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Meijer, Theo; Daan, Serge; Hall, Michael

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FAMILY PLANNING IN THE KESTREL (FALCO TINNUNCULUS): THE PROXIMATE CONTROL OF COVARIATION OF LAYING DATE AND CLUTCH SIZE

by

THEO MEIJER[1][3]), SERGE DAAN[1][4]) and MICHAEL HALL[2])

(Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands[1] and A.R.C. Research Group on Photoperiodism and Reproduction, Department of Zoology, University of Bristol, BS8 1UG, U.K.[2])

1. Introduction

Timing of breeding and mean clutch size in birds are adaptive properties evolved to maximize reproductive output (LACK, 1968). The idea has been advanced that variation in these properties between individuals, and indeed within the same individuals between breeding attempts in different years, also reflect adaptive responses to varying individual circumstances (HÖGSTEDT, 1980; DRENT & DAAN, 1980). This view implies that individual birds possess control mechanisms allowing them to adaptively adjust their reproductive decisions. Many species which raise a single brood per year show a characteristic seasonal decline in clutch size (Fig. 1; KLOMP, 1970). This decline offers the opportunity to analyse potential control mechanisms for the two major decisions in reproduction: when to start laying eggs (determining laying date) and when to stop laying eggs (determining clutch size).

The European kestrel, *Falco tinnunculus*, is a single-brooded species typically showing the seasonal decrease in clutch size (Fig. 1). We have elsewhere provided evidence that this decline reflects the variation in individual females laying at different dates in different years (MEIJER *et al.*, 1988). Furthermore the laying date-clutch size combinations
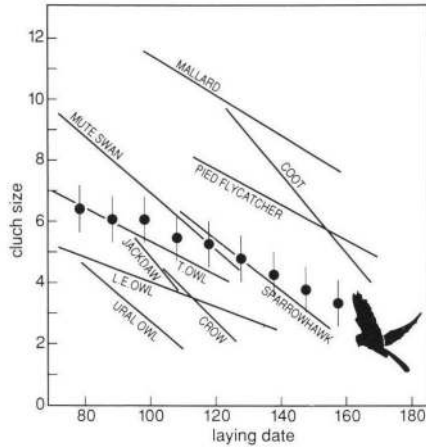

Fig. 1. Seasonal decrease in clutch size for single brooded bird species; mallard (KRAPU, 1981), American coot (ALISAUKAS & ANKNEY, 1985), mute swan (REYNOLDS, 1972), pied flycatcher (BERNDT & WINKEL, 1967), tengmalm's owl (KORPIMÄKI, 1987), sparrowhawk (NEWTON, 1986), jackdaw (RÖELL, 1978), carrion crow (YOM-TOV, 1974), long-eared owl (WIJNANDTS, 1984), ural owl (PIETIÄINEN et al., 1986) and kestrel (BEUKEBOOM et al., 1988).

observed approach those which theoretically maximize total reproductive value (of parents and eggs) and hence fitness in different conditions of food availability (DAAN et al., 1989, 1990). Thus it appears that kestrels must possess a complex mechanism adjusting laying date and clutch size to their nutritional circumstances. In this paper we outline the general, formal characteristics of this response mechanism, synthesizing the detailed conclusions from earlier publications (BEUKEBOOM et al., 1988; DAAN & ASCHOFF, 1982; DAAN et al., 1989; DIJKSTRA et al., 1982, 1988; MASMAN et al., 1988; MEIJER et al., 1988, 1989; MEIJER, 1989). We further present a model for the control mechanism which leads to larger clutches in early nests than in late nests. This model expands on a concept earlier presented by HAFTORN (1985). HAFTORN was aware of the speculative nature of his relatively simple proposition for the determination of clutch size by what "is undoubtedly a very complex procedure" (HAFTORN, 1985). Yet we think that such simple formal models may be helpful as a guide in experimental research unraveling this complexity. Finally, we present some new data on one potential candidate for one physiological component in this mechanism, prolactin.

2. Laying date

Food as a proximate factor.

