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Journal of Applied Ecology (1981), **18**, 355–371

ECOLOGY OF THE EUROPEAN WILD RABBIT *ORYCTOLAGUS CUNICULUS* (L.) IN MEDITERRANEAN HABITATS

II. DISTRIBUTION IN THE LANDSCAPE OF THE CAMARGUE, S. FRANCE

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SUMMARY

(1) Distribution of the European wild rabbit, *Oryctolagus cuniculus* (L.) on a 1000 ha west Mediterranean site (Tour du Valat, Rhône delta, S. France) was compared with an objective ecological classification of landscape. The study area has flat topography, and consists of marshlands, saline alluvial soils and generally halophytic vegetation with perennial grasses on higher ground.

(2) Rabbit distribution between nightfall and midnight and distribution of faecal pellets indicated that rabbits fed extensively on ground slightly lower than but adjacent to warrens and vegetated by halophytes, annual grasses and forbs. Warrens were associated with levées and ground which had been artificially raised or drained. Parcels of land suitable for warrens were small and infrequent in the west half of the study area, where rabbits were rare. Rabbits were abundant only where suitable juxtaposition of habitat for warren building and for feeding occurred.

(3) In the landscape classification hierarchy, the scale at which rabbits are related to the environment (*Umwelt*) is at the level of land facets rather than land systems.

INTRODUCTION

The wild rabbit, *Oryctolagus cuniculus* (L.), is of west Mediterranean origin (Zeuner 1963). Following changes in human land use since Roman times it has spread to its present European range (Van der Feen 1963) and, through introductions, to other continents and islands (Thompson & Worden 1956). Its distribution has been described in other sites with a mediterranean climate, e.g. eastern Australia (Myers & Parker 1965), southern Spain (Rogers & Myers 1979), but not in a deltaic environment.

The importance of measuring animal distribution is that it is a measure of the species' success in the environment. At the appropriate scale it may also indicate how the species uses different components of its habitat. In this paper measurement of distribution in relation to habitat in the Rhône delta is presented, using the landscape approach (Mabbutt 1968) to land classification.

The landscape approach was used for detailed description of the study area not only because of its importance in understanding the biology of the rabbit but because it also provided a fundamental frame of reference for a series of ecological studies being undertaken in the same area (e.g. Skelton 1978; Boy & Duncan 1979). This multiple use is possible because the approach provides an objective classification of land without reference to particular land use (Christian 1970).

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The study area comprises about 1000 ha of the estate of the Station Biologique de la Tour du Valat. Although considerably modified by centuries of human activity, particularly pasturage, the study area is agriculturally undeveloped, and the delta as a whole is famous as a wildlife sanctuary (see Weber & Hoffmann 1958).

LANDSCAPE ANALYSIS

Landscape analysis relies on recognition of recurrent patterns ('terrain patterns') on aerial photographs. Such patterns are called land systems. The components of the pattern are

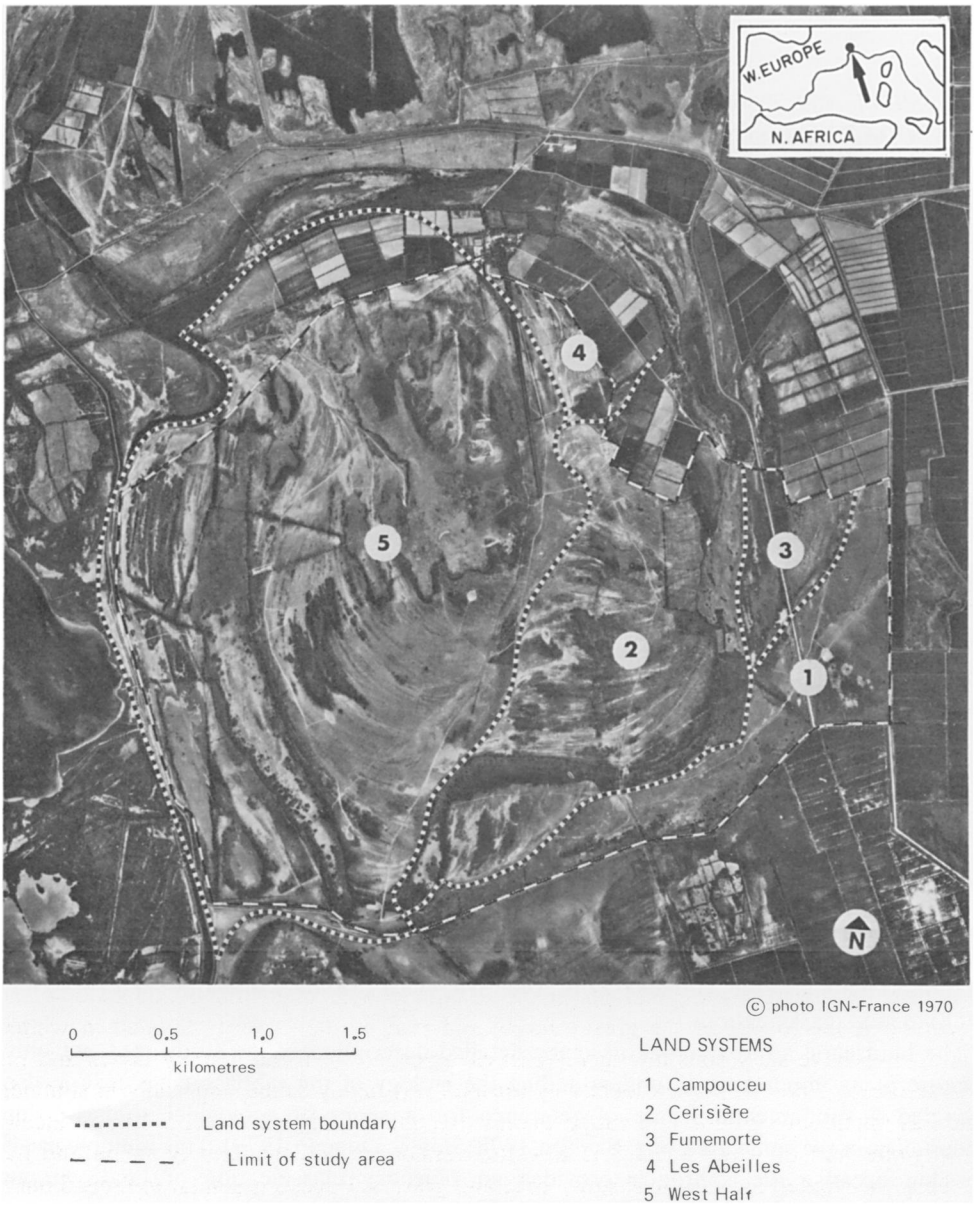


PLATE 1. Unrectified aerial photograph of la Tour du Valat estate, S. France, showing land systems and limits of the study area.

