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ORIGINAL ARTICLE

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Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*)

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Abstract Feral pigeons are descendants of wild rock pigeons that have adapted to the urban habitat. They have partially conserved the foraging behaviour of their wild ancestors (flights to agricultural areas) but have also developed new habits. Previous studies on the foraging strategies of feral pigeons have given various results, e.g. maximum distances reached by the pigeons (measured in a straight line from the resting places) differed between 0.3–0.5 km and 18–25 km. This study focuses on the spatio-temporal activity of feral pigeons in the urban habitat. We equipped 80 free-living feral pigeons from Basel, Switzerland with GPS receivers. We found three different foraging strategies for pigeons in Basel: (1) in the streets, squares and parks near the home loft, (2) in agricultural areas surrounding the city, (3) on docks and railway lines in harbours. The maximum distance reached by a pigeon was 5.29 km. More than 32% of the pigeons remained within 0.3 km of the home lofts and only 7.5% flew distances of more than 2 km. Females covered significantly longer distances than males, preferring to fly to more abundant and predictable food sources. Temporal activity patterns showed to be influenced by sex, breeding state and season. In contrast to wild rock pigeons and to feral pigeons in other cities, pigeons in Basel showed a clear bimodal activity pattern for breeding birds only. The differences between our results and those of other studies seem to be partly method-dependent, as the GPS-technique allows to record the pigeons' localisations continuously in contrast to other methods. Other differences might be due to different kinds of food supply in the various cities. Our study shows that feral pigeons have individual foraging strategies and are flexible enough to adapt to different urban environments.

Keywords Feral pigeon · *Columba livia* · GPS · Urban habitat · Spatio-temporal behaviour

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Introduction

Feral pigeons are descendants of wild and domesticated rock pigeons (Johnston and Janiga 1995) that have adapted to the urban habitat (Haag-Wackernagel 1998). Wild rock pigeons essentially forage on agricultural areas around the cliffs where they breed (Hewson 1967). They essentially feed on cultivated and wild seeds but also eat small snails and other invertebrates (Murton and Westwood 1966; Goodwin 1983). Feral pigeons have partially conserved the foraging habits of their wild ancestors, i.e., in some cities they still fly to surrounding agricultural areas to feed (Havlin 1979; Janiga 1983; Baldaccini and Ragionieri 1993; Little 1994). In other cities, they have adopted new foraging habits based on spilled food or feeding by humans. Johnston and Janiga (1995) define two principal foraging strategies for feral pigeons: (1) foraging in the streets, squares and parks near the home loft and (2) foraging in agricultural areas. They define foraging on docks and along railway lines in harbours and industrial areas as an intermediate strategy. In Brno (Havlin 1979) and in Bratislava (Janiga 1983), the majority of pigeons flew to adjacent agricultural areas to find food. Johnston and Janiga (1995) suggest that this is the most important foraging strategy for feral pigeons. In other studies, no flights to fields were recorded, and the pigeons fed in the streets and squares in the town (e.g. Gompertz 1957; Sol and Senar 1995; Slotta-Bachmayr et al. 1995). The great diversity of these findings indicates that the foraging habits of feral pigeons may greatly vary between cities with their different food resources in and outside the urban area.

Wild rock pigeons show bimodal foraging activity in the summer months and a single peak of foraging flights in the winter (Baldaccini et al. 2000). The same is reported for feral pigeons flying to agricultural areas (Havlin 1979; Janiga 1987). Lefebvre and Giraldeau (1984) analysed the daily feeding site use of urban pigeons. They also recorded a bimodal daily feeding schedule.

The studies, conducted to understand how the pigeons use their urban habitat, were done with various methods such as: (a) observation of individually marked birds in town (Lefebvre and Giraldeau 1984; Steiner and Zahner 1994; Sol and Senar 1995), (b) observation and counts of flying pigeons (Havlin 1979; Janiga 1987), (c) use of electronic rings detected by an antenna at a few feeding places (Dell'Omo 1997) and (d) telemetry (Scholl and Häberling, 1995 unpubl. data). All of these methods have limitations due to the length of time needed for observation, the difficulty in searching an entire town and its surroundings for marked pigeons and the difficulty in recognizing the rings in a highly structured urban habitat or in fields when pigeons show an increased escape distance.

We used the Global Positioning System (GPS) to study the spatio-temporal use of the urban habitat by feral pigeons in Basel, Switzerland. Satellite tracking was successfully used to monitor flight tracks of different bird species, e.g. albatrosses (Jouventin and Weimerskirch 1990; Weimerskirch et al. 1993, 1994, 2002; Waugh et al. 2000; Shaffer et al. 2001; Nicholls et al. 2002; Waugh and Weimerskirch 2003; Fukada et al. 2004; Waugh et al. 2005), frigatebirds (Weimerskirch et al. 2004) white storks (Berthold et al. 2002a,b), brent geese (Gudmundsson et al. 1995), gannets (Hamer et al. 2000, 2001; Grémillet et al. 2004), red-footed boobies (Weimerskirch et al. 2005), penguins (Guinet et al. 1997; Taylor et al. 2001) and homing pigeons (Von Hünerbein et al. 2000; Biro et al. 2002; Lipp et al. 2004). We showed that this method is also suitable for the monitoring of feral pigeons in the urban habitat (Rose et al. 2005). GPS tracking eliminates the bias due to the observation spots, as all places visited by the pigeons equipped with this design are automatically recorded. With other methods, it is not possible to record pigeons in hidden places like inner courts of buildings or on high buildings where the markings are not visible. GPS tracking not only provides information about all places visited by the pigeons, but also about the chronological sequence of a daily schedule. The method gives a better insight into individual strategies of feral pigeons than all other methods used previously.