Laying dates (of the first egg) among dutch kestrels are spread out over an annual episode of 70 days, from the end of March till early June. The negative association between mean laying date and annual food indices has been amply documented for the kestrel (CAVÉ, 1968; BEUKEBOOM *et al.*, 1988). It is thus possible that food supply acts as a proximate factor involved in the triggering of reproductive activities in spring. Male kestrels provide all of the females' food from courtship till half way the nestling phase. The male raises food provisioning to the female—some 2-3 weeks before laying—by increasing his hunting activity from an average of 1.6 till 2.9 hours/day, in combination with an increase in hunting yield (prey obtained per hour flighthunting). During egg laying, individual hunting yields fluctuate around 3 prey per hour of flighthunt (MEIJER *et al.*, 1989). Hunting yield is a useful measurement of the actual food availability to the individual pair and preferable over mean food indices for a whole study area as provided in many other studies. In continuous dawn-to-dusk observations of breeding pairs in the Lauwersmeer area, we established that female food intake (I in g/day) during late courtship $(I = 156\text{-}0.73 \ d)$ and during laying $(I = 161\text{-}0.59 \ d)$ was negatively correlated with the date of laying (d = day number of the year) (MEIJER *et al.*, 1989). This seasonal decline was associated with a trend towards lower hunting yields with progressive laying date in the males. Body mass of laying female kestrels decreased with progressive laying date (DIJKSTRA *et al.*, 1988).

Such correlations obviously do not prove a causal relationship between food supply by the male and the date when the female lays the first egg. However, experiments with extra food given to free-living kestrel pairs early and late in the breeding season, advanced their laying date on average by 10 and 6 days, respectively. Conversely, temporal food rationing of breeding pairs in captivity delayed the moment of laying until the birds were fed *ad libitum* again (MEIJER *et al.*, 1988).

In the kestrel, the male is able to collect food for the female as well as for himself by increasing his daily flight-hunting activity and by a simultaneous increase in hunting yield. Thus the male essentially determines when to bring enough food to his partner, and when she starts the formation of body reserves and eggs. In a sense, it is thus the male who decides when to breed. The female has only a slight modifying influence, since

late breeders start laying with a lower food intake and at a reduced level of body reserves compared to early breeders (MEIJER *et al.*, 1989). Environmental factors which are correlated with laying date, such as rain and temperature during winter and spring (CAVÉ, 1968; MEIJER *et al.*, 1988), are likely to act via the males' hunting activity. Decreasing male hunting time per day (*e.g.* by rain or wind, VILLAGE, 1983; RIJNSDORP *et al.*, 1981) and increasing energy demands (by lower temperature, MASMAN, 1986) may delay the date of laying.

This view of food supply as a proximate factor to which laying date is adjusted, is likely to be valid for other species of raptors. POOLE (1985, Table 3) recorded a similar trend in male food supply to laying ospreys *Pandion haliaetus:* females which laid 20 days later, received a 32% lower daily ration of fish. Like in the kestrel, body mass of laying females decreased with progressive laying date in sparrowhawks *Accipiter nisus* (NEWTON & MARQUISS, 1984), ospreys (POOLE, 1985), Ural owls *Strix uralensis* (PIETIÄINEN *et al.*, 1986) and Tengmalm's owls *Aegolius funereus* (KORPIMÄKI, 1986a). The advance in laying date of kestrel pairs given extra food is in agreement with the majority of surplus feeding experiments in the field in 18 species (Table 1). However, prolonged surplus feeding over 100-200 days (JONES, 1973; YOM-TOV, 1974; SMITH *et al.*, 1980; DAVIES & LUNDBERG, 1985; CLAMENS & ISENMAN, 1989) advanced laying only by 0-25 days. This suggests that in most species laying is somehow constrained to a small part of the year and that this laying "window" determines the earliest laying date. In some experiments the local food situation was apparently sufficient to let control birds lay at the same dates as experimentally fed birds (JONES, 1973; HOCHACHKA & BOAG, 1987; MEIJER *et al.*, 1988).

Daylength as a proximate factor.

