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A temporal analysis of the foraging flights of feral pigeons (*Columba livia* f. *domestica*) from three Italian cities

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Abstract

Foraging flights of feral pigeon populations may differ in occurrence and extent from town to town. In this paper, the annual pattern of such flights from three medium-sized Italian cities (Venice, Parma and Lucca) is described and compared with that recorded for a Mediterranean population of wild rock doves from Sardinia. The data provide evidence of the similarity of these flights both within urban populations and between feral pigeons and wild rock doves. On the other hand, the presented results point to a noticeable flexibility of this behaviour, whose features seem finely adapted to the environmental features of an urban habitat and its surroundings. In particular, the distribution of food resources and of the annual trend of reproductive attempts appear to exert a leading role in shaping the characteristics of these flights.

Keywords: *Feral pigeon, urban environment, foraging flight,* Columba livia, *nesting activity, flock size*

Introduction

The daily and seasonal pattern of pigeon displacements can be markedly affected by resource distribution and availability (Johnston & Janiga 1995). Indeed, diet requirements can be met only with difficulty within cities, for urban populations, and in the colony area for wild ones (see Toschi 1939; Goodwin 1983; Little 1994; Johnston & Janiga 1995; Baldaccini et al. 2000; Rose et al. 2006 and references therein). Consequently, a typical behavioural trait of the wild rock dove is the daily foraging flights from colonial sites to feeding grounds (Goodwin 1983). Although ferals have been under evolutionary pressure firstly to cope with the needs of the urban, rather than the natural environment, these daily movements, which have been basically "bred out" of domestic races (Goodwin 1983; but see e.g. Eber 1962), still remain in urban populations, which may fly for food to adjacent agricultural areas as wild doves do in the natural environment (Havlín 1979; Janiga 1987; Ragionieri et al. 1991; Baldaccini & Ragionieri 1993; Johnston & Janiga 1995; Rose et al. 2005, 2006). These movements may differ in occurrence and extent from town to town, sometimes involving only a fraction of the considered population (e.g. Sacchi et al. 2002; Rose et al. 2005), or even being extremely rare (e.g. Murton et al. 1972, Simms 1979; Sol & Senar 1995). This loss of acquired traits in favour of naturally selected ones is rather frequent in feral pigeons and also regards some morphological characters (atavism; Ballarini et al. 1989).

Foraging flights of feral pigeons are interesting not only in an evolutionary context, but also because they have important management implications, as for instance during pigeon census (Baldaccini & Ragionieri 1993). Indeed, one of the suggested pest-control methods for these birds is the limitation of food resources in urban areas (Haag 1993, 1995). Clearly, the effectiveness of this method is related to the movement of pigeons, and is more likely to be successful when pigeons move less. Foraging flight counts may also be employed to estimate the size of the urban population (Janiga 1987), given that under certain ecological conditions only a small proportion

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of the population has a strictly urban range, depending on how much food it gets from the public (Janiga 1987).

In this paper we investigated foraging flights by feral pigeons in three medium-sized Italian cities (Venice, Parma and Lucca). Our aims were:

(1) to describe the pattern of these commuting flights in different urban environments;
(2) to compare the patterns observed in the three considered cities with those previously recorded by Baldaccini et al. (2000) for wild rock doves breeding in NW Sardinia; and
(3) to investigate the possible influence of the spatio-temporal distribution of food resources, and of the annual trend of nesting activity on the temporal features of these flights (see Lefebvre & Giraldeau 1984; Janiga 1987; Johnston & Janiga 1995).

Materials and methods

The birds and their habitats

Data on feral pigeons' foraging flights were collected over a one-year period in three Italian cities: Parma (44°48′ N, 10°20′ E) in 1992, Lucca (43°50′ N, 10°30′ E) in 1996–1997, and Venice (45°26′ N, 12°19′ E) in 2003–2004. While the data regarding Venice have never been published before, parts of the observations regarding Parma and Lucca have been already published (Baldaccini & Ragionieri 1993; Baldaccini & Giunchi 1998). All data were completely rearranged and reanalysed.

The three cities host large populations of feral pigeons, not sympatric with wild rock dove populations, which have become locally extinct in those areas for a long time (Toschi 1939). Venice (urban area = ~7 km^2, inhabitants = ~70,000), the northernmost city, is an island in a large wetland (580 km^2) that pigeons must fly over to reach mainland foraging sites, i.e. cereal crops and a grain-loading and deposit site in the port of Marghera. Parma (~25 km^2, ~160,000) is surrounded by a large agricultural area characterized by extensive crops of cereals and alfalfa that are the main feeding grounds of feral pigeons (Baldaccini & Ragionieri 1993). Also Lucca (~5 km^2, ~80,000) is bordered by countryside where agriculture is, however, less extensive; contrary to the other two studied populations, in this area feral pigeons feed to a large extent in cereal processing mills which are relatively close to the city's medieval walls (Baldaccini & Giunchi 1998). The estimated feral pigeon population size at the time of data collection was at least 40,000–60,000 individuals for Venice (Baldaccini et al., unpublished data), 13,000–18,000 for Parma (Baldaccini et al., unpublished data) and 4000–8000 for Lucca (Bechelli G. 1996. M.Sc. thesis, Pisa University).