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known as land facets, units of land which are relatively homogeneous in lithology, form, soil and vegetation. Land systems and facets are natural units of land pertinent to the analysis of habitat (Rogers & Myers 1978). Methods and terminology of landscape analysis are given by Mitchell (1973). The following air-photo coverages of the study area were used: national coverage of 1970, scale 1:30 000, Institut Géographique National (IGN), Paris; Inventaire Forestier National (1975, scale 1:15 000); Resources Terrestres false colour infra-red (1974, scale 1:45 000 and enlargement scale 1:11 500); local coverage by the Photo Centre d'essais en vol, Istres (1974, scale 1:10 000). All except the infra-red were black and white panchromatic stereoscopic images.

Land classification

The study area was first classified for land systems using the IGN coverage. The study area is part of a Complex Land System (a land system exhibiting more than one morphogenesis) formed by a mosaic of deltaic erosion and sedimentation patterns. It includes five Simple Land Systems (those having a single morphogenesis), or parts of them (Plate 1) as follows: 1 Campouceu Land System; 2 Cerisière Land System; 3 Fumemorte Land System; 4 Les Abeilles Land System; 5 West Half Land System. Most facets were represented in each system, but the arrangement of facets differed between systems. Most analyses were done at the level of facets rather than systems.

Initial surveys of rabbit distribution (faecal pellets and warrens—see below) showed that few rabbits inhabited most of West Half Land System (L.S.), so facets were mapped only in the east half of la Tour du Valat (East Half). Facet boundaries were traced on an enlargement (scale 1:6000) of a single frame of the 1970 IGN coverage. The other aerial photographs were used to aid interpretation. The map was rectified using an existing 250 m grid marked on the ground by stakes, a system compatible with the National system (I.G.N., Paris). Landscape boundaries were verified in the field and dominant plants and other landscape features were identified. The map was digitized for use in computer analyses. To examine differences in altitude between facets, ground surface height above sea level (altitude) was measured along three transects at intervals of 5, 10 and 20 m, according to the size of the facets. Transects were chosen to give representative coverage of landscape units.

Land facets comprising the land systems are abandoned stream beds of different ages and their levées (Fig. 1, Table 1). Facets 1a and b are marshy abandoned river channels. Facets 2a and b are fragments of old stream beds which form deep and shallow marshes respectively. Facets 1a and 2a may remain flooded for about 10 months of the year, and facets 1b and 2b for shorter periods. Facet 7a is composed of levées beside existing abandoned stream beds (facet 1) and is generally well drained perennial grassland. Artificial levées comprise facet 7b which usually has vegetation similar to facet 7a. Facets 6a and b are modified forms of ancient levées; 6a is flat well drained mainly perennial grassland ('high grassland') and 6b is low grassland with many forbs and halophytes. Facet 6b is the lowest of the grassy facets and may be temporarily flooded in winter. Facets 3–5 have salty soils intermediate in elevation between the marshy facets and the grassy facets. Facet 4, known locally as *sansouire*, is highly saline, especially in summer, and has much bare ground and supports only extreme halophytes. Facet 5, known locally as *enganes* and of which facet 3 is a wetter version, is flat, moderately saline and has patchily distributed halophytic shrubs, forbs and grasses. Facet 3 is similar to facet 5 but is slightly lower, usually close to occurrences of facet 1.

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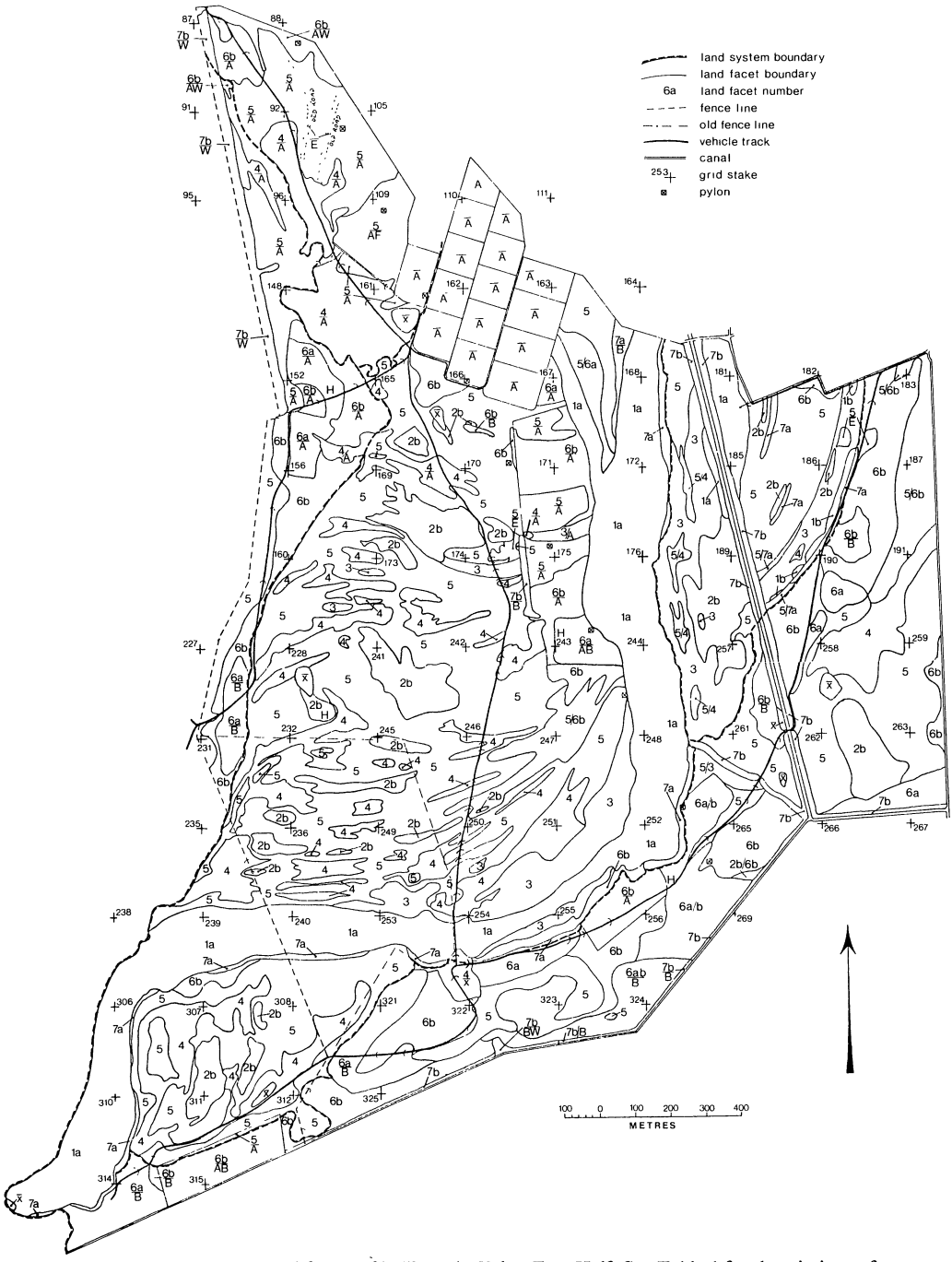


FIG. 1. Land systems and facets of la Tour du Valat, East Half. See Table 1 for descriptions of land facets and Plate 1 for names of land systems.

