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Hunting in the Kestrel, *Falco tinnunculus,* and the Adaptive Significance of Daily Habits *

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Summary. 1. In an attempt to evaluate the importance of individual daily habits to a freeliving animal, foraging behaviour of kestrels was observed continuously for days in sequence in open country. Data obtained in 2,942 observation hours were used. Flight-hunting was the prominent foraging technique yielding 76% of all prey obtained.

2. Flight-hunting was impeded by rain, fog and wind speeds below 4 m/s and above 12 m/s (Fig. 3). Flight-hunting tended to be suppressed also in response to recent successful strikes and more generally by a high level of post-dawn accumulated prey (Figs. 4, 5). Flight-hunting had a tendency to be enhanced in response to recent unsuccessful strikes (Fig. 6).

3. Trapping results demonstrated a fine-grained daily pattern of common vole trap entries, with peaks at intervals of ca. 2 h (Figs. 7, 8). The interpretation of some of this pattern as representative of vole surface activity was supported by overall strike frequencies of kestrels hunting for voles (Fig. 9).

4. Detailed analysis of the behaviour of three individuals revealed significant peaks in hunting yield and frequency, coinciding with each other and with peaks in vole trapping (Fig. 11). It is suggested that the kestrels adjusted their flight-hunting sessions to times of high 'expected' yield. Vole activity peaks sometimes remained unexploited.

5. Meal frequencies culminated shortly before nightfall except in incubating females. The difference between the daily distributions of hunting and eating was due to some of the prey being cached in daytime and retrieved around dusk (Fig. 13). Caching behaviour is interpreted as a circadian strategy allowing separate optimization of hunting – adjusted to prey availability – and eating – adaptive by retaining minimum body weight in daytime flight and by thermo-regulatory savings at night.

6. Some kestrels showed remarkable constancy from day to day in the temporal distribution of specific behaviours (Fig. 16) and of spatial movements (Figs. 18, 19). In three 1–2 week sequences of observation analysed, flight-hunting frequency peaked 24 h after prey capture (Fig. 17). This is probably based on day to day correlations in flight-hunting frequency as well as on increased motivation for hunting in response to prey capture 24 h ago (Table 5).

7. In one individual with three distinct hunting areas, the tendency to return to an area again was maximal 24 h after prey capture in that area (Fig. 21, Table 6). A field experiment tested the effect of prey capture on the daily distributions of hunting and site choice in this individual (Fig. 22). A significant concentration of flight-hunting activity in the experimental feeding area was observed at the daily time of feeding (Fig. 23). Two alternative hypotheses are compatible with the result. Favoured is the one that the birds use "time memory" for the optimization of their daily patterns of flight-hunting and site choice.

8. By adjusting her daily flight-hunting to times of high yield, one kestrel saved 10–22% on her total time spent flight-hunting. Maximal efficiency, by concentration of all hunting activity in the hour of maximal yield, was not attained, presumably because of information constraints. The generality of the contribution of daily habits to survival is discussed.

1. Introduction

Enright's Hypothesis

The cycle of day and night is the basic temporal unit of life on earth. Rotation of the earth has lent structure to our time. It has provided the evolutionary opportunity for organisms to develop sequences of behaviour matching predictable sequences in the world without. Such temporal programmes have become deeply rooted in the genetic make-up of a species. They exploit intricate localized structures as endogenous pacemakers to organize periodic behaviours with remarkable precision (Aschoff 1981). The functional discussion of circadian rhythms generally has stressed this evolutionary adjustment to the environment (e.g., Pittendrigh 1960, 1966; Aschoff 1964; Pittendrigh and Daan 1976). In contrast, Enright (1970, 1975) has emphasized the role circadian oscillators may play in adjusting an animal's daily sequence of behaviour to its own experiences with a periodic environment, rather than those of its ancestors. Enright's hypothesis is that biological clocks in higher animals primarily find adaptive significance in the repetition of behaviour patterns from day to day. Daily similarities in the time course of environmental change would put a premium on such repetition, provided that modifications in response to experience are continuously incorporated in the circadian programme. Enright (1975) hastened to add that most evidence in support of this hypothesis – except for the case of Zeitgedächtnis ("Time memory") in honeybees (Beling 1928) – remained anecdotal, and unsupported by adequate documentation. For proper evaluation of the hy-

pothesis it is obviously necessary to document the complete daily behaviour of individuals of a species in their natural conditions for many days in sequence.

We have taken up this challenge and embarked on a study of the daily behaviour patterns of European kestrels, *Falco tinnunculus*. In a flat and treeless study area it was possible to observe individual birds of this species nearly continuously, sometimes with help of a small radiotracking transmitter. We were able to quantify the foraging activity – both in flight and from perches – and record time and place for most of the prey taken. The main prey of the kestrel in the area is the common vole, *Microtus arvalis*. This species exhibits considerable changes in availability in the course of the day, associated with its need for above-ground feeding about every two hours (Daan and Slopsema 1978). This makes the temporal patterns of hunting in one of its predators of particular interest. The kestrel has occasionally been observed to cache prey for later retrieval (Parker 1977). This behaviour allows for separate temporal optimization of hunting activity and food intake, and is of prime importance in the analysis of temporal adjustment of foraging behaviour.

The present paper discusses benefits arising from temporal organization primarily in terms of the yield of hunting (voles caught per hour of flight-hunting). In a later paper we hope to evaluate the energetic costs and benefits of daily strategies in behaviour and estimate how the balance contributes to the fitness of the individual's genotype.

2. The Kestrel Study Area and Methods

The study was carried out in the "Lauwersmeer", a recent land reclamation in the Netherlands (53° 20′ N; 6° 10′ E). The area (ca. 9,000 ha) is a sandy flat, cut off from the Dutch Waddensea by a
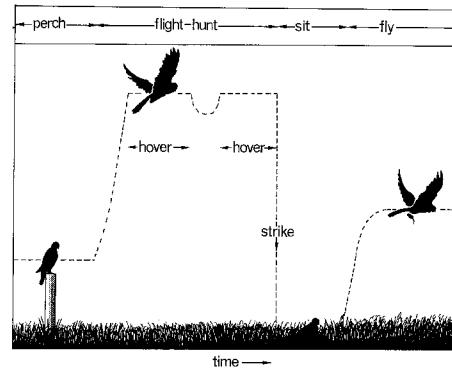

Fig. 1. Schematic representation of the four main behaviour categories distinguished. Flight-hunting includes the short flights in between bouts of hovering. In addition to these four, soaring occurs on warm summer days

dike in 1969. Since that time it has undergone a relatively undisturbed vegetational development (Joenje 1978). The area is inhabited by 20 to 30 pairs of kestrels, breeding in artificial nestboxes (see Cavé 1968). Many of these birds stay all year round. Some of the birds (see Table 1) were studied in the area itself, others in adjacent dairy farmlands.

Birds studied were marked individually by dyeing parts of their plumage with picrid acid. Occasionally birds were fitted with small (4–5 g) radio transmitters (AVM SM 1, 151 MC), attached to a single tailfeather (see Kenward 1978). This aided their detection when lost from sight, but only visual observations were used for analysis. Observation was carried out mainly from cars using telescopes (25 × 60) or binoculars (8 × 50), as this led to less disturbance than leaving the vehicle and walking about. Individuals were located at their roosts at dawn and usually followed until they returned at dusk.

For a crude analysis of time budgets the following behaviours were recorded (Fig. 1):

Table 1. Summary of data on individual kestrels studied

Bird No.	Sex	Age[a]	Name	Observation period	Hours of observation	Contact	Phase[b]	Remarks	Observers[c]
2	♀	>1	(nest 16)	May 3 – May 25, 1977	356.4	100%	I	incubating 6 eggs	AR, PK, SD*
3	♀	>1	(nest 18)	June 9 – June 13, 1977	76.2	100%	I	incubating 4 eggs	AR, CD
3	♀	>1	(nest 18)	June 19 – July 8, 1977	263.9	ca. 80%	N	feeding 4 nestlings	AR, CD
9	♂	2	Joep	July 9 – July 13, 1977	85.8	77%	N	feeding 4 nestlings	AR, CD
9	♂	2	Joep	July 31 – Aug. 19, 1977	135.6	79%	M		AR, CD
8	♂	>1	Pim	Oct. 15 – Oct. 20, 1977	88.0	95%	W	carrying transmitter	AR, CD, LV
9	♂	2	Joep	Dec. 7 – Dec. 23, 1977	124.9	90%	W		AR, CD, LV
5	♀	>2	Kiki	Jan. 17 – Feb. 3, 1978	165.2	93%	W	feeding experiments	AR, CD, LV
–	♀	>1	(nest 17)	Feb. 21 – Apr. 13, 1978	90.9	83%	W		CD, LV
9	♂	3	Joep	Mar. 31 – Apr. 5, 1978	62.3	74%	W		CD, LV
–	♀	>1	(nest 17)	May 2 – May 30, 1978	195.2	100%	I	incubating 4 eggs	CD,*
24	♂	>1	(nest 17)	May 2 – May 19, 1978	143.1	65%	I	feeding female	CD,*
9	♂	3	Joep	June 6 – June 15, 1978	70.1	87%	N	feeding 3 nestlings	AR, CD, LV, TV
45	♀	1	Blondie	Sep. 26 – Oct. 11, 1978	99.2	78%	W		PE, DM, FH,*
5	♀	>2	Kiki	Oct. 3 – Oct. 20, 1978	103.5	82%	W	carrying transmitter	PE, DM, FH,*
83	♂	>2	Parus	Mar. 22 – Mar. 29, 1979	73.3	80%	C		DM, FH
83	♂	>2	Parus	Apr. 10 – Apr. 24, 1979	59.8	83%	C		DM, FH
83	♂	>2	Parus	May 3 – May 10, 1979	92.4	73%	L	feeding female	CD, DM, FH,*
83	♂	>2	Parus	May 14 – May 22, 1979	122.8	56%	I	feeding female	CD, DM, FH,*
79	♀	>1	Ruba	May 3 – May 22, 1979	253.0	100%	I	incubating 6 eggs	CD, DM, FH,*
89	♀	>1	(nest 6)	May 15 – May 22, 1979	178.7	100%	I	incubating 5 eggs	CD, DM, FH,*
83	♂	>2	Parus	June 11 – June 12, 1979	34,5	80%	I	feeding 2 nestlings	DM, FH
9	♂	4	Joep	June 11 – June 15, 1979	67.2	92%	N	feeding 5 nestlings	AR, CD, LV, DM, FH