To compare the urban and wild populations, we considered the only published data on wild rock dove, which regard the Capo Caccia population (NW Sardinia, 40°36′ N, 08°10′ E; Baldaccini et al. 2000).

Foraging flights

Flocks of pigeons departing from (D) and returning to (R) each city were observed from a vantage point, whose location was chosen according to the pigeons' preferred routes, on the boundary of the built-up area. As reported for wild rock doves (Baldaccini et al. 2000), commuting flights were observed one day per month, from sunrise to sunset, using binoculars when necessary. The observations were performed in good weather conditions with no or moderate wind. For each flock, flight direction, time of sighting relative to local sunrise and flock size were recorded. As observed for wild rock doves (Baldaccini et al. 2000), the returning flight path of feral pigeons does not always coincide with the departing one (see also Baldaccini & Ragionieri 1993). Consequently, R-flights observations tended to be less consistent than those for D-flights. Therefore data analysis was mainly based on D-flights, except when specified otherwise.

In order to describe feral pigeons' D-flights for each day of observation, we analysed the annual trend of the same variables considered in Baldaccini et al. (2000): total number of pigeons observed per day (NTOT); total number of groups observed per day (NGR); median flock size per day (MED); numbers of hours since sunrise needed for 50%+1 of NTOT pigeons to depart from the city boundaries (T50). In addition, to better characterize the daily pattern of movement, we also included in our analysis the number of turning points (i.e. changes in trend direction, increasing or decreasing, during the day) of the D-flight daily trend (TP).

For each city, these variables were standardized across months, in order to make the level of variation comparable across measurements, and then used to compute a month's dissimilarity matrix (MDM), with 1–r Pearson product–moment correlation coefficient as distance index. The MDMs for the three cities were compared with those of wild rock doves, excluding September from the analysis as data for wild rock doves is not available for this month. The Mantel test, i.e. the correlation between two sets of dissimilarities (Legendre & Legendre 1998), based on 1000 permutations and adjusting the overall significance level by means of the sequential Bonferroni correction (Rice 1989; Sokal & Rohlf 1995) was used. To perform this analysis, the MDM of rock doves was recalculated with respect to that considered in Baldaccini et al. (2000) in order to include the TP variable.

The annual pattern of foraging flights was described by computing cluster analysis (complete linkage) on the above-mentioned MDM. That for rock doves was recalculated on the MDM including the TP variable. We did not report in detail the results of this analysis, as it was substantially analogous to that reported in Baldaccini et al. (2000).

In order to test the possible influence of the annual trend of breeding activity on the pattern of D-flights, during the same period of foraging flight observations, in Venice and Lucca we monitored the nesting activity of feral pigeons in a sample of nests (Lucca, $n=44$; Venice, $n=16$). These data were used to derive an index of nesting activity (NAI) in each considered month, by calculating the monthly percentage of monitored nests that contained eggs or nestlings (active nests).

One- and two-sample tests were performed by means of exact randomization (permutation) tests (Sokal & Rohlf 1995), while statistical significance of correlation coefficients was assessed by calculating two-sided nonparametric approximate bootstrap confidence intervals (DiCiccio & Efron 1996). All statistical calculations were performed using the R software (R Development Core Team 2005).

Results

As reported in Figure 1, the total number of departing (D) pigeons recorded in the three cities was different, while there was a substantial similarity in the annual trend of the total number of D-pigeons observed per day (NTOT). Indeed, movements were greater during the warm period of the year, while they were less extensive in wintertime. It is interesting to note that Parma and Venice showed relatively similar trends, with the maximum numbers of birds recorded in late summer–early autumn, while in Lucca this peak tended to come earlier (Figure 1). The differences in the total number of pigeons between maximum and minimum peaks, expressed as percentage of the maximum value of NTOT recorded during the year, were 80% in Venice, 91% in Parma, and 56% in Lucca. The values of NTOT recorded for returning (R) pigeons were substantially comparable to those of D-flights both in Parma and Lucca (Parma: $T=996$, $P=0.37$; Lucca: $T=346$, $P=0.21$; one-sample permutation test), while in Venice the daily records of R-pigeons tended to be consistently lower than those of D-pigeons ($T=3695$, $P=0.0005$, one-sample permutation test).

