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Foraging flights of wild rock doves (*Columba l. livia*): a spatio-temporal analysis*

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ABSTRACT

The first spatio-temporal analysis of foraging flights of wild rock doves is here reported. Birds living in one of the last relatively pure demes of wild *Columba livia* in the Mediterranean region (Capo Caccia, NW Sardinia) were observed on their foraging routes and in the course of daily movements to and from the colonial site. Foraging sites were located by systematic searches of colour-marked birds in the study area.

The pigeons followed rather stable routes in reaching foraging sites, which are mainly located in agricultural fields up to around 19 km from the colonial site. In autumn, doves tended to reduce the extent of foraging flights, feeding almost exclusively on lentiscus fruits located near the colony. Foraging flights in spring and summer differed from those in autumn and winter in the patterns of daily activity, the number of birds moving, and the sizes of the flocks. The possible relationships between the spatio-temporal characteristics of foraging flights and other aspects of the biology of rock doves, especially in the breeding season, are discussed.

KEY WORDS: Rock dove - *Columba l. livia* - Foraging flights - Activity pattern.

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INTRODUCTION

A typical behavioural trait of wild rock dove is the daily foraging flights form colonial sites to feeding grounds. The birds typically fly rapidly and directly to where they are going (fast 'commuting' flights of Goodwin, 1983). Despite the fact that the doves might find food in the vegetation of the cliff ledges where they nest, their main feeding sites are located mainly in agricultural areas, often far from their colonies (Toschi, 1939; Goodwin, 1983). These daily movements, 'bred out' in domestic races of pigeons (Goodwin, 1983), are still characteristic of feral populations, although their extent is reduced in urban areas (Simms, 1979; Sol & Senar, 1995); nevertheless most of our information on pigeon foraging flights deals only with ferals (Havlín, 1979; Janiga, 1987; Baldaccini & Ragionieri, 1993; Baldaccini & Giunchi, 1998). Additionally, foraging movements of wild rock doves often have been considered in the older literature to be nomadism or even migration (e.g., Toschi, 1939). Thus, we here present for the first time a spatio-temporal analysis of the foraging flights of rock doves, and include observations on the spatial range of this species.

Our study of this distinctive spatial behaviour of rock doves is significant for two reasons. First, it adds to our knowledge of the biology of a species whose European populations are now threatened by genetic extinction from interbreeding with feral and domestic pigeons (Murton & Westwood, 1966; Murton & Clarke, 1968; Cramp, 1985; Johnston *et al.*, 1988; Johnston, 1992). As a consequence, the nominate subspecies is regarded as endangered by the Convention on International Trade in Endangered Species of the European Community (CITES; EC regulations 3226/82 and 3418/83), and it has recently been included in the Italian 'Red List' (Bulgarini *et al.*, 1998). These problems of conservation have induced Johnston and Janiga (1995) to speculate that "...the disappearance of the ancestral [western European] rock pigeon could occur as early as in the last half of the 21st century...".

Secondly, and equally significant, is the fact that the need for pigeons daily to cover a number of kilometres to get food may have been one of the selective pressures on the evolution of the well-known homing abilities of rock doves (Alleva *et al.*, 1975; Visalberghi *et al.*, 1978), which have been further developed by artificial selection of carrier and homing breeds (Levi, 1965).

MATERIALS AND METHODS

The birds and their colony sites

Along the rocky cliffs of Capo Caccia (NW Sardinia, 40° 36', N 08° 10' E) rock doves (*Columba l. livia* Gmelin 1789) are widespread, nesting in crevices and large caves. We estimated a total of 3000 doves resident in that area. In Figure 1 the thickened stretch of coastal line indicates the approximate location of nesting and roosting sites of the birds in the study area. It is likely that doves from other parts of the coastal promontory joined the flocks that we observed.

The doves of the study region present a homogeneous wild phenotype (see Cramp, 1985) and other studies (Ragionieri *et al.*, 1991; Johnston & Janiga, 1995) have shown genetic and morphological differences of the birds at Capo Caccia from populations of neighbouring feral pigeons, despite the gradual intrusion of ferals. As a rough indication of the extent of the local gene flow from domestic or feral pigeons into the wild colony, in 1989 we found 0.9% of sample of 371 trapped birds with evident signs of hybridisation in the feather coat or bare parts; in 1997 the incidence had increased to 7.7% in a sample of 52 birds.