[a] *Age in calendar years*: 1 = born this year; 2 = born last year, etc.
[b] *Phase of the annual cycle*: C = Courtship; L = Laying; I = Incubation; N = Nestlings; M = Moult; W = Winter
[c] *Observers other than the authors*: D. Masman, F. de Haas, P. Koene, L. Vuursteen, P. Esselink, T. Vulink, * = assistance from student course

♀ #5   January 1978

? prey eaten, caught or retrieved
• prey caught and eaten
▲ prey caught and cached
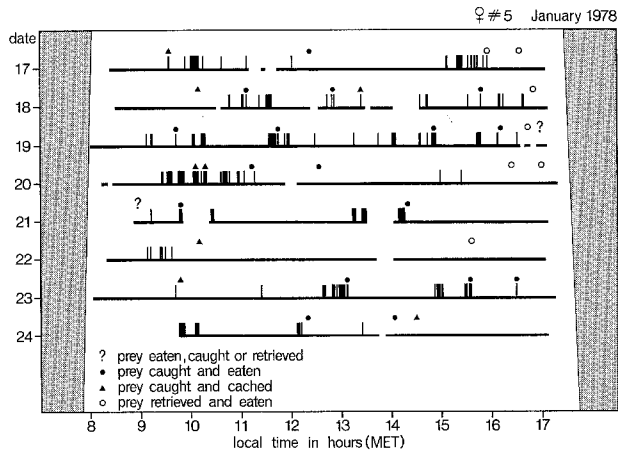○ prey retrieved and eaten

local time in hours (MET)

Fig. 2. Sample record of a sequence of observations on an individual kestrel ("Kiki"). Horizontal bars indicate periods of continuous observation; interruptions indicate loss of contact. Vertical bars are episodes of flight-hunting. Prey capture, caching, retrieval and eating as indicated

Flight-Hunting. In our definition this behaviour encompasses all hovering and the short (up to 1 min) flights between bouts of hovering. The term "hovering" is used here in the colloquial sense of flight which generates zero ground speed, and not in the more restricted aerodynamic sense of generating zero ground speed in still air.

Soaring. Slow movements upward in the thermal lift on warm summerdays; little or virtually no wing movements. Prey are taken by soaring animals, but soaring is not included in the category of flight-hunting.

Flying. This encompasses all behaviour in the air except flight-hunting, soaring and strikes.

Perching. The second important method of detecting prey. Perching is defined as sitting with a view of the ground surface over at least 180°, higher than 0.5 m above ground. Some behaviours of perched birds are strongly suggestive of presence or absence of hunting intentions. For instance head-bobbing and preening would be useful indicators for behaviour categories of *perch-hunting* and *perch-sitting*, respectively. Yet in many instances we have no unambiguous way of discriminating among motivational states of perched birds.

Sitting. This includes positions on the ground and sheltered positions like inside a nestbox or under the eaves of a house, typically occupied in rainy weather and at night. In both perching and sitting a number of behavioural modalities occur, such as bathing, preening, head bobbing, stone pecking, caching, retrieving, eating. Most of these do not concern us presently.

While the behaviours mentioned above thus have a precise operationally defined meaning we use the term *hunting* in a more relaxed sense for the whole process of search, pursuit and capture, but not intake of prey, and the term *foraging* even more loosely for hunting and food intake.

Time budget data were collected by recording the bird's behaviour every minute. When two observers were available, flight-hunting was recorded with bouts of hovering and flight accurate to the nearest second. These detailed data were used for an evaluation of the energetic cost of flight-hunting and are analysed in a subsequent paper. A survey of the 1-min-behaviour records for one intensively studied individual appears in Fig. 2. In addition, this kestrel (♀ # 5) was observed for another 10 days, during which her daily pattern was experimentally modified (see section 6).

3. Daily Variations in Hunting Activity

Of the five gross behavioural categories defined above, three concern activities in search of prey. Flight-hunting is by far the most effective method (Village 1980). It yielded on average 2.82 prey/h (see Table 2), compared to soaring (0.31) and perching (0.21). Sitting birds also incidentally catch prey at a very low rate (0.07 prey/h). Flight-hunting also is the most expensive method in terms of energy expenditure. It is probably more costly than flying with the most conservative speed. Energy expenditure in flight-hunt for a 250 gram kestrel is expected to amount at least to 10 times the Basal Metabolic Rate as calculated from a model by Pennycuick (1975). Perching and soaring are certainly much less demanding, although we cannot give power estimates at present. Soaring is restricted to warm and relatively quiet weather conditions, and hence to only some sunny days in summer. On days with thermal air lift, kestrel soaring is typically observed in the warmer hours of the day. Flight-hunting is also distinguished from perching and soaring in the type of prey taken (Table 2). While 97% of the prey seen taken by *flight-hunting* kestrels were small mammals (mainly common voles) and only 3% birds, bird percentages taken were 34% (mainly passerines) for *perching*, and 100% (mainly juvenile waders) for *soaring*. The figure for soaring is based on only 4 prey. However, 16 other prey seen captured by soaring kestrels were exclusively birds. To discuss temporal adjustment of kestrel food searching behaviour to vole activity, it is therefore appropriate to concentrate on flight-hunting, both from a point of view of the energetic implications and for reasons of prey specificity of the searching behaviour. An additional justification is that flight-hunting is the searching method yielding the majority (76%) of all prey collected.

3.1. Direct Effects on Hunting Motivation

In the analysis of hunting behaviour in relation to prey availability we are faced with the difficulty that hunting is continuously affected by other conditions. We illustrate below three effects on the amount of flight-hunting:

Table 2. Numbers of prey caught during various activities. Accumulated data for several individual birds with relatively complete time budget observations (# 5, 9, 24, 45 and ♀ nest 17)

Activity:	Flight-hunting	Soaring	Perching	Sitting
Hours of observation	106.2	12.9	295.4	358.6
Mammals:				
total prey	291	0	41	18
prey/hour	2.74	0	0.14	0.05
Birds:				
total prey	8	4	21	8
prey/hour	0.08	0.31	0.07	0.02
Total yield:	299	4	62	26
prey/hour	2.82	0.31	0.21	0.07
% birds	2.7	100.0	33.9	30.8
% of total catch:	76	1	16	7

Fig. 5. Effect of prior food supply on the tendency to hunt (**B**). Hourly data on flight-hunting were grouped with respect to the departure from average food supply level for each clock hour. Vertical lines are ±1 standard deviation
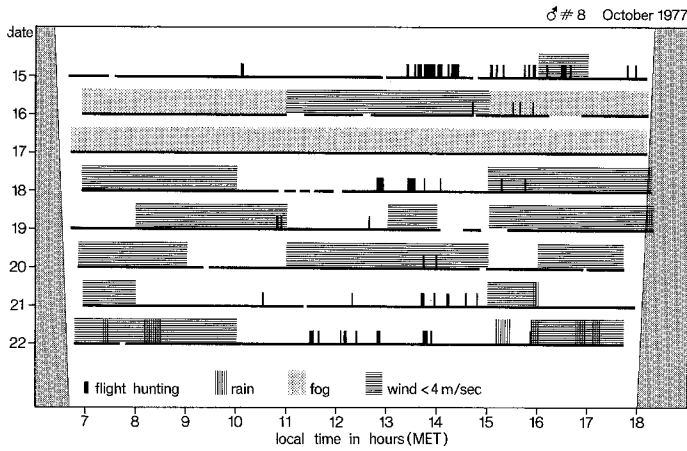
Fig. 3. Flight-hunting behaviour of a male kestrel ("Pim") in relation to weather conditions; conventions as in Fig. 2. Notice the reduction of flight-hunting behaviour during fog, rain and low wind speeds
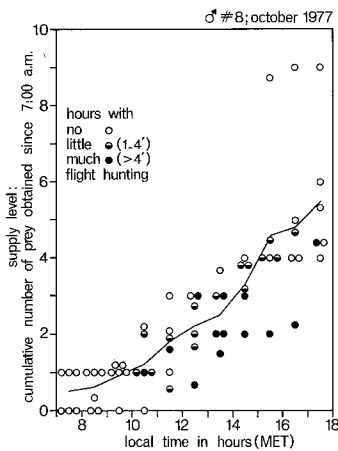

Fig. 4. Effect of prior food supply on the tendency to hunt (**A**). The curve connects the average numbers of voles collected since dawn up to any clock hour of the day. Circles show the actual number collected up to that hour on a particular day. The frequency of flight-hunting is indicated by degree of filling of the circles. Data from one male kestrel ("Pim")

Fig. 6. Effect of immediate prior experience on the tendency to hunt. Average frequencies of flight-hunting (±1 s.e.) are shown for 10 groups of 20 min intervals, pooled according to the frequency of flight-hunting in the preceding interval and to the occurrence of strikes in that interval, either successful or not successful

on the amount of flight-hunting:

1. Meteorological conditions.
2. Hunger or supply level.
3. Short-term experience.

3.1.1. Meteorological Factors

There are severe meteorological constraints on flight-hunting. Rain and dense fog are prohibitive, but also in very strong winds (> 12 m/s) and in still air (wind ≤ 4 m/s) flight-hunting is seriously impeded and reduced (see also Village 1980). This may be related to increased energetic demands away from the optimum flight speed (ca. 8 m/s, as calculated for kestrels from Pennycuick's model). A more detailed energetic account of flight-hunting at different wind speeds will be presented elsewhere. Here it suffices to illustrate (Fig. 3) how daily changes in weather conditions such as wind, fog, and rain can directly influence the expression of hunting tendency. As the example shows, ♂ # 8 undertook virtually no flight-hunting during fog and rain, and very little indeed in still air (wind speeds less then 4 m/s).
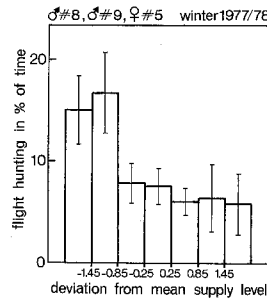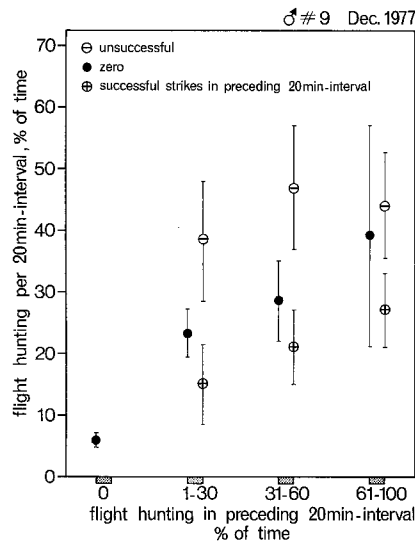
3.1.2. Supply Level

Hunting tendency is further directly affected by the time elapsed since the last prey was taken. Figure 4 indicates qualitatively the frequency of flight-hunting of ♂ # 8 at different times of day and in relation to the accumulated number of prey he had obtained in the time interval elapsed since dawn. The lower his *supply level* (including prey both cached and eaten) at any time of day, the more time he tended to spend in flight-hunt. Motivation for hunting in the course of the day may apparently be modified by the foraging return. In Fig. 5, flight-hunting frequencies were quantitatively assembled for three kestrels together in relation to various departures from the daytime-specific average supply levels. In those hours when the supply level lagged one prey or more behind the expected number of prey obtained since dawn, increased incidence of flight-hunting was observed.

