Behaviour of female Eurasian Kestrels during laying: are there time constraints on incubation?

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To investigate time, energy, and temperature constraints on hatching asynchrony in Eurasian Kestrels (*Falco tinnunculus*), we observed females during the laying period and quantified the time spent hunting to see whether this might limit time spent incubating. We predicted that females would hunt more in years when the density of voles was low in spring. Although females spent more time outside the nest box in poor-food years, there was only a weak trend for increased hunting. Only 22 of 68 (32%) of females either perch- or flight-hunted and they caught four prey in 389 hours of observation. There was no relationship between the tendency of females to hunt and the delivery rate of their mate. Time outside the box was not correlated with ambient temperature and the proportion of time hunting was not correlated with prey abundance on the territory. Females did not seem to increase their energy intake by being outside the box, but may still conserve energy by delaying incubation. We conclude that there are not time or temperature constraints on incubation, but we can not rule out energy constraints. It is also possible that delaying incubation when food is scarce is adaptive for kestrels.

1. Introduction

Recent reviews of hatching asynchrony in birds have stressed the importance of selective pressures during the laying period (Magrath 1990, Stoleson & Beissinger 1995, Stenning 1996). The hatching span within a clutch has consequences for the growth and survival of nestlings (review in Amundsen & Stokland 1991), but the degree of asynchrony is determined much earlier by the onset of incubation during the laying period. A female's control of hatching asynchrony by incubation schedules has been assumed but not well studied.

Thermometers placed in Eurasian Kestrel(*Falco tinnunculus*) nests showed that the onset of incubation varied among females and therefore was not controlled rigidly by physiology (c.f. Beukeboom et al. 1988, Wiebe et al. 1998). As well, the development of Eurasian Kestrel eggs matched the onset of incubation, but in other species, female body size (Bortolotti & Wiebe 1993), egg size (Viñuela 1997), and communication among hatching embryos (Vince 1964, Schwagmeyer et al. 1991) may all affect hatching patterns beyond parental control.

Although hatching patterns may be strongly

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correlated with incubation behaviour, female birds may not be able to "choose" optimal hatching patterns. The energy constraints hypothesis (Slagsvold & Lifjeld 1989, Nilsson 1993a) suggests that poor food supply during laying forces females to spend more time foraging and this, in turn, creates a time conflict with incubation. As a result, females are forced to delay incubation and hatch their eggs synchronously (maladaptively in this case). Consistent with this idea, female Blue Tits *(Parus caerulescens)* (Nilsson 1993a) and Wheatears *(Oenathe oenathe)* (Moreno 1989) supplemented with extra food during laying began incubating earlier and hatched their clutches more asynchronously than control pairs. In a similar experiment on American Kestrels *(F. sparverius)*, Wiebe and Bortolotti (1994) found exactly the opposite result; supplemented pairs had more synchronous clutches. They argued that time conflicts are less plausible for birds of prey because the male typically feeds the female during laying so that she can initiate incubation at any time.

Contrary to the pattern for American Kestrels, hatching in Eurasian Kestrel clutches was more synchronous in years with low vole densities when clutch size was controlled (Wiebe et al. 1998b), consistent with the prediction from the energetic constraint hypothesis, but also with adaptive (facultative) manipulation. Strong evidence for energetic constraint would be that female kestrels hunt more when food is scarce, and thus delay incubation. Observations by others suggest that female kestrels rarely hunt during laying (Village 1990), but previous studies have not quantified the foraging behaviour of females and how this relates to prey availability and the onset of incubation. In this study, we determined by direct observation whether time conflicts limited incubation for Eurasian Kestrels. Our main questions were: (1) is time spent off the nest during laying associated with prey density in spring, and (2) does the female gain energetic benefits (increased prey intake) by delaying the onset of incubation. We compared behaviour of laying females during five years with different spring abundance of voles, and examined the relationships between food abundance on the territory, male provisioning rate, and hunting effort of females. We also examined ambient temperature as another possible constraint on incubation behaviour.