The data Guyot *et al.* (1985) from near Corsica shows the pigeons there to have a short reproductive season, but at Capo Caccia the season is longer, probably spanning the entirety of late spring through summer. Nests with eggs and nestlings were found in May 2000, and in October 1989 9% of the trapped birds still showed juvenile traits.

Determination of departing flight paths and of foraging sites

The flight paths of departing birds were plotted by visually tracking the pathways of the largest flocks from vantage points located along routes usually followed by the birds in different seasons for 1989 to 1992 (sites A-E, Fig. 1). The location of these vantage points allowed tracking of the birds for most of their flights by observers who were in radio contact with one another. Successive positions of moving flocks were plotted on maps of the region.

Foraging sites of these birds were located by use of a variety of methods. Firstly, sites used by wild, feral, and domestic pigeons were located. Then, doves on departing flights were captured in mist nets near point A in Figure 1. Over a period of three years, some 371 birds were captured; these were marked by painting colours on the underwing coverts and the rump. Different colour combinations were used to distinguish the day of capture of the birds. Finally, systematic searches were made of the feeding areas previously located, in accord with the direction of vanishing points of birds for any given day from sites A to E. Sites where marked birds we found were plotted on a map.

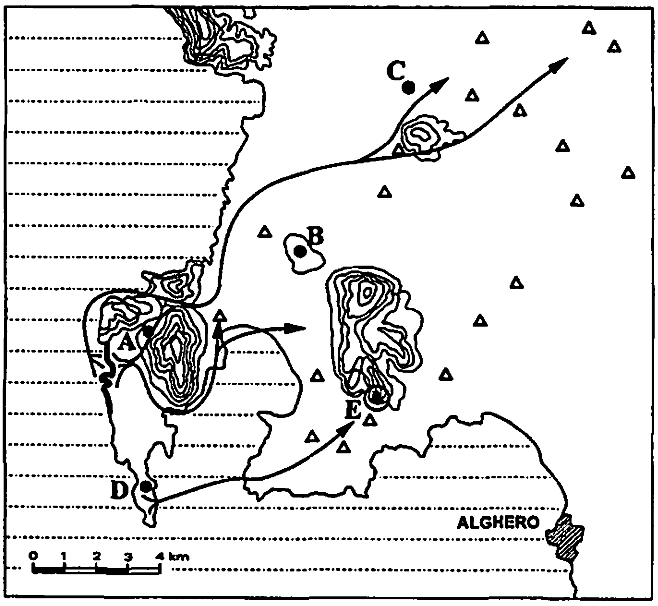

Fig. 1 - Schematic map showing the location of the nests and roost sites of the studied birds (thickened stretch of coastal line), the points of observation (A-E), the main foraging routes (arrows), foraging and watering sites (open and filled triangles, respectively).

Foraging flights

The flocks of doves departing from (D) and returning (R) to the colony in 1992 were observed from site A on one day per month (but not in September), from sunrise to sunset. For each flock, flight direction, time of sighting, and flock size were recorded. For all observations, the timing of movements was that relative to local sunrise. Flight paths of birds returning to the colony were sometimes completely different from those of birds leaving the colony, perhaps as a result of where the birds found good foraging, which changed from time to time. Thus, observations of returning flights (R-flights) were less consistent than those for departing flights (D-flights), and were in fact absent for January, February, and June. For this reason, data analysis was mainly of D-flights, except when noted otherwise.

The following descriptors were then determined: total number of doves observed per day (NTOT); total number of groups observed per day (NGR); median number (MED), range (R), and interquartile range (IQ) of birds per group per day. For D-flights, only the total time of activity per day (ATT) and the time since sunrise during which the number of pigeons that moved equal to 50% + 1 of NTOT (T50) were then determined. The latter variables were not considered for R-flights, due to lack of data.

The variables NTOT, NGR, MED, and T50 have been standardised, making the overall level of variation comparable across measurements (Wilkinson, 1990), and then used in cluster analysis, with the Pearson product-moment correlation coefficient as a distance index. This analysis aims to sort the different days of observation into groups based on their overall resemblance in pattern of the D-flights.

