The seasonal decline in clutch size: an experiment with supplementary food in the kestrel, Falco tinnunculus

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To test whether the seasonal decline in clutch size is proximately determined by laying date or by parental quality an experiment with supplementary food was performed in the kestrel Falco tinnunculus. The experiment showed that supplemented pairs laid earlier and larger clutches than control pairs. Comparison of clutch size between supplemented and non-supplemented pairs laying on the same dates, showed that supplementary food affects clutch size independently of laying date. The seasonal decline in clutch size seems to occur when there are among-pair differences in food supply, since clutch size declines among non-supplemented pairs but not among supplemented pairs.

I reviewed Daan et al.‘s model on optimization of clutch size and laying date. Contrary to what their authors defended, the model predicts that laying a clutch size in accordance with parental quality (or food supply) is more advantageous than doing it in accordance with laying date because there may be a change in the clutch size-laying date relationship. Independently of laying date, birds will maximize their fitness laying a clutch size as large as the number of young that can be adequately fed.


Seasonal declines in clutch size are common among single-brooded birds (review in Klomp 1970). Several hypotheses have been proposed to explain the proximate and ultimate factors determining such trends. The two hypotheses dealing with proximate factors are:

1) Differences in quality between individuals (including differences in age) and/or territories determine that pairs in better condition breed earlier and lay more eggs than others in worse condition (Darwin 1871, Askenmo 1982, Newton and Marquiss 1984, Hochachka 1990). In this case food supply independently affects both laying date and clutch size.

2) Other authors (Reynolds 1972, Drent and Daan 1980, Daan et al. 1988) postulate the existence of a condition threshold decreasing with time, which is governed either via an internal annual programme or via some external variable independent of food (e.g. day length). Crossing the threshold would induce laying date, which in turn determines clutch size. Both hypotheses lead to a seasonal decline in clutch size. If laying date determines clutch size, changes in the food supply would not alter the relationship between clutch size and laying date. On the other hand, if food supply independently affects both laying date and clutch size, changes in the relationship between clutch size and laying date would be expected from changes in food supply.

Until now, experiments with different species have led to different conclusions. Newton and Marquiss (1981) for Accipiter nisus, Arcese and Smith (1988) for Melospiza melodia, Hörnfeld and Eklund (1990), Korpimäki and Hakkarainen (1991) for Aegolius funereus, Nilsson (1991) for Parus palustris, and Bolton et al. (1992) for Larus fuscus, have shown that food supply affects clutch size independent of laying date; whereas Meijer et al.
(1988) for Falco tinnunculus, and several studies with multiple-brooded birds (review in Daan et al. 1988, Meijer et al. 1990) found that experimentally fed pairs laid clutch sizes equal to those expected from laying date.

At least four hypotheses have been proposed on ultimate factors affecting seasonal decline:

1. Lack (1966) and Perrins (1970) argued that the reduction in clutch size with the advance of the season is an adaptation to a worsening food supply for the young. However, seasonal declines in clutch size or reproductive success also occur when there is no seasonal deterioration in food availability (e.g. Hussell 1972, Daan et al. 1988, Korpimäki 1989, Hatchwell 1991).

2. Hussell (1972) proposed that young from late broods might have a smaller survival probability because of the shorter time available to them for moulting and building up energy reserves. Therefore, young of small broods might be at an advantage if their fledging mass is greater than that of young of large broods. According to this hypothesis, offspring from late broods would grow as well or better until independence than those from early broods, since they would receive more food. However, the opposite is most commonly found (e.g. Kluijver 1951, Perrins 1965, Newton and Marquiss 1984).

3. Toft et al. (1984) suggested that early and late breeders are extremes of a continuum of reproductive strategies, late birds being those whose low annual reproductive output is compensated by a longer life expectancy. Nevertheless, several studies have failed to demonstrate variation in energetic expenditure of parents raising different brood sizes (e.g. Ricks and Williams 1984, Williams and Nagy 1985, Masman et al. 1989, Moreno 1989, Tatner 1990). This suggests that there is only one optimal combination of effort (or clutch size) and parental survival.