Experiments with kestrels in captivity under natural photoperiod (nLD) showed that even under constant *ad lib.* food conditions the onset of egg laying was restricted to a range of 61 days (from April 8 till June 8; MEIJER, 1989). In experiments in constant photoperiods (LD) this laying window was shifted within the year; it was advanced by long days (MEIJER, 1989) and delayed by short days (unpubl. results). Food rationing in such constant photoperiods showed again that the amount of food (again delivered by male to female) determines whether laying is early or late within the window (MEIJER, 1989). These experiments led us to conclude that the reproductive window is largely endogenously deter-

TABLE 1. Effects of supplemental food on laying date and cutch size in 12 passerine and 6 non-passerine species

Species	Start	Period	Shift l.date	Shift c.size	Reference
1. *Parus major*	B	29	no	no	JONES, 1973; KREBS, 1971
2. *Parus major*	B	3	5 ***	no	KÄLLANDER, 1973
3. *Parus major*	B	14	2-5	-1.5	CLAMENS & ISENMAN, 1989
4. *Parus caeruleus*	B	14	5-6	0.8	CLAMENS & ISENMAN, 1989
5. *Parus cristatus*	B	3-4	5-7 **	0.3	VON BRÖMSSON & JANSSON, 1980
6. *Parus montanus*	B	7	2-5 **	0.3	VON BRÖMSSON & JANSSON, 1980
7. *Melospiza melodia*	B	30	25 ***	0.1	SMITH *et al.*, 1980
8. *Melospiza melodia*	B	5	18 ?	0.5 ***	ARCESE & SMITH, 1988
9. *Agelaius phoeniceus*	B	2-6	7-26 **	0.0	EWALD & ROWHER, 1982
10. *Agelaius phoeniceus*	B	2	2 *	no	WIMBERGER, 1988
11. *Erithacus rubecula*	?	?	no	incr.	HARPER, 1984 (in DAVIES & LUNDBERG, 1985)
12. *Prunella modularis*	B	14	10-22 ***	0.2	DAVIES & LUNDBERG, 1985
13. *Sturnus vulgaris*	B	3-4	5 ***	0.3	KARLSSON & KÄLLANDER, 1983
14. *Lanius collurio*	D	0.5	no	0.9 **	CARLSON, 1989
15. *Corvus corone*	B	15	5 **	0.2	YOM-TOV, 1974
16. *Pica pica*	B	5	2	0.5	HÖGSTEDT, 1981
17. *Pica pica*	B	4	0-8 **	0.4	HOCHACHKA & BOAG, 1987
18. *Pica pica*	B	3	4-6 *	no	KNIGHT, 1988
19. *Accipiter nisus*	D	2	2	0.8	NEWTON & MARQUISS, 1981
20. *Falco tinnunculus*	B	>4	23 **	0.7	DIJKSTRA *et al.*, 1982
21. *Falco tinnunculus*	B	>4	0-21 **	0.2	MEIJER *et al.*, 1988
22. *Falco tinnunculus*	D	2	6 *	0.4	MEIJER *et al.*, 1988
23. *Aegolius funereus*	B	3	6 **	0.9	KORPIMÄKI, 1989
24. *Pandion haliaetus*	B	2	4	no	POOLE, 1985
25. *Fulica atra*	B	?	no	?	HORSFALL, 1984
26. *Fulica americana*	B	4	no	no	HILL, 1988

Colums 2 and 3 indicate whether the experiment started before (B) or during (D) the breeding season and the duration of supplemental feeding from start till egg laying (in weeks). Levels of significance for shifts in laying date (days) and clutch size (eggs) are: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

mined, but that daylength affects the synchronization of this annual window with the environmental cycle.

Apparently, food supply determines when actual reproduction starts within the annual limits set by an endogenous program, synchronized via photoperiod. The decision to start breeding can be traced back to the male when he rather abruptly raises his daily flighthunt time. This occurs at different times of year for different males, but is usually simultaneous with an increase in hunting yield (MEIJER *et al.*, 1989). This yield

increase is unlikely to result from a change in behaviour, since experimental increases of food demand do not lead to an increase in yield in the kestrel (MASMAN et al., 1988). Apparently, the yield increase is due to increases in vole population density and/or vole surface activity as these primary kestrel prey start reproduction in spring. The actual trigger for reproduction thus presumably has to be sought in changes in behaviour, sexual condition or density of the prey, perceived initially by the male, and secondarily, when the male raises his daily work level, by the female.

3. Clutch size

Effects of food supply.

