

Foraging habitat selection, land-use changes and population decline in the lesser kestrel *Falco naumanni*

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Summary

1. The selection of foraging habitats by nine radio-tagged adult lesser kestrels (*Falco naumanni*) breeding in one colony in southern Spain, was studied in 1989 and 1990. Despite individual differences in the feeding habitat, there was a general tendency for grassland to be used more, and sunflower and woodlots to be used less, than expected by their availability.
2. The relatively higher food availability (measured as the number of hovering bouts by the lesser kestrels to catch one prey) of grasslands and cereals would explain the kestrels' preference for these habitats.
3. Since the 1950s, uncultivated grasslands in the area have decreased drastically and have been replaced by new crops, such as sunflowers. If grasslands continue to decrease in southern Spain, the progressive decline of lesser kestrel populations will probably continue in those areas.

Key-words: foraging habitat, lesser kestrel, grasslands, conservation.

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Introduction

The lesser kestrel (*Falco naumanni* Fleisch), a small falcon inhabiting open, cultivated areas, was long considered one of the most common European birds of prey (Irby 1895; Bijleveld 1974; Cramp & Simmons 1980). However, the size of lesser kestrel populations throughout Europe has declined markedly in the last three decades (Cramp & Simmons 1980; Biber 1990). The trend of the Spanish population, which forms 60–70% of the European total (Biber 1990), has been similar. At the end of the 1960s this population was estimated at more than 100 000 pairs (Bijleveld 1974). Since that time there has been a steep decline; the estimated population in the first half of the seventies being 20 000–50 000 pairs, falling to approximately 5000 in 1989 (González & Merino 1990). The reasons for this decline are not known. One of the suggested explanations is contamination by agricultural pesticides and heavy metals (Cramp & Simmons 1980). Recent studies (Negro *et al.* in press, b) show that the contamination in lesser kestrels' eggs is low. Hatching rates are high (about 80%) and comparable to that of other birds of prey not thought to have been appreciably affected by pesticides. Additionally, the annual survivorship of the adults (67%) (Negro 1991) is similar to that of other raptors of similar size (Merlin *Falco columbarius*, James *et al.* 1989; European

kestrel *Falco tinnunculus*, Village 1990; Sparrowhawk *Accipiter nisus*, Wyllie & Newton 1991).

Another suggested factor for the demise of the lesser kestrel has been the changes in agricultural practices in its breeding range (Biber 1990). These changes have occurred in large areas of the Iberian Peninsula in the last few decades (Fernández Alés *et al.* 1992), but their incidence upon lesser kestrels is unknown. If recent changes in land-use have contributed to the decline of the species, the habitats most favourable for the species should have suffered the largest reduction. To test this hypothesis we examined the habitat preferences and hunting behaviour of lesser kestrels in an area of mixed farmland.

Methods

The study area was in and around the lesser kestrel colony in the city of Mairena del Alcor (Guadalquivir valley, southern Spain), during 1987 and 1990. This colony was situated in a castle within the urban area, and on the edge of a plain situated 140 m a.s.l. The plain is intensively cultivated, being divided into small plots of olive trees, fruit trees (mainly oranges), cereal (wheat and barley) and sunflower crops, small woods (pine and *Eucalyptus* groves) and uncultivated grasslands (pasturelands, fallow lands, etc.). To the south of the plain is the lowland

area of the Salado river, where cereals and sunflowers are the main crops with small areas of fallow land. The area's climate is Mediterranean (Aschman 1973), characterized by a mild rainy winter season and a hot, almost rainless summer (for more details see Font 1983).

The lesser kestrel colony consisted of 42 breeding pairs in 1989 and 40 in 1990. In the course of these 2 years 13 adult birds (seven males and six females) were radio-tracked, two males in 1989 and four males and three females in 1990. Four of these birds produced little information and have been excluded from analysis. Radio-transmitters (Urmeneta SA, Arguedas, Spain) were attached to the two central tail feathers (Kenward 1978) and birds were tracked for 4–27 days, from mid-April to the beginning of August. The observations were made 2 or 3 days a week, when possible from dawn to dusk. Sometimes the bird was not located at the beginning of the tracking day, or was lost for long periods of time. While being tracked, the birds spent 13.3–35.4% of their time at the colony. When the bird hunted and could be effectively tracked by us, we could not always determine on which habitat it was hunting. In Table 1 we show the whole tracking time when we could determine where each individual hunted and the percentage of the tracking time, excluding the time spent in the colony. Each day of tracking, either one or two individuals were selected and were tracked simultaneously by one observer situated in the colony (see Negro, Donázar & Hiraldo 1992, in press, a), and by one or two observers who each followed one bird and were in contact by radio.