4. Daan et al. (1988) proposed a model based on the trade-off between delaying laying to be able to feed more nestlings and reducing the survival probability of the fledglings, which usually decreases with the season (Perrins 1965, Newton and Marquiss 1984, Daan and Dijkstra 1988). Daan et al.’s model leads to optimal clutch size-laying date combinations for different parental or territorial qualities. From the model, it was concluded that the optimum clutch size decreases with laying date. Accordingly, birds will adjust their clutch sizes to the optimum size for the date of laying, independently of food availability.

In this paper, I review Daan et al.’s model and reach different conclusions to those of the authors. Moreover I perform a supplementary food experiment with the common kestrel (Falco tinnunculus L.) in Spain, to test both hypotheses on the causal role of food. This species is appropriate because it was used by Daan and coworkers in other experiments (Dijkstra et al. 1982, Meijer et al. 1988), and their results had some bearing on their model. I repeat the experimental procedure of Dijkstra et al. (1982) and Meijer et al. (1988), thus allowing a comparison of results.

Ultimate determination of clutch size and laying date
Daan et al.’s model

Daan et al. (1988) proposed an interesting model on optimal clutch size-laying date combinations, considering two variables: (1) reproductive value of each egg $V_0(t)$ which depends on laying date, $t$, (2) number of feedable nestlings $C(q,t)$ that depends on territory or parental quality, $q$, and varies throughout the year (i.e. it depends on laying date, $t$). $C(q,t)$ is equivalent to clutch size. $V_0(t)$ declines with the advance of laying date, whereas $C(q,t)$ increases and then decreases with time of year.

The optimal laying occurs while $C(q,t)$ is increasing. Thus, females make a trade-off between the two variables; they may delay egg-laying to increase the number of feedable nestlings (i.e. clutch size) at the expense of reducing the reproductive value of each egg. The optimal laying date—clutch size combinations are given by the maximum clutch reproductive value, i.e. the product $C(q,t) \cdot V_0(t)$. When there are several parental qualities, the optimum clutch size from this trade off decreases with laying date because low quality females will benefit from postponing reproduction more than high quality females will (Fig. 1).

Other consequences from the model

Daan et al. (1988) did not go further in discussing the consequences of their model and concluded that in view of this, laying date would have evolved as a proximate determinant of clutch size. However, if there are changes in the optimum relationship between clutch size and laying date then clutch size will not be optimized when it is determined by laying date. Using Daan et al.’s model, two cases are shown which change the optimum clutch size-laying date relationship: (Case I) When different constraints independently affect egg laying and nestling feeding, (Case II) When there are interannual variations in the timing of maximum food supply.

Case I

There may be several situations in which different constraints independently affect egg laying and the capacity to feed nestlings. For example, when short periods with bad weather, such as rain, delay the beginning of laying, but do not affect food availability during the nestling period; or also, when some individuals of a migrant population arrive at the breeding site too late to lay on the optimal date according to their parental condition.

Suppose that a female of quality $q$, begin to amass energy for egg-laying a few days later than the rest. Therefore, she will not be able to lay as soon as the others of the same parental quality. It is beneficial for her to lay as soon as possible because the clutch reproductive value declines with time once the optimum laying date is reac-
Fig. 1. Model for the optimization of clutch size and laying date (based on Daan et al. 1988). The solid lines \[ C(q_i, t) \] and \[ C(q_i, t) \] show seasonal variation in number of feedable nestlings (or clutch size) for two different parental or habitat qualities. Dotted lines show variation of clutch reproductive value \( (Vo \cdot C) \) when \( Vo \) declines linearly. The optimal clutch size-laying date combinations for each parental quality (solid circles) occur when the functions \( Vo \cdot C \) reach the maximum. The dashed line represents optimal clutch size-laying date combinations depending on parental quality. Parameter values are: \( C(q, t) = (q \cdot \exp [-0.00015(t - Y)] - Gp + Gn \), \( q \) being an index of parental quality \( q = 8 \), \( q = 4 \), \( t \) day of year, \( Y \) is the day of year with maximum food availability \( (Y = 160) \), \( Gp \) is energy for parental maintenance \( (Gp = 3) \); \( Gn \) is energy demand per nestling \( (Gn = 1) \). The reproductive value of each egg is given by \( Vo = 2 - 0.01 t \).