The average clutch size is known to be strongly positively correlated with annual indices of vole density in the kestrel (CAVÉ, 1968; KORPIMÄKI, 1986b). Clutch size is further tightly associated with laying date, both between and within years (CAVÉ, 1968; MEIJER et al., 1988). Late breeding female kestrels, which are characterized by below average daily food intake and below average body mass (MEIJER et al., 1989), make raltively small clutches. Again only food manipulation experiments can tell us whether food supply is causally involved in the determination of clutch size. Free-living pairs—given extra food early in the season—laid large clutches, but late pairs—offered the same amount of food—laid small clutches (MEIJER et al., 1988; DAAN et al., 1989). Also in captivity, late laying pairs, temporarily food rationed but given ad lib. food from late courtship onwards, produced small clutches. Late breeding females, both free-living and captive, which received ad lib. food supplies, had an average body mass indistinguishable from the body mass of early layers (MEIJER et al., 1988). The conclusion must be that neither the daily rate of food intake nor the condition (as indicated by body mass) of the laying female kestrel itself determines the clutch size, independent of date. Hence food abundance apparently affects clutch size only through its modulation of the date of reproduction.

    This situation is probably more common, except maybe in species like swans, geese and ducks, which depend almost entirely on body reserves during laying (REYNOLDS, 1972; MILNE, 1976; ANKNEY & MACINNESS, 1978; RAVELING, 1979; KRAPU, 1981). It is unfortunate that to date no feeding experiments on such species have been performed. Feeding experiments in other species gave larger clutches in only one out of 8

multiple-brooded species (nrs 1-12, Table 1): the robin *Erithacus rubecula* (HARPER, 1984, cited in DAVIES & LUNDBERG, 1985), and in one (the red-backed shrike *Lanius collurio*) out of 10 single-brooded species (nrs 13-26, Table 1). The food-induced increase in clutch size in song sparrows *Melospiza melodia* remained below the ceiling values obtained in years of low population densities (ARCESE & SMITH, 1988), and food surplus experiments may thereby not have revealed the underlying relation between food and clutch size. In none of the experiments where supplemental food advanced laying significantly, was the increase in clutch size different from that expected for the earlier date. The general conclusion must be that food availability is a strong determinant for date of laying, but does not significantly affect the relationship between laying date and clutch size in most species.

Daylength.

Smaller clutches of late laying female kestrels are not an effect of differences in age, food intake or body reserves (MEIJER *et al.*, 1988). The tight negative association of clutch size and laying date, both between and within individuals, might suggest that daylength directly determines clutch size. In nature kestrels lay smaller clutches with progressively increasing photoperiod in spring. However, experiments testing the role of photoperiod showed that in constant long days (17.5L:6.5D, corresponding with early June) and in relatively short days (13L:11D, early April) the same natural range of clutches (3 to 7 eggs) was produced. Under both photoperiods, small clutches were laid only by females reproducing late in the ''reproductive window'', and large clutches early in the window (MEIJER, 1989). Hence daylength itself does not determine clutch size in the kestrel. Rather an internal time program for clutch size determination must exist within this window. Whether this program is part of a circannual rhythm (*i.e.*, whether it restarts itself spontaneously in constant conditions, GWINNER, 1986) can presently not be established.

For other species, BERNDT & WINKEL (1967), studying the seasonal decrease in clutch size of pied flycatchers *Ficedula hypoleuca*, have already suggested an endogenous rhythm of egg production. In a study on reproduction of captive mallards *Anas platyrhynchos*, BATT & PRINCE (1980) found that the main factor controlling clutch size was laying date, and suggested that the decline in clutch size was mediated through photoperiod. Unfortunately, there are no studies available to date on

clutch size regulation in experimental photoperiodic conditions other than in the kestrel (MEIJER, 1989).

In summary, all the descriptive and experimental evidence in the kestrel is consistent with the following interpretation:

a. There is an internally preprogrammed decline in clutch size within an annual "reproductive window" in individual females.
b. This window is synchronized with the external annual cycle by daylength.
c. Final follicle development and clutch initiation occur when the female within the window surpasses a threshold in daily food or energy intake.
d. This intake threshold shows a seasonal decline (thereby creating larger reserves in early breeders, which play no causal role in determining the larger clutch size).
e. The time at which the female passes this threshold is determined by the male when he increases his daily hunting activity, accompanied by an increase in hunting yield.