In all statistical analyses, parametric or nonparametric statistics were used according to whether or not the data were normally distributed (Sokal & Rohlf, 1995).

RESULTS

Departing pathway and foraging sites

Beginning just prior to sunrise, doves congregate, sometimes in large flocks, on tops of cliffs before they leave the colony site for feeding and drinking. Figure 1 shows the routes usually followed by most of the birds (D-doves). Such routes tend to avoid highest relief or the open sea, and they remain stable over long periods, as demonstrated by observations in October and November of 1989 and 1990. In particular, the route passing points A to C in Figure 1 seems to be the most stable, based on observations dating as far back as 1971 (Alleva *et al.*, 1975).

Foraging sites of marked birds are depicted in Figure 1; distances from the colony site range from four to 18.9 km. The doves find food on arable land, vineyards, pastures, Mediterranean scrub, or, occasionally, cereal stubble. In autumn the birds feed almost exclusively on fruits of lentiscus (*Pistacea lentiscus*), at sites near the colony; the importance of lentiscus was determined through field observations of feeding behaviour and by dissection of 30 mist-netted R-birds, sacrificed to assess their food preferences. Flowering and ripening of lentiscus does not occur every year, but when the fruits are widespread around the colony site the D-flights almost totally stop.

Figure 1 also shows a traditional watering site, an artificial basin.

Temporal distribution of movements

Figures 2 and 3 show the temporal distribution of movements in the course of a day of observation. In spring and summer, D-doves seem to leave the colony bimodally, with a large first peak early in the morning and a smaller peak six to nine hours after sunrise. The distribution of D-flights in fall and winter is described by a single peak early in the afternoon. The total time of activity per day (ATT) is highly significantly correlated with the effective length of the day ($r = 0.94$, $n = 11$, $P < 0.001$).

The temporal distribution of R-flights, considering days with a sufficient number of observations, is similar to that of D-flights, with a phase retard of two to three hours. This data do not represent mean foraging time, because of the variation in routes of return and the impossibility of identifying individual birds in the returning flocks.

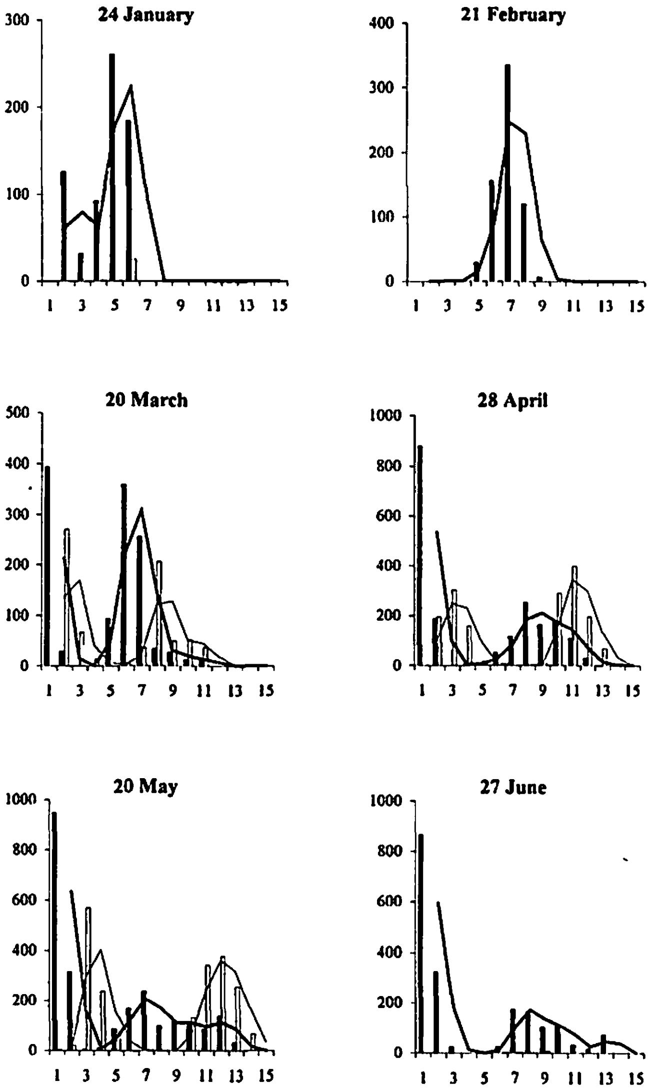
24 January
21 February
20 March
28 April
20 May
27 June

Fig. 2 - Time course of D-flights and R flights (filled and open bars, respectively) in the first six days of observation. Smoothing is calculated by means of running means, using two neighbouring points. Thick line, D-flights; light line, R-flights.