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TABLE 1. Characteristics of the land facets of la Tour du Valat

Facet	Type	Landform	Hydrology	Dominant plants
1	Recent stream bed	Abandoned channel	Up to 1·5 m deep } winter flooding Occasionally 2·0 m }	1a *Phragmites communis* *Scirpus maritimus*
	1a principal stream bed	1a continuous		
	1b subsidiary stream bed	1b fragmented	Summer drying out normal	1b *S. maritimus* *Aeluropus littoralis*
2	Marshy depression	Abandoned meanders		2a *Scirpus* spp. (3) *Typha* spp. (2) Other aquatic spp.
	2a deep marsh	May be contiguous with adjoining channels.	2a to 1·5 m deep } winter flooding 2b to 1 m deep }	
	2b shallow marsh	Adjoining natural levée on one side	Summer drying out normal	2b *Juncus gerardi* *Polypogon maritimum* Other aquatic spp.
3	Enganes—wet (local name)	Low land, slightly hummocky	Frequent winter inundation	Variable *Arthrocnemum fruticosum* *Limonium vulgare* *J. subulatus* *J. gerardi*
4	Sansouire (local name)	Low flat land	Frequent winter inundation	*A. glaucum* Bare ground
5	Enganes—dry (local name)	Medium elevation land, slightly hummocky	Minor winter inundation	*A. fruticosum* *Halimione portulacoides* *L. vulgare* *Puccinellia distans*
6	Grassland	Ancient natural levées		6a *Brachypodium phoenicoides* *Phillyrea angustifolia*
	6a high grassland		6a well drained	
	6b low grassland		6b occasional temporary flooding	6b *Agropyron pungens* *H. portulacoides* *L. vulgare* Annual forbs and grasses
7	Levée	Stream or canal bank	Well drained	As for 6a plus *Tamarix gallica*
	7a natural			
	7b man-made			

Additional characteristics of mapped facets (Fig. 1) are described by a capital letter, e.g. 6a/A or 6a/B. Designation of letters as follows:
A = altered, apparently irrevocably, by human land use. This subscript does not apply to facet 7b; B = bushes, these occur widely, and only concentrations of them have been marked; E = erosion, where induced recently by man; F = flooding, by other than natural means; H = building site, ruine or otherwise; W = wooded; X = excavation.

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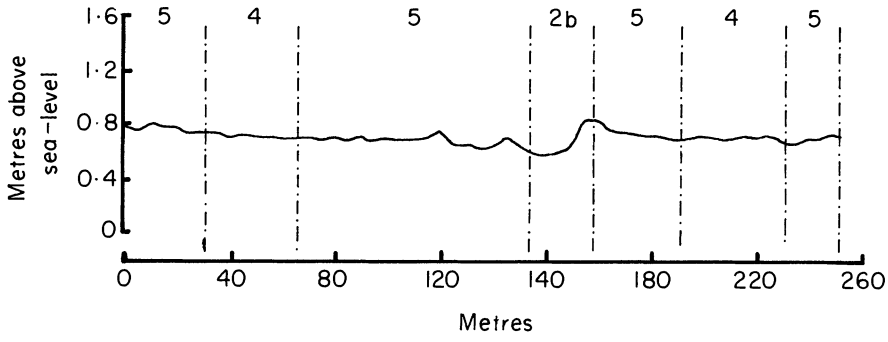


FIG. 2. Relief profile of land facets in Cerisière land system, la Tour du Valat.

The landscape of the Camargue is flat. The relief transects indicate a small general decrease in altitude, of the order of 1 to 2 m, from NW to SE in Cerisière L.S. Altitudinal differences between contiguous facets are generally of the order of a few centimetres (Fig. 2). Facet 1 is lowest, followed in order by facets 2 to 7 (highest). The difference between the lowest and highest altitudes measured is 1·4 m.

In each land system, facets are in characteristic patterns. All facets occur in Cerisière L.S. but it is dominated by a pattern of shallow marsh with a grassy levée on one side, surrounded by *enganes* with *sansouire* beyond (i.e. a recurring pattern of 4-5-2-5-4; see Fig. 2). An abandoned stream bed (facet 1a) bounded by levées is also a prominent feature of Cerisière L.S. Both Campouceu and Les Abilles L.S. are grassy with a facet pattern of 4-5-6. Les Abeilles L.S. is adjacent to the main group of farm buildings and has been subjected to more intensive or different land use from Campouceu L.S. Fumemorte L.S. has a facet pattern similar to that of Cerisière L.S. but is generally wetter. Thus, the 4-5-2-5-4 pattern of Cerisière L.S. is replaced by a 5-3-2-3-5 pattern in Fumemorte L.S. West Half L.S. is composed mainly of facets 1 to 5 and 7. Facet 2a occurs only in West Half L.S.

Vegetation and soils

The vegetation and soils of the study area have been described by Bassett (1978), who distinguished eight vegetation groups. The relationships between land facets and his vegetation groups are shown in Fig. 3. Clearly there is considerable correlation between the distribution of vegetation groups and land facets, but the relationship is not perfect since the landscape map is not a vegetation map but takes into account many environmental factors including landform, soils and hydrology. Only *sansouire* (facet 4) contains exclusively one (strongly halophytic) vegetation group (group C). Old stream beds (marsh facet 1a) include three vegetation groups (G, E and F), but those vegetation groups are little represented in other facets. *Enganes* and low grassland (facets 5 and 6b) are the facets having greatest heterogeneity of vegetation groups, and there is considerable overlap between those facets. High grassland, in which coarse perennial grasses frequently dominate, overlaps with those facets but halophyte vegetation groups are not found as they are in *enganes* and low grassland.

