme income breeders.

American Coot

Alisauskas and Ankney (1992) discussed the problems faced when breeding females are categorized into two or three small groups (e.g. prelaying, laying and incubation) thereby underestimating changes in the size of nutrient reserves relative to changes in nutrient use. To solve this problem, the change in nutrient reserves must be evaluated against rates of nutrient secretion into eggs by means of regression analysis. In this case, the slope and the intercept provide information about the amount of exogenous versus endogenous reserves, and about the existence of a nutrient threshold for egg-formation (Alisauskas & Ankney 1992). They used this method in their study of the breeding biology of the American Coot. After arriving on the breeding grounds in southern Manitoba, fat reserves (measured from carcass analysis) had to increase to a minimum of

27.5 g (i.e. the intercept) before egg-formation started. For every gram of fat in the eggs ('reproductive fat'), fat reserves declined by 0.55–0.85 g (i.e. the slope). Most of the protein was accumulated after arrival and only 24–28% of the egg protein resulted from endogenous protein (Alisauskas & Ankney 1985).

The underestimation by the classical method becomes clear by comparing their data from five prelaying coots with the six postlaying females. In the classical way, fat levels decreased by about 12 g and protein levels by only 1.6 g. While a mean clutch of 8.3 eggs contains 21 g of lipid and 32.4 g of dry protein (Alisauskas & Ankney 1985), endogenous fat and protein only cover 57% and 5% of the total demands, respectively. However, neither the classical nor the regression method take into account the energy and protein requirements of the laying female. Over the laying period, an additional 23.4 g of protein is needed and, of the total protein demands of 55.8 g, only 1.6 g (2.9%) could be endogenous (Table 1; with the regression method this figure increases up to 17–20%).

Of the total energy requirements, equivalent to 153 g of fat over 8.3 laying days, only 12 g (or 8%) comes from endogenous body reserves (Table 1). It seems that American Coots rely almost exclusively on direct food intake for the total energy and protein during laying.

Kestrel

The body mass of female Kestrels changes enormously during the breeding season. When the male started to feed the female, some three weeks before laying onset, she weighed 235 g (Meijer *et al.* 1989). During the last two weeks before laying, mass increased by 70 g, of which an estimated 28 g was due to development of oviduct (7 g) and eggs (on average 21 g), the other 42 g being accumulation of body reserves. At the end of laying, regression of the oviduct and ovary (14 g) and the loss of egg-material (21 g) would account for a mass loss of about 35 g. During early incubation, females weighed 268 g (Meijer *et al.* 1989), which means that additionally only 2 g of body reserves disappears during laying. It seems that energy and nutrients for egg-laying in the Kestrel come directly from the prey (Common Voles *Microtus arvalis*), which the male delivers to the female. Changes in female body mass suggest that the female first completes the build up of body reserves, after which she starts egg-formation. These reserves disappeared not during laying or incubation, but during the early nestling period (Dijkstra *et al.* 1988). Similar changes in body mass were observed for breeding

Sparrowhawks *Accipiter nisus* (Newton 1986).

Starling

The body mass of free-living female Starlings increased from 80.2 g before laying, to 91.5 g during laying, and decreased thereafter to 80–82 g during incubation (Ricklefs & Hussell 1984). During laying, no changes were detectable in carcass fat levels (around 3 g throughout) and in lean dry mass (around 24 g). The 11 g increase of mass is caused by development of the ovary and oviduct (4–5 g, see Ricklefs & Hussell 1984) and by the egg material in the rapidly growing follicles (around 7 g). A clutch of five eggs contained 1.9 g of fat and 3.5 g of dry protein (Ricklefs 1977). Changes in body-mass of captive laying Starlings with moderate food restriction paralelled exactly those of laying females fed *ad libitum* (Meijer & Langer 1995), suggesting that (as in the Kestrel) changes in body mass are caused by development and regression of the reproductive organs (and the loss of egg-material) and that during egg-formation female Starlings derive all energy and nutrients directly from dietary intake (Table 1).