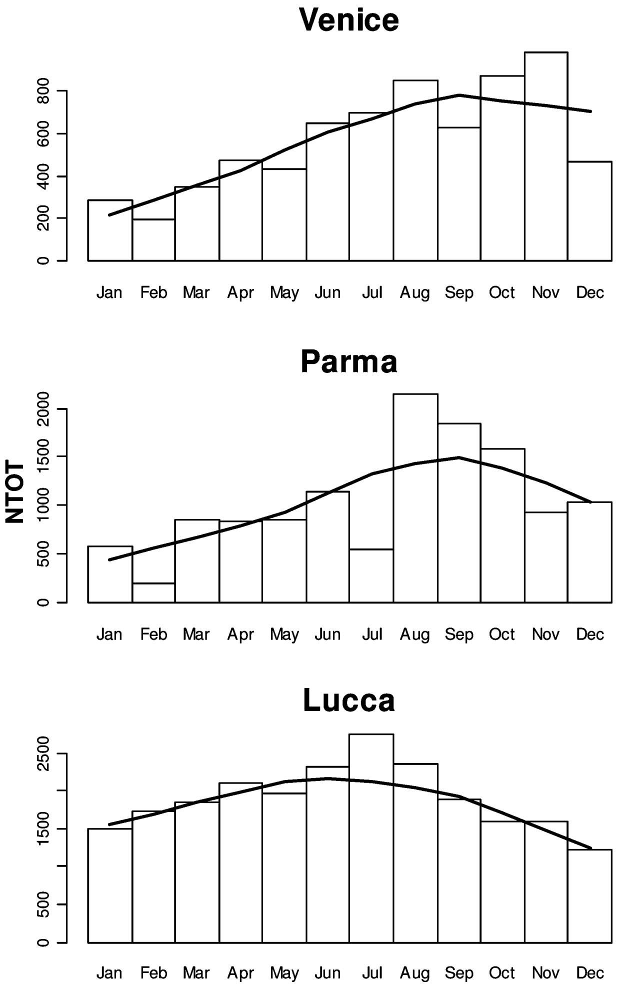

Figure 1. Annual trend of the total number (NTOT) of departing D-pigeons observed per day in Venice, Parma and Lucca. Smoothing lines were calculated using Locally Weighted Polynomial Regression (LOWESS) with a span=2/3.

As recorded for NTOT, also the number of groups observed per day (NGR) and the median flock size (MED) showed remarkable differences among cities (Figure 2). Indeed, Lucca pigeons left the city in rather small groups or even as single individuals, while in Parma and Venice flocking was more conspicuous. On the other hand, the observed seasonal trend of both variables was substantially similar in all three cities (Figure 2). Small groups were relatively common in the late spring and summer periods, while, in autumn–winter, flock size tended to increase. The median flock size of

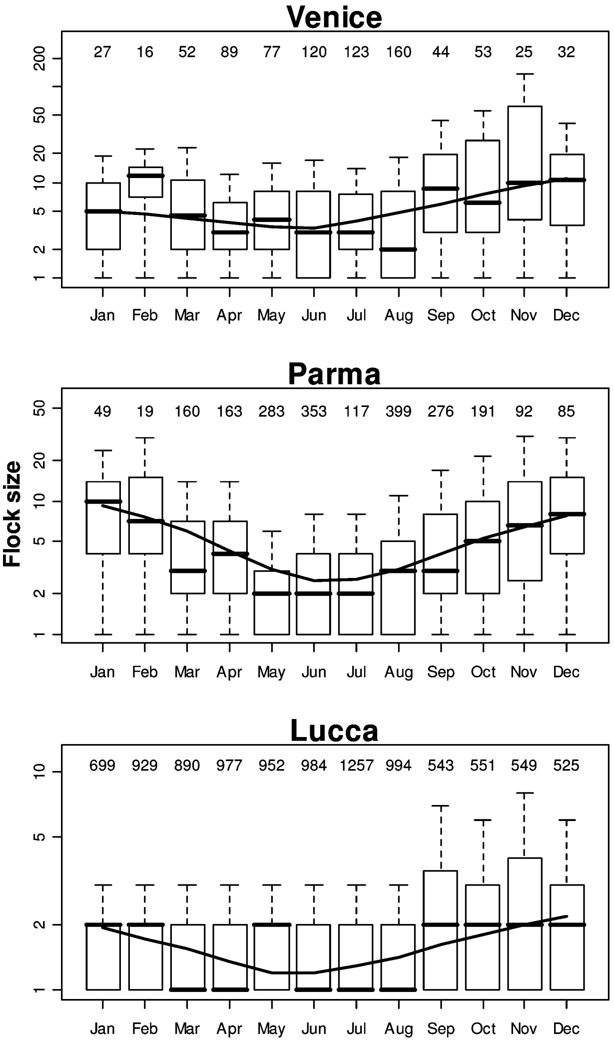

Figure 2. Box-and-whisker plot of the flock size of departing D-pigeons observed in Venice, Parma and Lucca (numbers above boxes=number of groups observed per day – NGR). Smoothing lines of the median flock size per day (MED) were calculated using LOWESS (see Figure 1).