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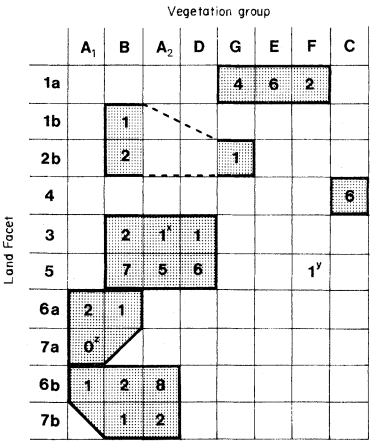


FIG. 3. Relationships between land facets and the vegetation groups of Bassett (1978) on la Tour du Valat, East Half. Figures in each cell represent the number of random plots common to the particular facet and vegetation group. Superscripts: [x]plot was within 1 m of a boundary between facets 3 and 5; [y]plot atypical of facet 5 owing to artificial flooding; [z]vegetation was not sampled in facet 7a, but vegetation group A_1 is typical

TABLE 2. Mean values (with standard error) of edaphic variables on la Tour du Valat, East Half

Facet	1a	1b	2b	3	4	5	6a	6b	7b
OM	16·2	16·8	19·4	16·1	7·9	8·9	9·0	10·1	6·0
	(1·5)		(6·0)	(2·5)	(1·0)	(0·8)	(2·0)	(1·2)	(1·3)
Na	593	878	195	472	1072	353	116	116	129
	(63)		(106)	(148)	(84)	(53)	(103)	(24)	(57)
K	68·7	–	59·7	63·3	24·6	46·8	42·7	49·1	33·7
	(4·6)		(3·9)	(5·8)	(5·7)	(3·6)	(14·1)	(4·3)	(13·1)
Ca	1452	1600	1443	1477	1390	1378	1410	1444	1243
	(61·6)		(213)	(15)	(23)	(20)	(59)	(35)	(41)
Mg	236	129	153	244	248	125	83	92	98
	(18)		(31)	(26)	(14)	(11)	(54)	(10)	(30)
TEB	2349	–	1851	2236	2735	1928	1651	1701	1504
	(90)		(76)	(165)	(110)	(66)	(175)	(43)	(130)
P	0·094	0·123	0·111	0·109	0·079	0·094	0·099	0·106	0·068
	(0·004)		(0·013)	(0·010)	(0·003)	(0·003)	(0·009)	(0·008)	(0·009)
N	0·64	1·05	0·98	0·55	0·08	0·27	0·40	0·41	0·22
	(0·08)		(0·33)	(0·17)	(0·01)	(0·04)	(0·09)	(0·05)	(0·04)
pH	7·7	7·4	7·7	8·0	8·0	8·2	8·2	8·3	9·1
	(0·1)		(0·3)	(0·2)	(0·02)	(0·1)	(0·1)	(0·1)	(0·3)
C:N	16·0	9·3	11·6	19·3	53·4	26·6	13·2	14·5	15·5
	(1·2)		(0·2)	(4·1)	(7·0)	(3·5)	(0·8)	(0·5)	(0·8)
MDM	5	6	7	6	3	10	31	24	27
	(1)		(1·5)	(2)	(1)	(2)	(15)	(3)	(2)
SWT	50	152	104	96	106	104	127	106	84
	(10)		(21)	(11)	(9)	(5)	(20)	(11)	(38)
EWF	*****	****	****	***	***	**	nil	(*)	nil
n	12	1	3	3	5	18	3	12	3

OM organic matter % LOI by weight; Na, K, Ca, Mg, TEB total extractable bases mg/100 g dry soil; P total %, N organic %, by weight; C:N carbon nitrogen ratio; MDM minimum depth mottling cm; SWT depth of water table in summer cm; EWF extent of winter flooding, 5 star scale.

Data source (except EWF): P. Bassett, personal communication.

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The relation of landscape units to soils is shown by additional data of Bassett (1978). Analysis of those data shows that facets are meaningful for chemical and other soil variables. For example, from one facet to another, organic matter may vary by a factor of 3, sodium by a factor of 9 and nitrogen by a factor of 12 (Table 2). All facets are very saline, particularly *sansouire*. Soils of the marshy facets (1 and 2) are hydromorphic gleys, those of *enganes* and *sansouire* facets (3, 4 and 5) are fluvial sodic soils (facet 4 highly saline) and those of grassland facets (6 and 7) are light brown soils with high sub-surface salinity (Astier *et al.* 1970). Soil salt levels are not constant throughout the year. In grassland, for example, chloride concentrations may vary from 2000 μg g in August to 100 μg g dry soil in February, although this fluctuation is reduced to a factor of four on ground some 25 cm higher (Heurteaux 1970). *Sansouire*, although frequently flooded in winter, has a thin salt crust in summer. Seasonal differences in soil variables result from the interaction of topography with a seasonally fluctuating water table (Heurteaux 1970; Bassett 1978). The small changes in relief have far-reaching consequences for both soils and vegetation. The landscape map (Fig. 1) thus not only delineates different categories of land, but also allows prediction of a number of habitat variables which may be of critical importance to wildlife, including rabbits.

Climate

The climate is typically mediterranean although more moderate than much of the Mediterranean region. Summers are hot (mean temp. 23 °C in July) and dry, and winters wet and mild (mean temp. 6 °C in January). Annual rainfall, of which about 50% falls from September to December and 30% from January to May, averages about 620 mm in the north of the Camargue (Arles) and 460 mm on the coast. Maximum temperatures are 2–3 °C higher and minimum temperatures 1–2 °C lower in Arles than on the coast. The sea thus has a considerable modifying effect on the climate. Strong winds from the NW and SE quarters are characteristic, particularly the *mistral*, a cold dry NNW wind which may blow for many days, especially in spring, at speeds up to 100 km/h or more.

Detailed weather records pertaining to the study area are maintained by the Centre National de la Recherche Scientifique, of which summaries are published periodically (e.g. Heurteaux 1976).

RABBIT DISTRIBUTION

Methods

Faecal pellet survey

Rabbit distribution was determined first by survey of faecal pellet distribution. A few pellets are deposited at regular sites (dung hills) but most are deposited haphazardly (Mykytowycz & Gambale 1969). Only haphazardly deposited pellets were surveyed, and were taken to be indicative of feeding habitat (see below). They were counted systematically at the intersections of a 125 m map grid (based on the existing 250 m grid—see above) over the study area (Plate 1—the main non-agricultural part of la Tour du Valat estate) from 21 May to 8 July 1975. At each grid intersection pellets were counted in ten 0·1 m^2 quadrats of 25 × 40 cm placed at 5 m intervals on the sides of a rectangle.