Red-billed Quelea

One of the most often cited papers 'showing' that endogenous fat and protein reserves regulate timing of reproduction is that of Jones and Ward (1976) on the breeding biology of the Red-billed Quelea in Africa. They suggested that in the very large, well-synchronized Quelea colonies the proximate control of breeding was provided by the individual's own body condition, and particularly the state of its protein reserves (measured as the labile component of the flight muscle protein). The number of eggs laid was determined by the rate at which the protein reserves fell during egg-formation (Jones & Ward 1976, Jones 1989). Figure 3 presents the data on daily fat and protein changes around laying, deduced from carcass analysis of hundreds of females, and the (calculated) daily amount of fat and protein needed for formation of the clutch. During the six egg-formation days, a total of 520 mg of fat and 160 mg of labile protein was lost. A three-egg clutch contained 300 mg of fat and 750 mg of protein (Jones & Ward 1976).

Total protein demands over the six-day period are 750 mg (clutch) plus 1620 mg (female; for comparison with the other species, the data in Table 1 are presented only for the three laying days). Only 160 mg comes from endogenous reserves (7%). A DEE of 3 × BMR over six days equals the energy of 16.3 g of fat.
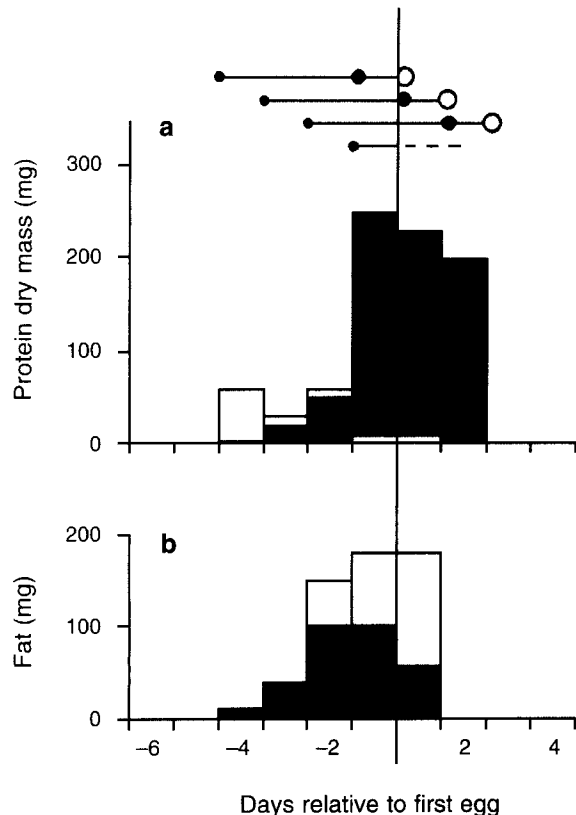
Figure 3. Comparison of the daily amount of protein (a) and fat (b) needed for egg-formation (■) in Red-billed Quelea and the daily amount of protein and fat lost from body reserves (□). Lines at the top represent the development of each egg in the clutch (●—●, rapid yolk development; ●, ovulation; ○, oviposition).

Together with 0.3 g clutch fat, the total energy requirement increases up to 16.6 g of fat (or 8.125g over three laying days, Table 1), of which 97% comes from food intake.

These data do not convincingly support the fact that, in Red-billed Quelea, protein reserves control both onset of breeding and clutch size; see also Jones (1989) and similar data for the Grey-backed Camaroptera *Camaroptera brevicaudata* in Uganda (Fogden & Fogden 1979). Jones (pers. comm.) suggests that, in Red-billed Quelea, the ability to breed is determined by a threshold 'capital' (i.e. some limiting micronutrient stored in the labile component of the breast muscle) and that the subsequent performance is determined by 'income'.

Pied Flycatcher

Pied Flycatchers arrive on the breeding grounds in northern Finland with small fat reserves (Ojanen 1983,

carcass analysis). Early-arriving birds waited up to one week, while late-arriving ones started egg-formation immediately (Lundberg & Alatalo 1992). Over the laying period, no change in the mass of the breast muscles was detectable (Ojanen 1983), which suggests that Pied Flycatchers rely completely on dietary protein for egg-formation and for nitrogen metabolism. If flycatchers live at 3 × BMR during egg-laying, they need the energy of 12.9 g of fat. Of the total fat requirements of 13.5 g, then only 0.7 g (5%) originate from endogenous depots (Table 1). As for the other passerines discussed earlier, flycatchers seem to be extreme income breeders.

