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Non-territorial behaviour and habitat selection in the Jay *Garrulus glandarius* in a Mediterranean coastal area during the reproductive period

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Spring territorial behaviour and habitat selection of the Jay *Garrulus glandarius* were investigated in two study areas in the Maremma Natural Park (Central Italy). Seven birds in 1990 and seven in 1991 were trapped and subsequently radio-tracked. Incremental area plots and the analysis of auto-overlap showed that most of the Jays did not have fixed home ranges, and that these overlapped greatly. Furthermore, many untagged Jays were seen inside the home ranges of the tagged ones and one pair of Jays successfully reproduced in 1991 inside other Jays' home ranges. No aggressive interactions were observed. These data seem to suggest that the Jays in Maremma do not show territorial behaviour. Home range sizes at one study area (Faunistico) were larger than in the other area (Pratini) (on average 36 ha versus 5 ha). This could depend on the higher habitat diversity or lower habitat quality of the first area.
Habitat use differed between the areas. At Pratini the maquis scrub was positively selected whereas the olive grove was avoided; at Faunistico the maquis, the olive grove and the cultivated fields were avoided whereas the meadows with scattered trees and the "open" scrub were positively selected.
The non-territorial behaviour of the Jays in the Maremma Natural Park may be determined by several local factors, such as resource abundance, high density of birds, low reproductive rates and food partly being collected outside the maquis. In particular, both in the case of resource abundance and in that of high density of birds, the cost of sharing resources would be less than the cost of defending the territory against all intruders and a non-territorial system would indeed be expected.

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Territorial behaviour is common in corvids (Goodwin 1986) and in some species (i.e. the Magpie *Pica pica*, Hooded Crow *Corvus corone cornix* and Steller's Jay *Cyanocitta stelleri*) territorial defence seems to be stronger in the period immediately prior to and during egg-laying (Brown 1963, Vines 1981, Loman 1985).

The Jay *Garrulus glandarius* is considered to be a territorial species which lives in pairs on year-round territories (Coombs 1978, Bossema 1979, Goodwin 1986, Keve 1985). Even though some observations in the Netherlands suggested that the boundaries were less clear-cut than in the other territorial corvid species (Bossema et al. 1986), detailed studies in Sweden have shown that territorial behaviour by resident Jays occurred during the breeding period (Grahn 1990) and that territories are well-defined with little overlap (Andrén 1990). In years with a high number of adult Jays at the beginning of the breeding season territories were compressed and, conversely, during low density years they were enlarged (Grahn 1990).

During periods of resource excess or during the non-reproductive season when resources are of less value, it might be disadvantageous to defend the territory from all intruders. Theoretically, if the resident bird is dominant over the intruders, it might allow them to stay in the territory part of the time (Grahn 1990); in this situation the cost of sharing resources would be less than the cost of defending the territory. When there is no resource excess, overlap between home ranges should be lower in the reproductive season (Davies and Houston 1984).

Predictions regarding territoriality are not easy to make. According to some models, territory size may change depending upon the goal of the territory holder (time minimization or energy maximization) and on whether, and how, food density and intruder pressure covary (Schoener 1983).

Food availability may influence territorial behaviour. The Jay is an omnivorous species. Acorns are usually an autumn staple food. Insects, especially caterpillars, are taken in great quantity during spring and summer and form the principle food given to nestlings (Owen 1956). Chestnuts, beech mast, grain, green peas and beans, cherries, raspberries and other fruit, buds, spiders, slow worms, slugs and small snails, young birds, eggs, mice and other small mammals, lizards and small snakes are also taken (Goodwin 1986).

A previous study of the movements of Jays in the Maremma Natural Park (Tuscany, Italy) gave no evidence of territorial behaviour either in summer or in autumn and showed a temporary, very high summer density of Jays in the coastal pine woods by day (Patterson et al. 1991). The diversity of habitats, with abundant insect food in summer and a supply of acorns in autumn, was suggested as the reason for the ranging patterns observed (Patterson et al. 1991).

This study investigated the spring territorial behaviour of the Jay in the Maremma Natural Park. Additional aims were: (a) to compare range sizes among seasons, habitats and areas and (b) to investigate habitat use.