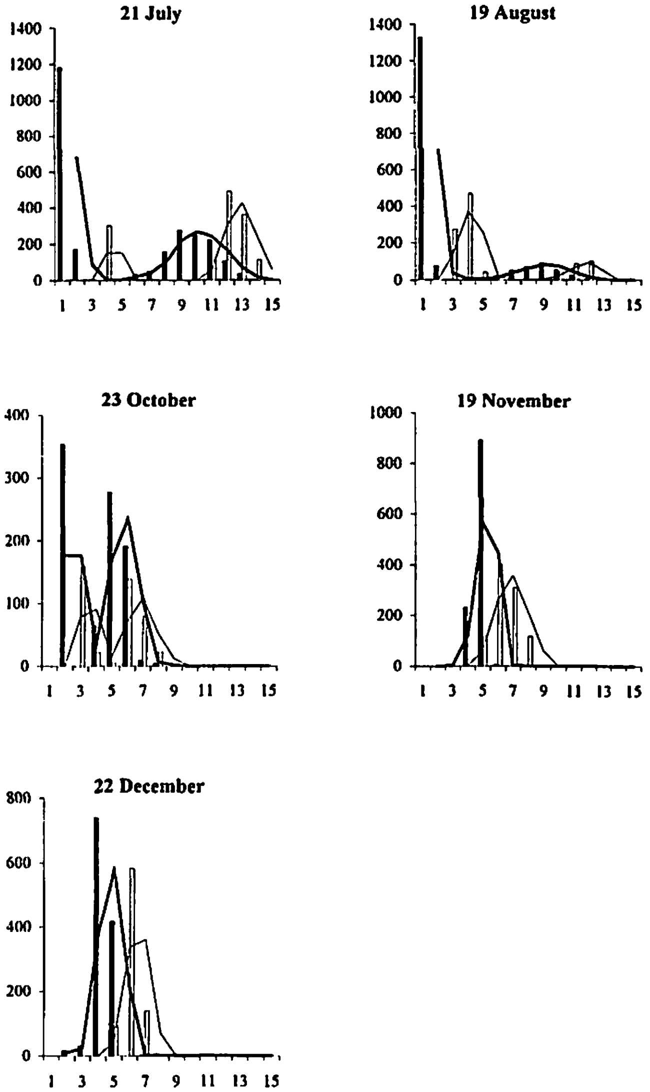
21 July
19 August
23 October
19 November
22 December

Fig. 3 - Time course of D-flights and R flights (filled and open bars, respectively) in the remaining five days of observation. Symbols as in Figure 2.

Tables I and II give the values of the variables used in analysing D- and R- flights (see Materials and Methods). The annual trend in NTOT is provided in Figure 4; for D-flights this variable increases from March to July and then decreases, reaching minimum values in winter months. For R-flights, the trend seems roughly similar, despite lack of data for some months (see Materials and Methods).

When flock size of D-flights is considered (Fig. 5A), a tendency to leave the colony in small flocks in spring and summer is evident. But, in fall and winter, it is often possible to see flocks with more than 40 doves. R-flights (Fig. 5B) show a similar, although less pronounced, trend. Excluding January, February, and June, MED of R-flights is significantly higher that that of D-flights ($W = 36.0$, $n = 8$, $P < 0.01$, Wilcoxon signed ranks test).