Zebra Finch

Houston *et al.* (1995) presented detailed information on the breeding biology of captive Zebra Finches, and concluded from carcass and clutch analysis that these finches (mean mass 15.25 ± 0.19 g) depend heavily on stored body fat and protein for egg-formation, which is unusual in small passerines. A clutch of four eggs contained 233 mg dry lipid and 540 mg dry protein. Females lost a mean of 895 mg lipid and 518 mg protein over the whole egg-formation period of eight days (Houston *et al.* 1995). Figure 4 combines the data on daily investment of lipid and protein in the production of a four-egg clutch (from Fig. 2 in Houston *et al.* 1995) and the changes in total lipid and carcass lean dry weight of female Zebra Finches during the period of egg-formation (their Table 2). Surprisingly, most of the endogenous lipid and protein loss occurred early in the yolk enlargement period. No change in food intake (of the pair) was measured, but a clear drop in female activity occurred during the egg-laying period (Houston *et al.* 1995). Energy normally used in activity was probably allocated to the egg-formation process. The measured seed intake of 2.85 g/day (Houston *et al.*1995) represents a DME of 40.2 kJ/day or 2.0 × BMR according to measurements by Marschall and Prinzinger (1991).

Energy demands over eight egg-formation days then increased up to 8.48 g fat (40.2/38 × 8) together with 0.233 g clutch fat. The loss of 0.895 g of endogenous fat represented only 10% of the total energy requirements.

Surprisingly, in the studies on free-living Red-billed Quelea (Jones & Ward 1976) and on captive Zebra Finches (Houston *et al.* 1995), endogenous protein and fat loss do not overlap with the period in which protein and fat are built up in the developing eggs. In fact, endogenous protein disappeared early in the egg-
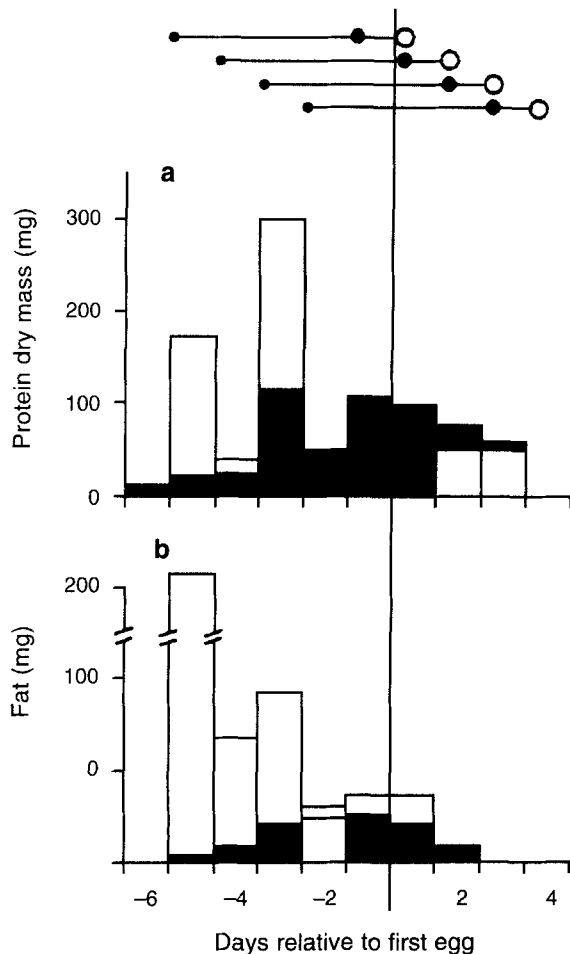
Figure 4. The daily amount of protein (a) and fat (b) needed for eggs (■), compared with the amount of protein and fat lost from body reserves (□) of laying Zebra Finches. Lines at the top represent the development of each egg in the clutch (see Fig. 3).

formation period in both species, and the same holds for fat in the Zebra Finch. Red-billed Quelea lost endogenous fat when protein demands were high, suggesting that stored energy was used for foraging on protein-rich food items. But the fat loss was small in relation to the total energy requirements during laying.

Zebra Finches lose 1–3 g of mass after introduction into small breeding cages, after which egg-formation starts (Rozman & Meijer unpubl data, Williams 1996). Maybe these finches decrease body mass before laying to reduce their maintenance costs.