Study areas

The study was carried out during April, May and June in 1990 and 1991 in the Maremma Natural Park, on the coast of Tuscany, Italy. The Park is characterized by three major vegetation types. Most of the area is covered by Mediterranean maquis scrub (hills named "Monti dell' Uccellina") but some portions of scrub have earlier been cleared to create olive groves. A pine forest extends behind the beach for about 6 km of the coast.

Two main study areas with different vegetation structure were chosen, Pratini and Faunistico (study area 1 and 2, respectively) which are about 3 km apart.

Limited human disturbance occurs both at Faunistico and Pratini. Vehicles pass along the road at Pratini and parties of visitors are conducted across, while access of vehicles is forbidden at Faunistico but visitors may walk freely. The coastal pine forest, where some car transects were made, is made up by *Pinus pinea* and *P. pinaster* with an understorey of *Cistus* spp., *Erica* spp., *Pistacia lentiscus*, *Myrtus communis*, *Juniperus oxycedrus* and *J. phoenicea* (Arrigoni 1988).

Study area 1

Pratini is a small olive grove (4 ha) located in the middle of the Park and surrounded by Mediterranean maquis scrub. The scrub contains *Quercus ilex*, *Arbutus unedo*, *Phyllirea latifolia*, *Fraxinus ornus*, *Erica* spp., *Pistacia lentiscus* and *Rosmarinus officinalis* (Arrigoni 1988).

Study area 2

Faunistico (40 ha) is close to the eastern border of the Park. One part consists of grazed meadows with scattered oak trees (*Quercus ilex*, *Q. pubescens*, *Q. suber*). This area is delimited by cultivated fields (cereals and fruit) in the east and Mediterranean maquis, prevalently made up of *Q. ilex*, in the west. Meadows of this area are grazed by fallow deer *Dama dama*, rabbits *Oryctolagus cuniculus* and cattle, and thus the grass is kept short. Because of the high densities of herbivores, coprophagous beetles are abundant. The part of the maquis close to the grazed meadows has recently been thinned and is much more open than the remaining scrub.

Methods

Jays were trapped (8 April–13 May) using mist nets (12 birds) or monofilament nylon nooses set in areas baited with small pieces of bread (2 birds). Jays can be classified as adults or 1-yr-old juveniles on the basis of the number of black crossbars on the outermost greater wing coverts. According to Svensson (1984) the typical number of black crossbars is 10–12 for adult birds and 6–8 for juveniles (1 yr-old). However, we found that the range of 10–12 bars used for classifying North European birds as adults was not valid for Mediterranean ones. In fact neither the 14 birds caught during this study nor the 24 specimens from different areas of Tuscany in the Museum of Natural History "La Specola" of Florence had more than 10 crossbars. Hence we also paid attention to the other cues suggested by Svensson, i.e. the regularity of the bars and their spacing, the width of the 2nd outermost tail feathers and the degree of feather wear. Accordingly, 10 out of 14 birds were classified as adults (at least 2 years old), one as a juvenile (one year old) and three as uncertain. We must emphasize that in the Jay also 1-yr-old individuals can reproduce (Grahn 1990).

All birds were fitted with small radio transmitters (2–4 g, i.e. less than 2% of the body weight) glued and tied to the base of the two central tail feathers (Kenward 1987). The radio-tagged individuals were tracked 1–3 days per week and located by approaching the birds closely or by triangulation.

Table 1. Home range sizes (ha) of the radio tracked Jays (for references to computational methods see "Methods"). Jay 2 had an insufficient number of fixes. Ad = 2 year old or older; juv = 1 year old. Study area 1 = Pratini; study area 2 = Faunistico. Jays 1–7 radio-tracked in 1990; Jays 8–14 in 1991.

Jay No.	Age	Study area	No. days tracked	No. of fixes	MCP	KER	HM
1	Ad	1	11	478	5.6	8.9	8.8
2	Ad	1	2	27	–	–	–
3	?	2	3	80	47.9	56.6	15.5
4	Ad	2	9	496	43.4	38.1	20.8
5	Ad	2	4	169	45.4	48.6	27.0
6	Juv	1	6	163	4.9	8.1	9.3
7	Ad	2	6	175	24.9	23.6	17.0
8	Ad	2	4	162	37.1	44.1	19.4
9	Ad	2	6	185	4.0	4.7	4.2
10	Ad	1	9	351	4.9	4.8	5.9
11	?	1	8	231	2.6	2.8	2.3
12	?	1	6	111	1.1	1.8	2.0
13	Ad	1	11	479	5.1	3.5	4.0
14	Ad	1	9	385	2.4	3.0	3.3

