

VARIATIONS IN THE DIET AND FORAGING BEHAVIOUR OF A WINTERING RED KITE (*MILVUS MILVUS*) POPULATION IN RESPONSE TO CHANGES IN FOOD AVAILABILITY

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INTRODUCTION

Theoretical models of optimal foraging have predicted variations in the diet and foraging behaviour of animals when prey availability changes in their environment (KREBS *et al.*, 1983; PYKE, 1984; STEPHENS & KREBS, 1986). It has been proven that a decrease in the main prey of a raptor results in: (a) an increase in trophic diversity (HERRERA, 1974; HERRERA & HIRALDO, 1976; JACSIK *et al.*, 1982), (b) changes in the use of the habitat, both in the breeding season (JAMIESON *et al.*, 1982; GREENE *et al.*, 1983; RUDOLPH, 1982), and during the winter (STEENHOF *et al.*, 1980) and (c) a decrease in the number of wintering raptors (BAKER & BROOKS, 1981).

This paper describes the changes in diet, activity patterns, habitat use and foraging behaviour of a wintering Red Kite (*Milvus milvus*) population in response to variations in prey availability resulting from a winter drought in a area usually flooded.

STUDY AREA

Field work was carried out in winter, between January 1981 and February 1982, mostly in the Biological Reserve of Doñana (37° 10' N, 6° 21' W), within Doñana National Park. The study area has been described elsewhere (VALVERDE, 1958; ROGERS & MYERS, 1980). It contains 3 main habitats: 1) The marsh, a shallow area usually flooded during winter, sustaining thousands of waterfowl; 2) the mediterranean scrubland, with dense cover of shrubs (*Halimium*, *Cistus*, *Erica*) and scattered woodlots of Stone Pine (*Pinus pinea*) and Cork Oak (*Quercus suber*); and 3) the interface between these two habitats, comprising sparse grassland with ferns and a few scattered Cork Oaks. This area is

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particularity rich in Rabbits (*Oryctolagus cuniculus*), which are also present in the scrubland in smaller numbers (ROGERS & MYERS, 1979).

The winter of 1981 was extremely dry. Rainfall was only 105.4 mm, compared with the normal annual average of 591 mm (AMAT *et al.*, 1979). January and February 1982 gave 327.5 mm precipitation, and the marsh was totally flooded. Thus, two clearly defined periods occurred: dry in January, February and December of 1981, and wet in January and February of 1982. In the dry period, the marsh was practically waterless except for scattered small pools, becoming essentially a dry plain with scarce vegetation. In the wet period, most of the marsh was flooded, leaving only small islands emerging above the water level. Changes in scrubland between the dry and wet periods were not noticed.

Prey distribution, abundance and mortality

During the dry period, the waterless marsh was occupied by animals that are usually found in the scrubland, like ungulates, hares (*Lepus capensis*) and non aquatic birds, for example. Large concentrations of greylag geese (*Anser anser*), ducks, rallids and other waterfowl gathered in the few remaining ponds. During the wet period, land animals confined themselves to the scrubland and the interface, while the waterfowl remained more uniformly distributed in the marsh.

The main differences in prey abundance during the two periods were in the numbers of waterfowl and shorebirds. In December 1981, 36,000 geese, 77,000 ducks and 2,300 shorebirds were counted in the National Park. In February 1982, the number of geese had not changed noticeably, but the number of ducks had doubled, and the number of shorebirds was 8 times greater (unpublished aerial census data from Doñana Biological Station). Although we have no such population estimates of most land animals, we did not detect any appreciable difference in their numbers between the two periods.

The most evident differences between both periods are related to the mortality of the species living in the study area. During the dry period there was a high mortality of waterfowl, especially geese, which, unlike other waterfowl, did not leave the National Park. During winters with little rainfall, geese cannot extract the subterranean bulbs of *Scirpus maritimus*, their main food, so they starve in great numbers (AMAT, 1986). After the rains, waterfowl mortality decreased considerably, but some land animals that had invaded the dry marsh died by drowning because of the sudden rise of the water level. One day, soon after the beginning of the rains, 60 hares were found dead or starving. The flood also produced mortality among cattle that had been weakened by the lack of food and then by the rain in the marsh.