Every time the bird was observed hunting, the habitat and the time the bird remained hunting in it were noted. The habitats used by the kestrels were classified in the following nine categories:

(1) woodland, (2) fruit trees, (3) olive trees, (4) uncultivated grassland, (5) cereals, (6) sunflowers, (7) legumes, (8) melons and other vegetables, and (9) urban areas. All the open habitats (numbers 4–9) offered good conditions for observing the birds. On the very few occasions in which the birds entered wooded areas, the lesser kestrels usually hovered above the trees. We always chose elevated points to track the birds and to observe hunting behaviour.

Crops statistics were obtained from the Annual Reports of the Carmona Chamber of Agriculture (those referring to the years 1958–78) which have already been published; Montaner *et al.* 1986). The data correspond to the municipalities of Carmona, Mairena del Alcor and El Viso del Alcor, in which the area of study was situated.

We studied habitat selection using the minimum convex polygon method (area of influence of the colony, see Negro *et al.* in press, a). We assumed that every bird was able to choose any part of this area for hunting. The lesser kestrel is a colonial bird and there were no active exclusions between individuals within this range. We think that this option was better than calculating the habitat availability only in the home range of every bird since home range size may be influenced, in turn, by habitat preferences.

The area of influence of the colony was subdivided using a grid with a cell size of 500 × 500 m. The different types of habitat inside every cell were determined. Additionally, and to estimate the distance of every patch to the colony, the central point of the cell was taken as a reference.

Foraging habitat selection was estimated for each tracked bird. In this way, we precluded the combination of samples from each of the 2 years since habitat availability showed interannual differences (see Discussion).

To determine if the habitats were utilized by the lesser kestrels randomly or if some kind of selection existed, we employed compositional analysis (see details in Aebischer & Robertson 1992; Aebischer *et al.* in press a, b). The main advantage of the compositional analysis in contrast with other methods is to avoid biases resulting from non-independence of proportions in habitat use (Aebischer *et al.* in press a). We utilized log ratios of available (area of influence of the colony, y_0) and utilized habitat (time spent by the bird in each habitat, y) compositions using the proportion of melon habitat as the denominator. Then, we calculated the difference $d = y - y_0$. Taking the data matrix of d values for each individual and habitat as a base we calculated the relation (λ) between the determinant of the matrix of mean-corrected sums of squares and cross-products (hypothesis to be tested: differential habitat use) and the determinant of the matrix

Table 1. Tracking patterns for radio-tagged lesser kestrels, (each individual identified by its PVC ring code and its sex; m = males, f = females). Given in detail are tracking months, the days spent at tracking, the minutes when the birds were located, the minutes in which the habitat they were hunting was accurately determined, and the percentage of the time spent by the birds located in habitats, out of the total time in which they were located (after the time spent at the colony was excluded)

Ind.	Period	Days	Minutes localized	Minutes habitat	% time in habit
AVm	Apr	4	3065	120	5.4
ATm	Apr–Jun	13	7200	416	7.9
MKm	Apr–May	15	11 885	1721	22.4
MVm	Apr–May	6	3080	332	12.8
CDm	Apr–Jun	27	13 892	2643	27.0
M4m	Jun–Jul	14	3350	1391	50.2
EEf	May–Jun	11	3514	633	20.8
MJf	Jun	5	5122	379	10.0
LPf	Jun–Jul	16	4750	757	19.0

of raw sums of squares and cross-products (null hypothesis: identical habitat use). The significance of λ was tested by means of the expression M/N where N was the number of lesser kestrels. This expression follows a chi-square distribution. To determine where the differences in habitat-use lie and to order the habitats according to their use for every lesser kestrel, we constructed a table of relative use of each habitat, calculating for each comparison between habitats the proportion in which it is used with respect to that available proportion (previously log-transformed). Finally, we compared the habitat preference in each habitat comparison with a random distribution.