Range IV software was used in the analysis of radio-tag data (R. Kenward 1990, Institute of Terrestrial Ecology, Wareham, U.K.). Incremental area plots were used to check the minimum sample size required to fully describe range areas. Range sizes and overlap between ranges were obtained through Kernel analysis (hereafter KER 95%) (Worton 1989). Range sizes were also estimated by minimum convex polygon (hereafter MCP 100%) and harmonic mean analyses (hereafter HM 95%) (Kenward 1987) in order to compare spring data with those of summer and autumn (Patterson et al. 1991). The minimum convex polygon was also used excluding the 5% of data points farthest from the harmonic centre (hereafter MCP 95%). Differences between home range sizes were tested by non-parametric techniques (Wilcoxon and Mann-Whitney tests).

The presence of stable home ranges was checked with 3 methods:

(1) by incremental area plots, adding fixes sequentially (animals with stable ranges are expected to reach an asymptote, while floaters should increase their ranges progressively);
(2) by calculating the distance between activity centres of the same Jay on successive tracking days (for a resident Jay, the distance should be small and should not increase systematically);
(3) by calculating a regression of the overlap between ranges of the same Jay with the length of time elapsed between the two tracking days (a Jay showing decreasing auto-overlap as a function of time would be classified as a floater). An analysis of eight daily ranges showed that in seven cases home range sizes did not vary (±20%) after five hours. Therefore only days with more than five daily hours of tracking were used in analyses 2 and 3. Only Jays with more than five days of tracking were considered.

The presence of territoriality was checked by range overlap and distance between activity centres among Jays frequenting the same area, and efforts were made at detecting all possible intraspecific interactions and territorial disputes.

In order to investigate habitat selection we compared the proportions of different habitat types (expected habitat use) in each study area (defined considering the outermost fixes) with the proportions of habitat types within the individual home ranges and with the proportions of radio-locations of Jays in the different habitats (observed habitat use). A third check of the habitat selection was carried out by comparing the proportions of different habitat types in each home range with those of fixes in these different habitats. Bonferroni confidence intervals were calculated to determine which habitat types were being preferred (Neu et al. 1974, Byers et al. 1984).