Fig. 2. Optimal clutch size when a female lays after her optimal laying date. (A) Arrows show possible decisions when a female of quality \( q_i \) cannot lay at her optimal laying date \( t_i \). Possibilities: (1) To lay the same clutch size as other females which lay on the same date, i.e. \( C(q_i, t_i) \). (2) To lay the largest clutch size whose nestlings can be adequately fed, i.e. \( C(q_i, t) \). Other symbols as in Fig. 1. (B) The clutch reproductive value according to decision about clutch size. The filled circle clutch reproductive value if female \( q_f \) would have laid at the optimal laying date-clutch size combination. Parameter values from Fig. 1.

Case II

Sometimes, the breeding season may occur at different dates every year because the food supply depends on unpredictable phenomena such as rainfall periods (e.g. Moreau 1950, Voous 1950, Marchant 1959, Fogden 1972, Millington and Grant 1984, Halse and Jaensch 1989, Wrege and Emlen 1991). In this case, there would be interannual variations in the optimal laying date-

Fig. 3. Optimal clutch size-laying date combinations when maximum food supply is reached at a different time in different years. Triangles are poor parental qualities and circles are good parental qualities. Filled symbols refer to years with early maximum food supply, and open symbols with late maximum food supply. Dashed lines show optimal clutch size variations for two different parental qualities when timing of maximum food supply varies. Parameter values from Fig. 1, \( Y \) being a variable.
clutch size relationship (Fig. 3). To demonstrate it, let us suppose that $t_i$ is the optimal laying date for pairs of quality $q_i$ in a year $Y_i$, and also for pairs of quality $q_i$ in another year $Y_j$ ($Y_i \neq Y_j$). Therefore, their optimal clutch size will be $C(q_i, t_i, Y_i)$ and $C(q_i, t_i, Y_j)$ respectively. The optimal laying date ($t_i$) occurs when the clutch reproductive value reaches maximum. Then its first derivative with respect to time is zero:

$$V_0'(t_i) \cdot C(q_i, t_i, Y_i) + V_0(t_i) \cdot C'(q_i, t_i, Y_i) = 0$$

and

$$V_0'(t_i) \cdot C(q_i, t_i, Y_j) + V_0(t_i) \cdot C'(q_i, t_i, Y_j) = 0$$

Since both terms are zero, equating and simplifying one obtains:

$$\frac{C(q_i, t_i, Y_i)}{C'(q_i, t_i, Y_i)} = \frac{C(q_i, t_i, Y_j)}{C'(q_i, t_i, Y_j)}$$

Hence, two females laying at the same date but in different years, will lay equal clutch size (i.e. $C(q_i, t_i, Y_i) = C(q_i, t_i, Y_j)$) when $C'(q_i, t_i, Y_i) = C'(q_i, t_i, Y_j)$. However, this condition will rarely occur if the pattern of seasonal variation of food supply changes between years.

Therefore, contrary to what Daan et al. (1988) concluded, their model predicts that laying a clutch size in accordance with parental quality (or food supply) is better than doing it in accordance with laying date.

**Supplementary food experiment**

**Methods**

A supplementary food experiment was carried out in the Alcarria region of the province of Cuenca, in Central Spain ($40^\circ 8'N, 2^\circ 18'W$) during the spring of 1990. The kestrel population breeds in natural rock cavities (95%) and to a lesser extent (5%) in old corvid nests in trees. Breeding data for this population have been collected from 1985, although more thoroughly from 1990. Parent kestrels were caught by using a “bal-chatte” (see Cavelio 1968) and ringed from 1990. Laying date was determined during the laying period of each nest.

Supplementary food was offered to two groups of ten pairs. The first of them (Early-fed) was supplemented from 28 February and the second (Late-fed) from 17 April. Feeding ceased when the pair had completed laying. Kestrels were supplemented with hen chicks; every two days 120–150 g of dead chicks were left in the nest of each selected pair. Yellow-coloured pellets indicated that the chicks were eaten by the kestrels.

Early-fed pairs were supplemented for a minimum of 50 d before egg laying (mean: 62 ± 7 sd) and Late-fed pairs for a minimum of 17 d (22 ± 5 sd). In both cases, the minimum supplementary feeding period was longer than the nine days that kestrels take to develop the first egg (Meijer et al. 1989). Thus, I assume that supplemented pairs had sufficient time to improve their condition.