The estimate of the habitat use diversity was carried out according to the Shannon Index using natural logarithms (Herrera 1974).

The overlap between individuals in the use of the habitat and in tracking time (categorized into weeks) was according to Pianka's Index (Pianka 1973).

Whenever possible, hunting sequences of the marked individuals were recorded. In these cases, the duration of the sequence (in seconds), the time that the bird hunted in the air or from a perch, the number of hovering bouts, and the number of prey captured, were noted. The approximate size of the prey was also estimated using the following four categories: (a) small arthropods (<1 cm), (b) medium arthropods (1–3 cm), (c) large arthropods (>3 cm), and (d) vertebrates. This information was obtained only for those habitats which were most used by the kestrels. Those sequences in which the kestrels hunted insects in the air were not considered, since in these cases the birds flew over various habitats.

Lesser kestrels hunt mainly while hovering, although they also hunt from perches. Nonetheless, the energy expenditure of the latter is negligible compared with hovering (Rudolph 1982; Masman & Klaassen 1987). Therefore, to study the hunting yield of each type of habitat we calculated the average number of hovering bouts required to catch one prey. Although birds could catch the prey among the vegetation, they usually took flight afterwards, and consumed the prey in the air. So it was possible to determine accurately the hunting yield in each habitat.

The vegetative cover of the habitat can affect the hunting yield of raptors (Bechard 1982; Toland 1987; Smallwood 1988). In our area of study the cereal habitat was the one in which, over the whole period of study, the greatest changes in vegetative cover were noted (from the period of seed formation to that of stubble). In consequence, the hunting yield for this particular habitat was estimated for two different periods, i.e. before and after the harvest.

Results

USE OF HABITAT

There were notable individual differences in the use of the several habitats by the kestrels studied (Table 1). In spite of these variations, some tendencies were clear. Four birds (44.4%) hunted mostly in grasslands (Table 2). Cereals were also the main hunting habitat for four birds. The area of melon bed was the only other habitat used frequently but only by three individuals (33%). The areas containing trees were hardly used by the kestrels, except for the olive groves which were used very seldom (Table 2). The woodland and urban areas were not visited by the hunting kestrels; consequently, they were excluded from further analysis.

We transformed the 'available' (area of influence of the colony) and 'used' habitat compositions using the proportion of melons as the denominator in the log ratio transformation of each of the other six proportions. The Wilk's lambda obtained was $\lambda = 0.0071$ ($P < 0.001$). Evidently, lesser kestrels did not use habitats randomly. The calculation of the ranking matrix (Table 3) gave uncultivated grassland > cereals > legumes > melons and vegetables > olive trees > sunflowers > orange trees. Grasslands were utilized significantly more than the other habitats (except cereals), cereals more than olive and orange trees, and legumes more than orange trees.

The different use and selection of habitats could be due to the way that the different habitats are distributed with respect to their distance from the colony. To check this hypothesis, the distances of

Table 2. Habitat use by nine radio-tagged lesser kestrels (each individual identified by its PVC ring codes and its sex; m = males, f = females). Habitats: orange trees (Or); olive trees (Ol); uncultivated grassland (Gr); cereal (Ce); sunflowers (Su); legumes (Le); melons and vegetables (Me). The two bottom lines indicate the availability of each habitat within the area of influence of the colony

	Or	Ol	Gr	Ce	Su	Le	Me
1989							
AVm	0.0	0.0	83.3	4.2	12.5	0.0	0.0
ATm	0.0	0.3	30.8	39.9	28.9	0.0	0.0
1990							
MKm	0.0	0.2	31.1	60.1	8.7	0.0	0.0
MVm	0.0	0.3	0.6	99.4	0.0	0.0	0.0
CDm	2.3	1.4	58.4	12.4	9.0	0.8	15.6
M4m	0.0	0.0	69.5	0.7	0.9	1.5	27.5
EEf	0.0	4.3	77.1	18.6	0.0	0.0	0.0
MJf	0.0	0.0	1.6	95.8	2.6	0.0	0.0
LPf	0.0	0.0	20.3	23.3	8.6	4.1	43.7
Habitat availability							
1989	4.0	5.1	0.7	51.4	33.7	1.2	3.6
1990	3.9	4.9	0.7	24.2	56.5	2.4	6.8