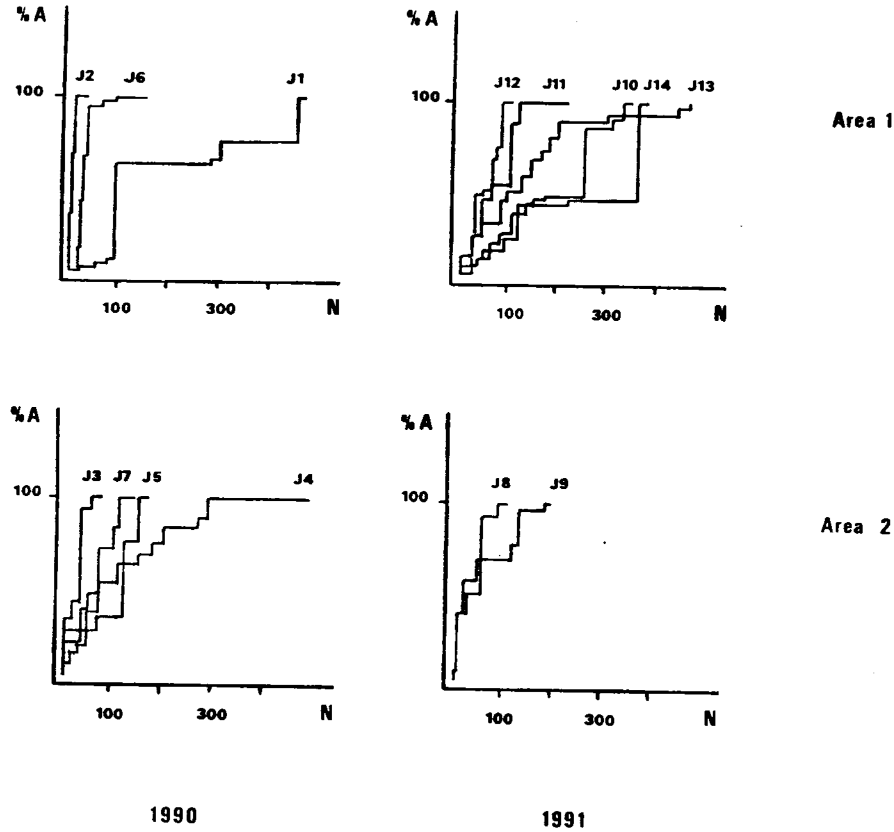
Results

Home ranges

Seven birds were captured in 1990 and seven in 1991. Home range sizes calculated with different methods and the number of fixes for each Jay are shown in Table 1. Jay 2 has been excluded from subsequent analyses because of insufficient number of fixes. Home range size was larger in study area 2 (35.9 ± 17.2 ha, KER) than in area 1 (4.7 ± 2.5 ha, KER) (Mann-Whitney's: $U = 3.0$, $P = 0.01$). No significant differences were found in the home range sizes calculated with different methods (Wilcoxon tests, $Z < 1.44$, $P > 0.15$).

Incremental area plots revealed that in 10 out of 13 cases the home range did not reach an asymptote even after a large number of fixes (up to 478) (Fig. 1). One range stabilized after 300 fixes (Jay 4) and another

Fig. 1. Incremental area plots of the radio-tagged Jays. % A = percentage of total area; N = number fixes.



showed an asymptotic slope after 200 fixes (Jay 13). The fact that most of the home ranges did not reach an asymptote was probably a biological phenomenon rather than the result of insufficient sampling. In fact even the ranges of two of the most intensively sampled birds (Jays 1 and 10, Table 1) did not stabilize.

Harmonic mean centres of the same bird were usually less than 100 m apart on successive tracking days with no substantial increase of distance with time. Exceptions were Jay 4, Jay 14 and in part Jay 9; in these birds the

Table 2. Analysis of daily range auto-overlap. Regression lines describe the percentage of auto-overlap (dependent variable) as a function of the number of days between successive samplings (independent variable). Coefficient b is the slope. The t-test was used to test the significance (P) of the regression coefficient.

Jay No.	Coeff. b	Intercept	P
1	−0.03	70.11	0.85
4	−1.78	79.90	<0.0001
6	5.59	2.89	0.36
7	−2.38	78.98	0.30
9	−0.91	24.57	0.07
10	0.16	55.58	0.66
11	−0.79	67.31	0.15
12	1.56	45.44	0.88
13	−0.17	76.46	0.64
14	−2.32	79.01	0.008

Table 3. Overlap matrix. Overlaps of the ranges of different Jays (J1–14) are given as percentages. Range areas in rows are overlapped by range areas in columns.

Pratini, 1990	J1	J2	J6		
J1	–	36.0	4.2		
J2	100.0	–	11.1		
J6	14.7	0.6	–		
Pratini, 1991	J10	J11	J12	J13	J14
J10	–	28.5	12.5	86.6	12.8
J11	81.8	–	50.2	62.3	45.5
J12	64.0	82.9	–	57.7	73.9
J13	92.1	39.9	26.7	–	27.3
J14	30.9	28.3	43.9	24.7	–
Faunistico, 1990	J3	J4	J5	J7	
J3	–	23.8	62.5	17.5	
J4	37.3	–	35.3	42.3	
J5	66.3	26.6	–	27.8	
J7	52.0	81.1	60.0	–	
Faunistico, 1991	J8	J9			
J8	–	34.6			
J9	100.0	–			

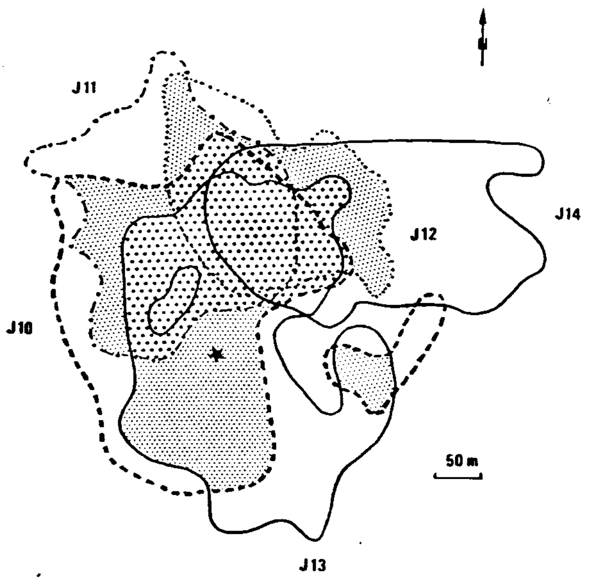


Fig. 2. Pratini. Ranges of radio-tagged Jays in 1991. Contours obtained by Kernel Analysis (95%). The star specifies the position of one nest (untagged pair). Smaller dots show areas where two ranges overlapped; larger spots show where three or more ranges overlapped. The whole dotted area was placed within the maquis. Note that the actual degree of overlap among Jays was certainly much higher than that represented because many untagged birds were seen within the same areas.