When the experiment began, not all pairs had been located, so that the random selection of 10 pairs (one of them in a twig-nest) of the Early-fed was made from only 16 pairs. The Late-fed (10 pairs) and Control (23 pairs, two of them in twig-nest) groups were randomly selected from all pairs except the Early-fed group. One pair in the Early-fed group and two more in the Late-fed group did not consume the chicks and later abandoned the area, four Control pairs did not lay, and a pair in the Late-fed group and four Control pairs lost the clutch before completion. These pairs were excluded from analysis, leaving 15 Control pairs, 9 Early and 7 Late supplemented pairs.

Laying date and clutch size are compared between Late-fed and Control groups to see the effect of food supply on both laying date and clutch size. Laying date and clutch size are also compared between Early and Late-fed to test whether similar feeding conditions during prelaying and laying periods lead to equal clutch size at different times. I also compare the clutch sizes of supplemented pairs (Early and Late groups) with those of non-supplemented pairs which laid within the same date range but in different years (from 1985 to 1992) to test whether laying date determines clutch size. I assumed that data from different years were independent even if individual birds provided data in more than one year because the repeatability of clutch size and laying date are not significantly different from zero in the kestrel (Meijer et al. 1988), as well as in other birds of prey (review in Korpimäki 1990). This suggests that most of the interannual variation in breeding performance is due to environmental factors, and successive records of the same individual can be treated as nearly independent observations (Korpimäki 1990).
Table 1. Laying date and clutch size in early-fed, late-fed and control pairs of kestrel.

<table>
<thead>
<tr>
<th></th>
<th>Early fed (E)</th>
<th>Late fed (L)</th>
<th>Control (C)</th>
<th>Comparison (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>E-L L-C</td>
</tr>
<tr>
<td>Laying date (2)</td>
<td>Mean</td>
<td>120.0</td>
<td>128.7</td>
<td>135.3</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>7.1</td>
<td>4.3</td>
<td>6.0</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>108–131</td>
<td>124–136</td>
<td>122–146</td>
</tr>
<tr>
<td>Clutch size</td>
<td>Mean</td>
<td>5.11</td>
<td>5.14</td>
<td>4.27</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.60</td>
<td>0.38</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>4–6</td>
<td>5–6</td>
<td>3–5</td>
</tr>
</tbody>
</table>

(1) U-test, 2-tailed. (2) January 1 = 1.

Results

Clutch size and laying date in the population

Clutch size and laying date were recorded for 85 nests in unmanipulated conditions, between 1985 and 1992. Laying date ranged from 8 April to 7 June. Clutch size ranged from 3 to 6 eggs. Clutch size declined significantly each year with laying date (in 1990: r = −0.69, n = 15, P = 0.03; 1991: r = −0.48, n = 21, P = 0.025; 1992: r = −0.48, n = 26; P = 0.01; in other years n ≤ 7), and when all years are pooled (Fig. 4: r = −0.33; n = 85; P = 0.002).

The largest clutch sizes of 6 eggs were present in 5 years; these were, however, never the earliest (1988: 15, 1989: 6, 1990: 15, 1991: 24, 1992: 5 d later than the first clutch). According to Daan et al.’s (1988) model, that result is expected if some females of high quality delay the laying date, and if clutch size is not determined by laying date.

Effect of supplementary food on the seasonal decline in clutch size

The Late-fed group laid significantly larger clutches (Mann-Whitney U-test, P = 0.013) at significantly earlier dates than the Control group (Mann-Whitney U-test, P = 0.012; Table 1). Thus, food availability affects both laying date and clutch size, but it is not possible to discern whether clutch size was determined by food supply or laying date.

Both Early and Late-fed groups received equal daily amounts of supplementary food but from different dates; in this manner, I experimentally created two groups with similar feeding conditions but prepared to lay at different times. The Early-fed group laid significantly earlier than the Late-fed group (Mann-Whitney U-test, P = 0.019), yet there were no significant differences in clutch size between the two groups (Mann-Whitney U-test, P > 0.95, Table 1). Such a result was expected if food availability determines clutch size, but it does not permit the rejection of the hypothesis of determination by the laying date.