Table 3. Habitat ranking matrix for the nine radio-tagged lesser kestrels. Positive signs below figures indicate significant deviation from random at $P < 0.05$

	Or	Ol	Gr	Ce	Su	Le	Me	Rank
Or		-0.452	-6.667	-2.924	-0.362	-1.242	-1.103	0
			+	+		+		
Ol	0.452		-6.215	-2.471	0.090	-0.789	-0.651	2
			+	+				
Gr	6.667	6.215		3.744	6.306	5.426	5.564	6
					+	+	+	
Ce	2.924	2.471	-3.744		2.562	1.683	1.820	5
Su	0.362	-0.090	-6.306	-2.562		-0.879	-0.741	1
Le	1.242	0.789	-5.426	-1.683	0.879		0.138	4
Me	1.103	0.651	-5.564	-1.820	0.741	-0.138		3

the different patches of each habitat from the colony were obtained in an area of 87.75 km² in which more than 90% of the hunting locations were situated. The results obtained do not support the hypothesis, no significant differences being found (chi-square = 20.01, df = 27, $P = 0.83$) in the distributions of the distances of the different habitats from the colony.

In spite of the fact that lesser kestrels are not territorial, each tracked individual ranged over a different area. These individual home-ranges overlapped to varying degrees (Negro *et al.* in press, a). In each individual home-range, the proportion of habitat could be different and this would contribute to the individual variations found in habitat use and selection. If this were the case, a positive correlation between the overlap of individual home-ranges and the overlap in the use of the habitat should be expected. However, the correlation between the two variables turned out to be weak and not significant ($r_s = 0.199$, df = 20, $P > 0.05$).

On the other hand, the study took place over a long period of time, such that the conditions in the habitats may vary with time, and hence those birds whose tracking periods did not coincide could make different habitat use and selection. However, the correlation between the overlap of the tracking periods and the overlap in the use of the habitat between individuals was weak ($r_s = 0.06$, df = 20, $P > 0.05$) and not significant.

As lesser kestrels tend to flock temporarily in habitats in which there are temporary population explosions of insects, for those birds were tracked for only a few days, the tracking period could, by chance, coincide with local population explosions of prey in certain habitats, and this would overestimate the importance of the habitat. A positive correlation would be expected between the diversity of habitat use and the number of days of tracking, and this is what was observed (Fig. 1). The two individuals that deviated most from the general tendency in habitat selection were tracked for only a short number of days.

Use of the different habitats was not constant over the time of the study. While grassland, cereals

and sunflowers were used by the kestrels throughout the whole tracking period, others, e.g. legumes and melons, were only used for a few weeks (Fig. 2). On the other hand, while pastures were regularly exploited throughout the day, melons and legumes were used for only a few hours a day.

HABITAT YIELD

The application of a one-way ANOVA to the rate of hunting success achieved by each individual in the most used habitats revealed that there were no significant differences between individual birds (grassland, $F = 0.707$, df = 3.22, $P = 0.55$; cereal, $F = 0.368$, df = 2.12, $P = 0.70$). In consequence, the data for all individuals were pooled. The number of hovering bouts required to catch one prey (Fig. 3) was the lowest in the area of melon beds (1.5), followed by grassland (5.6) and cereals, where the values were 7.9 during the period of seed formation and 6.9 after harvesting. The least profitable habitat was sunflower fields, with 11.7 hovering bouts per prey. The size of the prey in the different habitats (Table 2) did not vary significantly (chi-square = 1947, df = 3, $P = 0.538$) and hence does not appear to be an influencing factor in the yield of the habitat.

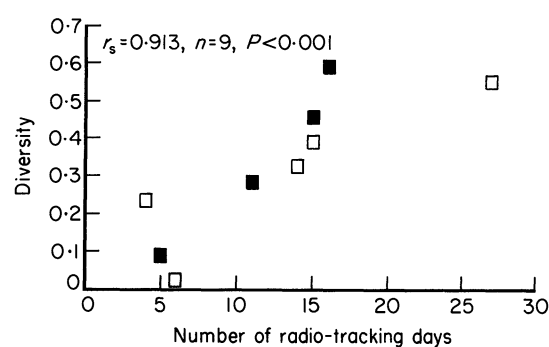


Fig. 1. Relationship between the diversity of habitat use and the number of radio-tracking days. Each point represents a radio-tagged lesser kestrel. The result of the Spearman rank correlation is shown.