distances between daily range centres were up to 1100 m, suggesting the possible lack of a stable home range.

These results were confirmed by the analysis of daily range auto-overlap. The same three Jays (4, 9 and 14) had ranges whose auto-overlap decreased with time (with a significant level of association between the two variables in Jays 4 and 14), while other birds showed constant auto-overlaps (Table 2). The size of the daily home ranges varied from 0.6 to 114.2 ha, with large individual variations.

In territorial animals, one should expect non-overlapping or only slightly overlapping ranges; in our case ranges overlapped to different degrees (45% on average) and no range was exclusive (Table 3 and Fig. 2). Furthermore, many untagged Jays were seen inside the home ranges of the tagged ones and one pair of Jays successfully reproduced in 1991 inside the home ranges of Jays 10 and 13 (Fig. 2). No aggressive interactions were ever detected.

Habitat use

Habitat use differed from individual to individual and from area to area (Table 4). At Pratini the maquis scrub was positively selected (10 selections were positive and only 3 were negative) whereas the olive grove was avoided (10 negative versus 3 positive). At Faunistico habitat use was more complex because of the greater

Table 4. Relative habitat use (%) by the different Jays at Pratini and Faunistico. The relative extension of the different habitat types in each area given in brackets. Observed frequencies of habitat use calculated both as percentages of the different habitat types within individual home ranges (% H.R.) and as percentages of fixes in the different habitat types (% Fixes). Ol = olive groves; Sc = maquis scrub; Me = meadows with scattered trees; Os = "open" maquis scrub; Fi = cultivated fields (fruit, cereals, olives etc.). Differences between observed and expected frequencies tested by using Bonferroni simultaneous confidence intervals analysis. + = positive selection ($P<0.05$); – = negative delection (avoidance) ($P<0.05$); no signs = no selection.

Pratini (Ol = 15.7%; Scr = 84.3%)

Jay No.	% H.R.		% Fixes	
	Ol	Sc	Ol	Sc
1	20.8+	79.2–	15.0	85.0
2	9.7+	90.3	0.0–	100.0+
6	7.5–	92.5+	1.2–	98.8+
10	14.3	85.7	2.3–	97.0+
11	5.0–	95.0+	3.0–	96.7+
12	5.6–	94.4+	1.8–	98.2+
13	24.3+	75.7–	8.6–	91.4+
14	26.0+	74.0–	4.4–	95.6+

Faunistico (Me = 12.1%; OL = 16.3%; Sc = 39.7%; Os = 4.3%; Fi = 27.6%)

Jay No.	% H.R.					% Fixes				
	Me	Ol	Sc	Os	Fi	Me	Ol	Sc	Os	Fi
3	47.2+	0.0–	16.3–	11.3	25.2	83.7+	0.0–	16.3–	0.0–	0.0–
4	40.3+	0.0–	19.1–	17.4+	23.2–	39.7+	0.0–	13.3–	28.4+	18.6–
5	41.2+	0.0–	15.6–	12.1+	31.1	54.4+	0.0–	14.8–	8.3	22.5
7	13.8	0.0–	57.0+	29.2+	0.0–	6.9	0.0–	33.1	60.0+	0.0–
8	39.2+	0.8–	38.1	21.9+	0.0–	33.9+	0.0–	27.2–	38.9+	0.0–
9	9.9	0.0–	5.2	84.9+	0.0–	2.2–	0.0–	7.0–	90.8+	0.0–

habitat diversity. The meadows with scattered trees and the "open" scrub were positively selected (8 positive versus 1 negative and 9 positive versus 1 negative respectively) whereas the olive groves and the cultivated fields were often avoided and never positively selected. Also the dense maquis scrub was avoided (8 negative versus 1 positive), possibly as a result of the preference shown for the open areas of the maquis.