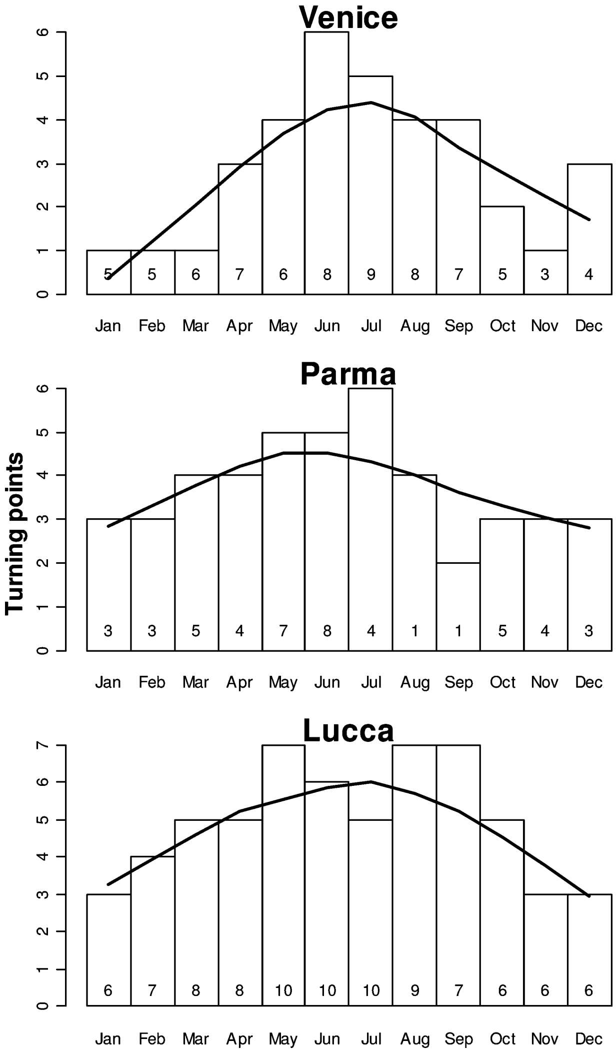

Figure 3. Number of turning points (TP) of the daily trend of D-flights recorded in each month in Venice, Parma and Lucca. Smoothing lines were calculated as in Figure 1. Numbers refer to the hours after sunrise needed for 50%+1 of NTOT pigeons to depart from the city boundaries (T50).

R-flights was relatively similar to that of D-flights both in Parma and Lucca (Parma: $T=95$, $P=0.31$; Lucca: $T=40$, $P=0.12$; one-sample permutation test), while in Venice it tended to be slightly lower in all months, with the exception of February ($T=295$, $P=0.01$; one-sample permutation test).

The temporal distribution of movements during each day of observation showed significant variability during the year (Figure 3). In wintertime, birds tended to leave the cities over a shorter period (a small number of hours after sunrise needed for 50%+1 of NTOT pigeons to depart from the city boundaries –T50) and with a single peak of departure (low numbers of turning points –TP). Conversely, in warmer periods, corresponding with an increase in day length, we observed a longer activity span, which is clearly indicated by a parallel increase of T50. In this period the daily pattern of D-flights was more complicated, as indicated by the clear increase of TP (Figure 3), although there was a general tendency to have two main peaks of movement, the first one in the morning and a second one during the afternoon (Figure 4). These two patterns are illustrated in detail in Figure 4, taking as examples a mid-winter (January) and a summer month (June). On the whole, the pattern of daily R-flights was substantially similar to that of D-flights in Venice and in Parma, as testified by the significant correlation of D- and R-TP (respectively, $r=0.79$, $P=0.01$; $r=0.64$, $P=0.02$). On the other hand, no correlation emerged between the TP of D- and R-flights of Lucca pigeons ($r=0.25$, $P=0.4$).