2. Material and methods

Kestrels were studied from 1992 to 1996 in the vicinity of Kauhava, western Finland (approx. 63°N, 23°E). The main study area (Alajoki, ca. 100 km²) is a flat, agricultural landscape broken by small patches of trees and peatland bogs, and by ditches (Korpimäki 1984, Korpimäki & Norrdahl 1991). The rest of the area (ca 200 km²) consists of smaller agricultural fields (1 to 10 km²) surrounded by coniferous forest. Kestrels bred in nest boxes (basal area 30 × 30 cm) and the density of breeding pairs varied from 0.04 to 0.98 per km² depending on the phase of the vole cycle (Korpimäki & Norrdahl 1991). Eurasian Kestrels at this latitude are migratory and arrive on the site in April and early May to choose territories and mates (Palokangas et al. 1992). *Microtus* voles are their main prey with bank voles *(Clethrionomys glareolus)*, shrews and small birds taken as alternative prey (Korpimäki 1985).

Nest boxes were checked regularly with a mirror to record accurately the laying date and number of eggs. We observed kestrels during the mid-laying period, on the day or the day following the laying of the antepenultimate and penultimate eggs of a 5–6 egg clutch (smaller clutches were rare). Females remained near the nest boxes in non-overlapping territories and many were colour-banded, so we were certain of observing different individuals. Previous data on hatching patterns of clutches indicated that partial incubation was usually initiated around the penultimate egg (Wiebe et al. 1998a), so it was an appropriate time to detect differences in the onset of incubation among individuals. For each breeding pair, two observation periods of 4 hours each were done in the morning and afternoon on two different days without rain, except for some instances in 1992 when time budgets were 3 hours each. This resulted in an 8 hour time budget for most females. Observers with spotting-scopes, stationed at least 200 m from the box, recorded behaviour of focal individuals continuously as described by Altmann (1974). The behavioural categories we analyzed were: (1) in box (either incubating, laying or sitting beside the eggs); (2) perch-hunting (perched above ground, focusing intently on the ground, or "head-bobbing", sometimes interrupted by strikes, see Village 1983); (3) perched (all other time

perched above ground excluding "maintenance" behaviour such as preening or eating (4) flight-hunting (soaring, hovering and directional flight). We didn't measure incubation directly with temperature probes, but time in the box is an adequate measure of time constraints on the female, because clearly she has the time to incubate if she is in the box. We recorded the number of prey delivered by the male but, because the focus was on the female, we did not follow him except when he was in her vicinity. Whether the female ate, or cached, prey items was also noted. For additional details about the methodology of behavioural observations, see Tolonen and Korpimäki (1994).

We have trapped small mammals, mainly sibling voles (*Microtus rossiaemeridionalis*), field voles (*M. agrestis*) and bank voles on the study area since 1977. Each year, snap-traps were placed in 2–3 grids (each 0.5–1 ha) in both Alajoki and the smaller agricultural fields representative of the habitat where kestrels hunted, and were checked for four consecutive nights. We trapped during two sessions each year: one in May, and one in September (for more details about the trapping design see Korpimäki & Norrdahl 1991). This long-term data showed that populations of small mammals on our study site cycle regularly with a period of three years (Korpimäki 1993), that the phase of the cycle is the same for the two parts of the study area, and that actual densities in the two areas are similar (Spearman correlation on 24 trapping sessions $r^2 = 0.8$, $P < 0.001$). Thus, data on small mammals and reproduction of kestrels were combined from both parts of the study area. For analyses in this paper, we used spring trapping results (May number of small mammals/100 trap-nights) to rank years in terms of prey abundance.

In 1996, we censused small mammals on an additional 20 active kestrel territories prior to incubation using the method of Norrdahl and Korpimäki (1993). We chose ditches and fields representative of the surrounding habitat 100–300 m from the nestbox. One hundred traps were placed 10 m apart and checked on two consecutive nights for a total of 200 trap-nights per territory. These trapping data were correlated with the behaviour of females on those specific territories in 1996.

For each female, we calculated the proportion of time spent on different behaviours excluding the part of the time budget she was out of sight (all females were in view at least 92% of the time) and arcsine-transformed the values if they did not have a normal distribution. Because the time incubating tends to increase during the laying sequence (Beukeboom et al. 1988), we used stage of laying (penultimate or antepenultimate egg) as a fixed factor in the ANOVA models. In nine cases, a female was observed during two different stages so we randomly chose one observation period to analyze in order to insure independence of observations. We did not consider stage of laying in the categorical analyses of hunting, because hunting was so rare.