Similar results were obtained after comparing the proportions of different habitat types in each home range with the proportions of fixes in these same habitats, but the number of comparisons showing no selection was higher in this case, especially at Faunistico (13 out of 30 cases).

Therefore, we conclude that the preferred habitats (i.e. those used significantly more often than expected, cf. Andrén 1990) were the maquis scrub at Pratini and the meadows with scattered trees and the open areas of the maquis scrub at Faunistico. All radio-tagged birds moved within ecotonal areas, where the maquis was bordering to other more open habitats. Also at Pratini, where the Jays did not abandon the maquis, home ranges were bordering on the olive grove.

All sampled nests (N = 149) were in the maquis scrub (mainly in *Quercus ilex* and *Arbutus unedo*), but only two were occupied. Undamaged nests were very few (8.5%) and most were classified as having lost 2/4 or 3/4 of their original material (52.8%), indicating that they were at least one year old.

Discussion

In both study areas Jays seemed to be non-territorial because home ranges overlapped extensively during the reproductive period. Incremental area plots showed that most of the Jays did not have fixed home ranges, while the analysis of daily range auto-overlap showed that they had essentially constant auto-overlap. These results suggest that most of the home ranges increased in area, but did not drift away during the reproductive period and, in fact, most of the activity centres remained approximately at the same place.

In Sweden both Andrén (1990) and Grahn (1990) found that during the breeding period Jays had well defined territories with no or little overlap. In the Netherlands pairs of Jays bred solitarily and defended all-purpose territories (Bossema et al. 1986). In Maremma the lack of territorial behaviour was also suggested by the occurrence of breeding birds attending eggs or chicks within the home range of other Jays, and by the apparent lack of territorial disputes, such as those reported between neighbours in South Central Sweden (Andrén 1990). Even though intraspecific interactions are difficult to observe in the dense maquis, they were not observed in the more open habitat at Faunistico either. There, by contrast, some observations suggested that individuals may join to form temporary feeding flocks.

Even though it is possible that non-territorial birds had been caught selectively, we believe that this cannot explain our results in both years and areas. The non-territorial system of Jays in the Maremma Natural Park may be determined by several factors.

(1) Previous observations suggested a situation of resource abundance in both summer and autumn. Jays caught cicadas which were plentiful in the pinewood during summer and fed on acorns which were abundant in the maquis during autumn (Patterson et al. 1991). No specific, rich food source was detected during spring although a previous study suggested that the abundance and variety of food resources in Maremma were high throughout the year, with the highest availability of beetles during spring (Cavallini and Lovari 1991). Moreover, in the Maremma Park, Jays use these resources flexibly during the different seasons (Patterson et al. 1991), so presumably they are not forced to migrate as their northern conspecifics are (Andrén 1985, Schmitz 1986). If so, the cost of sharing resources would be less than the cost of defending a territory against all intruders (Davies and Houston 1984) and a non-territorial system would be expected. Nevertheless, resource availability may change from year to year (oaks, for instance, show cycles of acorn abundance) and occasional food shortage in some periods cannot be excluded.
(2) All radio-tagged birds showed an ecotonal distribution, which was perhaps facilitated by the availability of food in the ecotone (birds could feed in the maquis or in the more open habitats). Hence, it might be hypothesized that, assuming that the density of birds was very high in the ecotone, the energy expenditure for defending territories might have been too high to make defence a viable option. Unfortunately we could not estimate bird density within the maquis scrub because visibility was very limited and the canopy was usually completely closed along road edges.
(3) The fact that only two occupied nests were found seem to suggest a rather low reproductive rate. All of the tagged birds should potentially have been able to reproduce (even 1-yr-old individuals can reproduce in the Jay; Grahn 1990) but we could not find their nests even though core areas were searched for them. The low reproductive rate may be partly responsible for the lack of definite home ranges. Birds with no centres of activity (nests) may easily move on, in response to local food availability. Opportunistic or erratic behaviour may be advantageous in such conditions and in fact a few individuals showed increased distances between activity centres on successive tracking days.
(4) The movements of Jays at Faunistico suggest that, during the spring, the birds need to forage also out-

side the maquis scrub, which remains, however, the nesting and roosting habitat. This fact is not necessarily incompatible with a territorial system and, in fact, some territorial bird species feed outside their territories. Jays have been observed to forage outside their territories and join "ceremonial gatherings" in the Netherlands (Bossema et al. 1986). Great Reed Warblers *Acrocephalus arundinaceus* display intra- and interspecific territorial behaviour during the breeding season but also feed outside their territories (Rolando and Palestrini 1991). Nevertheless, if territories had existed in the Maremma Park, only the few holders of territories close to the open foraging areas could have taken advantage of this proximity. In a territorial system, the great majority of birds would have been forced to establish territories far from the ecotonal areas.