In addition to this effect of the accumulated number of prey obtained since dawn, our data suggest that the capture of prey had an instantaneous suppressing effect on the tendency to flight-hunt afterward (see below and Fig. 6).

3.1.3. Short-Term Experience

The tendency to flight-hunt may be modified in response to immediately preceding experience. We will show below that unsuccessful strikes had a significant tendency to be followed by increased flight-hunting in the next 20 min, while successful strikes generally led to reduced flight-hunting in the next interval. The differences between the fractions of time spent in flight-hunt following zero strikes, a positive strike or only negative strikes were similar in all three animals for which we have extensive data (Table 3). Flight-hunt percentages were lower when at least one positive strike had been made in the preceding 20 min than when hunting had not led to any strikes, although this difference is vanishingly small in one of the three birds ($\female$ # 5). In contrast, average hunting frequencies were highest when only negative strikes had been made in the preceding interval. For the pooled data of the three kestrels, the differences between mean values were tested with Wilcoxon's two-sample ranking test. All differences were statistically significant except the difference between flight-hunting following zero strikes and flight-hunting following at least one positive strike (Table 3).

This does not prove that the negative strikes were indeed causally involved in increasing the tendency to flight-hunt. Positive correlations between one 20 min interval and the next are to be expected for instance on the basis of prevailing weather conditions. In fact the lowest flight-hunting frequencies were observed in intervals following 20 min intervals without any hunting (Table 3). Also, the probability of strikes to occur will increase with increasing flight-hunting frequency. For a proper analysis of the effect of strikes on subsequent flight-hunting we therefore have to compare 20 min intervals with similar flight-hunting frequencies and differing only in the occurrence of strikes. Figure 6 shows for the bird for which we had the most abundant data ($\male$ # 9) the flight-hunting frequencies following 20 min intervals with different experiences. It turns out that in all groups of intervals positive strikes were followed by suppressed hunting, and negative strikes by increased hunting. After negative strikes the frequency of hunting was even larger than after more hunting but no strikes. This supports the suggestion that the effect is attributable to increased hunting in response to unsuccessful strikes. The detection of prey may stimulate hunting while the capture of prey seems to suppress hunting immediately afterwards.
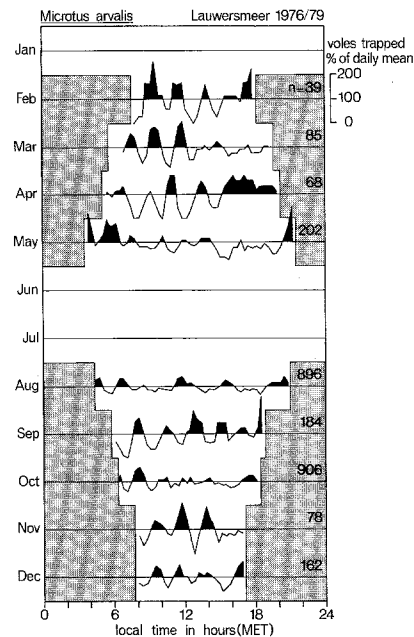

Fig. 7. Daily variations of vole trapping frequency. The 3-pt running mean number of vole trappings per 20 min was expressed as a ratio of the average over the daylight. Each monthly graph is based on 2–9 days of trapping and on a total number of voles caught indicated as n

3.2. Patterns of Prey Availability

The main prey of kestrel, the common vole, lives in burrows and occasionally emerges to the surface for feeding. In daytime, the rodent makes such feeding excursions in regular cycles of about two hours. To some extent the cycles of different members of the population run in synchrony. We obtained a rough indication of the surface feeding activity by recording trapping times in a live trapping programme with frequent trap checks (3 checks per hour). The procedure and main results have been described earlier (Daan and Slopsema 1978). An updated account summarizing all vole trapping data we collected so far is presented in Fig. 7. The data are expressed as hourly deviations from the average number trapped during daylight. For each month data from several samples were pooled, sometimes originating from

Table 3. Frequencies of flight-hunting in 20-min intervals with different immediate prior experience. Frequencies are expressed in % of time, and in the last column in % of the individual average frequency. Mean values ± 1 standard error. Numbers of intervals appear in parentheses

Bird:	$\male$ # 8 October	$\male$ # 9 December	$\female$ # 5 January	All birds
Preceding 20-min interval with:				
No hunting, no strikes	0.9 ± 0.3 (182)	6.2 ± 1.2 (194)	3.4 ± 0.8 (110)	29.4 ± 39.7 (486) A
Hunting, no strikes	12.9 ± 3.1 (30)	24.9 ± 3.2 (72)	10.6 ± 2.9 (30)	157.2 ± 19.5 (132) B
Hunting, negative strikes only	18.2 ± 7.5 (13)	44.6 ± 5.7 (25)	20.4 ± 5.2 (14)	269.7 ± 45.1 (52) C
Hunting, at least one positive strike	5.4 ± 2.6 (13)	18.7 ± 4.0 (35)	10.4 ± 4.4 (12)	103.8 ± 19.8 (60) D
Individual average frequency:	4.8	21.6	7.2	100.0
		% of time		% of individual average frequency

Wilcoxon-two sample test on averages in last column: A–B: $p < 0.001$; A–C: $p < 0.001$; A–D: $p < 0.001$; B–C: $p < 0.005$; B–D: $p < 0.10$; C–D: $p < 0.001$

different areas and habitats in the Lauwersmeer nature reserve. The pattern emerging is different for summer and winter. From September through April predictable trapping peaks and troughs, alternating with a periodicity of ca. 2 h, occur in the first half of the light period and gradually fade away in the afternoon. Sometimes three, sometimes only two trapping peaks are clearly pronounced. In records obtained in May and August deviations from average are much less systematic, although the first morning peak is usually present.

Such patterns in trapping probably reflect seasonal changes in individual activity patterns such as documented for captive common voles by Ostermann (1956) and Erkinaro (1969). We postpone a full discussion of the physiological and evolutionary forces shaping these patterns (see Daan et al., in prep.). Here it suffices to note that the physiological need for daytime feeding in the voles is large during the winter months, with high energy requirements and low quality food. The feeding cycles may have been more regular in winter because of increased daytime activity. We consider the partial synchrony of such cycles in the vole population to be the result of the general solution for the optimization of feeding cycles: time above ground in the daylight is always minimized by starting the day with a rest phase rather than an active phase of the ultradian cycle. Additional benefits may under some circumstances accrue from reduced individual risk of predation as a consequence of synchronous vulnerability (Daan and Slopsema 1978).

Be all this as it may, we are left with relatively systematic and predictable daily variations in prey behaviour. The trapping variations are of course merely correlated with prey activity, but they are presently the best indications we have. The pattern of peak times of vole trappability is sumarized in Fig. 8. This figure includes estimates of the time of the first nocturnal trapping peak in the evening ("dusk peak") as well as of the last peak in early morning ("dawn peak"). There appears to be some seasonal variation in the time relative to civil twilight at which these peaks occur. The onset of night activity, as far as reflected by an increase in trapping, and also the end of activity around dawn occur at a considerably higher light intensity in summer than in winter. (The high values at the end of the light period in Fig. 7, February and December, represent only the incline towards the dusk peak, not the culmination of activity itself). In this respect, the voles seem fairly typical for the general seasonal changes of phase relationships between circadian activity rhythms and the natural light-dark cycle in nocturnal mammals (Daan and Aschoff 1975): onset and end of daily activity shift with sunset and sunrise in their seasonal course but do not follow them completely. More observations, based on techniques other than trapping, are needed to confirm this interpretation. One confirmation is derived from the frequency of strikes of kestrels hunting for voles (Fig. 9), as discussed below.

For the analysis of kestrel hunting activity in relation to vole availability we are confronted with the problem that vole activity patterns are likely to vary slightly from one habitat to the next. This variation, which will be documented elsewhere, may create slight asynchrony for the 2-h trapping rhythm between samples. Even though the rhythm in each sample is usually discernable for up to three trapping peaks per day, the combination of several samples taken at the same time of year (such as in October, Figs. 7, 8), may obscure the second and third peak by phase differences. We face the same problem when we use the predictions from vole activity in the trapping areas for vole activity in the kestrel hunting ranges. A further complication is that we cannot assume that all peaks we distinguish in the trapping record have equal strength as indicators of maxi-
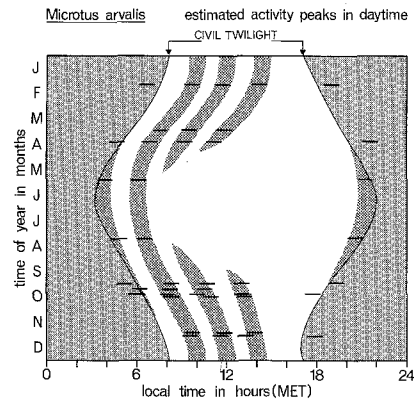

Fig. 8. Summary figure showing the timing of vole trapping peaks. Horizontal bars (1 h long) indicate actually observed peaks in trapping series. Shaded areas are our interpretation of the timing of such peaks throughout the year
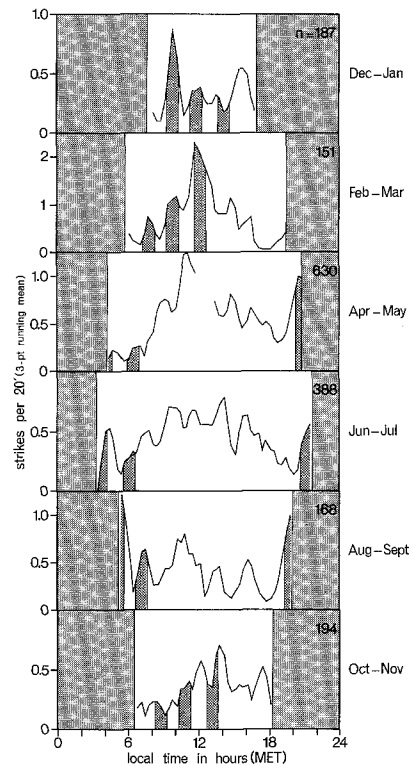

Fig. 9. Daily curves of strike frequency based on continuous kestrel observations pooled in six bimonthly intervals of the year. Shaded areas under the curves indicate vole trapping peaks as derived from Fig. 8

ma in vole availability. It is likely that the amplitude of some of the trapping rhythms is particularly shaped by a few trap-prone individual voles. The trappings therefore do not necessarily give a quantitatively accurate picture of vole availability, as tacitly assumed by Daan and Slopsema (1978).