TABLE I - *Summary statistics of D-flights (see Materials and Methods for abbreviations).*

Month	NTOT	NGR	MED	IQ	R	ATT (min)	T50 (min)	Cluster
Jan	695	36	11.0	3.0-25.8	1-110	289	253	I
Feb	647	65	5.0	2.0-11.0	1-80	229	377	I
Mar	1222	88	10.5	5.0-18.0	1-50	619	323	I
Apr	1990	244	7.0	4.0-11.0	1-40	712	72	II
May	2353	310	5.0	3.0-9.0	1-60	742	79	II
Jun	1914	208	6.5	3.8-12.0	1-65	739	66	II
Jul	2485	248	7.0	4.0-13.0	1-85	768	59	II
Aug	1747	118	7.0	3.0-15.0	1-150	654	34	II
Oct	897	54	10.0	6.0-24.8	2-70	375	238	I
Nov	1132	27	23.0	6.0-62.5	1-250	121	250	I
Dec	1205	40	14.0	5.0-47.8	1-120	299	229	I

The pattern of clustering of the eleven days considered for D-flights, using the four variables listed in Materials and Methods, is summarised in the dendrogram in Figure 6. Two clusters are clearly evident in this analysis: the first (I) includes spring and summer months, April to August, the second (II) fall and winter months, October to March. Based on the data in Table I, the monthly periods in cluster I have lower values of NTOT and NGR, and higher values of MED and T50, relative to cluster II.

DISCUSSION

Our rock doves undertook stable and extended daily 'commuting' flights in order to reach food sources far from the colony site. Flights varied in respect of the varying availability of food throughout the year. The flight activity of these wild birds shares several characteristics with those reported for feral pigeons, presumably as a response to common selective pressures (Havlín, 1979; Janiga, 1987; Baldaccini & Giunchi, 1998). However, the yearly patterns observed for the wild birds prove to be more consistent and predictable than those for ferals. Indeed, cluster analysis of the D-flights shows two distinct and rather homogeneous phases, April to August and October to March. Several environmental factors probably affect such ordination, and include day length and temperature or meteorological conditions, which are thought to influence patterns of movements of feral pigeons (Havlín, 1979; Janiga, 1987; Johnston & Janiga, 1995). It is worth noting, however, that the flight activity pattern of our wild pigeons correlates reasonably well with their strongly seasonal annual reproductive cycle (but see Cramp, 1985; Guyot *et al.*, 1985). A causal relationship between the pattern of movements and breeding activity has already been hypothesised for feral pigeons (Janiga, 1987), in which the bimodal schedule of foraging in early spring is related to the alternation of the sexes at the nest (see also Johnston & Janiga, 1995).

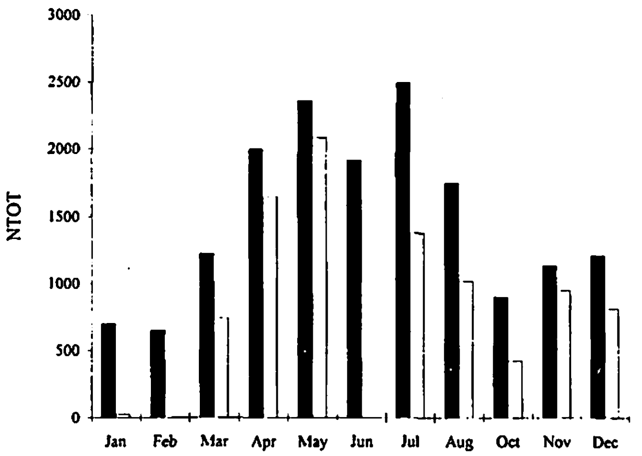

Fig. 4 - Annual trend of the total number of observed doves per day. Filled bars, D-flights; open bars, R flights.

TABLE II - *Summary statistics of R-flights (see Materials and Methods for abbreviations).*

Month	NTOT	NGR	MED	IQ	R
Jan	25	1			
Feb					
Mar	739	57	11.0	6.0-18.0	1-37
Apr	1644	124	10.0	5.0-20.0	1-50
May	2079	149	10.0	5.0-18.0	1-65
Jun	1	1			
Jul	1374	100	10.0	6.8-19.0	1-70
Aug	1018	37	14.0	4.0-30.0	1-160
Oct	425	21	16.0	10.0-32.0	2-60
Nov	946	24	32.5	8.0-51.0	1-150
Dec	812	19	30.0	19.0-65.0	1-130