Blue Tit

In comparison with the other passerine species, tits lay a large number of eggs and thereby need an enormous amount of additional nutrients for laying. For the Blue

Tit, which typically lays eggs of 1.2 g (Nilsson 1994), total clutch mass exceeds the body mass of the female (10–11 g). The Blue Tit clutch contained 0.9 g of dry protein and 0.7 g of fat (Perrins 1996). Because during the early laying and late nestling periods no reduction in flight muscle or fat reserves was observed, Perrins (1996) concluded that tits obtain the necessary extra protein and fat for egg-formation from their daily diet.

DISCUSSION

Total energy and nutrients of the laying female

During the egg-formation period, protein and lipid are deposited in the developing eggs, but at the same time both nutrients are needed by the laying female herself for nitrogen metabolism and as an energy substrate. It seems that, for all species discussed, protein rather than energy is the limiting factor for reproduction. Clutch protein (Table 1: clutch/total) represented 33% (Blue Tit) to 70% (Lesser Snow Goose) of the *total* requirements of the laying female, against clutch fat only 4% (Red-billed Quelea and Blue Tit) to 28% (Snow Goose and Eider). This means that for laying females, on average, protein demands double compared with the non-laying period (see also Robbins 1981). If the efficiency of egg-protein synthesis in these species is similar to that in chickens (i.e. 55%; Scott *et al.* 1976), the nitrogen intake (or nitrogen metabolism) during egg production may be increased to about four times (Robbins 1981).

Especially for energy, but also for protein, the 'additional' cost of laying is much higher in larger species than in smaller ones. In large species such as Mallard, Eider and Snow Goose, clutch fat represents 24–28% of the total energy need, whereas in smaller species such as Starling, Red-billed Quelea, Pied Flycatcher, Zebra Finch and Blue Tit (all with body mass under 100 g) it is only 3–5% (Table 1). This is not because smaller species have relatively smaller eggs or smaller clutch mass; the opposite is true (Table 1: egg mass/ body mass and clutch mass/body mass; Rahn *et al.* 1975). However, smaller species have a much higher metabolic rate per gram body mass. Mass-specific BMR is 7–8 times higher for species such as flycatchers and tits than for geese and eiders (1.7–1.9 versus 0.23–0.27 kJ/g, respectively, Table 1). When related to DEE, smaller species have a 15–20 times higher mass-specific BMR than larger species. This means that for the formation of eggs, larger species have to collect more additional energy, in both absolute and *relative* terms,than smaller species.

For protein the differences are less extreme, but again clutch protein represents a higher percentage of the total protein requirements in large species (56–70%, see Table 1) compared to the smaller (passerine) species (33–50%). This is because the larger species have lower energy expenditure levels (between 1–2 × BMR) than smaller species (3 × BMR, see Methods), and thereby relatively lower protein costs. The storage of fat before laying and the longer laying-intervals between eggs in larger species reduce the additional cost of laying. Smaller species seem to store almost no energy before laying and are able to lay eggs with the shortest egg-interval possible (i.e. 24 hours).

Of the 12 species presented, only the Eider fasts completely during egg-formation and therefore relies fully on endogenous energy and protein for both processes (maintenance and egg-formation). In the Adelie Penguin with an extremely long egg-formation period of three weeks, 25% of the clutch energy and protein originate directly from feeding; however of the total requirements of the laying female it is only a few percent (Table 1). For the Lesser Snow Goose, half of the total energy and protein requirements comes from endogenous reserves, the other half directly from the diet. The other species, from Mallard to Blue Tit, rely on direct food intake for more than 90% of their total energy and protein.

Thus, most laying females have to search intensively for protein-rich food items on the days albumen is being built up. During these days, they also have to search for calcium-rich food items for egg-shell formation. We could not find data on the decrease in food intake caused by selective searching for proteins. To collect calcium for egg-shell formation, Graveland (1995) observed that captive Great Tit females spent 20% of their time handling and eating snail shells (even though they had immediate access to an unlimited calcium supply). Swallows *Hirundo rustica* spent up to half an hour per day collecting calcium (in an area where grit and snail shells were easy to obtain) (Turner 1982).