Thus we surmise an intricate interplay between environmental information of two kinds: daylength synchronizing the internal program and food setting actual reproduction time within the internal program. The nature of the internal program remains to be discussed.

4. Incubation and follicle resorption

Like many other birds species, kestrels have ovaria which develop a larger number of ova than will eventually be laid. This is clear from egg removal experiments, done both in the American kestrel in captivity (PORTER, 1975), and the European kestrel in field experiments (BEUKEBOOM et al., 1988): With repeated removal of eggs from the nest, kestrels produce more than they would ever lay under normal conditions. Thus the regulation of clutch size is accomplished by the "decision" to resorb further developing follicles, and information from the number of eggs already present in the nest affects this decision.

That a larger number of ova undergo enlargement in the period prior to egg laying than are actually laid is true also for the black-headed gull *Larus ridibundus* (WEIDMANN, 1956), for the herring gull *Larus argentatus* (PALUDAN, 1951; PARSONS, 1976), and, from examination of the ovary, also for the lesser black-backed gull *Larus fuscus* (HOUSTON et al., 1983). In these three species, which normally lay three eggs, resorption of the

d- and e-follicle starts four days before the last egg (egg c) is laid, when incubation behaviour develops normally. Likewise, Adélie pinguins *Pygoscelis adeliae* lay 2 eggs and develop three follicles (ASTHEIMER & GRAU, 1985).

HAFTORN (1981, 1985) showed that in the great tit *Parus major* the rate of development of incubation behaviour during the laying period was related to the size of the clutch: the faster the daily incubation time of a female increased, the smaller was the clutch she eventually produced. HAFTORN suggested that further development of follicles is suppressed when the total incubation time during laying has surpassed about 1000 minutes. This happened consistently about three days before the last egg was laid. HAFTORN (1985) went on to suggest that the increase in incubation behaviour during laying is slow in females laying early in the year, and fast in females laying late in the year, and that this difference is instrumental in the relatively long laying period and large clutches in early breeders among the great tits.

With slight modification, this theory is also consistent with the data obtained in the kestrel. Incubation behaviour in this species also develops more rapidly in females laying late in the season, and producing small clutches (Fig. 2). Using lipophylic dyes (ASTHEIMER, 1986; GRAU, 1984) we have shown that in the kestrel a follicle enters its rapid growth phase nine days before the egg is laid (MEIJER *et al.*, 1989). Furthermore, from egg removal experiments we know that the decision to resorb extra follicles, and hence to terminate laying is taken circa four days before the last egg is laid (BEUKEBOOM *et al.*, 1988). Since eggs are laid in two-day intervals, at least two extra follicles are being developed and later resorbed unless eggs disappear. The decision to terminate follicle development shifts from late in the laying period in early females (around egg 4) to early in the laying period in late females (around egg 2), and is associated with approximately 50% of the day devoted to incubation, both in early and late breeders. Our experiments with egg additions and removals moreover have shown that both incubation behaviour and final clutch size are affected by the number of eggs in the nest. Egg additions to the nest just after—or before—the first egg was laid increased the incubation tendency of free-living kestrels. Egg removal reduced the incubation tendency at least when the removals started before incubation behaviour had reached 50% of time (Fig. 2 and BEUKEBOOM *et al.*, 1988). We surmise that the extent of incubation behaviour on the one hand and the number of eggs present in the nest on the other both positively affect a regulating variable which controls the further increase in incubation

and the decision to resorb further eggs. The fact that egg removal may prevent the normal increase in incubation behaviour and also prevent clutch termination suggests that contact between eggs and adult somehow reinforces incubation, and thus enhances further contact. This positive feedback loop would then eventually lead to clutch termination. If incubation tendency in laying females would spontaneously increase with progressive laying date, a progressive advance in the onset of follicle resorption and hence reduction of clutch size would emerge.