Statistical analyses were performed using SAS (1988); ANOVA models were first run with interaction terms but if these were not significant, they were subsequently dropped from the model. Significance was based on Type III (unique) sums of squares which controls for all effects in the model simultaneously. To test for differences among years, year was treated as a factor with five levels. For increased power, another set of analyses was done with years grouped into three categories according to the number of voles in spring: low (1993 and 1996), medium (1995) and high (1994 and 1992). Logistic regressions used the log-likelihood method with significance based on the Wald statistic. Temperature data were obtained from the weather station at Kauhava airport within the study area.

3. Results

3.1. Time in the nestbox

The median number of *Microtus* voles in spring, the main prey of kestrels, varied about six-fold across the five years of the study (Fig. 1). Spring densities were lowest in 1993 and 1996, "low" phases of the three-year cycle and highest in 1992, although the population crashed later that summer (see Tolonen & Korpimaki 1995).

There was considerable variation in the amount of time females spent in the box during the laying period. As expected, they were more often in the box after the penultimate egg than after the antepenultimate egg (2-way ANOVA: $F_{1,67} = 25.7$, $P < 0.001$, Fig. 1). At the early stage of laying, females were in the box as little as 38%
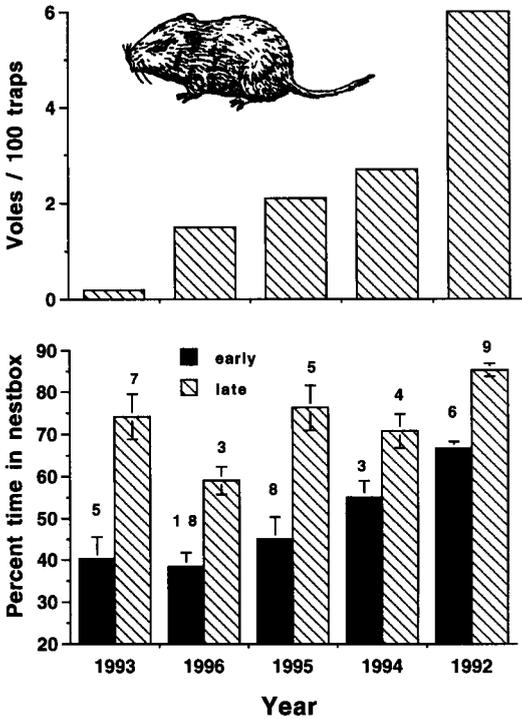
Fig. 1. Annual density of *Microtus* voles in May (top) and the percent of time female Eurasian Kestrels were inside the nest box (bottom) during the early (antepenultimate) and late (penultimate) egg laying stages. Years are ordered according to vole abundance based on 1080 trap-nights each year. Means and standard errors are shown with the number kestrels observed above the bars.

some years and as much as 66% in others. There was also a significant effect of year ($F_{4,67} = 4.21$, $P = 0.005$). Scheffé post-hoc tests indicated that

Table 1. Percent of female Eurasian Kestrels (sample size *n*) flight-hunting, perch-hunting and hunting (both methods combined). Years are ordered according to decreasing spring density of *Microtus* voles (number per 100 trap-nights) and both stages of laying are combined.

Year	*n*	Vole density	Flight %	Perch %	Hunt %
1992	15	6.0	20.0	0.0	20.0
1994	7	2.7	0.0	14.3	14.3
1995	13	2.1	23.1	0.0	23.1
1996	21	1.5	38.1	23.8	47.6
1993	12	0.2	33.3	8.3	41.6

females spent more time in the box in 1992 (a high vole year) compared to 1993 and 1996 (low vole years) and also in the box more in 1994 compared to 1996 (Fig. 1). A non-parametric correlation showed a significant relationship between the annual spring number of voles and the percent time in the nestbox during the antepenultimate egg ($r_s = 0.81$, $n = 5$, $P = 0.037$) but not during the penultimate egg ($r_s = 0.25$, $n = 5$, $P = 0.40$). Even when outside the box, females usually stayed within 200 m of it. Only 10 of 62 females (16%) made short flights out of sight of the box.

To see whether ambient temperature might affect incubation, we used the daily minimum and daily mean temperatures from the same day as the behavioural observations as covariates in two ANCOVAs (year and stage as factors). However, neither minimum nor mean temperature was associated with time in the nestbox (T_{min}: $F_{1,67} = 0.13$, $P = 0.71$; T_{mean}: $F_{1,67} = 1.26$, $P = 0.26$).