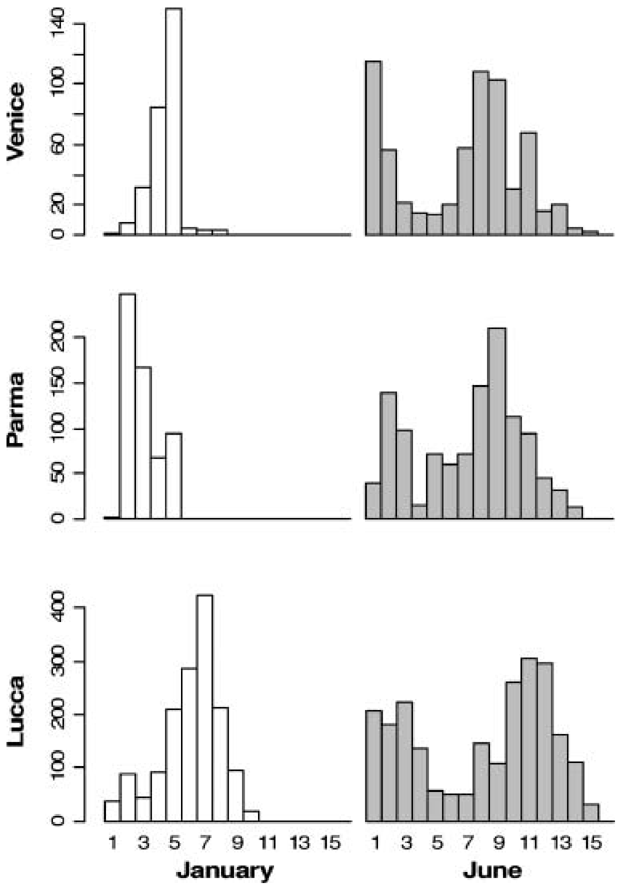

Figure 4. Time course (hours after sunrise) of the number of departing pigeons (D-pigeons) recorded in January and June (open and filled bars, respectively) in the three considered cities.

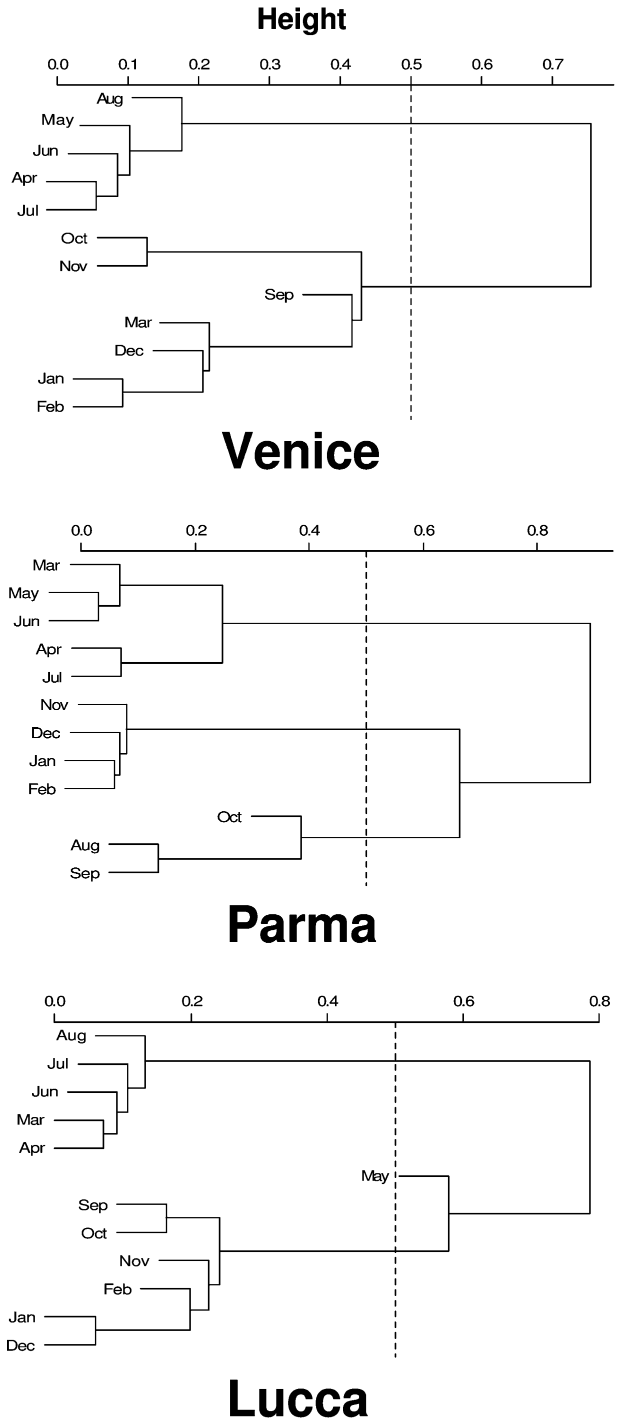

Figure 5. Dendrograms showing the pattern of clustering of the 12 days considered for departing flights. Note the different scales of the three plots. Broken lines indicate the cut height=0.5.

The analysis of the month's dissimilarity matrixes (MDMs), performed using the Mantel test after sequential Bonferroni correction, revealed a significant correlation both within feral populations ($r_{\mathrm{Venice,\,Parma}}=0.54$, $r_{\mathrm{Venice,\,Lucca}}=0.65$, $r_{\mathrm{Parma,\,Lucca}}=0.67$; all $P<0.05$) and between feral pigeons and wild rock doves (all $P<0.05$). On the whole, the D-flights in Venice tended to show characteristics more similar to the wild population ($r=0.78$) than did those of Parma and Lucca (respectively, $r=0.46$ and $r=0.44$).