HAFTORN (1985) suggested in his model that incubation tendency in the great tit shows a faster daily increase in late breeders, but the rise starts sooner after the first egg in late breeders (Fig. 2). Obviously both will lead to the same result of a shorter laying period—and hence smaller clutch—later in the year.
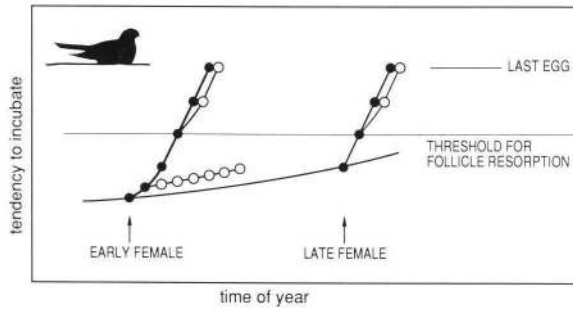

Fig. 2. Development of incubation behaviour during the laying period (mean ± se) in female kestrels laying six (n = 5) and four eggs (n = 3). Removal of eggs suppresses the development of incubation behaviour early in the laying period in two early laying females.

Our view is formally summarized in a model—modified from HAFTORN's model—for the seasonal control of clutch size in Fig. 3. The moment an early or late female starts egg formation is determined by when the female's daily food intake, itself determined by the male's daily hunting activity, passes a threshold value. An early female starts at a low incubation tendency, a late female with a high tendency. This initial tendency to incubate is based on an endogenous seasonal program, synchronized by daylength. Following deposition of the first egg, the feedback loop between egg-broodpatch contact and incubation tendency starts to operate. The early female can lay 4 eggs before daily incubation reaches the 50% level, whence follicle resorption starts. Two further eggs

are laid after this moment, one of which has just ovulated and the other has almost reached its final volume (MEIJER *et al.*, 1989), and neither is affected by inhibitory feedback induced by incubation (MURTON & WESTWOOD, 1977). A late laying female has a higher initial tendency to incubate her first eggs, and reaches the 50% level already after two eggs, so that her clutch is only 4 eggs.
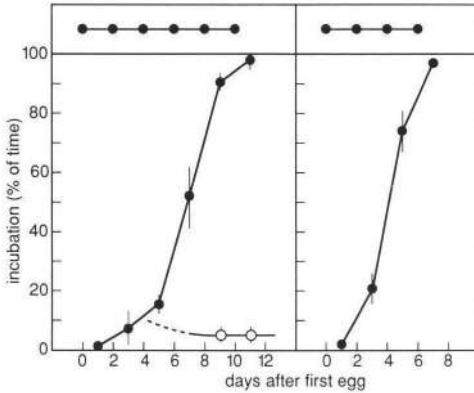

Fig. 3. Proximate model for the seasonal control of clutch size. Indicated is the development of normal incubation behaviour of an early and a late female (laying six and four eggs respectively), and of a non-breeder. Egg removal (o--o--o) has only an effect on incubation behaviour and clutch size during the first days of the laying phase, early in the season. For further explanation see text.

Repeated removal of eggs (except one) during the laying period in the model would lead to an interruption of the egg-broodpatch-incubation loop, hence to a slower rise in incubation behaviour, and to the excessively large numbers of eggs observed, since the 50% incubation is reached much more slowly if at all. Removal experiments have this effect only early in the season. When the second egg of a late breeder is laid and taken away, the clutch is already fixed. The same holds for removals late in the laying period of early females (see Fig. 3). The model further explains why addition of eggs to the nest just before laying caused an earlier increase in incubation behaviour and hence a slight tendency toward smaller clutches (BEUKEBOOM *et al.*, 1988). If an endogenous rise in incubation tendency in females with the progress of season would cause the decline in clutch size, the model also offers an explanation why food availability determines laying date but does not affect clutch size independent of date.