Laying females not only have to search for both protein and calcium-rich food items during egg-laying, but both females of altricial and precocial species spend more and more time on the nest (Meijer 1990, Meijer & Siemers 1993) which decreases foraging time and thereby food intake. It is therefore not surprising that during this period some endogenous energy (when available) is used (Figs 2 & 3). During the period off the nest, most females become inactive to reduce the chance of predation and of damaging the developing eggs. In individual non-laying Zebra Finches, body

mass increased by 7% between dawn and dusk which decreases flight speed by over 30% (Metcalfe & Ure 1995). Due to the development of oviduct and (non-ovulating) ovary (representing 6% of adult mass; Ricklefs 1974) and the developing follicles (on average the mass of one egg, or 3–11% of female body mass; Table 1) body mass in income breeders would *additionally* increase by 9% (larger species) to 17% (smaller species, such as most passerines). This greatly increases predation risk in laying females, especially when energy stores for the night are built up during the second half of the day and when the egg in the oviduct reaches it maximum volume. For females of capital breeders, body mass would not increase but would drop steadily during the egg-formation period and thereby reduce predation risks.

The models of Reynolds (1972) and Drent and Daan (1980) concentrated on the decisions affecting laying date and clutch size. Thomas (1988, p. 353) extended the income and capital (laying) models of Drent and Daan over the whole reproductive period to species which reproduced on 'capital' and those which reproduced on 'income'. It would be more correct to distinguish between capital layers and capital breeders, because both breeding strategies are quite different. The Adelie Penguin, where the female fasts from 10 days before laying until laying is complete, is a capital layer. The Eider, which arrives at the breeding grounds with large reserves and fasts during both laying and incubation, would be a capital breeder. At the other extreme are the income layers, represented by passerine species.

However, data for the Lesser Snow Goose and the Mallard show that even within the same species, there are large differences in the amount of endogenous versus exogenous nutrients used during the egg-formation period. For female Lesser Snow Geese laying clutches of six eggs, 39% and 70% of the total protein and energy needed during egg-laying originates from endogenous reserves, but only 10% and 46% for females laying clutches of three eggs (Table 1).

There are also large differences within the same season. Of the total energy needed during egg-laying, early females with large clutches cover 45% of the total requirements by endogenous fat, whereas late females with smaller clutches obtain almost all energy by foraging (Table 1). For proteins, both early and late-laying Mallards have to forage for almost all of it.

Laying date, clutch and egg-size decisions

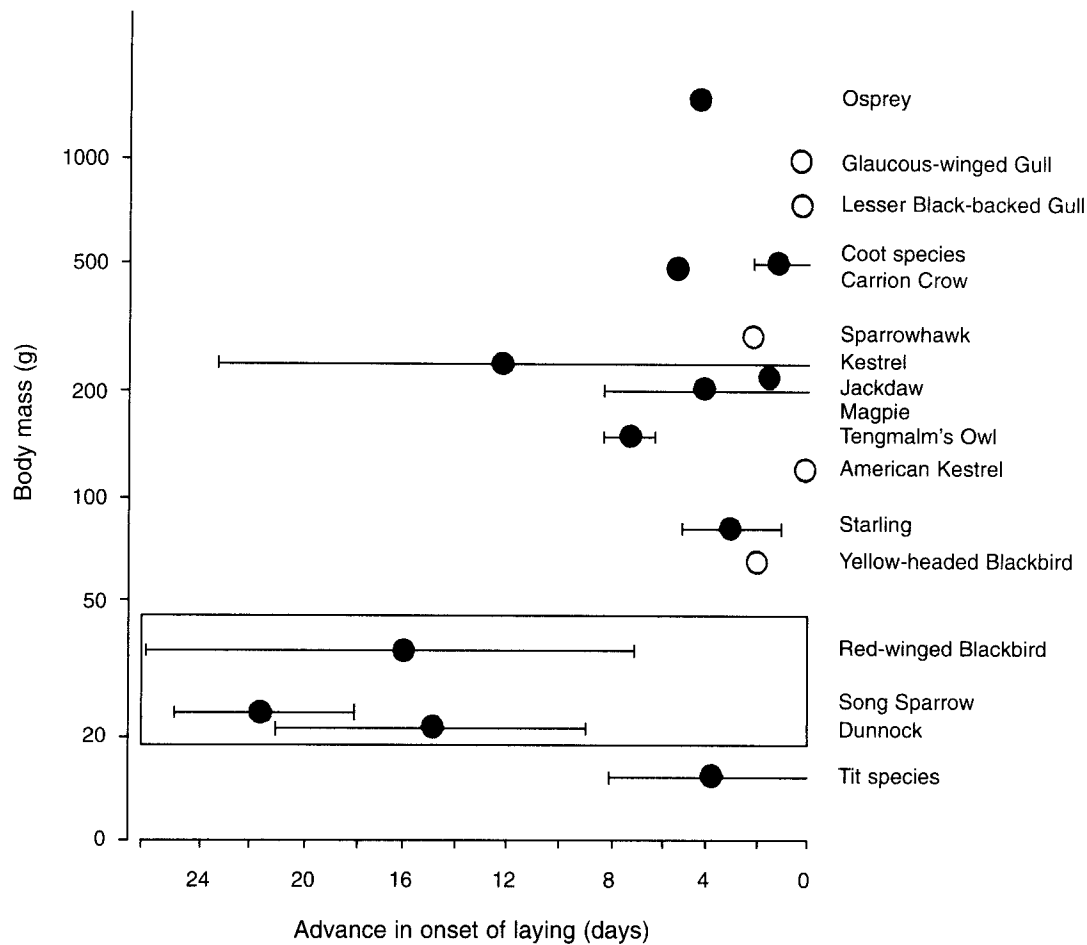It is therefore not surprising that timing of laying is