Figure 5 and Table I report the pattern of clustering of D-flights recorded in each month calculated on the MDM obtained from the five descriptors listed in the Methods section. Although the distance among clusters is relatively variable among the three cities, the general pattern is comparable. Using a cut height=0.5 we can identify two main clusters in Venice, and three in Parma and Lucca, although in the last case one cluster includes only a single month (May). In all cities, spring and summer months tend to cluster together and the same is true regarding autumn and winter months. Exceptions are March in Venice, which is included in the winter cluster, and May in Lucca, which, as mentioned previously, forms a single cluster, well separated from the other two. It is interesting to note that in Parma late summer and early autumn months form a third

Table I. Summary of clusters identified using a cut height=0.5. Data on rock doves are also reported for comparison (see also Baldaccini et al. 2000).

	Feral pigeons			
	Venice	Parma	Lucca	Rock doves
January	A	A	A	A
February	A	A	A	A
March	A	B	B	A
April	B	B	B	B
May	B	B	C	B
June	B	B	B	B
July	B	B	B	B
August	B	C	B	B
September	A	C	A	/
October	A	C	A	A
November	A	A	A	A
December	A	A	A	A

cluster, which is not evident in the other two cities. This main separation between spring–summer and autumn–winter parallels what was observed in wild rock doves (Table I), although the distinction between these two periods in the latter case is more evident (see Baldaccini et al. 2000).

The monthly values of the index of nesting activity (NAI) recorded in Venice and Lucca were highly correlated ($r=0.87$, $P<<0.0001$), and in both cities we observed a clear difference regarding this parameter between the two main clusters identified using 0.5 as split distance [Venice: $T=183$, $P=0.005$; Lucca (only considering clusters A and B): $T=116$, $P=0.006$; two-sample permutation test; Figure 6]. It is interesting to note, however, that the NAI values recorded in the two clusters were not completely separated. In particular, February NAI in Lucca was clearly at variance with respect to the relatively low values recorded in the other months grouped in cluster A.

Discussion

The patterns of feral pigeons' foraging flights of the three populations show remarkably common features. Indeed, the month's dissimilarity matrixes (MDMs), calculated on the five considered variables, proved significantly correlated both within ferals and between ferals and wild rock doves. It is reasonable to assume that these similarities probably reflect comparable selective pressures. Given the close relationship between feral pigeons and wild rock doves (Johnston et al. 1988; Johnston 1992), we could not exclude a possible effect of a shared endogenous component. This innate component, however, probably has a marginal effect at most on the annual pattern of these flights. Indeed, commuting flights are differentially expressed both by wild rock doves and feral pigeons depending on a number of ecological factors (e.g. the type of food resources, their spatio-temporal variability, the annual breeding cycle), which could be responsible both for the similarities and peculiarities recorded for the considered populations (Havlín 1979; Janiga 1987; Johnston & Janiga 1995). Actually, the strong effect of these ecological factors on the foraging behaviour of these birds is clearly testified by the substantial suppression of commuting flights when the available