Hence for a variety of reasons it is useful to consider another indicator of vole surface availability. In Fig. 9, the frequency of strikes made by kestrels is plotted as a function of time of day. Data were pooled in twomonthly periods and assembled in such a fashion that before-noon data were aligned with respect to dawn civil twilight, afternoon data with respect to dusk civil twilight. This composition is obviously subject to variations from various sources: there are daily effects of weather conditions,

and different individual kestrels, with differently daily trends in hunting behaviour are included. The strike frequency of course depends directly on the frequency of flight-hunting, and gives no quantitative estimate of vole availability. Yet if the vole trapping peaks correspond with real maxima in vole availability, we should expect them to be usually reflected as elevations on the daily curves of strike frequency, as long as at least some hunting is done. Going from morning to evening, we see the *dawn peak*, predicted by trapping, clearly recurring in the strike records of June through September. This is likely to be a true summer phenomenon, although it does not show up in April/ May. *Morning peak 1*, present in trapping records at all times of year causes a pronounced relative increase in strike frequency only in the composite data for December–March and August–September. *Morning peak 2* is much less pronounced in December through March and clearly disappeared in summer. *Morning peak 3* is indicated only in February–March, but this may just as well be a coincidence with the maximum in a diurnal trend and is anyway based on a single individual kestrel (δ # 83). The *dusk peak*, reflecting the onset of nocturnal vole activity, is present all through the summer as an increased strike frequency; also in conformity with the vole trappings, this peak is absent in winter.

We conclude that the following peaks in vole availability are general enough to allow an analysis of adjustment of hunting frequency: In summer dawn and dusk peaks, in winter morning peak 1 and, to a lesser extent, morning peak 2. (In addition, uncertain vole availability peaks, are indicated in Fig. 10 with question marks). This restrictive assumption is only concerned with the patterns generalizable across seasons and areas. Individual kestrels, on a smaller scale, are presumably faced with patterns predictable from day to day in much greater detail. Our analysis is, however, of necessity restricted to the strongly generalizable patterns.

3.3. Hunting Yield and Frequency

Figure 10 presents, by way of illustration, the average frequencies of flight-hunting (in % of time) in the course of the day for 6 individual kestrels. The patterns vary widely, with average frequencies of flight-hunting from 3.6% (δ # 8, October) up to 21.6% (δ # 83, May). The difference between winter and summer patterns in the extent of short-term variation is only apparent: the noise in the winter samples is much smaller since they were based on more days of observation. In some instances we see a close correspondence between a peak in flight-hunting frequency and a vole trapping peak: a concentration of flight-hunting at the time of morning peak 1 in δ # 9 (December, June) and $\female$ # 5 (January). Flight hunting was concentrated at the dusk vole peak in δ # 9 (July). In other instances a vole trapping peak was not associated with a concentration of kestrel flight-hunting.

We shall take a closer look at the three winter birds, for which the data are most complete: δ # 8 October, δ # 9 December and $\female$ # 5 January. These data allow us to investigate the relation of variations in hunting *frequency* with variations in hunting *yield*. As with the trapping data, 3-pt running averages were used as a smoothing procedure (Fig. 11). The yield of flight-hunting was estimated by multiplying actual strike rates per hour of hunting with the overall average strike success (i.e. the fraction of strikes which were successful: 0.34 for δ # 8; 0.48 for δ # 9; 0.26 for $\female$ # 5). In the hunting yield curves of both δ # 9 and $\female$ # 5 a morning peak can be distinguished which coincides with vole peak 1. A slight elevation at peak 2 is also
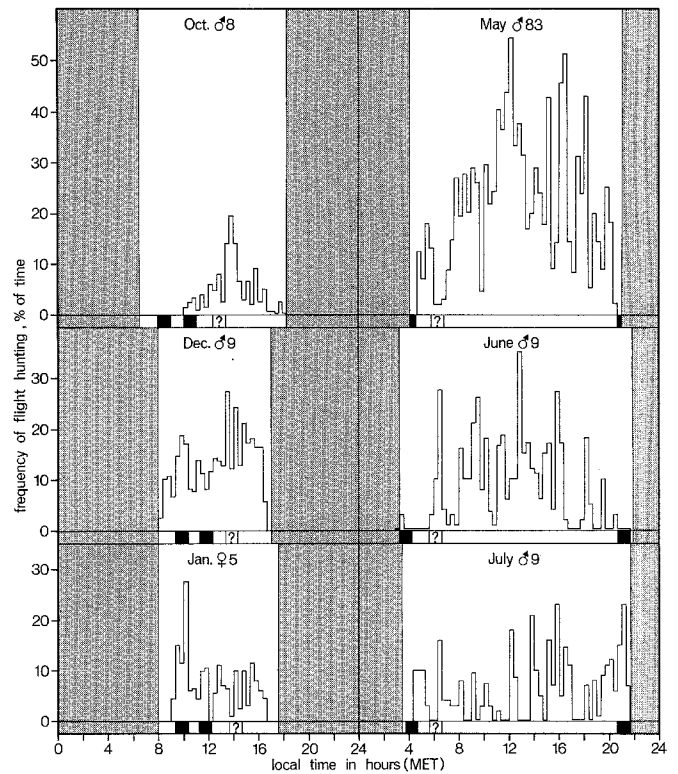

Fig. 10. Flight-hunting frequency as a function of time of day in six individual kestrels observed at different times of year for several days continuously
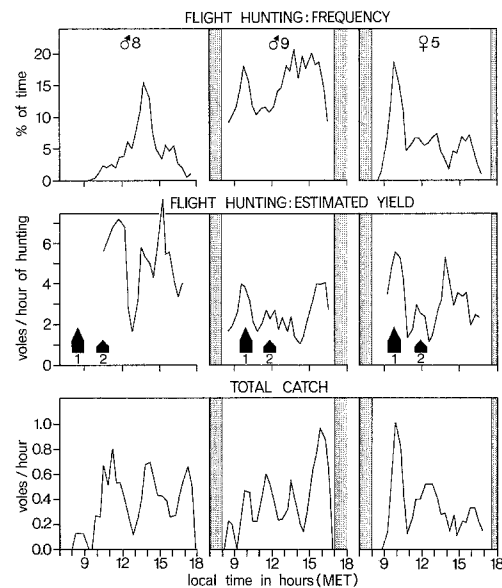

Fig. 11. Flight-hunting frequency, estimated yield and total food intake as a function of time of day. Data from three individual kestrels observed during the winter. All data points are 3-pt running means for 20 min intervals. Yield was estimated by multiplying strike frequency per hour of hunting with average fraction of successful strikes. Arrows indicate vole trapping peaks 1 and 2

indicated. For δ # 8 the relevant data are missing. This is not due to gaps in the observations but to the fact that δ # 8 did not hunt at all at the time of morning peak 1. This male had a pronounced daily rhythm of hunting activity with a sharp rise in the early afternoon. This seems to have nothing to do

with vole availability, and is more likely related to weather conditions which were usually poor (no wind) in early morning in the observation period (cf. Fig. 3). ♂ # 9 and ♀ # 5 showed a clear increase in hunting frequency in the hour of elevated hunting yield. In addition, ♂ # 9 did a considerable amount of flight-hunting in the afternoon. The concentration of hunting at times of high yield naturally is reflected in the pattern of total vole catch frequency (lower panels of Fig. 11) although these graphs in addition contain the voles caught in perch-hunting.

The concentration of hunting at times of high yield as is seen in some animals is clearly adaptive for improving the catch per effort ratio of these raptors. That some birds, such as ♂ # 8, may not show such adaptive timing of hunting behaviour is critical for understanding the mechanism by which others arrive at the optimal solution. We shall come back to this problem in section 5. Here it suffices to summarize that each time of year is characterized by its own daily distribution of prey availability, and that there are further local variations confronting the foraging kestrel. Sometimes such vole peaks are truly exploited, by adjusting hunting frequencies to times of optimal hunting yield, sometimes they are not.

4. Daily Patterns in Food Caching, Retrieving and Intake

In section 3 we saw that a kestrel hunting for voles faces the problem of adjusting its activity to variations in the availability of its prey. If all prey were eaten immediately upon capture, we would expect these variations also to determine the daily course of food intake. This, however, is not the case. In Fig. 12 the frequency of meals is plotted as a function of time of day. A meal is easily defined as any continuous period of eating; it may be interrupted by incidentally looking around but not by flying (unless disturbed) or hunting or the like. Durations of meals are not specified but are typically in the order of 1 to 7 min for voles and up to 45 min (including plucking time) for avian prey. A meal may consist of any food item from the head of a vole up to a complete starling. Some meals were classified by the observers as uncertain, and a minimum and a maximum estimate of meal frequency were obtained by exclusion and inclusion of the uncertain meals, respectively. All the graphs in Fig. 12, pooling data from several individuals (excluding incubating ♀♀) in 2-month intervals, show a peak in meal frequency at the end of the day. The peak reaches a level of circa 1 meal/h, so on average the kestrels consume about one meal in the hour before returning to their roost. The average meal frequency over the whole day varied from 0.28 meals per hour in summer to 0.53 per hour in winter (Table 4). Simultaneously there was a seasonal shift in the daily distribution. The evening peak was least pronounced during the summer months and most conspicuous in late winter: meal frequencies in the last two hours of the day were 1.3 times average in June/July and 3.3 times average in February/March (Table 4).