Warren surveys

Between 28 October 1975 and 12 January 1976 all warrens (groups of interconnected rabbit holes) on the study area (Plate 1) were surveyed. A second survey, 4–29 May 1976,

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was made in East Half (Fig. 1), which was shown by the first warren survey and by the faecal pellet survey to be the area of major rabbit activity, in every fourth 250 m grid square. In both surveys the area was searched systematically from a horse to locate warrens. Heavily vegetated areas were searched on foot. The number and category of holes were recorded qualitatively as follows:

(1) active, showing positive sign of recent use, e.g. footprints, diggings, etc.;
(2) assumed active, but no definitive positive sign;
(3) assumed inactive, but no definitive negative sign;
(4) inactive, showing negative sign, e.g. cobwebs, digging required, flooded, etc.

To compare winter and spring data only those squares searched in both surveys were considered.

Spotlight counts

Seasonal changes in population levels were monitored by direct counts of rabbits. The counts were made along a 7·9 km route (transect) following established vehicle tracks. A preliminary count was made in June 1975. Subsequent counts by a standardized method were made from October 1975 to September 1977. Counts were made shortly after nightfall, using a 100 W quartz-halogen spotlight mounted on the roof of a Land-Rover, driven at 10 km/h. The light was directed regularly approximately 45° either side of the transect line to a maximum distance of about 100 m. Most rabbits counted were within 30 m of the transect because vegetation limited visibility. A sample, generally consisting of six transect counts, was made approximately once per month. The direction in which the transect was driven was alternated to compensate for possible time differences. Numbers of rabbits counted in 100 m sections of transect marked by numbered signs were noted on a tape recorder. To allow comparison of numbers of rabbits counted in different landscape units, the areas of land facets and systems extending 30 m either side of the transect were calculated. The total number of rabbits in each 100 m section was allocated proportionally to the area of each landscape unit in a section. Areas outside East Half were categorized as 'unclassified'.

To compensate for variability in the visibility of rabbits in different land facets, seasons and years, a visibility index (I_v) based on simple counts of model rabbits in different seasons and facets and made in the same way as counts of wild rabbits was established. I_v was proportional to the reciprocal of the proportion of model rabbits seen out of the total number placed in the field. Derivation of the index is described by Rogers (1979). The number of rabbits assigned to each landscape unit was multiplied by the appropriate value of I_v.

Results

Faecal pellet survey

Distribution of faecal pellets on the study area was strongly related to land systems (Fig. 4) and facets (Table 3). Highest densities of pellets were in Campouceu L.S. and lowest in West Half L.S. ($P < 0{\cdot}0005$). Most pellets in West Half L.S. occurred along its elevated eastern border which adjoins Cerisière L.S. and Les Abeilles L.S. Of the dry facets, 6b had the highest density of pellets and facet 4, the lowest ($P < 0{\cdot}0005$). In two-way analyses of variance of counts in East Half (facets *v.* systems) differences between means were greater between facets than between systems (Table 3).

Distribution of faecal pellets reflects above ground distribution of rabbits. As feeding is the predominant activity when rabbits are above ground (Myers 1955; Mykytowycz & Rowley 1958), pellet distribution will reflect mainly the feeding distribution.

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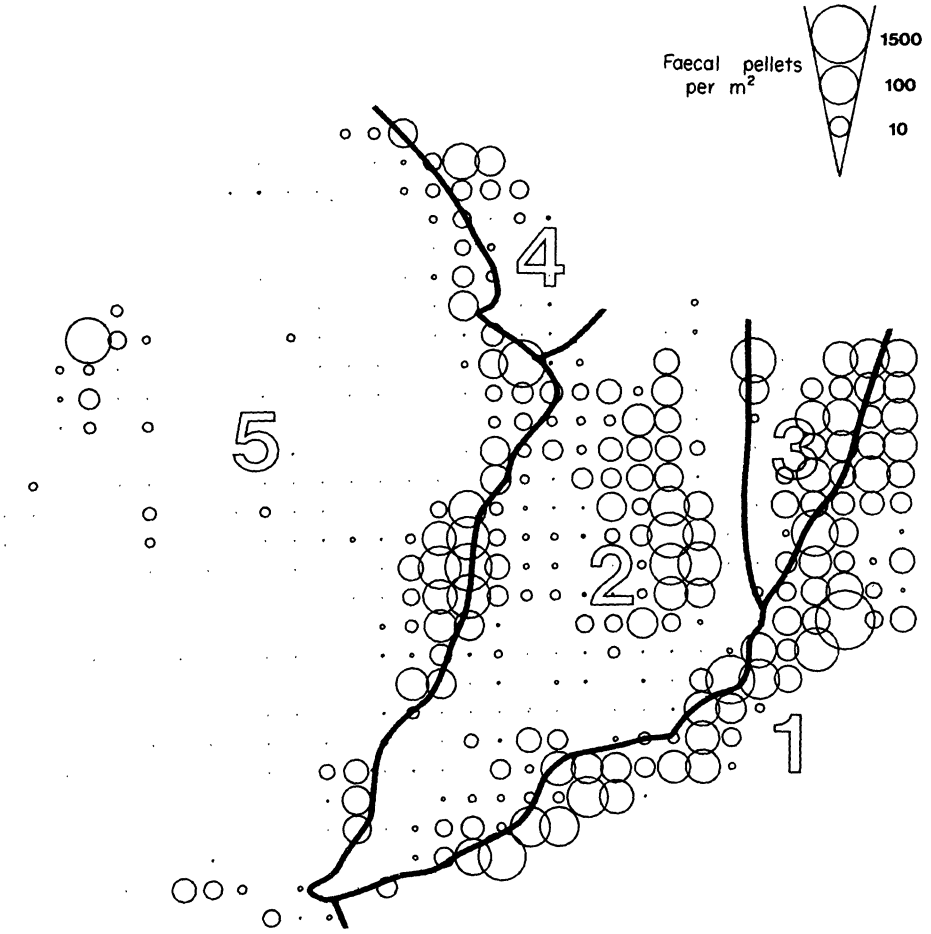


FIG. 4. Distribution of faecal pellets on la Tour du Valat estate. Circle diameter is proportional to logarithm of mean number of pellets in ten 0·1 m² quadrats, June 1975. Dots indicate samples in which pellet counts were zero. Hollow numbers refer to land systems (see Plate 1).

Warren surveys

Distribution of warrens was also strongly related to land systems (Fig. 5) and facets (Table 4). Densities of warrens were highest in the elevated grassy part of West Half L.S. in East Half, but elsewhere in West Half L.S. only twenty-six warrens (of which all but two had only one active entrance) were found. Campouceu L.S. had next highest densities of warrens. Lowest densities of warrens were found in Les Abeilles L.S. ($P < 0{\cdot}0005$).