MATERIAL AND METHODS

To study the Kite's feeding habits, 1,100 pellets were collected under 6 roost-sites in the dry period (January and December 1981), and 359 under 3 roost-sites during the wet period (February 1982)

To estimate the actual biomass consumed of each prey-species we carried out a food test with two captive Kites during 14 days. The birds consumed an average of 99.6 g (± 22.5) and regurgitated an average of 1.06 (± 0.57) and 1.21 (± 0.55) pellets daily, respectively. These results about food intake are consistent with the theoretical estimates of CRAIGHEAD & CRAIGHEAD (1969), though slightly lower than those found by other authors (KENDEIGH, 1969; BROWN, 1970; DAVIES & DAVIS, 1973). Thus, we assume that each pellet would correspond to 95 g of fresh food. Total biomass contributed by each prey was calculated adding their partial contributions to each of the pellets. When there was only one species on the pellet we assigned it the value of its weight, unless it was over 95 g. If there were more than one species we divided 95 among the number of species, except when they were small enough as to suppose that these prey-items had not been shared by several Kites (eg. insects, reptiles, small mammals). In these cases we assigned to the small prey the value of their weight and for the large ones we subtracted this value from 95 g. Obviously, this method provides approximate figures.

The wintering population of Red Kites was estimated by counting the number of individuals at each roost at dawn or dusk. Surveys were carried out simultaneously by one observer at each roost in January 1981, December 1981 and January 1982.

Studies of foraging behaviour were carried out during 5 days in the dry period (12-6 December 1981), when the average temperature was 15.2°C, and during 7 days in the wet period (3-9 February 1982), when the average temperature was 12.4°C. There was no rainfall during these periods. Field observations were made from a 28 m tower located between the scrubland and the marsh, from which we had an extensive view in all directions. From sunrise to sunset, observations of the number of Kites, habitat they were flying over, type and height of flight and grouping behaviour (number of Kites flying less than 50 m from each other) were taken every 10 min.

Trophic diversity was calculated with the Shannon-Weaver index (H'), considering the 12 groups of prey established in Table 1. For testing goodness of fit, the G test (d.f. = 1) was used (SOKAL & ROHLF, 1981). Spearman rank correlations and Mann-Whitney U-test were also used (SIEGEL, 1956).

RESULTS

1. *Number of Kites*

One hundred and nine, 128 and 119 Red Kites were counted at roost sites in January 1981, December 1981 and January 1982, respectively. Thus, there was not an obvious decrease in the number of Kites during the wet period.

2. *Diet*

In both periods the Kites' diet consisted mainly of birds and mammals (99.3 to 99.8 % of the biomass). This was consistent with results of previous studies (DAVIES & DAVIS, 1973; ORTLIEB, 1980; DAVIES & DAVIS, 1981). Insects, a group frequently preyed on, comprise less than 0.5 % of the biomass (Table 1). A detailed description of the diet has been given in an earlier paper (BLANCO *et al.*, 1987).

The diet showed statistically significant differences between the dry and wet periods. During the wet period the percentage of «Geese» decreased sharply, while the groups of prey with higher mortality («Hares» and «Big mammals») and the heterogeneous group «Other birds» increased significantly. Changes in «Rats» and «Rallids» could be related to a local specialization of the individuals of two roost-sites (Appendix 1). The differences in the percentage of «Reptiles» and «Insects» are unimportant since the contribution of these groups to the biomass is hardly noticeable. «Rabbits», «Ducks» and «Waders» did not show significant differences (Table 1).

Trophic diversity increased during the wet period, both in percentage of prey-items (H'i) and biomass (H'b) (Table 1). The means of H'i and H'b in the roost-sites (Appendix 1) during the wet period ($\bar{x} = 2.131 \pm 0.043$, $\bar{x} = 2.001 \pm 0.055$, respectively) were also higher than in the dry one ($X = 1.833$, 0.167 , $X = 1.659$, 0.055 , respectively), the differences being significant ($U = 0$, $n = 6$ and 3 , $p = 0.012$, in both cases). Among the groups of prey considered, only «Geese» maintained a negative correlation with H'i ($r = -0.700$; $p < 0.05$) and H'b ($r = -0.816$; $p < 0.01$). «Big mammals», «Waders» and «Other birds» correlated positively with H'i ($r = 0.616$, $p < 0.05$; $r = 0.620$, $p < 0.05$; $r = 0.916$, $p < 0.01$, respectively) and H'b ($r = 0.783$, $p < 0.01$; $r = 0.650$, $p < 0.05$; $r = 0.850$, $p < 0.01$, respectively; $n = 9$ in all cases).