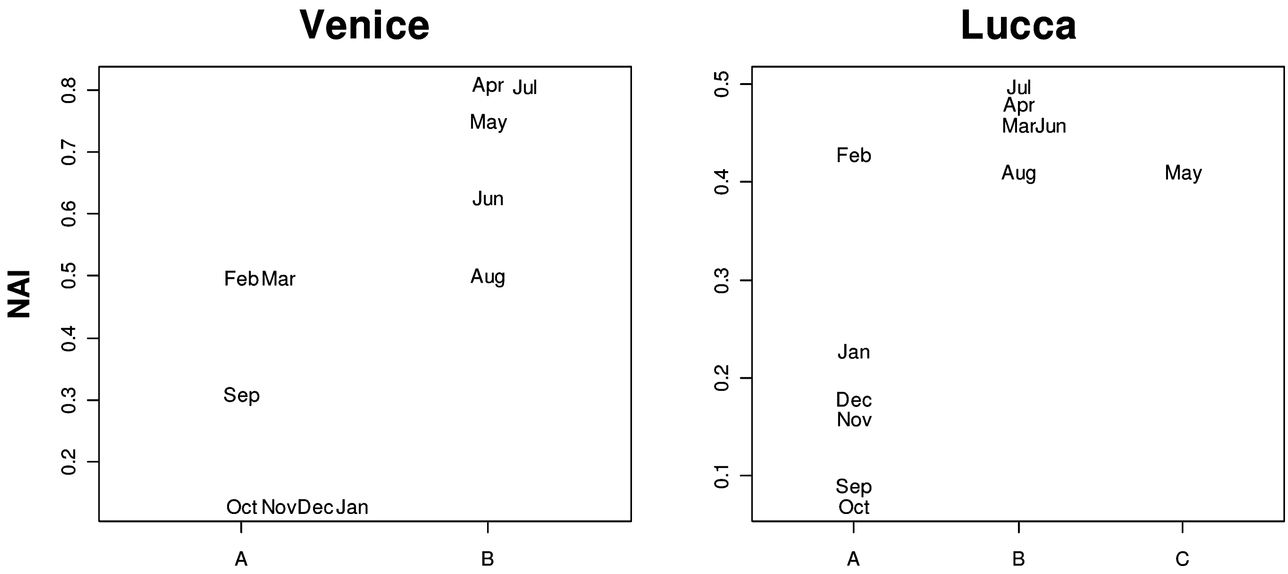

Figure 6. Values of the index of nesting activity (NAI) recorded during the months grouped in the two (Venice) and three (Lucca) clusters identified using a cut height=0.5. Cluster identifiers as in Table I.

resources within cities or in the colony area can fulfil the food requirements (see e.g. Baldaccini et al. 2000 and unpublished data).

Considering the general pattern of clustering, it is evident that nesting activity exerts an important role in shaping the characteristics of foraging flights. Indeed, the mean values of the index of reproductive activity (NAI) vary significantly according to the clusters identified using 0.5 as split distance both in Venice and in Lucca. In this respect, it should be noted that a correlation between the flight activity pattern and the annual reproductive cycle has been previously suggested both for feral pigeons (Janiga 1987) and also for wild rock doves (Baldaccini et al. 2000). As hypothesized by Janiga (1987; see also Johnston & Janiga 1995), nesting activity should affect the daily schedule of movements, determining the roughly bimodal pattern observed in warmer periods as a consequence of the alternation of sexes at the nest. It is interesting to note that while cluster analysis produces a separation between spring–summer and autumn–winter periods both in ferals and in wild pigeons (see Baldaccini et al. 2000), the distinction is rather more evident in the latter, probably reflecting their markedly seasonal annual reproductive cycle, typical of all temperate latitude species of columbids (Murton & Westwood 1977; see also Cramp 1985; Guyot et al. 1985). Even though we have no data regarding the Parma NAI, it seems reasonable to hypothesize that, considering the relatively comparable latitudes of the three cities, the close relationship between nesting activity and foraging flights can explain a significant part of the above-mentioned homogeneity among the annual flight pattern of the considered feral populations.

Besides nesting activity, the spatio-temporal distribution of food resources is another important variable to be taken into account when trying to interpret our results. In particular, since flying to extra-urban areas in order to feed is costly, it seems reasonable to assume that the availability of food within a given city has a significant effect on the fraction of the population that moves. In this respect, Venice and Lucca probably represent opposite extremes. Venice hosted the highest population density of feral pigeons among the considered cities (more than 8000 birds km^{-2}) and one of the highest ever reported in literature (see Johnston & Janiga 1995), but the number of birds foraging in the mainland is rather small. This result suggests a high availability of food resources within the city, which could not be explained simply by considering the extension of the urban area and the number of its inhabitants. Instead, we should take into account the tourist traffic (about 4 million tourists in 2003; COSES 2004), which is especially high during spring and summer periods. This consistent human presence not only means a high intensity of pigeon-feeding by the public, but especially a high production of organic waste, which, as suggested by Buijs & Van Wijnen (2001) for Amsterdam, notably affects pigeon population density, and, in the case of Venice, reduces the number of commuting pigeons. On the other hand, the fraction of commuting pigeons we observed in Lucca is rather high, probably as a consequence of the availability of a highly predictable food resource (cereal processing mills) rather near the city (<2 km, considering the closest sites; see also Baldaccini & Giunchi 1998).

The characteristics of food resources not only affect the total number of "commuters", but also its annual trend. Indeed, in all cases, analyses evidenced a remarkable variability of the number of pigeons observed per day (NTOT) during the year, with low numbers in the winter and a noticeable increase during spring and summer. The explanations of this seasonal pattern could be several, such as the variability of foraging routes, the annual trend of population size, and the variable exploitation of different food resources. Actually, the variability of foraging routes seems substantially unlikely, especially for Lucca and Venice pigeons, which, according to our observations, in practice leave their cities following a single route only. On the other hand, the annual trend of NTOT broadly fits the plausible demographic trend of the considered population. Indeed, the maximum number of pigeons recorded during the observations tends to occur when pigeon populations usually reach their peaks, i.e. as reported for several European cities, during late summer and autumn, just before the more or less severe decrease due to high winter mortality (Johnston & Janiga 1995). This pattern is confirmed in Venice, where we observed an increase of birds counted until late autumn and a sudden decrease from December to March (Baldaccini et al., unpublished data). It should be noted, however, that the differences reported between maximum and minimum NTOT peaks are generally far more extreme than those that could be reasonably hypothesized simply considering the demographic trend, which probably does not exceed ~40% of the annual maximum population size, according to the available data (Johnston & Janiga 1995; Baldaccini et al., unpublished data). On the other hand, it seems likely that this pattern also reflects the exploitation of different food resources. Indeed, as recorded for other European cities (see Johnston & Janiga 1995), during the winter months external food sources are generally low, and breeding activity is generally suspended (which means fewer nutritional requirements than in the reproductive season; see Murphy 1994), feral pigeons mainly remain within the city, exploiting internal resources, and only a relatively small part of the population moves during the warmer hours of the day. This pattern shares some similarities with that recorded for wild rock doves, which tend to exploit resources close to residential areas (mainly lentiscus berries, when available) during colder months, while they move to inland agricultural areas in warmer periods (Baldaccini et al. 2000). Our hypothesis regarding the seasonal variability of use of differently distributed food resources is confirmed by the relatively anomalous behaviour recorded in Lucca. Indeed, in this city, given that the outside food resource is relatively constant and probably easily reachable, differences between winter and summer periods are less evident, and probably fit more closely the annual population size trend.