Within land systems warrens were concentrated in the elevated facets, particularly high grassland and man-made levées (facets 6a and 7b). The high density of warrens found on man-made levées indicates the important influence of human land use on distribution and, probably, numbers of rabbits. Largest warrens and large numbers of warrens were found at the sites of ruined buildings. Fumemorte L.S., because of its natural pattern of facets (2, 3 and 5), none of these facets characterized by high densities of warrens (Table 4), would have had few warrens but for the man-made levées of the canal. The high density of warrens noted in old stream beds (facet 1, a marshy facet) is an artefact. That facet is frequently bordered by natural levées (facet 7a). In rare cases small errors in grid reference

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TABLE 3. Relationship between densities of rabbit faecal pellets in land systems and facets of la Tour du Valat, East Half (Fig. 1). Numbers of observations are given in brackets

Systems	Facets 1a	1b	2b	3	4	5	6a	6b	7a	7b	Overall mean
1	–	–	28·50 (2)	97·00 (1)	3·00 (3)	170·95 (19)	72·91 (11)	135·19 (32)	–	302·50 (2)	130·63 (70)
2	5·17 (35)	–	18·67 (6)	0·50 (4)	11·18 (22)	46·57 (72)	50·75 (4)	284·29 (7)	32·50 (4)	–	40·37 (154)
3	0·0 (2)	82·00 (2)	50·67 (4)	37·13 (8)	3·00 (3)	121·00 (11)	–	–	47·00 (1)	0·0 (2)	62·15 (33)
4	–	–	–	–	0·43 (7)	30·38 (8)	–	198·00 (1)	–	–	27·75 (16)
5	–	–	–	–	33·00 (4)	78·14 (7)	357·00 (4)	99·00 (7)	–	25·00 (1)	136·30 (20)
Overall mean	4·89 (37)	82·00 (2)	31·00 (12)	30·46 (13)	8·33 (36)	74·55 (117)	128·05 (19)	153·34 (47)	35·40 (5)	126·00 (5)	70·25

Significance of differences between means (ANOVA)

	d.f.	Mean square	F	P
Facet (Adj. systems)	9	70·22	16·2	0·0005
System (Adj. facets)	4	23·15	5·3	0·0005
Interactions	17	11·08	2·6	0·005
Remainder	262	4·30		

of warrens on narrow levées resulted in them being assigned to facet 1 in the automated classification process. In the dry facets, lowest warrens densities were observed in *enganes* and *sansouire* (facets 4 and 5, $P < 0{\cdot}0005$; Table 4), facets with the least plant cover.

Warren size differed between seasons at the level of facets but not at the level of systems, but more entrances per warren were active in spring than winter at the level of both systems and facets, notably in grassy elevated areas (facets 6a, 6b and 7b, $P < 0{\cdot}05$; Table 5). Since warrens are most easily observed in areas of sparse vegetation (where in fact fewest were found), any bias from differences in warren visibility in different facets will tend to obscure significant differences rather than to create false ones. In spring, vegetation makes warrens less visible than in winter. This may account for the smaller number of entrances per warren found in spring, when rabbit population levels are higher, compared to winter. The proportion of active entrances, which is relatively free from that kind of error, was higher in spring than in winter, consistent with changes in rabbit abundance. In Australia, numbers of rabbits were related to numbers of warrens in sandy soils (Myers & Parker 1965, 1975), whereas in soils in which warrens were more or less permanent, as is the case at la Tour du Valat, numbers of rabbits were related to the number of active burrow entrances (Parker *et al.*, 1976). The distribution of warrens was, therefore, concentrated in the middle of areas with many pellets. Rabbits built their warrens on high grassland or levées and used surrounding low grassland and *sansouire* for above ground activities.

Spotlight count index

Spotlight counts made during a period of high feeding activity showed that rabbits were distributed non-randomly between different land facets and systems. Greatest densities of

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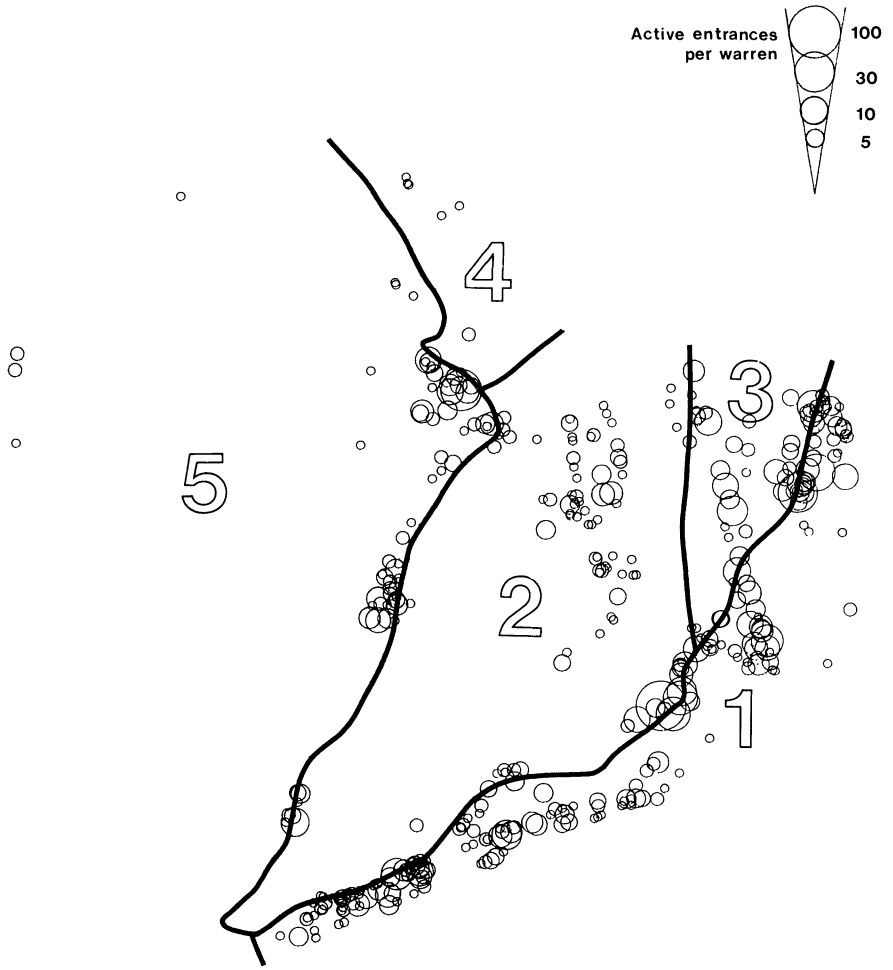


FIG. 5. Distribution of all active rabbit warrens on la Tour du Valat estate. Circle diameter is proportional to logarithm of total active entrances per warren in winter, 1975–6. Hollow numbers refer to land systems (see Plate 1).