5. Prolactin?

While this model has been formulated as a formal model, regardless of the physiological nature of the controlling variable which rises spontaneously in spring, it is of course tempting to speculate on this variable. HAFTORN (1981) has suggested a role for prolactin here. Indeed, plasma prolactin concentration is known to rise gradually in spring in starlings *Sturnus vulgaris* (DAWSON & GOLDSMITH, 1985), in mallards *Anas platyrhynchos* and canvasbacks *Aythya valisneria* (BLUHM *et al.*, 1983a, b), even in non-laying females. This slow increase is followed by an acceleration during egg laying in ducks (HALL & GOLDSMITH, 1983) and in starlings (DAWSON & GOLDSMITH, 1982) or with onset of incubation in bantam hens *Gallus domesticus* (SHARP *et al.*, 1979; LEA *et al.*, 1981), in turkeys *Meleagris gallopova* (BURKE & DENNISON, 1980; PROUDMAN & OPEL, 1980) and in barheaded geese *Anser indicus* (DITTAMI, 1981). Prolactin is associated with incubation patch development in many bird species (JONES, 1971; DRENT, 1975) and is further thought to be involved in the termination of egg laying (BURKE & DENNISON, 1980; EL HALAWANI *et al.*, 1981; LEA *et al.*, 1981). Sitting on the eggs may—by tactile stimulation of the broodpatch by the eggs—enhance prolactin secretion at the onset of incubation and also help to maintain high levels during incubation (LEHRMAN & BRODY, 1964; JONES, 1969). Plasma prolactin concentration decreases by broodpatch desensitization in ducks (HALL & GOLDSMITH, 1983), by removal of nestbowl and eggs in ringdoves (RAMSEY *et al.*, 1985), by removal of eggs in turkeys and in canaries *Serinus canarius* and increases in both species after resumption of incubation (EL HALAWANI *et al.*, 1980; GOLDSMITH, 1984). For this variety of reasons, prolactin is an obvious first candidate for a physiological component in our proximate model for sesonal clutch size determination.

We measured plasma prolactin concentrations in paired female kestrels in captivity during winter and spring of 1986-88. These birds went through the normal reproductive cycle of breeding and raised young successfully, under *ad lib.* feeding and natural light-dark cycles. Details of feeding conditions and blood sampling have been presented elsewhere (MEIJER *et al.*, 1988; MEIJER & ŞCHWABL, 1989). The analysis of plasma prolactin concentrations at the University of Bristol followed the procedures described by HALL *et al.* (1987).

In the context of the model presented, the prolactin (P) data for birds before egglaying are of special interest. In Fig. 4 half-monthly averages are plotted of all the plasma P concentrations obtained in paired female
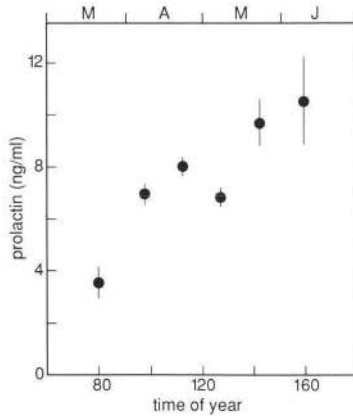
Fig. 4. Plasma prolactin concentrations (mean ± se) of captive, paired female kestrels during early courtship (until the last 10 days before laying) from March to early June.

kestrels before the 10th day prior to egglaying. These levels increased slowly, but significantly (y = 0.0726 × d-0.966 ng/ml, n = 67, r_s = 0.482, p ≪ 0.01) in the course of spring, from 3.6 (± 2.5) ng/ml plasma in February to 10.3 (± 5.9) ng/ml in early June. This suggests a spontaneous rise, by wich late breeders would start laying at higher P levels than early breeders. This can be checked more directly by comparing P levels measured in the last 10 days before laying. In this interval the female kestrel builds up large body reserves and the follicles develop rapidly (MEIJER et al., 1989). There was a seasonal increase in plasma P levels during late courtship (y = 0.154 × d-12.2, n = 10, r_s = 0.72, p < 0.01). In contrast, there was no seasonal increase in P levels during egg laying (y = 0.003 × d + 10.8, n = 13, r_s = -0.017).

Thus prolactin concentrations showed: (a) a gradual increase in spring; (b) in early breeding females a lower level just before egg laying compared to late females and (c) the same levels during laying in early and late females. These phenomenona are all consistent with the hypothesis that a spontaneous rise in prolactin secretion is involved in the regulation of the increasing initial tendency to incubate the first eggs of a clutch, and hence the advancing tendency toward follicle resorption and seasonally declining clutch size in the kestrel. Definitive evaluation of this hypothesis obviously awaits experiments specifically manipulating prolactin concentrations in early and late laying females.