During the dry period Kites fed more frequently on large species («1,000-10,000 g» class, which includes Geese), while in the wet period they were mainly eating prey in «100-1,000 g» class, which includes most other bird species. The consumption of prey «over 10,000 g», which includes dead cattle, increased almost fivefold in the wet period. There were significant differences

TABLE 1

Diet of the Red Kite in the dry and wet periods. I: percentage of prey-items; B: percentage of biomass. Central column shows G test values and their significances when comparing I in both periods (n.s. = not significant, * = $p < 0.01$, *** = $p < 0.001$). H'i and H'b: trophic diversity considering I and B, respectively; P: number of pellets analysed; N: number of prey-items.

[Alimentación del Milano Real en los periodos seco y lluvioso.

I: porcentaje del número de presas; B: porcentaje de biomasa. La columna central muestra los valores de G y sus significaciones al comparar I en ambos periodos (n.s. = no significativo, * = $p < 0.01$, *** = $p < 0.001$). H'i y H'b: diversidad trófica considerando I y B respectivamente; P: número de egagrópilas analizadas; N: número de presas.]

	Dry period			Wet period	
	I	B	G	I	B
Rabbits	8.3	9.9	0.01 n.s.	8.4	9.7
Hares	0.2	0.3	37.71 ***	3.2	6.0
Rats	5.3	8.2	11.10 ***	2.3	3.8
Small mammals*	3.9	2.1	6.83 **	1.8	0.8
Big mammals**	2.3	3.5	68.11 ***	10.6	15.5
Geese	28.4	42.8	62.05 ***	13.6	19.1
Ducks	9.1	13.4	0.57 n.s.	8.1	9.8
Rallids	0.7	0.9	56.29 ***	5.9	7.8
Waders	5.8	9.2	1.93 n.s.	7.3	9.4
Other birds	8.3	8.9	29.45 ***	16.1	17.7
Reptiles	0.4	0.4	6.49 *	1.4	0.3
Insects	27.3	0.4	9.34 **	21.3	0.1
H'i	1.946			2.231	
H'b		1.803			2.142
P		1100			359
N		1998			639

(* Rats excluded; ** Mammals > 1000 g, lagomorphs excluded).

TABLE 2

Size of the prey consumed during the dry and the wet periods. Results are expressed as percentages; n = number of prey. Values of G test and their significances (symbols as in the Table 1) are also shown.

[Tamaño de las presas consumidas durante los periodos seco y lluvioso. Los resultados se expresan en porcentajes; n = número de presas. Se muestran también los valores de G y sus significaciones (como en la Tabla 1).]

	0-10 g	10-100 g	100-1000 g	1000-10000 g	> 10000 g
Dry period (n = 1998)	28.0	8.2	29.4	31.8	2.6
Wet period (n = 639)	23.8	8.1	40.7	16.0	11.4
G	4.49 (*)	0.00 (n.s.)	27.67 (***)	65.20 (***)	70.09 (***)

between both periods in all classes considered, except the «10-100 g», that mainly includes small mammals (Table 2). The diversity for size classes was higher in the wet ($H' = 1.451$) than in the dry ($H' = 1.380$) period.

3. Activity

In both periods Kites became active at sunrise and finished at sunset. There is a relative maximum in the first hour, probably related to the communal departure from the roost-sites, after which most individuals perched and resumed their activity gradually (Fig. 1).

Though the number of wintering Kites in the study area did not change noticeably throughout both periods, the average number of Kites observed flying each day in the dry period ($\bar{x} = 84.4$, 19.3) was smaller than in the wet one ($\bar{x} = 136.1$, 40.2), the difference being significant ($U = 2$, $n = 7$ and 5 respectively, $p < 0.005$). Thus there was an increase in the foraging activity of the Kites during the wet period, mainly in the central hours of the day (Fig. 1).