3.2. Hunting

We only saw 7 of 68 (10%) females perch-hunting and the average proportion of time these individuals spent hunting was small (median 10%). In an analysis with low, medium and high year categories, the proportion of females that perch-hunted did not vary according to year type (Fisher-exact test, $P = 0.17$). Flight-hunting is more energetically expensive than perch-hunting but has more success (Masman & Klaassen 1987). Only 19 of 68 (28%) females soared, hovered, or kited during time budgets, and these spent a median of 0.9 % of time flying. There was no difference in the probability of flight-hunting between year categories (Fisher-exact test, $P = 0.35$). Because hunting was so rare, we combined perch- and flight-hunting and found a weak trend that the proportion of females that hunted increased as vole density decreased, but it was not significant (Fisher-exact test, $P = 0.09$, Table 1). During 389 hours of observation in all years, 10 strikes on prey were seen, and 4 of these were successful. For the 19 territories in 1996 for which we had small mammal densities and records of female behaviour, there was no correlation between the abundance of voles and female's perch- and flight-hunting combined (Spearman Correlation: $r_s = -0.05$, $P = 0.82$).
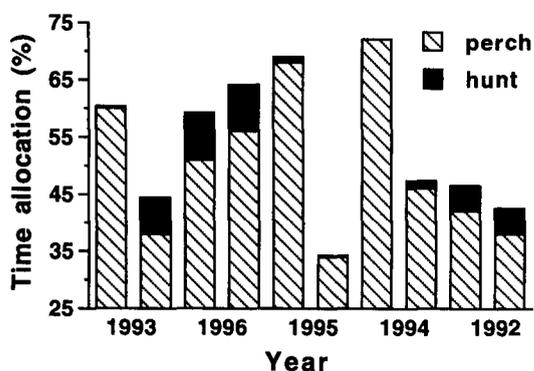
Fig. 2. The allocation of time by female Eurasian Kestrels outside the nest box to perching and active hunting (perch and flight). The rest of the time out of the box was spent in activities exclusive of hunting (see text). The first bar for each year is the day of the antepenultimate egg, the second bar represents the penultimate egg stage, and years are ordered according to increasing vole abundance as in Fig. 1.

Fig. 3. Delivery rates of male Eurasian Kestrels during the laying period in relation to the number of small mammals near their nest box in 1996.

Although females did little active hunting, they may detect prey opportunistically when perched above ground. Thus, we combined all time spent above ground looking over the surrounding landscape to estimate potential "passive" hunting. Not surprisingly, females spent less time above ground as laying progressed to the penultimate egg (2-way ANOVA: $F_{1,69} = 13.8, P < 0.001$). However, variation in time perched above ground was only marginally significant between years ($F_{4,69} = 2.4$, $P = 0.06$, Fig.2). Thus, although total time outside the box did vary significantly among years, females were engaging in considerable "non-hunting" behaviours such as sitting on the ground, preening, eating, caching prey items, copulating or chasing predators.

3.3. Prey deliveries

Delivery rates by males varied from 0 to 1.25 prey hr^{-1} (median 0.38) but we did not find a relationship with the abundance of prey. There were no overall differences in delivery rates between years (Kruskal-Wallis ANOVA: $\chi^2 = 2.9$, $n = 68, P = 0.56$) or between the low/med/high year categories (Kruskal-Wallis ANOVA: $\chi^2 = 1.04, P = 0.59$). Neither were deliveries by males correlated with vole (*Microtus*) abundance in spring on different
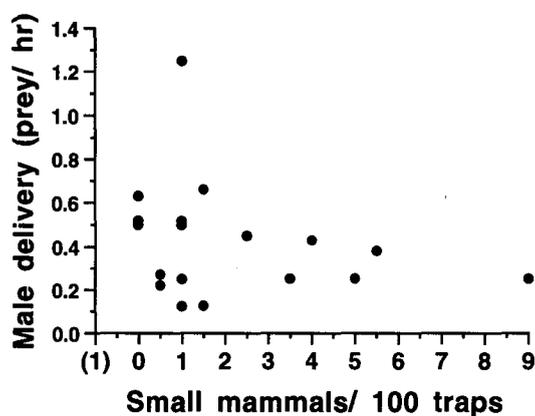
territories in 1996 (Spearman Correlation: $r = -0.31, n = 19, P = 0.21$) or with the abundance of all small mammal species combined ($r = -0.17$, $P = 0.49$; Fig. 3). Females that hunted (flight and perch hunting combined) did not have mates with lower provisioning rates than females that did not hunt (Mann-Whitney U-test, $Z = 0.31, P = 0.75$).