6. Concluding remarks

The seasonal decline in clutch size is a very general phenomenon in temperate zone birds, at least in species which breed once per year (KLOMP, 1970). It is not restricted to birds alone, but has been reported also in reptiles (*e.g.* NUSSBAUM, 1981), insects (TURNBULL, 1973) and in litter size of mammals (MYERS & POOLE, 1962; KOTT & ROBINSON, 1963). There are good ultimate reasons for such a decline in single-, not in multi-brooded species (DAAN *et al.*, 1989), which apply probably fairly generally. The gradual seasonal improvement of nutritional conditions and temperature in spring and the declining prospects for offspring raised with progress of laying date seem to be involved, and this has been worked out as a life history optimalisation problem in particular for the kestrel (DAAN *et al.*, 1990).
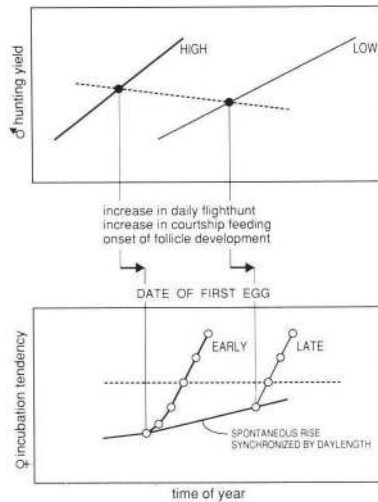

Fig. 5. Summary of proximate regulation of kestrel reproduction. For explanation see text.

While the ultimate forces shaping the clutch-date association may be fairly similar across species, its proximate regulation mechanism is likely to vary from species to species or from group to group. Thus we do not claim that our model of an endogenous time program, hypothesing the hormone prolactin to cut down on number of eggs when clutch initiation is late, should apply to other birds. However we do expect that on a formal level some elements in the model, as summarized in figure 5, may

apply fairly generally. The most general feature of the model is probably that there are two proximate factors involved: one providing general information on time of year, the other specific information on nutritional conditions of the individual concerned. For time of year daylength is probably the most precise cue the temperate environment has to offer for any organism, and its use, either as trigger or as Zeitgeber for endogenous annual programs is widespread (GWINNER, 1986). We also expect that tuning to individual conditions within a reproductive window is a general phenomenon. The role of food availability itself as a proximate trigger for reproduction is less likely to be general. In the kestrel it makes sense that the male responds to food supply in spring and "decides" when to raise courtship feeding to his partner and to trigger her reproduction. It is the male who experiences the food supply directly and who can "predict" the food supply two months later when the nestlings have to be fed, by virtue of the correlation between hunting yields in early spring and midsummer (DAAN et al., 1990). In other species, not relying on one single major prey type, food availability early on may contain less relevant information and other predictors of the food situation in the nestling phase may be used. Whatever the trigger, we feel that a strongly anchored internally driven clutch-date relationship is likely to hold for all species with only a single opportunity for breeding per year.

The problem of clutch size variation has fascinated evolutionary ecologists for quite some time. The physiological basis of clutch size control in birds has however hardly been investigated, and this renders any generalizations highly speculative. Species with a predictable seasonal dependence of clutch size seem to offer an excellent opportunity to study its adaptive regulation, and we are at the beginning of a fascinating episode of manipulative experiments.

Summary

The time in spring when a male kestrel rapidly increases his daily hunting time and his hunting yield, and thereby the amount of food delivered to the female, determines the date when she lays the first egg. Food experiments in free-living and captive kestrels gave a significant advance in laying date. Clutch size, which decreases with progressive laying date, did not change independent of date in response to food manipulation. These effects are in agreement with most other feeding experiments. Photoperiod experiments in kestrels advanced the reproductive cycle in constant long days, and a similar seasonal decline in clutch size was found. It seems that there is an internally preprogrammed decrease in clutch size within an annual "reproductive window". A proximate control model for the seasonal decline of clutch size is proposed, modified from an earlier model by HAFTORN (1985). This incorporates an increasing tendency to incubate the first eggs with progression of the season, an egg contact-incubation positive feedback loop, and the

resorption of further follicles in the ovary when the laying female incubates 50% of the time. This follicle resorption fixes the clutch size ca. four days before the last egg is laid. the 50% incubation level is reached earlier in late females and consequently resorption starts earlier and the resulting clutch is smaller than in early females. Experiments in kestrels with removal and addition of eggs, in combination with measurements of incubation behaviour are discussed in relation to the model. Plasma prolactin data of female kestrels show that this hormone is a serious candidate for a physiological component relaying time of year in our model for clutch size regulation.

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