Figure 5. Summary of the change in onset of laying (indicated as range and mean) for free-living species supplemented with extra food. The box contains three multiple-brooded species, all other species are single or double-brooded. ○, Insignificant advance; ●, significant advance. One data point summarizes the experiments on different species of tits and coots (see also Table 2).

directly influenced by the food availability for the laying female. This seems to be supported by a number of feeding experiments on free-living species. Of the 24 species in which supplemental feeding experiments have been carried out, 20 species were fed at least two weeks before egg-laying started (we consider this a minimum time to see a reaction on laying date at all). Of these 20 species, 15 showed a significant advancement in laying date (Table 2). Although in most studies an enormous amount of food was supplemented, advancement of laying was less than seven days in ten out of 14 species; in the other four species, the supplemented females advanced laying up to 3–4 weeks. Three of these species, Dunnock *Prunella modularis*, Song Sparrow *Melospiza melodia* and Red-winged Blackbird *Agelaius phoeniceus* are multi-brooded and have extremely long 'laying windows' of 3–4 months (see also Svensson 1995). The fourth

species, the Kestrel, is single-brooded with a relatively long laying window of almost three months. In years when vole density was low in particular, food supplementation advanced the onset of laying by up to three weeks (Dijkstra *et al.* 1982; Meijer *et al.* 1988).

In five food-supplemented species there was no significant advancement in laying. Three species were fed only for two weeks (Yellow-headed Blackbird *Xanthocephalus xanthocephalus*, American Kestrel *Falco sparverius* and Sparrowhawk) which was maybe too short to see any effect. The other two species failing to react were gulls (Lesser Black-backed Gull *Larus fuscus* and Glaucous-winged Gull *L. glaucescens*), both colonially breeding birds. Colonially breeding birds in particular show an extreme synchronization of breeding activities, probably controlled by social stimulation (Fraser Darling effect). It seems that food supplementation to only a part of the colony cannot

Table 2. Summary of food supplementation experiments.