Because caching occurred at infrequent intervals, we used only data for females with complete, 8 hour time budgets. Most prey items were eaten immediately by females, but each year we saw 13–28% of females cache prey, typically in grass clumps on the ground. The proportion of prey cached did not vary among years (Kruskal-Wallis ANOVA, $\chi^2 = 1.25, P = 0.86$), but a logistic regression showed that the probability a female cached increased as the number of prey delivered by the male increased (Wald-statistic = 11.0, $P = 0.009$; Fig. 4).

4. Discussion

4.1. Temperature constraints

Ambient temperature may be one constraint that forces females to initiate incubation early. If it is too warm during laying, embryos may develop abnormally or be less viable (Arnold et al. 1987, Viega & Viñuela 1993). If it is too cold, eggs may freeze (Williams & Croxall 1991). We found no relationships between ambient temperature and
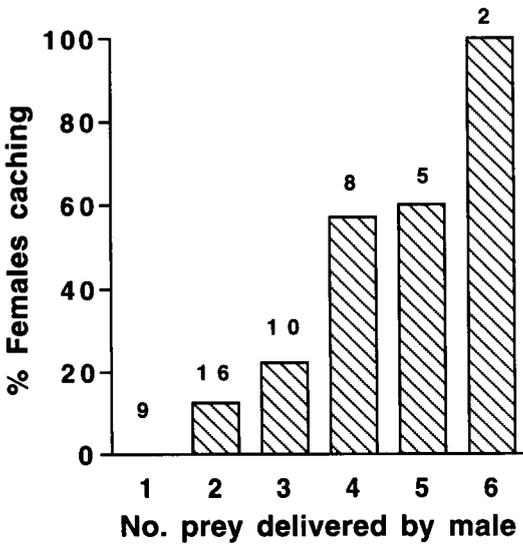
Fig. 4. The percent of female Eurasian Kestrels caching at least one prey item according to the number of prey delivered by their mate during an 8 hour time period. Numbers of females are above the bars.

time inside the nest box, although males and females sometimes took shelter in the box during windy and wet weather. On our northern study area, daily temperatures during laying did not exceed the 26°C necessary for embryonic development (Webb 1987), so egg viability was probably not a concern. Temperatures occasionally went below freezing at night, but unincubated kestrel eggs seem tolerant of cold because thermometers placed inside nests showed that eggs hatched even after being exposed to 0°C (Wiebe et al. 1998a). Similarly, eggs laid and not incubated during laying gaps of 3 and 6 days hatched in a normal pattern. Thus, unincubated eggs in our population seem tolerant of ambient temperatures for periods of at least 6 days, and temperature constraints cannot explain variation in the onset of incubation which occurs over a shorter time period (Wiebe et al. 1998a).

4.2. Energy and time constraints

Egg-laying in birds is generally considered to be energetically costly (Perrins 1996). Meijer et al. (1989) quantified energy consumption in the field for female Eurasian Kestrels at different stages of

breeding and found the greatest intake during the laying period. Food supplementation experiments in Blue Tits have demonstrated that the transition from laying to incubation is one of the main energy bottlenecks during reproduction (Nilsson 1994). Thus, when food is scarce during laying, one may expect females to compensate by foraging more to increase energy intake. Increased foraging seems to be an option for passerines, and bi-parental incubation may be a strategy by which males liberate females to forage for themselves during the laying period (Nilsson 1993b).

The behavioural data in this study confirm that females spent less time in the box in poor food-years (Fig.1) but our results did not support time constraints. Little of the roughly 30–60% of the time outside the box was spent actively perch- or flight-hunting (Fig. 2). Although there was a slight tendency to hunt more when voles were scarce, hunting usually comprised less than 5% of the total time budget. This generally agrees with other reports that female kestrels do not hunt during laying (Village 1983, Masman et al. 1988), although we did observe rare hunting and four instances of prey capture by females in this period. Of the time outside the box, only between 33–70% was spent perched (Fig.2), so even passive hunting did not seem to be a main goal of females. Although the amount of time outside the box increased as food decreased, the proportional allocation of that time showed no consistent pattern across years (Fig.2), so females did not use the extra time to hunt more. Thus, contrary to the energetic constraints hypothesis, foraging time did not conflict with incubation, and females did not increase their food intake by being outside the box.