Of course we cannot interpret meal frequencies as equivalent to rates of food intake, before analyzing the size of the meals consumed at different times of day. There are some indications that average meal size varied with time of day in the same way as meal frequency. Kestrels that caught a starling in the morning or early afternoon typically ate only the head and cached the rest, flight muscles and legs. Such a cache was retrieved and eaten at the end of the day. While we do not have exact weights of the various parts of the body, this indicates that meal sizes generally may have been slightly larger at the end of the day. It was further observed that voles cached –
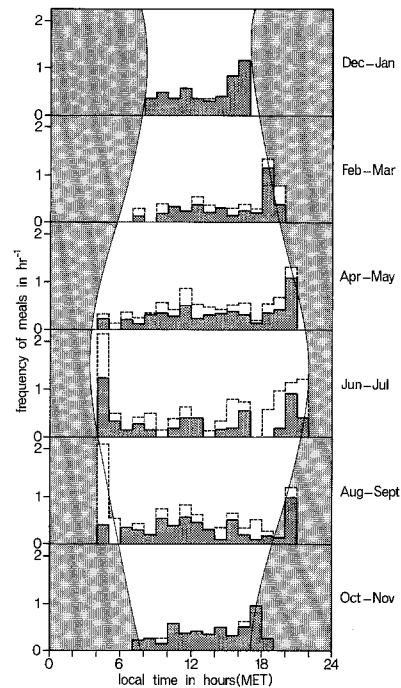

Fig. 12. Daily curves of food intake, expressed as the number of meals seen taken per hour of observation. Data from several kestrels pooled. Shaded histogram is the minimum frequency, dashed histogram the maximum frequency of meals

Table 4. Seasonal changes in the frequency of meals and their distribution over the day

Time of year	Meals per hour		Retrieved prey as fraction of meals (last 2 h of the day)
	whole day	last 2 h of the day	
December/January	0.53	0.98	0.31
February/March	0.31	1.01	0.79
April/May	0.32	0.71	0.48
June/July	0.28	0.74	0.20
August/September	0.33	0.43	0.00
October/November	0.42	0.86	0.26

and retrieved at the end of the day – were often larger than voles eaten immediately (Rijnsdorp and Dijkstra, in prep.). Mueller (1973) found in laboratory experiments with the American kestrel, *Falco sparverius*, that the size of meals taken at the end of the day was significantly larger than earlier in the day. Similar data from the European kestrel obtained by J. de Vries in our laboratory will be included in a later study on daily caloric intake. For present purposes it is safe to assume that the temporal pattern of food intake will resemble the pattern of meal frequency but with an even more pronounced peak at the end of the day.

The daily pattern of food intake (Fig. 12) thus contrasts with the pattern of flight-hunting (Fig. 10). The way in which the two are reconciled is the principle of caching and retrieving (see also Rijnsdorp and Dijkstra, in prep.). Some (but not all) prey are cached upon capture, either wholly or in part. Caching is done at any time during the day, but rarely in the last two hours before dusk. It is in these hours that most of the cached prey are retrieved (Fig. 13). This daily pattern of caching and retrieving is very distinctive in autumn, winter and spring. It
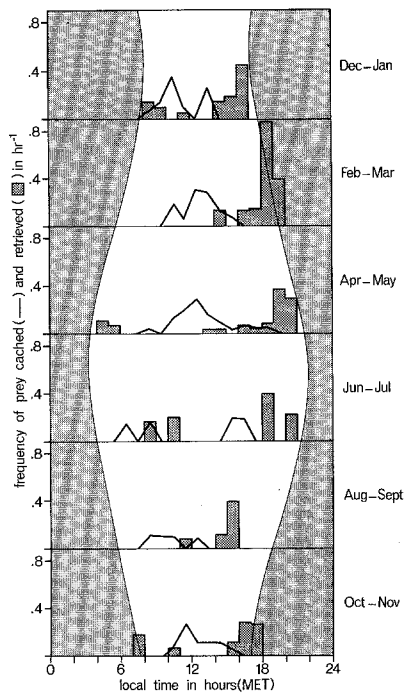
Fig. 13. Daily variations in the frequency of food caching (*solid lines*) and retrieving (histograms). Data from several individual kestrels pooled per bimonthly period

Fig. 14. Daily curves of food intake, expressed as number of meals per hour of observation, for a pair of kestrels during incubation

Fig. 15. Daily variations in the frequency of food caching and retrieving by incubating female kestrels. Conventions as in Figs. 12 and 13

seems much less pronounced in summer (June through September), although sample sizes were relatively small for this period. In wintering females of the American kestrel, *Falco sparverius*, Collopy (1977) found a closely similar pattern in caching and retrieving. Naturally, the prey retrieved at the end of the day contribute to the evening peak in meal frequency. However, this contribution varies greatly between the different seasons (Table 4). In August and September none of the meals observed in the last two hours were retrieved caches, in later winter retrievals accounted for up to 79% of such meals.

Incubating females were excluded from the above analysis, for good reason. Such females do not show an evening peak in meal frequency. Their daily pattern of food intake is in sharp contrast with that of their mates (Fig. 14). A female during incubation does not herself hunt and relies almost totally on food brought to the nest by the male (Tinbergen 1940). She does cache prey and retrieve it, however, in much the same temporal fashion as foraging kestrels (Fig. 15). This did not result in a peak in food intake at the end of the day, in any of the three incubating females for which we have the relevant data. The cache-retrieval tactic in the incubating female merely seems to level out fluctuations in the male's food provisioning. Her increased retrieval tendency in the evening is apparently just sufficient to compensate for the male's reduced rate of delivering prey to the nest which again may be related to his own increased motivation for eating.

The principle of caching and retrieving allows the kestrels to optimize the times of hunting with respect to both weather conditions and prey availability while they simultaneously can arrange their meal schedules according to different criteria. It enables them to uncouple food searching from its consummatory act, eating, and to optimize these separately as to time of day. The question remains what sort of benefit is derived from concentrated feeding shortly before nightfall. It is unlikely that this has anything to do with an improvement in the quality of the
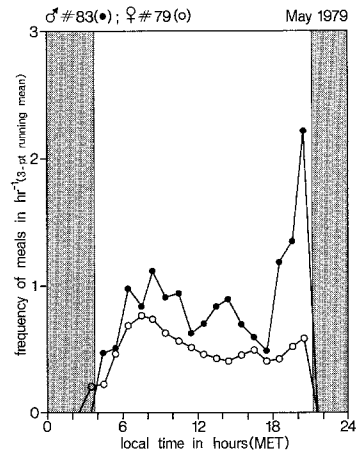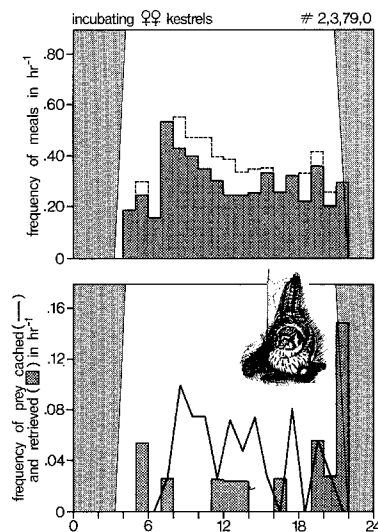
prey by the act of caching (e.g. increased digestibility; reduced risk of parasite infection), since such principles would apply to all prey and to all kestrels. However, we should not preclude that warm summer conditions may effect the palatibility of cached prey and therefore the strategies followed by the raptors.

A more attractive hypothesis is suggested by the difference in meal frequency pattern between incubating and non-incubating kestrels. It should be a general energy-savings policy to keep body weight during flight at the lowest possible level. By delaying the consumption of that part of the food which is needed to balance the nocturnal maintenance, a kestrel would keep its body weight in daytime at a low level. A rough estimate – using Pennycuick's (1975) flight energy model – of the savings from postponing one 22 gr vole meal (10%) from morning till evening for a 220 gr kestrel spending 20% of its time (2.4 h) in flight-hunting at optimal flight speed (8 m/s) is 12 kJ per day. This is nearly 7% of the daily subsistence energy for captive kestrels of the same weight (Kirkwood 1979) and a considerable advantage. The fact that breeding females do not concentrate feeding in the evening is consistent with the fact that they do not hunt and thus would not benefit from reduced daytime body weights. Actually body weights of females are sharply increased during incubation as compared with weights in the rest

of the year (Daan et al., in prep.). The flightcost hypothesis clearly would predict evening feeding at any time of year. Any seasonal variation in daily feeding patterns needs other functional explanations.

A second benefit may derive from the efficient use of the heat produced in food digestion (Specific Dynamic Action – SDA; see Kleiber 1975). Nocturnal heat production by SDA is less likely to be wasted than SDA in daytime. This is because ambient temperatures at night are more likely to be below the thermo-neutral zone, while thermoregulatory requirements at night are not met by extra heat produced by muscle activity. Although little is known about the role of SDA in the energy budget (Ricklefs 1974) it is potentially a factor by which the balance can be considerably adjusted. This is subject of further research. Yet on theoretical grounds it is clear that night temperatures in the zone of thermoneutrality would not allow the exploitation of SDA for thermoregulatory purposes. There is thus a potential basis for seasonal changes in strategies of circadian organization of feeding times, with respect to the daily balance of energy.

5. Daily Routines in Individual Kestrels

We have described the general daily patterns of hunting and feeding behaviour in a functional context. In order to discuss how these patterns are generated by the birds in response to experience and how the circadian system may be involved, it is now appropriate to have a closer look at individual characteristics of daily behaviour. This analysis is inspired by Enright's hypothesis (see Introduction) which surmises two elements in the daily behaviour pattern of animals: Firstly a tendency to repeat circadian changes day after day, and secondly, flexibility in this repetitive pattern such that new experiences are incorporated every day in tomorrow's motivational sequence. The first element is undoubtedly present in the kestrel. We have often come across instances of daily patterns characteristic of individual birds, such as exemplified in Fig. 16. Female # 5 was occasionally observed pecking stones by the roadside, used as grinders in the stomach. All such observations were before 11:00 a.m. Female # 3 took a sandbath customarily in the late afternoon. It would be a prohibitive task to work out the benefits to ♀ # 5 from pecking stones in the morning rather than the afternoon, or decide why ♀ # 3 sandbathed around 6 p.m. But then, it would be even harder to explain why the same benefits would not lead other birds to develop the same behaviour. The patterns are characteristic of individuals, not of populations. Some may be characteristic of individuals for only a short time of their life. It is our contention, however, that such individual patterns are of tell-tale significance for understanding general daily strategies.

Behaviours such as stone pecking and sand bathing are rare and thereby unsuitable for a more detailed analysis. We chose to investigate the temporal pattern in flight-hunting behaviour and site choice. As before, we concentrate on the three birds with the most complete data: ♂ # 8 in October 1977 (8 days in sequence), ♂ # 9 in December 1977 (14 days) and ♀ # 5 in January 1978 (8 days prior to experiments). These data were collected with the aim of complete continuity of observation such that correlations between consecutive days might be revealed. The winter situation is further characterized by more reliably predictable daily fluctuations in vole availability.