To test whether laying date determines clutch size, the laying date and clutch size of supplemented females were then compared with clutches of all years in unmanipulated conditions, which were laid in the same laying date range. If clutch size was determined by laying date, independently of food availability, there would be no differences in clutch size between supplemented and non-supplemented pairs. Laying date in supplemented pairs ranged from 18 April (108) to 16 May (136). However, the samples within that differ in distribution (D = 0.28, n1 = 16, n2 = 58, P < 0.3, Kolmogorov-Smirnov two-sample test). In order to get samples with similar distributions, the first and the last clutch were removed because they were laid 6 d earlier and 5 d later than the rest, respectively; such intervals include 12.5% of the sample of supplemented pairs, but 36.2% of the non-supplemented. Thus, the analysis includes clutches between days 114 and 131, and the sample distributions are significantly equal (D = 0.16, n1 = 14, n2 = 37, P > 0.95, Kolmogorov-Smirnov two-sample test). Clutch size was significantly larger for the supplemented than for the non-supplemented group (Mann-Whitney U-test, P = 0.013), even though there were no differences in laying date (Table 2). Clutch size declined with laying date in the non-supplemented group, but not in the supplemented group (Fig. 5).

Table 2. Comparison of laying date and clutch size of supplemented (Fed) versus unmanipulated (Unfed) pairs, which laid within the same range of laying date.

<table>
<thead>
<tr>
<th></th>
<th>Fed</th>
<th>Unfed</th>
<th>Comparison (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laying date (2)</td>
<td>Mean</td>
<td>124.1</td>
<td>124.0</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>5.7</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>37</td>
<td></td>
</tr>
<tr>
<td>Clutch size</td>
<td>Mean</td>
<td>5.14</td>
<td>4.59</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>0.53</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>37</td>
<td></td>
</tr>
</tbody>
</table>

(1) U-test, 2-tailed. (2) January 1 = 1.
may determine uncontrolled differences between pairs, affecting both clutch size and laying date.

The case of the Dutch kestrel population
Daan et al. (1988, 1990) have presented the Dutch kestrel population as a clear case in which laying date determines clutch size independently of food supply. In that population, two supplementary food experiments did not produce any difference in clutch size between experimentally fed pairs and control pairs laying at the same date (Dijkstra et al. 1982, Meijer et al. 1988). Yet reanalysis of their data (published in Daan and Dijkstra 1988) leads to a different conclusion.

Daan and Dijkstra (1988) classified the breeding seasons into three categories (peak, trough, and other) according to the index of vole abundance (see Daan and Dijkstra 1988: p. 94, Table 3 and p. 98, Fig. 3a). They found a significant linear correlation between annual mean clutch size, c, and laying date, d; the linear regression is given by e = 9.495 - 0.03647 d (r = -0.86; n = 20; P < 0.001). If laying date determines clutch size independently of food supply, data points would be distributed equally on both sides of the regression line for any breeding season category. In peak years, however, all points in unmanipulated conditions and two groups of experimentally fed kestrels are above the regression line.

### Table 3. Differences between observed and expected mean clutch size, according to mean laying date, of Dutch kestrel populations for three vole categories. Data from table 3, p. 94, in Daan and Dijkstra (1988).