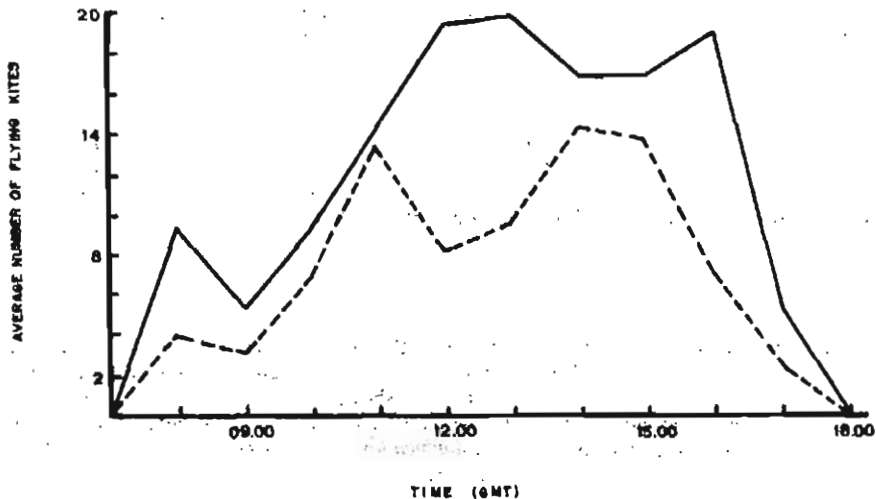


FIG. 1.—Red Kite activity during the wet (full line) and dry (broken line) periods. Activity during each period is expressed as the daily average number of flying Kites observed from a fixed point. Every hour shows the total birds seen every 10 min.

[Actividad de los Milanos Reales durante el período seco (línea continua) y el lluvioso (línea discontinua). En cada período la actividad se expresa como el número medio diario de Milanos volando observados desde un punto fijo. En cada hora se representa la suma de los conteos realizados cada 10 min.]

4. Use of the habitat, flight patterns and grouping behaviour

During both periods, Kites searched for food in the 3 habitats considered. The marsh was used most in the dry period, but was used least in the wet one. The scrubland had the opposite pattern of use (Table 3a).

Red Kites fly in search of food by soaring, gliding combined with flapping, or flapping, each one demanding more energy than the previous (PENNY-CUICK, 1972). Soaring was significantly more used in the wet period, and the opposite occurred with gliding-flapping (Table 3b).

Kites usually fly at medium (20-40 m) or low (0-20 m) heights. The only significant difference between the two periods are in the highest class of flight-height (Table 3c).

Red Kites in Doñana tend to roost together in winter but usually search for food alone. The differences in the number of Kites foraging together are not statistically significant except when groups of more than 3 individuals are considered. These groups were seen most often in the dry period (Table 3d).

DISCUSSION

Although we were unable to measure the availability of food during the two periods, it was clearly much higher during the dry period than the wet one. This was mainly due to the abundance of Goose carcasses during the dry period.

In the wet period, when Red Kites reduced the proportion of Geese in their diet, trophic diversity increased. As we have seen, the frequency of feeding on Geese is the only variable negatively correlated with trophic diversity. This would indicate that this prey was more profitable than its substitutes in the wet period (SCHOENER, 1971). In any case, the diet in both periods seemed to reflect the availability of carrion. Assuming that animals over 500 g are consumed by Kites as carcasses (BLANCO *et al.*, 1987), the percentages of prey items taken as carrion were almost the same in the dry period (50.1 %) and in the wet one (48.9 %), the difference being not significant ($G = 0.08$, $p > 0.75$).

The increase of activity during the wet period seemed to occur in response to the decrease in food availability. For Ospreys (*Pandion haliaetus*) and American Kestrels (*Falco sparverius*), an increase of foraging activity at the expense of resting and preening has been shown when the availability of food decreases (JAMIESON *et al.*, 1982; SMALLWOOD, 1987). In Kites, this increase of activity during the wet period occurred in the middle of the day, when temperatures were higher, facilitating soaring (HENTY, 1977; GERRARD *et al.*, 1980), a more energy-saving kind of flight. In contrast, during the dry period Kites found food early in the morning and then remained perched most of the time, explaining why maximum flight activity did not occur at midday.