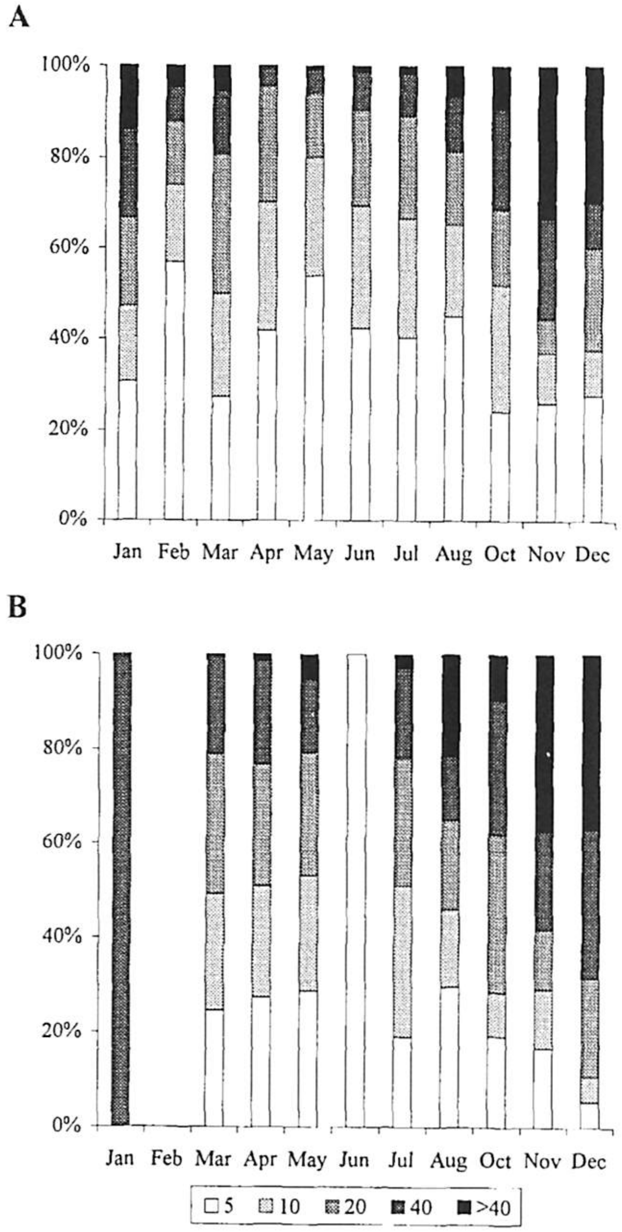

Fig. 5 - Annual trend of flock size distribution of D- and R-flights (**A** and **B**, respectively).

The hypothesis of a causal relationship between the pattern of D-flights and reproductive duties of the sexes sounds reasonable. It is likely that the higher degree of homogeneity in the daily schedule of movements of wild rock doves in spring and summer relative to that of ferals is owing to the higher degree of breeding synchrony in the wild birds.

Even so, if we consider the number of variables that differ in the two periods (Table I), it seems unlikely that reproductive activity is the sole cause of the pattern observed. Columbids and many other diurnal birds have bimodal feeding schedules (Murton *et al.*, 1972; Lefebvre & Giraldeau, 1984; Johnston & Janiga, 1995), probably caused by lack of night-time foraging (Zeigler *et al.*, 1971) and use of the crop as a food storage chamber (Griminger, 1983). At least in urban environment, this kind of schedule is evident for feral pigeons (Lefebvre & Giraldeau, 1984). Therefore, at least part of the bimodal course of spring-summer D-flights could be due to feeding schedules that are absent in colder months probably because of the shorter daylength and the delay in onset of D-flights with respect to sunrise.

Clearly, it is difficult to distinguish the effect of a single environmental variable on the temporal course of flights, because a number of interacting biotic and abiotic factors probably affect the observed patterns. Nevertheless, given the predictability of these movements, it is likely that reproductive activity and daily feeding schedules are the most important influences, sharing the same characteristic of seasonal and annual stability.

The variables discussed just above do not seem to explain seasonal variation in the size of D-groups. Our pigeons are typical social foragers that form into feeding flocks that are not, at least in feral pigeons, social units (Lefebvre & Giraldeau, 1984). The advantages of flocking are various, including transfer of information about foraging sites, assistance in finding food (Ward & Zahavi, 1973; Giraldeau, 1984; Johnston & Janiga, 1995), and probable reduction of risk of predation (Goodwin, 1977; Kenward, 1978; Johnston & Janiga, 1995; see Brown and Brown, 1996, for additional references). Moreover, although the evidence is not consistent, flocking may also have a function in accuracy of orientation (Walraff, 1978; Tamm, 1980; Burt de Perera & Guilford, 1999; but see also Keeton 1970, Wagner, 1975; Benvenuti & Baldaccini, 1985; Guilford & Chappel, 1996), as well as in homing speed (Burt de Perera & Guilford, 1999).