TABLE 4. Distribution of rabbit warrens among the land facets of la Tour du Valat, East Half, winter 1975–6

Facet No.	Area (ha)	Number of warrens			Density O/ha
		observed (O)	expected (E)	$\frac{(O-E)^2}{E}$	
1a	55·04	12	74·1	52·0	0·22
1b	0·77	3	1·0	4·0	3·90
2b	22·66	16	30·5	6·9	0·71
3	24·76	18	33·3	7·0	0·73
4	50·01	16	67·3	39·1	0·32
5	163·79	199	220·5	2·1	1·22
6a	27·72	112	37·3	149·6	4·04
6b	72·09	154	97·0	33·5	2·16
7a	5·21	14	7·0	7·0	2·69
7b	10·33	38	13·9	41·8	3·68
Total	432·38	582	582·0		

Significance of differences $\chi^2 = 34$, $P < 0{\cdot}0005$. d.f. $= 9$.

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TABLE 5. Relationships between warren characteristics and land facets in la Tour du Valat, East Half

Land facet	1a	2b	3	4	5	6a	6b	7a	7b
Winter 1975–76									
Total entrances per warren	4·75	5·00	6·67	2·00	4·43	6·41	6·53	1·00	9·50
Active entrances per warren	1·75	1·00	4·00	0·00	1·42	1·32	1·23	1·00	3·67
Proportion active per warren	0·30	0·20	0·51	0·00	0·38	0·23	0·30	1·00	0·34
No. of observations	4	1	3	1	48	50	30	1	6
Spring 1976									
Total entrances per warren	3·50	4·00	3·29	1·50	2·53	2·92	2·96	0·00	4·00
Active entrances per warren	2·75	2·50	0·71	0·25	0·96	1·19	1·54	0·00	1·86
Proportion active per warren	0·62	0·63	0·11	0·25	0·36	0·45	0·54	–	0·39
No. of observations	4	2	7	4	48	26	39	0	14

Significance of differences between means (ANOVA)

Source of variation	d.f.	Mean square	*F*	*P*
Total entrances per warren				
Seasons (adj. facets)	1	20·40	22·43	0·001
Facets (adj. seasons)	8	1·314	1·444	0·25
Interactions	7	0·2348	0·258	1
Remainder	271	0·9097		
Active entrances per warren				
Seasons (adj. facets)	1	0·0387	0·057	1
facets (adj. seasons)	8	1·009	1·489	0·25
Interactions	7	0·8703	0·258	1
Remainder	271	0·6778		
Proportion of total entrances active per warren				
Seasons (adj. facets)	1	0·8176	5·001	0·05
facets (adj. seasons)	8	0·2291	1·401	0·25
Interactions	7	0·2197	1·344	0·25
Remainder	271	0·1635		

TABLE 6. Analysis of variance of spotlight counts of rabbits on la Tour du Valat, 1975–7

	Source of variation	d.f.	Mean square	*F*	*P*
A	Facets	9	89·01	778	0·0005
B	Direction	1	0·158	1·4	0·75
AB	Interactions	9	1·179	10·3	0·0005
C	Months	19	4·904	42·9	0·0005
AC	Interactions	171	0·645	5·6	0·0005
BC	Interactions	19	0·370	3·2	0·0005
Residual		171	0·114		
Total		399			
A	Facets	9	47·65	63·8	0·0005
B	Direction	1	0·023	0·34	0·75
AB	Interactions	9	3·350	5·67	0·0005
C	Months	19	15·43	26·1	0·0005
AC	Interactions	171	0·687	1·16	0·50
BC	Interactions	19	0·516	0·87	0·75
Residual		171	0·590		
Total		399			

rabbits were found in low grassland and *enganes* (facets 6b and 5), and moderate densities in high perennial grassland (facet 6a). Marshy facets (nos 1 and 2, represented by less than 2·5% of the transect) and levées (facets 7a and b, represented by 2·2% and 2·4% of the transect, respectively) had low densities of rabbits, as did *sansouire* (facet 4,

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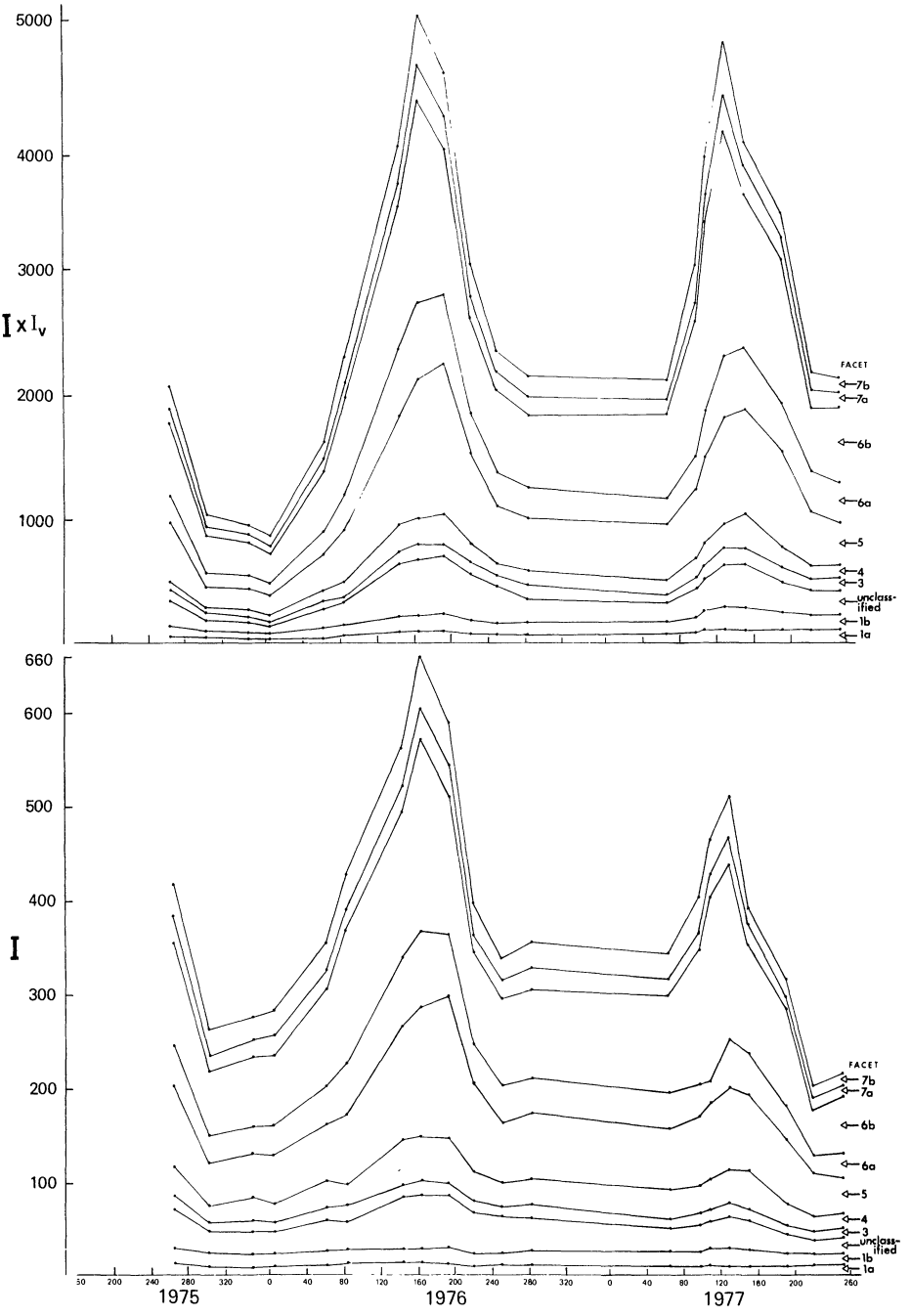