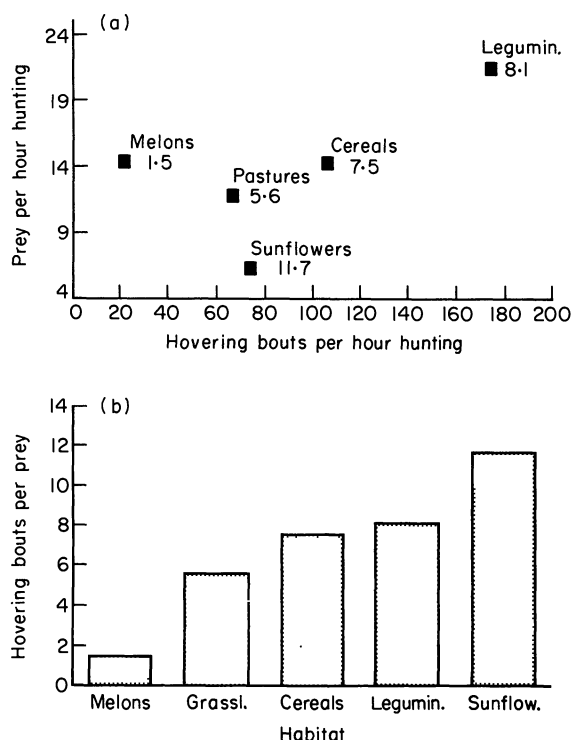


Fig. 2. Hunting performance in the five most used habitats. (a) Relationship between hunting yield (prey obtained) and hunting effort (hovering bouts) per hour hunting. (b) Number of hovering bouts required to catch a prey in five different habitats.

Discussion

The individual differences found in our study could be due to a variability in habitat selection, such as has been observed in other species (e.g. common snipe *Gallinago gallinago*, Green, Hirons & Cresswell 1990). Additionally, a part of the observed variation may be due to the low number of tracking days available for some individuals. This might have been caused by local and short-time variations in prey availability and could have influenced the results. But, even allowing for this, our results strongly suggest that the lesser kestrel does not use farmland habitats in proportion to their availability and that some very clear preferences exist.

As is to be expected considering the lesser kestrel's general distribution in the world (Brown & Amadon 1968), they avoid wooded areas. This could be due to the dense vegetative cover which would make prey less accessible (Toland 1987) to lesser kestrels, or to the fact that in these areas prey may be scarce. Olive groves, in spite of their relatively low tree density, were not used, probably due to the prey scarcity.

Hunting yield would explain why grassland and cereals tend to be the most used habitats, and why others, such as sunflowers, tend to be almost totally avoided. However, it cannot explain why the area