In order to analyse the consequence of experience on flight-hunting the next day, we first standardized all the data so as to pool results from three different individuals: Relative flight-
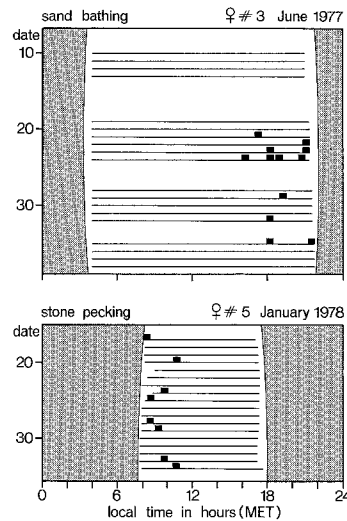

Fig. 16. Daily habits: Times of occurrence of rare behaviours: sand bathing in ♀ # 3, stone pecking in ♀ # 5

Table 5. Relative frequencies of flight-hunting depending on prior history. Frequencies of flight-hunting (in % of time) were calculated for each clock hour of observation, then expressed in % of the individual average frequency, and averaged across individuals in 4 classes of flight-hunting frequency 24 h ago, either with or without prey. Means ± standard error (nr of hours)

Relative flight-hunting 24 h ago:	No prey 24 h ago	Prey 24 h ago	Significance of difference[a]	Total
0	69% ± 16 (43)	87% ± 36 (7)	$p < 0.1$	71% ± 15 (50)
1– 66%	53% ± 24 (9)	167% ± 97 (6)	$p < 0.1$	98% ± 42 (15)
67–133%	103% ± 36 (10)	134% ± 46 (11)	n.s.	119% ± 29 (21)
>133%	119% ± 37 (14)	143% ± 40 (9)	n.s.	128% ± 27 (23)
Total	81% ± 13 (76)	148% ± 22 (33)	$p < 0.01$	96% ± 12 (109)

[a] Wilcoxon's two-sample test

hunting frequencies were calculated for each hour of observation by dividing the percent of time spent in flight-hunt by the individual average percentage. For the three birds used in the analysis, we had together 70 observation hours in which at least one prey was captured and for which also some of the behaviour of the bird on the next day is known. Such hours contained, of course, significantly more flight-hunting than hours without prey captures (Table 5; and data points on the left side in Fig. 17). We have also calculated the mean relative frequencies of flight-hunting one hour later, two hours after prey capture, etcetera, up to a lag time of 30 hs. These figures were plotted as a function of lag time in Fig. 17 (closed symbols). This graph has a gap between 6 and 18 h after prey capture, where data were too sparse since these hours fell mainly in the night. The graph displays a characteristic peak 24 h after prey capture. We cannot say whether this peak is a statistically significant elevation on the curve. This is because a particular hour may be 24 h after one prey capture and 23 h after another prey; hence the mean flight-hunting frequencies at different lag times are based to some extent on the same values. They are not independent and the significance of their difference cannot be tested. We can, however, do exactly the same calculation for the behaviour during the first 30 h following all such hours in which *no* prey was caught. These data (open symbols in Fig. 17) reach a
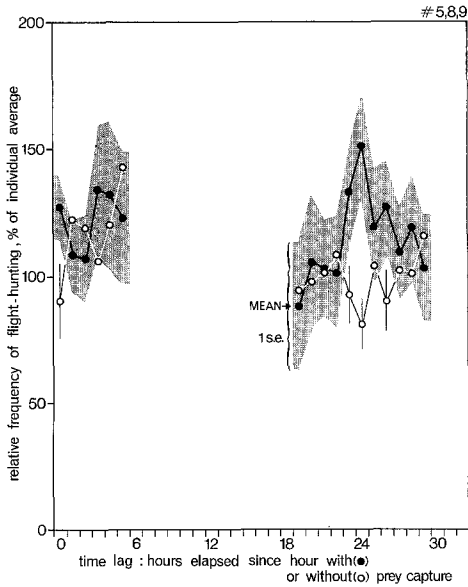
Fig. 17. Effect of experience 24 h ago on the tendency to hunt. Average frequencies of flight-hunting (as % of the individual average frequency) in the first 30 h following hours either with (●) or without (○) prey capture. Shaded areas represent ±1 s.e. around the mean (●), vertical lines ±1 s.e. around the mean (○) when outside the shade

minimum value at 24 h lag time, in contrast with a *maximum* 24 h after prey capture. Statistical comparison of the mean relative frequencies of flight-hunting 24 h after prey and 24 h after no prey reveals a significant difference (Wilcoxon's two-sample test, $p < 0.01$, see Table 5). There are two plausible causes for this result, and we will demonstrate that both are involved.

Firstly, there was a positive correlation in the frequency of flight-hunting in the same clock hour on two consecutive days. This day-to-day correlation was statistically significant by Spearman's rank correlation test ($r_s = 0.310$; $n = 109$; $p < 0.01$). Since there was – obviously – more flight-hunting in hours with prey capture than in hours without prey (as demonstrated in Fig. 17 left side) this led to more flight-hunting 24 h after prey capture than 24 h after no prey. Secondly an increased tendency to flight-hunt in response to prey capture 24 h ago contributed further to the result. This can be observed by comparing situations 24 h after prey and after no prey for different narrow classes of hunting frequencies 24 h ago. Within such classes the first mechanism can not have been responsible. Yet within each class (Table 5), flight-hunting was on average more frequent 24 h after prey capture than after no prey. In any class, flight-hunting 24 h after prey capture was more frequent than 24 h after no prey in the next class. By cutting up the data like this, however, sample sizes became too small for more than marginal statistical significance *within* classes (Table 5).

Hence in flight-hunting behaviour of the kestrels both elements of Enright's hypothesis are present. There is a correlation in the temporal pattern of hunting behaviour on consecutive days and this pattern tends to be modified by experience such that prey capture is followed by increased hunting frequency 24 h later. Since the immediate effect of prey capture is a depression in hunting tendency (Table 3), the increase 24 h later is not simply another expression of the same day-to-day correlation, but a clear adaptive adjustment.

Along similar lines as with the tendency to hunt we can discuss the daily pattern in site choice of hunting places. Two striking examples of day-to-day correspondence in hunting sites
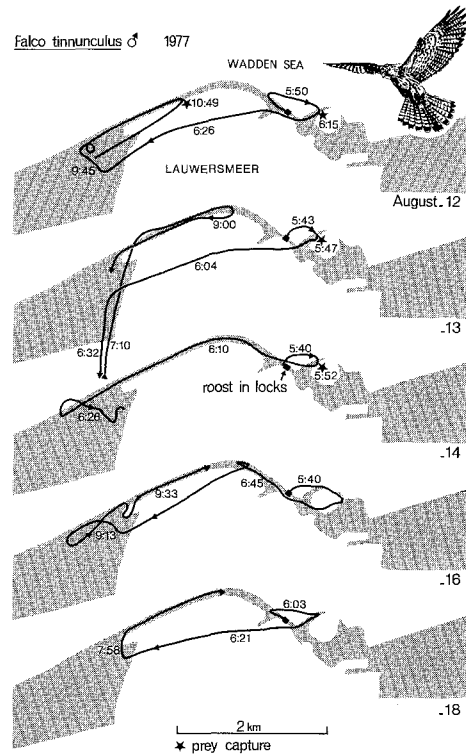

Fig. 18. Spatial daily habits. Flight movements of a male kestrel upon leaving its roost (■) in the morning are plotted for five days in August 1977. Notice the correspondence in time and place of prey captures (*) on three consecutive days
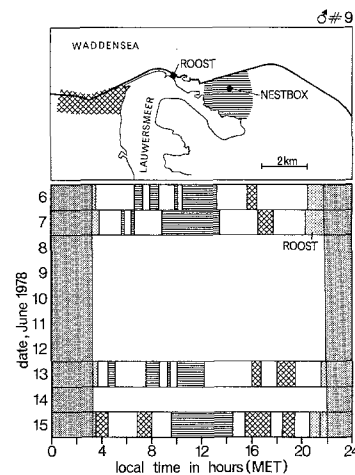

Fig. 19. Spatial daily habits. The same kestrel (♂ # 9) as in Fig. 18, using the same roost a year later. The lower panel indicates daily times of presence in three separate areas; I around nestbox; II (*crosshatched*); III (*stippled*), around roost

are shown in Figs. 18 and 19, both using data from ♂ # 9. In August 1977, after leaving the roost at dawn, this bird chose to hunt for several days in sequence on a very small part of a dike (ca. 200 m). Usually after having caught a vole he flew off, heading for the western part of his home range (Fig. 18). The next summer, the bird has slightly shifted its home range, now centered around a new nest site. Figure 19 illustrates its choice of hunting sites in June 1978, while it was taking care of a brood of three young. In the area around the nestbox (I) ♂ # 9 hunted in flight for voles. In another area (II, cross
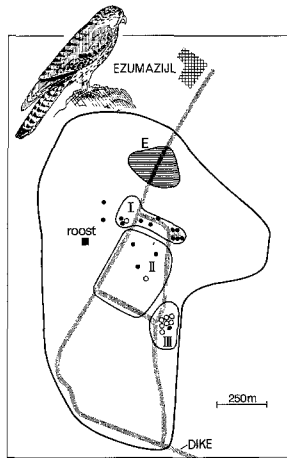
Fig. 20. Home range, main hunting areas (I, II, III) and experimental feeding area (E) of kestrel ♀ # 5 ("Kiki") in January 1978. All prey captures in the pre-experimental period are indicated (● prey taken from flight-hunt, ○ from perches)
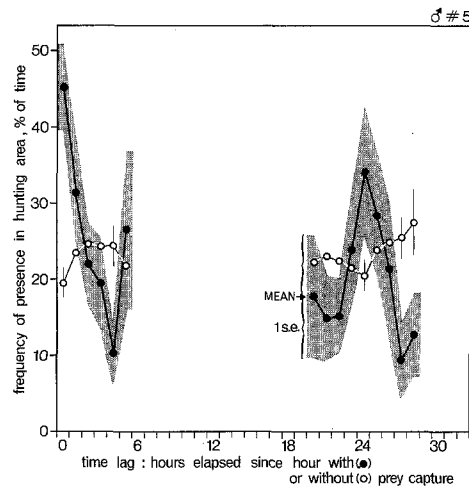
Fig. 21. Effect of experience 24 h ago on the tendency to select a hunting area. Per area hours were pooled in groups either with (●) or without (○) prey capture t hours ago, plotted against time lag t. Shaded area represents ±1 s.e. around the mean (●), vertical lines ± s.e. around the mean (○) when outside the shaded area

Table 6. Presence of kestrel # 5 in various parts of her home range depending on prior history. For each of three hunting areas (see Fig. 20) the frequency of presence was calculated in % of time for each of 59 observation hours. Data were then pooled in five classes according to behaviour 24 h ago, and expressed as means±s.e. Numbers in parentheses are observation hours per area. Differences were tested by Wilcoxon's two-sample test (two-tailed)

Presence in area I, II or III →	Without prey capture	With prey capture	Total		
↓					
	Presence in same area 24 h later:				
0%	17±3% (73)	–	17±3% (73) ⎫		
1–33%	21±3% (52)	25±12% (6) n.s.	22±3% (58) ⎬ n.s. ⎫		$p<0.001$
>33%	30±4% (35)	39±11% (11) n.s.	32±4% (46) ⎭ $p<0.05$ ⎬		
Total	21±2% (160)	34± 2% (17) n.s.	22±2% (177)		

hatched in Fig. 19) he hunted mainly from perches for starlings and juvenile waders. On four days of observation, a clear habitual pattern emerged of vole hunting in the mornings in area I and of bird hunting in the afternoon in area II.