4.3. Delivery rates and caching

At least in 1996, a low vole year, the numbers of voles near the nest box did not affect the delivery rate of males but it may have had an indirect effect on their energy balance. For example, as central-place foragers, males may need to travel farther to maintain a certain delivery rate (see Korpimäki et al. 1994). Females did not respond to low delivery rates by hunting more, but did reduce the amount of prey they cached. In contrast, the probability of caching was not associated with year or

with local abundance of small mammals on the territory so the short-term performance of the male seems to be more important in determining the feeding behaviour of the female. Because the probability a female hunted was not related to food abundance on the territory near the nest, or to the provisioning rate of her male, there appeared to be little overall motivation to hunt whatever the local circumstances.

Caching seems to be common in kestrels (Village 1990), and it may dampen fluctuations in prey delivery by a male bird of prey (Rijnsdorp et al. 1981, Korpimäki 1987). Consistent with this idea, captive American Kestrels deprived of food for longer periods cached more prey when later given surplus food (Mueller 1974). However, when the densities of voles are low in spring, female Eurasian Kestrels may usually be hungry, and prey deliveries too infrequent to permit regular caching. Our data suggest that caching is a behaviour which only a fraction of the females could afford to invest in (Fig. 4).

4.4. Energetic cost of incubation

Our results do not support the classic energetic constraints hypothesis which acts by a mechanism of time constraints on incubation (see above). However, a lack of hunting by female kestrels does not mean they were not energetically constrained. Delaying incubation may be a tactic to conserve energy rather than to increase energy intake during laying. In most birds, incubation requires considerable input of energy above the basal metabolic rate (Tatner & Bryant 1993) although exceptions may be cavity-nesting birds in benign thermal regimes (e.g. Gessaman & Findell 1979). In a detailed analysis of energy expenditure using doubly-labelled water on breeding female Eurasian Kestrels in the laboratory, Meijer et al. (1989) estimated that full incubation costs about 300 kJ day^{-1}. They also calculated that the peak of egg formation, in isolation, costs about 72 kJ day^{-1}. Three females measured early during the laying sequence when incubation was almost absent had an energy expenditure of about 312 kJ day^{-1}. Thus, adding the cost of egg formation to the cost of full incubation would mean roughly 372 kJ day^{-1} which is a 20–24% increase in expenditure com-

pared with either incubation or laying alone. Females in our study may have delayed incubation when food was scarce because if it was too costly to simultaneously form eggs and incubate them. Direct measurements of energy expenditure (e.g. by doubly-labelled water) on wild kestrels would be useful in evaluating this idea (cf. Beukeboom et al. 1988).

If females delayed incubation to save energy, it is still unclear why they spent more time outside the box rather than minimizing energy expenditure by sitting beside the eggs in the sheltered nestbox microclimate. Females may save some energy by delaying incubation but this does not mean they are forced by energy constraints to do so. Synchronous broods have better fledging success than asynchronous broods in low vole years (Wiebe et al. 1998b) so females may be "choosing" to delay incubation to maximize success in the nestling period, and any energy saved during laying may just be a bonus. Food supplementation during the laying period would help to determine if egg laying is a short-term energy bottleneck that determines the onset of incubation for kestrels and other species.

Selostus: **Tuulihaukkanaaraiden käyttäytyminen muninta-aikana: rajoittaako aika- tai energiapula haudonnan aloitusta?**

Tuulihaukoilla ja useimmilla muillakin petolinnuilla pesyeen esikoisen ja kuopuksen välinen ikäero voi olla huomattava. Etelä-Pohjanmaalla, Kauhavalla ja Lapualla kerätyssä 12 vuoden aineistossa ko. ikäero vaihteli nollasta kymmeneen

päivään, mutta enemmistö pesistä (52%) kuoriutui kahden–kolmen vuorokauden kuluessa. Tuulihaukkojen poikaset kuoriutuivat lähes samanaikaisesti huonossa ravintotilanteessa (myyriä maastossa vähän), mutta hyvässä ravintotilanteessa (myyriä enemmän) esikoisen ja kuopuksen välinen ikäero oli suurempi, mikä on ristiriidassa lähes kaikkien kuoriutumisen eriaikaisuutta selittävien hypoteesien kanssa.