TABLE 3

Habitat use, type and height of flight, and grouping behaviour of the Red Kites during the dry and wet periods. Results are expressed as percentages; n = number of records. Value of G test and their significances (symbols as in the Table 1) are shown under each table. [Uso del hábitat, forma y altura de vuelo y agrupamiento de los milanos durante los periodos seco y lluvioso. Los resultados se expresan en porcentajes; n = número de observaciones. Los valores de G y sus significaciones (símbolos como en la Tabla 1) se muestran debajo de cada tabla.]

	a) Habitat use		b) Type of flight		c) Height of flight		d) Grouping behaviour: number of Kites flying together.								
	Marsh	Scrub-land	Soaring/flapping	Glide-Flap	0-20 m	21-40 m > 40 m	2	3							
Dry period (n=385)	39.8	27.0	33.2 (n=389)	55.8	36.5	7.7	(n=385)	34.0	42.9	23.1	(n=426)	64.9	18.8	6.7	9.6
Wet period (n=960)	10.2	67.7	22.1 (n=926)	67.0	23.0	10.0	(n=947)	36.4	46.4	17.2	(n=976)	64.8	22.7	6.8	5.7
G	27.13 (***)	186.98 (***)	14.56 (***)	24.51 (***)	1.81 (n.s.)	0.69 (n.s.)	1.36 (n.s.)	6.04 (*)	0.16 (n.s.)	2.74 (n.s.)	0.78 (n.s.)	6.64 (**)			

During the wet period, the scrubland was used more often than the marsh, and the opposite occurred in the dry one. This could be expected if the scrubland were more profitable for raptors during the wet season, but it is not the case. Prey that can only be taken in the marsh made up 60.4 % and 48.0 % of the total number of prey-items in the dry and wet periods respectively (insects not included). Thus, the marsh was always the most profitable habitat, considering the percentage of time it was used (Table 3a). Besides, foraging in the scrubland would be more difficult for Kites because of the thicker vegetation, as has been proven for other raptors (BECHARD, 1982; SMALLWOOD, 1988). Kites spent more time foraging in the scrubland (a less favourable habitat) during the wet period possibly because the amount of food available daily in the marsh was lower than the needs of the Kite population.

During the wet period, energy-saving flight patterns were used more often in spite of the lower average temperatures, that would make soaring more difficult. This could partially compensate for the higher consumption of energy required by longer periods of daily activity. This behaviour agrees with results obtained in earlier field studies carried out on American Kestrels (COLLOPY & KOPLIN, 1983; SMALLWOOD, 1988) and are consistent with theoretical predictions stating that predators should shift to less energy-consuming search methods when prey density decreases (NORBERG, 1977; ANDERSSON, 1981; STEPHENS & KREBS, 1986).

Groups of more than 3 Kites were seen significantly more often in the dry period than in the wet one. It could be related to the higher concentration of carcasses during that period. Hunting techniques did not vary much, as expected from the fairly constant proportion of carrion in the diet.

In conclusion, when the availability of profitable prey decreased, food diversity, foraging activity and the amount of time spent searching in less favourable habitats increased, and energy-saving flight patterns were used more frequently.

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SUMMARY

The foraging behaviour of a wintering Red Kite population in Doñana was studied in two periods with different food availability. Diet, daily activity, habitat use, and flight and aggregation patterns were examined in both periods.

Variations in the diet reflected changes in prey mortality. When carrion availability decreased,

food diversity, foraging activity and amount of time spent searching in unfavourable habitats increased, and energy-saving flight patterns were employed more frequently.

KEY WORDS: Diet, foraging, food availability, *Milvus milvus*, Red Kite, Doñana, Spain.

RESUMEN

Variaciones en la alimentación y en el comportamiento de búsqueda de una población invernante de Milanos Reales (Milvus milvus) en respuesta a cambios en la disponibilidad de alimento.

Se estudia el comportamiento de búsqueda en una población de Milanos Reales invernantes en Doñana en dos periodos con diferente disponibilidad de alimento. En ambos periodos se examinaron la alimentación, la actividad diaria, el uso del espacio y los patrones de vuelo y agregación.