In analogy with the tendency to hunt we can analyse how such temporal patterns in site choice come about. We restricted this analysis to one individual, ♀ # 5. The data for the other two birds (♂♂ #8, 9) are less suitable for evaluation: ♂ # 8 shifted from one hunting place to the next in the course of the 8 days of continuous observation, while ♂ # 9 in december 1977 hunted nearly all the time in one small area, along a dike of 2.5 km. In the home range of ♀ # 5 three major hunting areas, which were partly isolated from each other, can be distinguished (Fig. 20). In area I the bird hunted mostly in flight, in area II and III mostly from perches. The approximate location of all prey captures observed is plotted in Fig. 20. We have quantified the presence in any of the three areas in terms of the number of 5-min episodes spent there for every hour of the day.

Figure 21 plots the average presence of the bird following hours with and without prey capture in the same area. Again we see a maximal tendency to choose an area when prey had been captured there 24 h ago, rather than any other time lag. This is not the case when no prey had been captured there 24 h ago. Although the effect seems quite pronounced, it is statistically not significant (Table 6). There were only 17 prey for which the behaviour of the predator on the next day was known.

This small number apparently is insufficient to allow statistical significance of the trend observed. If we pool the available data with respect to the degree of presence in the same area 24 h ago, a significant trend is observed of increased average time of presence with increased presence 24 h ago (Table 6). Both when presence was less than 33% or more than 33% 24 h before, prey capture apparently was associated with increased presence in the same area 24 h later. Of course, the numbers of prey within classes are even smaller and again allow no statistical significance.

Thus at least in one bird where several distinct hunting areas could be discerned we have modest support for the idea that the choice of area was partly determined by daily habits, but was modified by experience with the foraging return 24 h previously. Both elements of Enright's hypothesis were likely to be present, but more prey captures need obviously be observed for a strong support of the hypothetical effect of prey. Naturally the causal involvement of prey capture in the modification of both flight-hunting and site choice can only be established experimentally. The experiment we attempted is described in the next section.

6. Daily Routines: a Field Experiment

If daily patterns in motivation for hunting and in site choice indeed emerge from accumulating experience with time and place

of rewards this should be testable in a crucial field experiment. This is the classic experiment in which Beling (1928) demonstrated the use of "time memory" by foraging honeybees. We have performed one such experiment with a freeliving kestrel. The results do not unequivocally distinguish between two main alternative intepretations. This is partly due to our design of the experiment. Yet we insert a discussion of the experiment for a variety of reasons. The results bear directly on the motivational mechanism involved in the behaviour of our topic. But they also make clear how exceedingly complicated the problem of time and space is and what careful knowledge of natural behaviour is needed for an optimal experimental design. In addition the experiment requires considerable effort, and is not lightly repeated. Our failure may help others to avoid the pitfalls of experimental design.

The aim of the experiment was to test if the daily pattern in site choice of a kestrel ($♀ \# 5$) was modified by offering her live prey at a selected place and time of day. In addition, we examined the effect on daily variations in flight-hunting behaviour. The areas within the home range used by the bird, "Kiki" – including the experimental feeding spot E – are shown in Fig. 20. The complete data on site choice together with the experimental protocol are shown in Fig. 22. The experiment can be divided into three parts:

1. Pre-experimental uninfluenced observation: January 17–24, 1978.

2. Experimental feeding and continuous observation: January 24–February 1, 1978.

3. Post-experimental uninfluenced observation: February 2–3, 1978.

In the period of experimental feeding, we offered the kestrel each day between 8:00 and 10:30 (MET) one to three lab mice (total weight 18–50 gr) by releasing them from a car in the vicinity of the perch (area E). Kiki usually caught the prey offered immediately.

In the pre-experimental period, Kiki typically visited hunting area I in the morning around 10:00, and again in the late afternoon. The habit of visiting area I in the morning was associated with a tendency to flight-hunt during morning peak 1 of vole availability (Figs. 2, 10). The return to area I in the late afternoon was connected with the retrieval of cached prey (Fig. 22, open circles). The experimental feeding area E was rarely visited until January 24. On this day we gave Kiki two mice when she happened to be in this area. On the next day, the experiment started with daily feedings in E around 10:00 a.m. This time was selected with the aim of affecting Kiki's site choice without greatly influencing her daily hunting pattern.

The influence of the mice fed on the site choice was considerable. Kiki not only came back to E every morning but also stayed there for almost the entire day following capture of the prey offered (Fig. 22). In the two postexperimental days, Kiki returned and spent 77% of her time available from 8:00 till 10:30 in area E, against only 45% of her time in the remainder of the day.

Of her total presence in area E, some may have been truly associated with foraging and "expectation" of prey, and some visits, especially those in late afternoon, may have had to do with the retrieval of cached prey. However, much of the time Kiki spent in area E may be more properly interpreted as a casual tendency to remain in an area after prey capture. To avoid such ambiguity we looked, more closely, at the site choice during flight-hunt (Fig. 23). In the pre-experimental days Kiki very rarely flight-hunted in area E and did not catch any prey there. She concentrated her flight-hunting around 10:00 as ex-
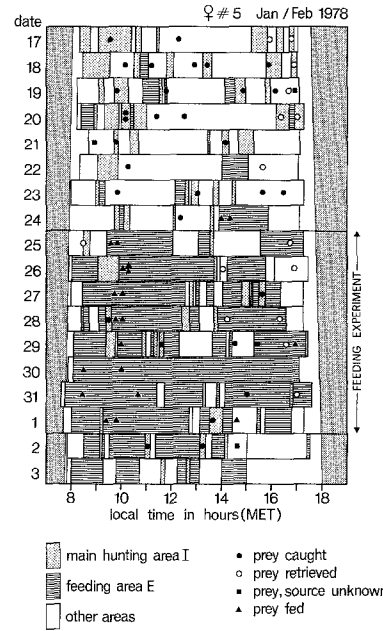

Fig. 22. Site choice of kestrel "Kiki" during the feeding experiment. Horizontal blocks indicate time of continuous observation. Presence in main hunting area I and experimental feeding area E are indicated by different hatching. Symbols show prey captured (●), retrieved (○), experimentally fed (▲) and uncertain (caught or retrieved; ■)
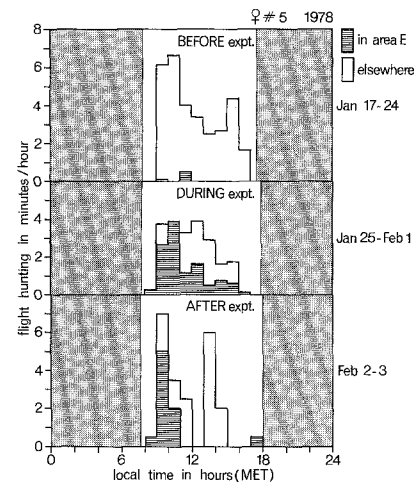

Fig. 23. Frequency of flight-hunting as a function of time of day, within and without experimental feeding area, before, during and after the feeding experiment

plained before. In the experimental period, total flight-hunting around 10:00 was considerably reduced. In fact, the amount of flight-hunting during this experimental feeding time dropped to a level characteristic of the rest of the day. Most flight-hunting between 8:00 and 10:00 a.m. was done in the experimental area E. This hunting preference for area E around feeding time clearly persisted after the experiment was stopped (Fig. 23 lower panel), when the morning hunting peak returned.

While the effects mentioned are quite obvious, their interpretation is not unambigous. Flight-hunting during the feeding time was suppressed in the experimental period relative to pre- and post-experiment control days. The immediate suppressive effect of prey capture on hunting tendency shown above (Fig. 6) may have been stronger than the stimulating effects of prey captures 24 h ago (Fig. 17). This is unclear, but our experiment was hardly

designed to manipulate hunting tendency. Had we wished to investigate this part of Enright's hypothesis we should have selected for feeding time a time of day with normally little flight-hunting (e.g. 14:00).

Site choice during flight-hunt was more convincingly affected by the experimental manipulations in the sense that around feeding time a preference for area E was clearly indicated, during both experimental and post-experimental days. However, as feeding time was also the first major hunting episode of the day, due to our experimental design, the results are compatible with two different mechanisms. Both of these functionally make sense. One is Beling's principle of time memory: the kestrel selects the site which rewarded her 24 h ago. The other is a mechanism whereby the bird selects every morning during its first hunting session the site which yielded the best rewards during the whole previous day. Such behaviour has been demonstrated in starlings (Tinbergen 1976). The possibility that the kestrel also employs such a strategy cannot be lightly disregarded. The experimental feeding area E was far more profitable than the major hunting areas I, II and III (19 prey caught in E, and 7 in the rest of the home range during the experiment). Kiki may have been selecting this site every morning regardless of the time of feeding. The data therefore cannot be interpreted as a strong experimental support for time memory in the kestrel, but they are at least compatible with the proposition.

7. Daily Habits: their Meaning to Predator and Prey

The temporal organization of kestrel foraging behaviour discussed so far is most aptly summarized by the compilation of data on ♀ # 5, Kiki, shown in Fig. 24. Because of cyclic vole surface activity the yield of kestrel flight-hunting varies in a predictable manner in the course of the day. By adjusting her daily motivational pattern to her experience with vole abundance, Kiki was able to catch most of her daily supply in morning peak 1 of prey availability. By eating only some of the prey and caching the rest for retrieval at dusk, she was in addition able to keep her feeding concentrated just before nightfall.