Seurasimme tutkimusalueemme tuulihaukkanaaraiden käyttäytymistä muninta-aikana vuosina 1992–96 selvittääksemme, rajoittaako esim. aikapula, energiapula tai alhainen lämpötila haudonnan aloitusta, minkä seurauksena poikaset kuoriutuvat eriaikaisesti. Tuulihaukkanaaraat eivät tavallisesti saalista ennen munintaa ja muninta-aikana, vaan koiraat huolehtivat niiden ruokinnasta. Ennustimme, että jos naaraat saalistavat munintavaiheessa, niiden tulisi käyttää enemmän aikaa saalistukseen huonoina kuin hyvinä myyrävuosina. Munivat naaraat viettivät enemmän aikaa pesäpöntön ulkopuolella huonoina myyrävuosina (Kuva 1), mutta niiden saalistukseen käyttämän ajan osuus oli tällöin vain aavistuksen suurempi. Ainoastaan 22 naarasta 68:sta seuratusta yksilöstä (32%) saalisti aktiivisesti munintavaiheessa (Taulukko 1), mutta ne pyydystivät vain neljä saalista 389 havaintotunnin aikana. Naaraiden pesäpöntön ulkopuolella vietetyn ajan osuus ei ollut riippuvainen ulkolämpötilasta eikä pesäpöntön ympäristön myyrätiheydestä. Naaraiden saalistusaktiivisuus ei ollut myöskään yhteydessä niiden puolisoiden tuoman saaliin määrään, mutta paljon koiraalta ruokaa saavat naaraat varastoivat saalista enemmän kuin muut (Kuva 4). Siten paljon aikaansa pesäpöntön ulkopuolella viettävät naaraat eivät näytä lisäävän ravinnonsaantiaan munintavaiheessa, mutta ne saattavat viivyttää energiaa kuluttavan haudonnan aloitusta, kun ravintotilanne on huono.

References

Altmann, J. 1974: Observational study of behaviour. — Behaviour 49: 227–267.

Amundsen, T., & Slagsvold,T. 1991: Hatching asynchrony: facilitating adaptive or maladaptive brood reduction. — Proc. Int. Ornithol. Congr. 20: 1707–1719.

Arnold, T. W., Rowher, F. C. & Armstrong, T. 1987: Egg viability, nest predation and the adaptive significance of clutch size in prairie ducks. — Am. Nat. 130: 643–653.

Beukeboom, L., Dijkstra, C., Daan, S. & Meijer, T. 1988: Seasonality of clutch size determination in the Kestrel, Falco tinnunculus: an experimental study. — Ornis Scand. 19: 41–48.

Bortolotti, G. R. & Wiebe, K. L. 1993: Incubation behaviour and hatching patterns in the American Kestrel Falco sparverius. — Ornis Scand. 24: 41–47.

Gessaman, J. A. & Findell, P. R. 1979: Energy cost of incubation in the American Kestrel. — Comp. Biochem. Physiol. 63A: 57–62.

Korpimäki, E. 1984: Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. — Ann. Zool. Fenn. 21: 287–293.

Korpimäki, E. 1985: Diet of the Kestrel Falco tinnunculus in the breeding season. — Ornis Fenn. 62: 130–137.

Korpimäki, E. 1987: Prey caching of breeding Tengmlam's Owls (Aegiolus funereus) as a buffer against temporary food shortage. — Ibis 129: 499–510.

Korpimäki, E. 1993: Regulation of multiannual vole cycles by density-dependent avian and mammalian predation? — Oikos 66: 359–363.

Korpimäki, E. & Norrdahl, K. 1991: Numerical and functional responses of Kestrels, Short-eared Owls and Long-eared Owls to vole densities. — Ecology 72: 814–826.

Korpimäki, E., Tolonen, P. & Valkama, J. 1994: Functional responses and load-size effect in central place foragers: data from the Kestrel and some general comments. — Oikos 69: 504–510.

Magrath, R. D. 1990: Hatching asynchrony in altricial birds. — Biol. Rev. 65: 587–622.

Masman, D. & Klaassen, M. 1987: Energy expenditure during flight in trained and free-living Kestrels, Falco tinnunculus. — Auk 104: 603–616.

Masman, D., Daan, S. & Dijkstra, C. 1988: Time allocation in the Kestrel (Falco tinnunculus), and the principle of energy minimization. — J. Anim. Ecol. 57: 411–432.

Meijer, T., Masman, D. & Daan, S. 1989: Energetics of reproduction in female Kestrels. — Auk 106: 549–559.