FIG. 6. Indices (I) of mean densities of rabbits in the land facets of la Tour du Valat estate, from monthly spotlight counts, with (above) and without (below) visibility correction (I_v).

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15% of the transect) (Fig. 6). Differences between facets were highly significant ($P < 0{\cdot}0005$; Table 6).

Interpretation of this pattern of distribution depends upon the diurnal activity pattern of rabbits in space and time. Rabbits are mainly crepuscular and nocturnal. They feed for 2·6–6 h with peak activity some 2 h after dark (Myers 1955; Mykytowycz & Rowley 1958; Myers & Poole 1961; Nelissen 1975). Nocturnal feeding in the Camargue has been verified (Rogers 1979). Since spotlight counts were made shortly after nightfall, during the main feeding period, areas with the highest densities of rabbits were the main feeding grounds.

The effect of application of the visibility index was to emphasize seasonal differences in numbers of rabbits and to suggest that numbers of rabbits counted in *sansouire* (facet 4) may have been biased upwards relative to other facets.

Sansouire (facet 4) and natural levées (facet 7a) had greatest seasonal changes in rabbit densities. There was little or no seasonal variation in rabbit densities in facets which were usually flooded in winter (facets 1 and 3) and therefore unavailable to rabbits. The records of rabbits in them during winter (Fig. 6) arose from the method of apportioning rabbits counted to facets. In other respects seasonal variation in rabbit densities was similar in different facets. Statistical interactions between numbers of rabbits counted in different facets and months concerned principally those facets which had low occurrence along the transect. The distribution of rabbits measured by spotlight corresponded to distribution of pellets, confirming that low grassland and *enganes* facets were the most important feeding habitats.

DISCUSSION

Inasmuch as all species have evolved in response to limited variability of environmental pressures, an exploratory study of this kind must emphasize environment as much as it does the animal itself. Particular questions can then be placed in proper perspective. The number of kinds of environmental pressures on an animal is, potentially at least, very large. To avoid premature selection of environmental factors in this study, habitat was described holistically using the concept of landscape, rather than by a number of environmental factors more or less arbitrally chosen.

As shown for southern Spain (Rogers & Myers 1979) rabbit distribution in the Camargue is determined by a complex of factors closely associated with land systems and their constituent facets. Features which determined their suitability for rabbits differed according to the way in which the rabbit used its habitat, principally for breeding and feeding.

Warrens not only provide cover, but are vital for breeding, and little burrowing occurs outside the breeding season (Myers 1958; Myers & Poole 1961). Thus high grassland and levées (facets 6 and 7), in which greatest densities of warrens occurred, provided breeding habitat. In these facets danger of winter inundation and short-term flooding from heavy rain are least. Burrows in *sansouire* (facet 5) appear less favourable for breeding because of the increased likelihood of flooding. The absolute number of warrens in *sansouire* was higher than in high grassland or levées simply because it was more widespread, but the density of warrens was lower and warren size was smaller.

Although intensive feeding occurs in high grassland in the immediate vicinity of warrens, distribution of pellets and of rabbits themselves indicated that adjacent facets (low grassland and *enganes*) were the main feeding grounds. Microscopic analyses of the

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diets of rabbits in the study area (Rogers 1979) confirm this conclusion. The dominant plants of high grassland, *Brachypodium* and to a lesser extent *Agropyron*, are tough perennial grasses and are little eaten. Low grassland and *sansouire*, floristically rich facets, contain the plants eaten most by rabbits. Therefore rabbits probably feed in *enganes* and low grassland facets because they are adjacent to warren areas and they contain the plants rabbits eat. In addition, wet *enganes* and *sansouire* (facets 3 and 4) are further from warren areas and are more frequently inundated, particularly in winter and early spring, and are less available to rabbits at those times than *enganes* (facet 5) and low grassland (facet 6b).

It has been shown elsewhere in the Mediterranean region that high densities of rabbits occur where good warren building ground is juxtaposed with suitable feeding habitat (Rogers & Myers 1979). Evidently the same conditions hold in the Camargue, although the factors governing suitability of facets for breeding and feeding are not necessarily the same.

Patterns of plant communities on the study area, which largely determine the favourability of facets for feeding, result from patterns of relief and hydrology, through the intermediary of soils. Warrens are limited to high ground adjacent to moderately elevated feeding areas. Thus, primary determinants of rabbit distribution in the Camargue are relief and hydrology. Similar patterns of distribution have been reported in the Southern Tablelands of New South Wales (Australia) where relatively low densities of warrens were found in flooded or water-logged areas (Parker 1977). In Queensland, most rabbits were found in well drained areas (Parker *et al.* 1976). The water table in the Camargue has been rising in modern times because of human activities (Heurteaux 1975). Any long term lowering of water levels would increase the amount of land available to rabbits and provide greater opportunity for an increase in their number if numbers are limited by available breeding habitat.

Klopfer (1969) has discussed the problem of describing habitat in a way which takes account of the animal's *Umwelt* (von Uexkull 1921), i.e. the environment as perceived by the organism as distinct from the whole environment. Insofar as the problem is one of scale—different scales may be required to measure habitat for mice and elephants—factors comprising the *Umwelt* of rabbits in the Camargue are at the scale of land facets rather than land systems. This conclusion is justified by the stronger association of faecal pellets with facets than with systems, and confirmed by comparison with landscape of the other indices of distribution measured.

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