<table>
<thead>
<tr>
<th>Index of volves</th>
<th>Year</th>
<th>Area</th>
<th>Mean laying date</th>
<th>Mean clutch size</th>
<th>Expected difference (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak</td>
<td>1960</td>
<td>F</td>
<td>107.4</td>
<td>5.65</td>
<td>5.58</td>
</tr>
<tr>
<td>Peak</td>
<td>1964</td>
<td>F</td>
<td>110.0</td>
<td>5.50</td>
<td>5.48</td>
</tr>
<tr>
<td>Peak</td>
<td>1986</td>
<td>F</td>
<td>120.3</td>
<td>5.24</td>
<td>5.11</td>
</tr>
<tr>
<td>Peak</td>
<td>1977</td>
<td>L</td>
<td>113.4</td>
<td>5.42</td>
<td>5.36</td>
</tr>
<tr>
<td>Peak</td>
<td>1981</td>
<td>L</td>
<td>114.4</td>
<td>5.53</td>
<td>5.32</td>
</tr>
<tr>
<td>Peak</td>
<td>1983</td>
<td>L</td>
<td>119.0</td>
<td>5.44</td>
<td>5.16</td>
</tr>
<tr>
<td>Peak</td>
<td>1986</td>
<td>L</td>
<td>122.9</td>
<td>5.15</td>
<td>5.01</td>
</tr>
<tr>
<td>Peak</td>
<td>(2)</td>
<td></td>
<td>109</td>
<td>5.55</td>
<td>5.52</td>
</tr>
<tr>
<td>Peak</td>
<td>(3)</td>
<td></td>
<td>132</td>
<td>4.85</td>
<td>4.68</td>
</tr>
<tr>
<td>Trough</td>
<td>1961</td>
<td>F</td>
<td>118.1</td>
<td>4.94</td>
<td>5.19</td>
</tr>
<tr>
<td>Trough</td>
<td>1963</td>
<td>F</td>
<td>121.9</td>
<td>5.24</td>
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</tr>
<tr>
<td>Trough</td>
<td>1965</td>
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<td>103.4</td>
<td>5.69</td>
<td>5.72</td>
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<tr>
<td>Trough</td>
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<tr>
<td>Trough</td>
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</tr>
<tr>
<td>Trough</td>
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<td>L</td>
<td>115.3</td>
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</tr>
<tr>
<td>Trough</td>
<td>1987</td>
<td>L</td>
<td>128.5</td>
<td>4.84</td>
<td>4.81</td>
</tr>
<tr>
<td>Trough</td>
<td>1962</td>
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<td>4.03</td>
<td>4.30</td>
</tr>
<tr>
<td>Trough</td>
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<td>120.6</td>
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</tr>
<tr>
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<td>127.8</td>
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<td>4.67</td>
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<tr>
<td>Trough</td>
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<td>L</td>
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<td>4.91</td>
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<tr>
<td>Trough</td>
<td>1985</td>
<td>L</td>
<td>132.7</td>
<td>5.00</td>
<td>4.66</td>
</tr>
</tbody>
</table>

F = Flevoland, L = Lauwersmeer.

(1) Difference: Mean - Expected clutch size.

(2) Early surplus feeding (Meijer et al. 1988).

(3) Late surplus feeding (Meijer et al. 1988).
The result differs significantly from that predicted by Daan et al.'s hypothesis (Table 3, P < 0.01; signs-test).

Daan et al. (1988) knew the functions of Vo(t) and C(t) (see above) for their population; thus, they estimated the clutch size-laying date combinations which maximize clutch reproductive value. Their predictions are adjusted to mean laying date at which each clutch size was laid (Daan et al. 1988: Fig. 7), but this is not repeated when predictions are compared with observed mean clutch sizes at each laying date (Fig. 6). These results indicate that there are also changes in the clutch size-laying date relationship for the Dutch population of kestrels. Therefore it seems that clutch size is not proximately determined by laying date in the Dutch kestrel population.

The optimal laying date and clutch size

Daan et al.'s (1988) model predicts optimal clutch size-laying date combinations which result from a trade off between delaying breeding to be able to feed more nestlings and reducing the survival probability of the fledglings. According to the model, the optimal solution for pairs of low quality is to lay later than those of high quality because they increase their clutch reproductive value by waiting longer; however, they cannot feed broods as large as those of better parental quality. Thus, seasonal decline in clutch size will occur whenever there are several parental or territorial qualities within any population.

In spite of such covariation between laying date and clutch size, to lay a clutch size according to the laying date, as suggested by Daan et al. (1988), is not the best solution when some females lay after their particular optimal laying date or when the timing of high food supply varies among years. However, independently of laying date, females maximize their fitness whenever her clutch is as large as the number of young that can be adequately fed (Figs 2 and 3). Thus, if there is any correlation between pre-laying food supply and nestling-period food supply (e.g. Benkman 1990, Davis and Graham 1991, Donázar et al. 1992, Tye 1992) then daily food intake should be a cue for number of feedable nestlings. Therefore, such proximate mechanisms, in which the daily food intake proximately determines clutch size, should be favoured by natural selection. This point of view of the model diverges from Daan et al.'s (1988) conclusions, but is supported by the results since the largest clutch sizes are not the earliest, and there are changes in the clutch size-laying date relationship depending on food supply.

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