In the above, we have given some functional considerations on this organization. It is not yet possible to develop the precise cost-benefit functions for optimalization, although with the assay of the energy balance at least the energetic costs and benefits of a particular behavioural organization may become measurable. Currently we can clarify the savings only by estimating the total time Kiki would have needed for hunting had she opted for various alternative strategies. Let us look first at two such alternative solutions: (a) hunting randomly during the day and (b) hunting in such manner that the daily pattern of prey capture matches the observed pattern of food intake.

(a) in January 1978, the kestrel Kiki (♀ # 5) had an active day of 9.12 h, of which she spent 6.2% or 0.57 h in flight-hunt. She caught 0.327 voles per hour of observation, i.e. 2.99 voles per day. Of these, 1.90 on average were caught in flight-hunt, and 1.09 from perches. Her average hunting yield over the day, weighing data from all 20′ intervals equally, was 3.01 voles per hour of flight-hunting. Hence if Kiki had spent equal amounts of hunting all through the day, she would have needed 0.63 h to catch 1.90 voles. Her daily strategy saved her 0.06 h of flight-hunting per day, or ca. 10%, when compared with the alternative strategy of random hunting. This is not, however, a very realistic alternative, since random hunting would obviously imply a large deviation from the daily change in eating tendency.

(b) The other alternative for the falcon would be to adjust its hunting activity to its needs for food intake, i.e. to capture
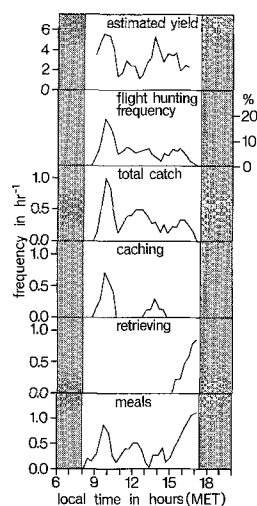

Fig. 24. Summary of daily variations in foraging in a female kestrel. All curves are 3-pt running means of 20 min estimates

prey with the same diurnal variations as with which it ate. We calculated for every hour of the day the hunting time needed to obtain the observed number of vole meals by dividing this number by the hunting yield for the same hour (both values shown in Fig. 24). The sum of such hourly hunting times is 0.73 h. Compared with this value, the actually realized flight-hunting of 0.57 h entails a reduction by 22%. Thus by using the routine of caching and retrieving, Kiki was able to shift her hunting episodes to times of day which were more profitable than the times selected for eating, and thereby she saved 22% of total hunting time.

So the daily strategy chosen by the kestrel Kiki is superior to two obvious alternatives. It involves considerable daily savings on the most expensive article of its time budget. Caching behaviour allows it to reconcile the exploitation of prey with pronounced daily variations in availability and the separate optimalization of feeding time. Food caching can probably more generally be interpreted as a circadian strategy. Among raptors in the field, it has been well documented in the American kestrel (Collopy 1977) and in Eleonora's falcon, feeding on mediterranean migrants (Walter 1979). It is characteristic that in these cases the main prey species is subject to strong daily variations in availability. The circadian nature of the meaning of food storage is also indicated in some herbivorous hoarding behaviour (Toates 1978).

Should we conclude that the kestrels are optimizing their daily behavioural programs? Of course in functional analysis one is not really testing the hypothesis that nature optimizes (Maynard Smith 1978). What is done in practice is hypothesize that some parameter is maximized. One then tests whether the animals behave according to the hypothesis by comparing its behaviour with alternatives, imagined with or without help of mathematics. Kiki behaved much as though she were minimizing the time and thus energy spent every day on hunting, But did she really approach the optimal solution? Let us look at a third alternative.

(c) A third solution to Kiki's hunting problem would be that she did all her flight-hunting in the hour of maximal yield of the day. In her case, this was during vole morning peak 1, i.e. from 9:20 to 10:20. The hunting yield at this hour was 5.61 v/h. Hence Kiki would have needed only 0.34 h of flight-hunting to cover her total daily needs of 1.90 v (in addition

to 1.09 v taken from perches). This would have meant a reduction of flight-hunting time of 60% as compared to the time she needed in reality.

The third alternative demonstrates that the solution of minimal daily hunting time has not been reached. Does this prove that nature did not optimize in this case, or that we did not correctly identify the factor optimized by the bird? Neither of these is a necessary conclusion. The fact of the matter is that alternatives we invent may not be truly alternative possibilities for the animal making its choices and decisions. There are obvious constraints on these decisions unknown to us in detail, but clearly concerned with the information the animals possess. This is illustrated by the behaviour of another kestrel, Pim ($\male$ # 8). The alternative solutions for this bird cannot be reconstructed since the data on hunting yield for early morning, including vole peak 1 are missing. Pim did not hunt at the time of day which might well have been the most rewarding for flight-hunting. On several days, weather conditions had been bad for hunting in the morning (Fig. 3) and when the weather improved, Pim may simply have lacked the information that one hour after sunrise is among the best times for vole hunting. The problem of information constraints in testing optimalization hypotheses may be a very general one, although not generally realized. The rejection of null-hypotheses may not distinguish between the alternatives of a wrongly chosen maximization function or ill understood constraints on animal decision making. Only thorough knowledge of the natural situation may indicate which is the more likely of the two.

The role of information in the system is crucial for understanding not only the adaptiveness of the fine daily patterns in behaviour, but also how they come about. Is it primarily an innate, preprogrammed daily change which is responsible for variations in motivation for flight-hunting, relatively independent of individual experience but satisfactorily evolved in the course of thousands of generations of vole-hunters? This possibility has not been experimentally investigated. Yet we have a strong feeling that the genetic contribution to short-term variations is at most small, compared with the role of experience. This is supported (1) by the absence of any indications of a morning peak in foraging behaviour in many birds we have held in captivity so far. Similarly (2) this peak may also be absent in field conditions as demonstrated by $\male$ # 8 (Figs. 3, 11). (3) The most powerful argument is that the tendency to hunt at any time of day is under direct influence of prior experience. As we have shown, hunting frequency may be suppressed following prey capture. More importantly, it is promoted by prior unsuccessful strikes, and thus by information on prey availability. Successful strikes have a positive effect on the hunting frequency 24 h later. Finally (4), from a functional point of view, a rigid system would seem maladaptive since in many places where other prey are hunted than voles, and even in one locality the daily pattern of abundance of the voles may differ from one habitat to the next and may further change dramatically in the course of the year (Fig. 8).

It is not *a priori* impossible that natural selection should have produced a system spontaneously choosing in any set of environmental conditions the optimal daily programme from a stored set of routines; but it is difficult to imagine that evolution discarded the opportunity for the individual to improve on such routines in response to experience. This is apparently what we see happening. The kestrels show day-to-day correlations in details of the behaviour patterns, illustrated by rare behaviour slike stone pecking and sand bathing but also in the more basic phenomena of hunting behaviour and site choice.

Together these patterns constitute a set of individual daily habits, continuously improved and adjusted as further information on where and when prey are easily caught is incorporated.

The possible general validity of such daily habitual strategies remains to be discussed. Is it specific for the kestrel or for similar animals, which rely on a few prey items per day? One might propose that the characteristic discontinuity of foraging behaviour would put an extra premium on endogenous timing of hunting behaviour, related to the kestrel's restricted information on prey availability and the high energy cost of hunting. Other predators, such as waders (Goss Custard 1969) or small passerines (Tinbergen 1980) typically have a more continuous intake of small food items and thereby a more continuous flow of relevant information. Decisions in such foragers may be based on instantaneous information rather than on experience from preceding days. Yet also for them at any time of day there are necessarily parts of the hunting range and parts of the prey menu excluded from the flow of information. To approach optimal foraging decisions they too need to apply some expected value on intake rates in such non-visited areas and unexploited prey. If some prey fluctuate daily in availability it may pay the foraging bird to incorporate any information obtained 24, 48 or 72 h ago in such expectations. Starlings appear to make some of their foraging decisions in the field accordingly and can be easily trained to do so in the lab (Daan 1981).

If of general use to predators with rhythmic prey, would the strategy of daily habits be useless for herbivores with a more continuous food supply? No. The existence of individual daily habits has been documented for the common vole in both lab and field conditions (Daan and Slopsema 1978). For a prey species such habits may be part of an antipredator defence strategy rather than related to maximization of food intake rates. It may seem paradoxical that a predator and its prey should exploit essentially the same mechanism as a strategy against each other. The better known crypsis of both hunter and hunted illustrate that such sharing of defence mechanisms is not unique. The meaning to the prey of daily habits may be based on slight correlations in predator behaviour from day to day. For a vole exposing itself to predator detection in the pursuit of a mouthful of grass it may pay to stick to yesterday's time schedule: not because that schedule is generally superior to any other; but because, remaining undetected in yesterday's exposures to predation, the vole has no better information to go by. That schedule helped him to survive yesterday and is a tiny bit more likely to help him again today than any departure from it.

Finally, a few points should be made on the behavioural mechanism generating daily habits. Enright (1970, 1975) proposed that they are a major functional property of self-sustained circadian oscillations. Are they therefore implicitly a feature of circadian pacemaking systems? Enright's (1980) own recent neurophysiological model for vertebrate circadian pacemakers contains no provision for the incorporation of experience in the daily program. One may envisage a pacemaker which sets and resets an array of physiological oscillations, such that each time of day is characterized by its own physiological state of the organism. As a consequence each time of day may have its own probability distribution for various behaviours. Such circadian changes in motivational state may be continuously modified when conditioning stimuli are associated by the organism with the state of its internal milieu. In honeybees, time associated learning was shown to freerun in circadian fashion (Beier 1968). A related behaviour in rats, the 24-h periodicity of performance in appetitive and avoidance tasks depends on the presence of a circadian pacemaker, the suprachiasmatic nuclei (Wansley and

Holloway 1975; Stephan and Kovacivic 1978). In the kestrel, we have no empirical support for the endogenous circadian control of individual daily routines in either hunting motivation or site selection. Yet it is an attractive hypothesis that all of these phenomena reflect the same general mechanism of learning performance associated with the internal physiological state of the organism. By keeping the internal oscillations in synchrony with the day outside circadian pacemakers may create the temporal substrate on which individual experience can be exploited for continuous optimization of daily patterns of behaviour.

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