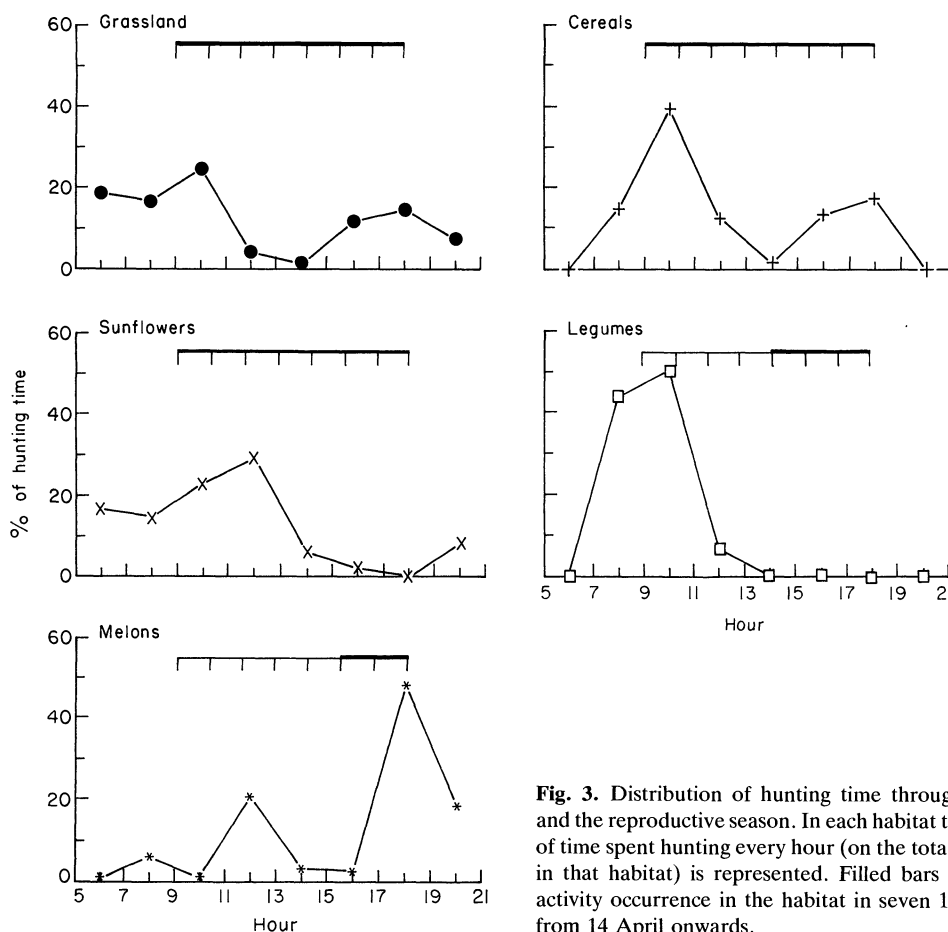


Fig. 3. Distribution of hunting time throughout the day and the reproductive season. In each habitat the percentage of time spent hunting every hour (on the total time hunting in that habitat) is represented. Filled bars show hunting activity occurrence in the habitat in seven 15-day periods from 14 April onwards.

of melon cultivation, a more profitable habitat, was not positively selected by all the individuals. This could be due to the fact that the yield of this habitat is high only during the period of fruit formation (July). The only three birds which were tracked during this period spent greater fractions of their hunting time in the melon habitat. Nonetheless, the degree of selection was lower than that of less productive habitats such as grassland. Perhaps this is related to the fact that the melon area can be exploited only during a short number of hours per day. The reason for this is unknown. Insect populations can have local explosions and/or variable circadian activity rhythms (Smallwood 1988) which would imply that availability might be time-limited and that the prey caught in melon beds may be different from that captured in other habitats. In

addition, the kestrels can probably cause prey depletion and will exploit this habitat only when the probability of capture is higher than the one expected in other habitats (Charnov, Orians & Hyatt 1976; Ferrer, in press). Unfortunately, we do not have enough information to test these hypotheses.

During the last 35 years great changes in land-use have taken place in the area of study (Montaner *et al.* 1986; Fernández Alés *et al.* in press). The surface area of the preferred habitats, such as uncultivated grassland, has decreased, whereas those habitats avoided by the lesser kestrels have increased (Fig. 4). Some of the new crops (e.g. sunflowers) also involve intensive chemical treatments against arthropods, the main prey of the kestrels. On the other hand, the mechanization of agriculture, together with government – sponsored reorgan-