Moreno, J. 1989: Energetic constraints on uniparental incubation in the Wheatear Oenanthe oenanthe. — Ardea 77: 107–115.

Mueller, H. C. 1974: Food caching behaviour in the American Kestrel. — Z. Tierphsychol. 34: 105–114.

Nilsson, J.-Å. 1993a: Energetic constraints on hatching asynchrony. — Am. Nat. 141: 158–166.

Nilsson, J.-Å. 1993b: Bisexual incubation facilitates hatching asynchrony. — Am. Nat. 142: 712–717.

Nilsson, J.-Å. 1994: Energetic bottle-necks during breeding and the reproductive cost of being too early. — J. Anim. Ecol. 63: 200–208.

Norrdahl, K. & Korpimäki, E. 1993: Predation and interspecific competition in two Microtus voles. — Oikos 67: 149–158.

Palokangas, P., Alatalo, R. V. & Korpimäki, E. 1992:

Female choice in the Kestrel under different availability of mating options. — Anim. Behav. 43: 659–665.

Perrins, C. M. 1996: Eggs, egg formation and the timing of breeding. — Ibis 138: 2–15.

Rijnsdorp, A., Daan, S. & Dijkstra, C. 1981: Hunting in the Kestrel (Falco tinnunculus) and the adaptive significance of daily habits. — Oecologia 50: 391–406.

SAS Institute, Inc. 1988: SAS/STAT user's guide release 6.03. — Sas Institute, Inc., Cary, North Carolina.

Schwagmeyer, P. L., Mock, D. W., Lamey, T. C. & Beecher, M. D. 1991: Effects of sibling contact on hatch timing in an asynchronously hatching bird. — Anim. Behav. 41: 887–894.

Slagsvold, T. & Lifjeld, J. T. 1989: Constraints on hatching asynchrony and egg size in Pied Flycatchers. — J. Anim. Ecol. 58: 837–845.

Stenning, M. J. 1996: Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. — Trends Ecol. Evol. 11: 243–246.

Stoleson, S. H. & Beissinger, S. R. 1995: Hatching asynchrony and the onset of incubation in birds revisited: when is the critical period? — Current Ornith. 12: 191–270.

Tatner, P. & Bryant, D. M. 1993: Interspecific variation in daily energy expenditure during avian incubation. — J. Anim. Ecol. 231: 215–232.

Tolonen, P. & Korpimäki, E. 1994: Determinants of parental effort: a behavioural study in the Eurasian Kestrel Falco tinnunculus. — Behav. Ecol. Sociobiol. 35: 355–362.

Tolonen, P. & Korpimäki, E. 1995: Parental effort of Kestrels (Falco tinnunculus) in nest defense: effects of laying time, brood size, and varying survival prospects of offspring. — Behav. Ecol. 6: 435–441.

Veiga, J. P. & Viñuela, J. 1993: Hatching asynchrony and hatching success in the House Sparrow: evidence for the egg viability hypothesis. — Ornis Scand. 24: 237–242.

Village, A. 1983: Seasonal changes in the hunting behaviour of Kestrels. — Ardea 71: 117–123.

Village, A. 1990: The Kestrel. — Poyser, London.

Vince, M. A. 1964: Social facilitation of hatching in the Bobwhite Quail. — Anim. Behav. 12: 531–534.

Viñuela, J. 1997: Laying order affects incubation duration in the black kite (Milvus migrans): counteracting hatching asynchrony? — Auk 114: 192–199.

Webb, D. R. 1987: Thermal tolerance of avian embryos: a review. — Condor 89: 874–898.

Wiebe, K. L. & Bortolotti, G. R. 1994: Food supply and hatching spans of birds: energy constraints or facultative manipulation? — Ecology 75: 813–823.

Wiebe, K. L., Wiehn, J. & Korpimäki, E. 1998a: The onset of incubation in birds: can females control hatching patterns? — Anim. Behav 55: 1043–1052.

Wiebe, K. L., Korpimäki, E. & Wiehn, J. 1998b. Hatching asynchrony in Eurasian kestrels in relation to the abundance and predictability of cyclic prey. — J. Anim. Ecol. 67: 908–917.

Williams, T. D. & Croxall, J. P. 1991: Chick growth and survival in Gentoo Penguins Pygoscelis papua: effect of hatching asynchrony and variation in food supply. — Polar Biol. 11: 197–202.