The social organization of the Jay in the Maremma Park therefore seems very different from that observed in northern Europe. This is not surprising if we consider that one study area in Sweden lies outside the distributional range of the oaks *Quercus robur*, *Q. petraea* (Andrén 1990, Hultén 1971) and that territoriality seemed to be less clear-cut in the Dutch study areas which, conversely, were inside these oaks' distributional range (Bossema et al. 1986). In our oak-dominated Mediterranean area, the high density of birds and high food abundance, may make territoriality uneconomical.

Mean home range size in Sweden ranged from 14 ha (Grahn 1990) to 35 ha (Andrén 1990), whereas in the Netherlands home ranges were between 2 and 10 ha (Bossema et al. 1986). In Maremma we obtained (Kernel Analysis) mean values of 35.9 ± 17.2 and 4.7 ± 2.5 ha, at Faunistico and Pratini respectively. These differences may be related to the different degree of habitat diversity, Faunistico having a much higher diversity than Pratini. The larger home ranges at Faunistico than at Pratini were likely due to the Jays abandoning the maquis in order to forage in other habitats, i.e. open maquis areas, meadows with scattered oaks and cultivated fields. Hence, in the Maremma, home range size was positively related to habitat diversity.

Andrén (1990) could ascertain that territory size was negatively related to habitat quality (in terms of percentages of preferred habitats). Birds in poorer habitat might have to enlarge their territories to compensate for lower food density. At Pratini the preferred habitat (scrub) accounted for 84.3% of the total area, whereas at Faunistico the preferred habitat types (meadows, open scrub) accounted for only 16.5%. Differences in home range size between the two study areas were therefore in accordance with Andrén's observations. However, the percentage of time spent in a certain habitat type may not necessarily be positively correlated with the amount of foraging within the same habitat, as found by Cavallini and Lovari (1991) in the red fox *Vulpes vulpes*.

The maquis scrub is the only natural habitat of the Maremma Park. Apart from nesting there, Jays were particularly dependent on this habitat for resting and tagged individuals always stayed there overnight during spring and also during summer and autumn (Patterson et al. 1991). Apart from roosting, home range sizes in all seasons (spring, summer and autumn) seemed to depend mostly on the distribution and availability of food. During summer the Jays' movements probably depended on the abundance of cicadas *Cicada orni* in the coastal pine wood, and during autumn on the occurrence of scarab beetles in the olive groves and of acorns in the maquis (Patterson et al. 1991). During spring, the maquis may be avoided by foraging birds if more attractive habitats are available. At Pratini, apart from a small olive grove, the maquis was practically the only available habitat. At Faunistico, in contrast, there was greater habitat diversity and Jays clearly avoided the maquis scrub and preferred the open maquis and the grazed meadows with scattered oaks. Positive and negative selections may vary seasonally. Cultivated fields, for instance, were not attractive during spring because fruits (hazels, grapes, and peaches) were still not ripe, whereas many Jays were observed there in late summer and autumn. The present data seem to suggest that also during spring the Jays' movements partly depended on the availability of food outside the maquis. Hence food location and availability might be one important determinant of the ranging behaviour of Jays in the Maremma Natural Park.

Nesting certainly is expected to be another determinant of the ranging behaviour of Jays. In Sweden Jays strongly preferred to locate their nests in Norway spruce *Picea abies* (Andrén 1990), perhaps because nests in deciduous trees are poorly hidden (Loman 1975, 1979). In Maremma nests were placed in trees (*Q. ilex* and *A. unedo*) which occurred widely in the maquis whereas no nests were found in other habitat types. Maquis might also be selected since it gives shelter against predators (man, other Corvids, raptors). It is perhaps relevant that the Hooded Crow, which is dominant over the Jay (Bossema et al. 1986, Rolando 1988, Rolando and Giachello 1992), occurred in the other habitat types.

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