It does not seem that the kind of flocking formation of rock pigeons in flight, which is of clusters of individuals, can confer an aerodynamic advantage to the birds, because pigeon flocks lack precise interindividual spacing (see Speakman & Banks, 1998). The sizes of D-groups are probably determined by a trade-off between variables noted above and the costs of flying and foraging in groups (e.g., competition for resources and in-

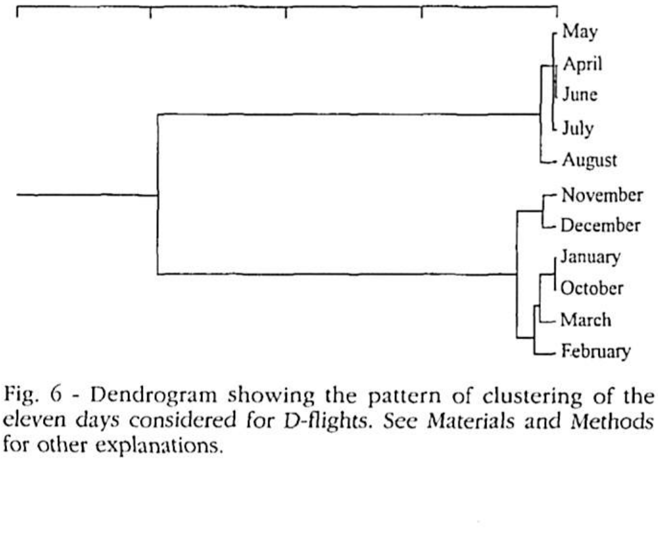

Fig. 6 - Dendrogram showing the pattern of clustering of the eleven days considered for D-flights. See Materials and Methods for other explanations.

creased attraction of predators). For our birds, the greater frequency of small groups is probably a consequence of the greater availability of food in the spring-summer period, which in turn is related to the agricultural practices in this area. Greater availability of food reduces the advantage of large flock size in searching for food and thus of paying the costs of interindividual competition that tends to increase with group size (Wittenberger & Hunt, 1985).

Notwithstanding these considerations, it is not reasonable to assume either (1) possible variation of antipredatory benefits with flock size (because the presence of predators, mostly peregrines, *Falco peregrinus*, shows no substantial change at Capo Caccia in the course of a year) or (2) possible orientational advantages. We note that for R-flights, when the doves have an urgency to reach the colony swiftly and safely, the median size of the flocks tends to be greater than that for D-flights.

Concerning routes of departure from the colony, rock doves initially follow topographic features of the region; the route is regular and perhaps traditional. Only after a flock reaches the inland agricultural area do the birds disperse, in accord with seasonal variation in food availability. Thus, the spatial range of our birds was relatively large, but we cannot put this into perspective, owing to lack of data on home range of this and related species. In colder months, the number of pigeons commuting is reduced, and, although this could be caused by reduction in the number of birds in the colony, it is possible that some doves do not move from the colony at all, feeding at *Pistacea* shrubs growing near the cliffs.

As noted earlier, commuting flights may cease completely in years with full ripening of *Pistacea* fruits. Although the total content of proteins and essential amino acids of lentiscus berries is fairly high compared to other fleshy fruits of Mediterranean habitats (Izhaki, 1993, 1998), they provide an unbalanced profile of essential amino acids (Izhaki, 1998). It thus seems unlikely that rock doves could feed exclusively on these fruits for long periods of time, even though their nutritional requirements in the colder months may be less than in the reproductive season (Murphy, 1996). The birds probably adjust their foraging behaviour to variation in their food supply as well as to their physiological state, carrying out behavioural strategies that are difficult to perceive using indirect approaches such as ours. But, we can say that extensive foraging flights characterise the daily activity of wild rock doves, which was previously known only from studies on feral pigeons. These flights are strongly predictable in their temporal and spatial pattern at any given time period of the year.

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