Las variaciones en la alimentación reflejaron los cambios en la mortalidad de las presas. Al disminuir la disponibilidad de carroña, aumentaron la diversidad trófica, la actividad de búsqueda y la cantidad de tiempo empleado en hábitats desfavorables. Además, los Milanos utilizaron formas de vuelo que conllevan menor gasto energético.

PALABRAS CLAVE: Alimentación, comportamiento de búsqueda, disponibilidad de alimento, *Milvus milvus*, Milano Real, Doñana.

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APPENDIX 1

Diet of the Red Kites in every roost-sites studied. Letters at the top the columns indicate the different roost-sites; numbers show the months when the pellets were collected; 1 and 2: January and December 1981, respectively (dry period); 3: February 1982 (wet period). I: percentage of prey-items; B: percentage of biomass; H₁ and H₂: trophic diversity considering I and B, respectively; P: number of pellets analysed; N: number of prey-items.

[Alimentación de los Milanos Reales en los dormitorios estudiados. Las letras situadas sobre las columnas indican los diferentes dormitorios, y los números muestran los meses en que fueron colectadas las egagrópilas; 1 y 2: enero y diciembre de 1981, respectivamente (período seco); 3: febrero de 1982 (período lluvioso). I: porcentaje del número de presas; B: porcentaje de biomasa; H₁ y H₂: diversidad trófica considerando I y B, respectivamente; P: número de egagrópilas analizadas; N: número de presas.]

	A1		B1		C1		D1		E1		E2		D3		E3		F3	
	I	B	I	B	I	B	I	B	I	B	I	B	I	B	I	B	I	B
Rabbits	9.3	14.0	9.2	11.9	5.3	8.5	5.1	5.9	5.7	6.5	12.5	17.1	8.5	10.7	6.0	6.2	15.1	18.7
Hares	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.5	0.0	0.0	4.0	7.0	3.3	3.8	8.5	10.8
Rats	3.5	6.4	1.2	1.8	1.0	2.1	20.1	30.7	3.7	3.9	1.5	2.1	2.5	4.8	2.1	3.4	1.9	2.1
Small mammals*	4.2	1.6	1.2	0.6	5.8	2.9	7.3	3.9	2.2	0.8	4.6	2.9	4.0	1.9	0.6	0.3	0.9	0.3
Big mammals**	2.3	4.7	2.4	2.1	4.3	7.4	1.4	1.9	0.8	1.0	3.6	4.6	18.5	31.3	8.1	10.0	2.8	3.4
Geese	15.1	30.8	54.1	66.6	15.0	29.2	15.9	25.2	33.6	55.8	35.7	47.0	7.0	10.6	19.5	27.0	6.6	10.3
Ducks	8.8	15.5	8.8	11.3	9.2	15.5	7.1	10.9	11.5	15.2	8.8	11.7	4.5	5.5	10.2	11.6	7.6	12.6
Rallids	0.9	1.2	1.7	2.5	0.0	0.0	0.3	0.4	0.2	0.3	0.7	0.7	2.0	2.5	9.9	13.4	0.0	0.0
Waders	9.2	16.4	1.5	1.6	11.6	20.2	5.5	8.1	3.8	5.8	4.6	4.8	5.5	6.9	6.3	8.5	13.2	17.8
Other birds	8.9	9.9	2.5	0.3	11.1	12.6	12.5	12.2	8.7	10.0	7.1	8.6	18.0	18.3	13.0	15.4	21.7	23.8
Reptiles	0.0	0.0	0.6	0.8	0.0	0.0	1.6	0.6	0.0	0.0	0.3	0.3	0.5	0.3	1.2	0.3	2.8	0.1
Insects	37.8	0.5	16.8	0.5	35.3	0.5	23.2	0.2	29.6	0.2	20.6	0.2	25.0	0.2	19.8	0.1	18.9	0.1
H ₁	1.902		1.516		1.927		2.047		1.744		1.865		2.116		2.190		2.088	
H ₂	1.899		1.195		1.911		1.845		1.452		1.652		2.024		2.054		1.925	
P	200		200		100		200		200		200		200		100		59	
N	431		334		207		353		368		306		200		333		106	

(* Rats excluded; ** Mammals > 1000 g, lagomorphs excluded).