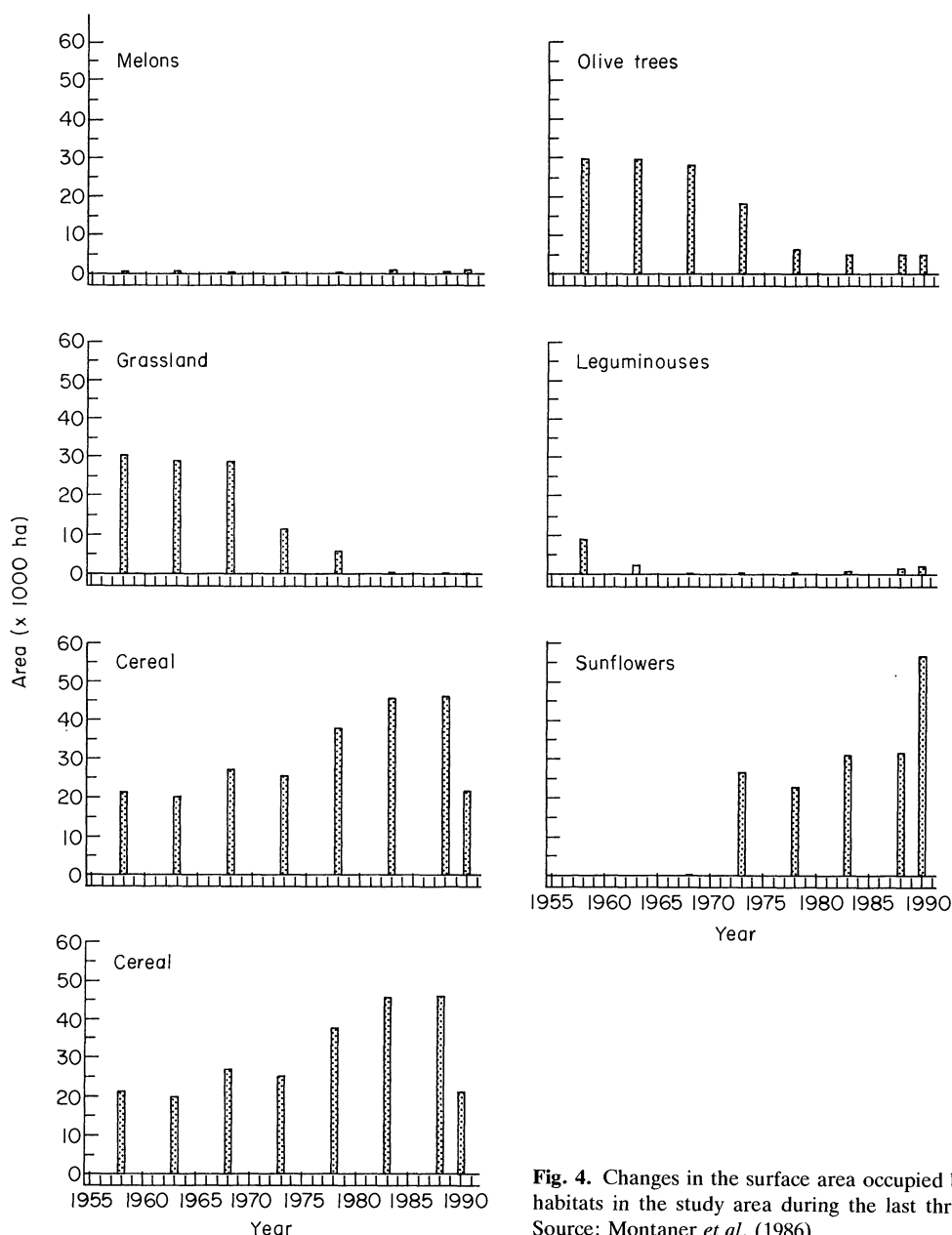


Fig. 4. Changes in the surface area occupied by the main habitats in the study area during the last three decades. Source: Montaner *et al.* (1986).

ization of field distribution from the 1960s onwards, have also caused an increase in field size and the almost complete disappearance of field margins (Fernández Alés *et al.* in press). Similar changes have taken place throughout the Guadalquivir valley (Senra & Alés, in press), and in other cultivated areas of the Iberian Peninsula.

If the tendency in lowland land-use in the south of Spain continues, a progressive decline in lesser kestrel numbers is to be expected in these areas. To conserve the populations by returning to the land-use patterns in use 40 years ago does not seem to be possible. The most feasible solution would be to increase the areas of grassy field margins and hedges or river banks where small areas of grassland are often conserved. This conservation strategy may also benefit small game populations through the creation of nesting and brood-foraging areas (Sotherton, Boatman & Rands 1989). In Spain, hunting generates a large income and hence the promotion of field margins could lead to important socio-economic benefits and ensure the conservation of this habitat as well. Initially, this conservation strategy should be encouraged by economic incentives from the Spanish Government, the European Community or both. In fact, the introduction of new crops in Spain has always been encouraged by state subsidies (Montaner *et al.* 1986).

This analysis may not be applicable to Mediterranean mountain areas where the lesser kestrel is also declining or has even disappeared (González & Merino 1990). In these areas, the loss of pastureland has been due to factors such as the abandoning of extensive livestock farming and the subsequent replacement by either successional scrub (dominated by, e.g. *Cistus* spp., *Genista* spp.) and tree plantations (Fernández Alés *et al.* 1992). It would therefore be necessary to study the changes in lesser kestrel populations in those areas in relation to these changes in land-use.

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