Species		Period of food suppl. (weeks)	Advance in laying date (days)	Increase in clutch size (eggs)	Increase in egg mass (g)	Reference
Willow Tit	B	7	2–5	ns	?	von Brömsson & Jansson 1980
Crested Tit	B	4	5–8	ns	?	von Brömsson & Jansson 1980
Marsh Tit	L	–	–	0,9	?	Nilsson 1991
Blue Tit	B	14	5–6	ns	?	Clamens & Isenman 1989
Blue Tit	B	5	4–6	ns	ns	Nilsson & Svensson 1993 Nilsson 1994, Svensson & Nilsson 1995
Great Tit	B	3	5–6	?	?	Källander 1974
Great Tit	B	14	ns	ns	?	Clamens & Isenman 1989
Robin	?	?	ns	+	?	Harper 1984 in Davies & Lundberg 1985
Red-backed Shrike	L	0,5	ns	0,9	ns	Carlson 1989
Dunnock	B	14	9–21	ns	?	Davies & Lundberg 1985
Song Sparrow	B	30	25	ns	?	Smith *et al.* 1980
Song Sparrow	B	5	18	0.5[a]	ns	Arcese & Smith 1988
Red-winged Blackbird	B	3–6	12–26	ns	?	Ewald & Rowher 1982
Red-winged Blackbird	B	2	4–7	ns	?	Wimberger 1988
Yellow-headed Blackbird	B	3	(2)	ns	ns	Arnold 1992
Starling	B	4	1–5	ns	ns[b]	Källander & Karlsson 1993
Magpie	B	5	ns	(0.5)	+	Högstedt 1981
Magpie	B	4	0–8	ns	ns	Hochachka & Boag 1987
Magpie	B	3	4–6	ns	?	Knight 1988
Magpie	B	35	6–7	ns	?	Dhindsa & Boag 1990
Jackdaw	B	9	2	0,6	ns	Soler & Soler 1996
Carrion Crow	B	15	5	ns	ns	Yom-Tov 1974
Tengmalm's Owl	B	3	6	ns	ns	Korpimäki 1989
Tengmalm's Owl	D	3	8	0.9[f]	?	Hörnfeldt & Eklund 1990
American Kestrel	B	2	ns	?	+	Wiebe & Bortolotti 1995
Kestrel	B	>4	23	ns	?	Dijkstra *et al.* 1982
Kestrel	B	>4	0–21	ns	?	Meijer *et al.* 1988
Kestrel	D	2	6	ns	?	Meijer *et al.* 1988
Kestrel	B/D	9	–	–	?	Aparicio 1994[c]
Sparrowhawk	D	2	ns	ns	?	Newton & Marquiss 1981
European Coot	B	?	ns	?	ns	Horsfall 1984
American Coot	B	4	ns	ns	+	Hill 1988
American Coot	B	2	1.5	1.0	(+)	Arnold 1994 Arnold *et al.* 1991
Lesser Black-backed Gull	B	3	ns	0.4[d]	+[d]	Hiom *et al.* 1991
Lesser Black-backed Gull	B	3	ns	ns	+[e]	Bolton *et al.* 1992
Glaucous-winged Gull	B	3	ns	ns	(+)	Reid 1987
Osprey	B	2	4	ns	ns	Poole 1985

B, Food supplementation started before the breeding season; D, food supplementation started during the breeding season; L, food supplementation started during laying. Period of food supplementation, how many weeks food was added before laying started. [a]Density-dependent effect. [b]In one of 4 years a 4% increase. [c]Same controls for early and late feeding experiments. [d]Larger eggs and clutches on one of two islands. [e]Increase only by protein supplement. [f]No date correction. Numbers in parenthesis have *P* level of 0.05–0.10; ns, not significant; ?, no data.

override the synchronization, and it therefore hardly affects the onset of laying. Support comes from food supplementation experiments in Starlings. When all Starlings of a breeding colony were given extra food, laying advanced by five days (compared with a nearby, unfed colony). When in one colony only half of the starling pairs were fed, laying onset differed by only one day between fed and unfed pairs (Källander & Karlsson 1993).

Food supplementation over a long period seems to be able to advance laying in multiple-brooded species by up to three or four weeks, but in single and double-brooded species by only up to one week (Fig. 5). Maybe females would have reacted more strongly if natural food had been supplemented (e.g. caterpillars for tits or leatherjackets for starlings) or if protein-rich food had been offered. In most supplementary feeding experiments it is assumed that it is energy which is limiting egg-production and therefore the quality of the diet was usually ignored. But Lesser Black-backed Gulls reacted differently to energy-rich and protein-rich food supplement (Bolton *et al.* 1992) as did Zebra Finches (Williams 1996, Houston pers. comm.).

We think that food quality and, especially for smaller bird species, the indirect role of ambient temperature on onset of laying has been insufficiently studied. A clear increase in spring temperature seems to trigger egg-formation immediately in Starling (Korpimäki 1978), Pied Flycatcher (Lundberg & Alatalo 1992), tits (Kluijver 1952, Perrins and McCleery 1994) and House Sparrow (Seel 1968).