Our hypothesis that the distribution and availability of food resources are one of the main factors to influence the characteristics of commuting flights is further supported by the annual trend in flock size. In all three populations, winter flocks are larger than summer ones, and this pattern was also recorded for wild rock doves in Sardinia (Baldaccini et al. 2000). This could be explained considering the studies of Lefebvre & Giraldeau (1984), which show that when quantity and location of food is unpredictable, pigeon flocks tend to be bigger, as a result of a sort of mutual parasitizing of specialization, which provides group foraging individuals with a wider range of foods than does solitary foraging (Giraldeau 1997; Giraldeau & Beauchamp 1999; Rafacz & Templeton 2003; see also the information centre hypothesis: Ward & Zahavi 1973; Sonerund et al. 2001; Dall 2002, and references therein). Following this line of reasoning, the greater frequency of small groups in the spring–summer period is probably a consequence of a greater predictability of food, which in turn is related to agricultural practices in areas surrounding the cities. In this case, the costs of group foraging, which increase with group size (Wittenberger & Hunt 1985; Milinski & Parker 1991), being mainly related to inter-individual competition, probably exceed the advantage of large flocks in searching for food (see also Waltz 1982). The data for Lucca further support this hypothesis. In this city, we observed indeed a large majority of birds that commuted singly or in pairs and no substantial differences in flock size over the year. As previously noted regarding the annual trend of NTOT, the exploitation of a predictable food resource, whose distribution does not vary significantly during the year, likely influences the foraging strategy of pigeons, acting against the formation of large flocks.

Obviously the advantages of flocking are not only limited to food searching; also the reduction of predation risk should be considered (see Hamilton 1971; Pulliam 1973; Bertram 1978; Kenward 1978). In this respect, it is interesting to note that feral flocks in all the three cities tended to be smaller than wild flocks recorded in Sardinia (Venice: $T=70$, $P=0.02$; Parma: $T=20$, $P=0.003$; Lucca: $T=0$, $P=0.001$; one-sample permutation test), where, especially during autumn and winter, flocks of more than 40 pigeons were relatively frequent (Baldaccini et al. 2000). This tendency of ferals to form small flocks has been recorded also in other cities (see Johnston & Janiga 1995), and could probably be related with a reduced presence of aerial predators in urban and suburban environments. In this context, it should be mentioned that R-flights flock size tends to be even greater than that of D-flight in wild rock doves (Baldaccini et al. 2000), while not different or even smaller in feral pigeons. Although we cannot rule out a possible orientational advantage of flocking (see Guilford & Chappel 1996; Burt de Perera & Guilford 1999, and references therein), when pigeons have the urgency to reach the colony swiftly and safely, it seems likely that this result could be explained in terms of antipredatory strategy. Indeed, when pigeons return to their colony the costs of flocking in terms of competition for food resources are null and birds could gain advantage from the probable reduction of the risk of predation due to grouping. This benefit is relevant when predation is relatively intense (i.e. for wild rock doves), while probably not relevant when predation risk is low (i.e. feral pigeons), and birds could also risk paying the cost of an increased attraction of the scarce predators that might be present.

To sum up, our data show at the same time both the constancy and the noticeable flexibility of feral pigeons' foraging flights, whose characteristics seem finely adapted to the environmental features of an urban habitat and its surroundings. Obviously our approach, while allowing a broad comparative description of the temporal patterns of this phenomenon, does not permit a fine analysis of the behavioural strategies involved, and thus our explanations of the results remain speculative. Given the complexity of the urban environment, the population size of these birds and their mobility, an in-depth study of the spatio-temporal behaviour of feral pigeons is actually not easy to carry out. Nevertheless, the recent advances in the GPS-tracking method indicate that this analysis could be performed in the near future (Rose et al. 2005, 2006), thus allowing the hypothesis derived from our coarser-grained approach to be tested.

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