Advancement of laying could have a negative effect on the fitness of the parents. Drent and Daan (1980) proposed that the optimal laying date varies between individuals in the population and that animals maximize their fitness by each adjusting the date of breeding to the optimal time in their circumstances. Experiments show that advancement of breeding lowered local survival in female Blue Tits (Nilsson 1994) and female European Coots *Fulica atra* (Brinkhof 1995). Therefore, breeding too early seems to be associated with costs and supports the view that a whole complex of proximate factors times breeding, in which the role of food is not directly related to the energetics of the laying female but is part of a more strategic decision on when to start breeding.

How food availabilty affects the number of eggs laid and what role endogenous and exogenous (dietary) nutrients play in the determination of clutch size has been discussed intensively for waterfowl (Drobney & Fredrickson 1985, Ankney & Afton 1988, Ankney *et al.* 1991, Drobney 1991). Arnold and Rohwer (1991)

argued that although most female waterfowl use reserves during laying, nutrient reserves have only a small effect on clutch size, except for arctic-breeding waterfowl. This seems to be more generally true. Of the 24 species which were food-supplemented, almost no fed females laid larger clutches or larger eggs than the unfed ones (Table 2). There are seven species in which clutch size slightly increased; in four of these the results were not confirmed in a second study. In two species (Marsh Tit *Parus palustris* and Red-backed Shrike *Lanius collurio*) feeding started three or four days before (Carlson 1989) or after the first egg was laid (Nilsson 1991).

The effect of extra food on egg mass or egg size was not measured in all studies, but again very few species showed an increase in egg mass (only in American Kestrel *Falco sparverius* and both *Larus* species; Table 2). This suggests that both clutch size and egg mass are more or less independent of female body reserves and actual food intake.

In most single-brooded species, clutch size decreases progressively with laying date – as is the case for Mute Swan *Cygnus olor* (Reynolds 1972), all species of arctic-nesting geese (Hamann & Cooke 1989), captive and free-living Mallards (Batt & Prince 1979, Krapu 1981), Willow Grouse (Myrberget 1986), American Coot (Arnold 1994), free-living and captive Kestrels (Cave 1968, Meijer *et al.*1988), free-living and captive Starlings (Karlsson 1983, Feare 1984, Meijer 1991), and Pied Flycatchers (Berndt & Winkel 1967). For Zebra Finch and Red-billed Quelea, no such data are available. Experiments with groups of Zebra Finches breeding in captivity showed that laying in this species is highly synchronized and that clutch size decreased sharply with progressive laying date (almost 0.50 egg/day; Rozman & Meijer unpubl. data). Similar phenomena are observed for colonial breeding Starlings (Karlsson 1983).

It seems that laying date itself controls the number of eggs laid, independent of food intake and body reserves, although small differences between years exist, for example in Mallard (Batt & Prince 1979), American Coot, (Arnold 1994) and Starling (Karlsson 1983, Feare 1984). Batt and Prince (1979) have suggested that, for Mallard, the decline in clutch size was mediated by photoperiod. For Kestrel, Meijer's experiments with breeding pairs under artificial photoperiods (Meijer 1989) showed that clutch size was not determined by photoperiod at the moment of laying, but that an endogenous programme triggered by photoperiod was responsible for smaller clutches later in the season (see also Meijer *et al.* 1992). This

had already been proposed by Berndt and Winkel (1967) from their work on the reproduction of Pied Flycatchers.

It seems that some large species, with their low mass-specific metabolic rate and a wide thermoneutral zone, can start laying in cold regions at a time when food is not yet locally available, depending exclusively on endogenous nutrients and energy during egg-laying (e.g. Adelie Penguin) and incubation (e.g. Eider). Smaller species, and especially passerines with their high mass-specific metabolic rate, depend almost exclusively on dietary nutrients and energy for egg-laying. Larger species such as Kestrel, Sparrowhawk, coots and ducks also rely directly on food intake for more than 90% of the total protein and fat needed during laying. Energy, in particular, but also protein, of the clutch represents (both absolute and relative) a much higher fraction of the *total* energy and protein requirements of large species than of small species. Finally, for both small and large species, the additonal cost of laying is much higher for protein than for energy.

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