The aim of this study is to gather precise information about the spatio-temporal use of the city of Basel by feral pigeons and to identify factors influencing this behaviour. We compared our results to those obtained with wild rock pigeons and with feral pigeons in other cities.

Materials and methods

GPS receivers

For our study, we first used three GPS-MS1 receivers (Steiner et al. 2000) from July 2002 to February 2003. From February to November 2003, we used ten SAM receivers (GPS Smart Antenna Module, based on the TIM module) designed by u-blox AG Thalwil, Switzerland, and CabTronix GmbH, Kloten, Switzerland (for technical features see u-blox AG 2003). Our receivers were 60×32×14 mm in size and weighed 36–38 g, depending on the size of the battery. The GPS receiver was 10–15% of a feral pigeon's body weight. When equipped with a 960-mA battery, recording lasted about 30 h in low-power mode (with one position recorded every 3 s). We expect an accuracy in the range of 0–25 m away from the real location in 40–95% of the recorded positions, depending on the proportion of open sky. Expected to lie within 100 m of the real location (Rose et al. 2005) are 86–100% of the positions.

We set the GPS receivers to store their position every 3 s. We used the software μ-logger (u-blox AG, Thalwil, Switzerland) for downloading. The stored positions were represented on an electronic map of Basel (from the Grundbuch- und Vermessungsamt, Justizdepartement des Kantons Basel-Stadt) by the software MapInfo Professional (MapInfo Corporation Troy, New York). For more details about the method, see Rose et al. (2005).

The pigeons

The feral pigeons used for this study are living in three lofts situated in public buildings in Basel, Switzerland (for a description of the lofts, see Rose et al. 2005). The pigeons are free-living and use the lofts as breeding or sleeping places, but they must search for their food themselves like all urban feral pigeons. Before and during the GPS study, we observed the pigeons in the lofts once a week to identify the sex of the birds (through their behaviour), the pairs, and we controlled their fidelity to the loft and their breeding state. To ensure the return of the pigeons equipped with GPS receivers, we chose pigeons which were closely bound to the loft, mostly birds that had regularly bred during the months preceding the GPS flights. We studied 35 females (average weight 344±25 g), 44 males (average weight 356±27 g) and one pigeon of unknown sex (340 g). Forty-two pigeons were caught in the Matthäus loft, 15 in the Peters loft and 23 in the Stapfelberg loft. All birds were in good physical condition, i.e., they weighed more than 300 g and showed no sign of disease such as soiled plumage or grey and soiled nostrils (Vogel et al. 1983). The GPS method constrained us to choose this non-random sampling of 80 birds.

Dummies and receivers were fixed on the pigeons' back with Velcro tape (one part glued onto the GPS, the counterpart glued onto the feathers of the birds) and with a harness consisting of two loops passing around the body and joined at the breast (Rose et al. 2005).

Before equipping the pigeons with the GPS receivers, we trained them with dummies of the same size and weight as the receivers. The pigeons carried the dummies for 4 to 9 days to become used to the load. The training allowed us to observe the pigeons' reaction to the load. For the GPS records, we caught the pigeons in the morning to fix the receivers on their backs and released them immediately in the loft. The records started when the pigeons flew out of the loft, as there is no reception of satellite signals inside buildings. The same day after dark, we removed the GPS receivers from the homed birds to download the data onto the PC and to charge the batteries. We intended to obtain ten successful GPS records with each trained pigeon, but this was not always possible. Some pigeons lost the Velcro tape before we could perform the ten records. We let the same pigeon undisturbed between two consecutive GPS records for at least one day. We started the records at 8:00 (local time). In the evenings of the day before equipping the pigeons with GPS receivers, we closed the Stapfelberg loft and the Peters loft to prevent the pigeons from escaping before or at our arrival in the morning. This precaution was not necessary in the Matthäus loft, as the pigeons did not escape before or on our arrival. Our presence in the loft made some pigeons leave immediately after being released. They turned back soon after our departure. These data were valuated as if the pigeons had been inside the loft and we corrected the data set to eliminate these obviously biased parts of the records.

Between July 2002 and November 2003, we performed a total of 575 records. Individual pigeons were equipped on 1–17 days altogether with the receivers (mean 7.2±3.3). From July 2002 to February 2003, we worked with three GPS receivers and could, therefore, equip a maximum of three pigeons each day. From February to November 2003, we worked with ten GPS receivers. Two hundred sixty-six records were performed with pigeons from the Matthäus loft, 104 from the Peters loft and 205 from the Stapfelberg loft. Eighty-seven records were obtained in winter, 174 in spring, 61 in summer and 253 in autumn. The records stored between 1 and 19,505 positions (mean 3,631± 3,036).

The captures and the experiment were performed with the permission of the Cantonal Veterinary Office of Basel Town, Switzerland (authorization no. 1859).

Data processing and statistics

For the analysis, we classified the records in six categories: 1) complete records that started and ended at the loft, 2) records that did not start at the loft (due to the technical delay to get the first position), 3) records that did not end at the loft (due to the end of the battery duration), 4) records that did not start nor end at the loft, 5) records where the pigeon remained only on the roof of the loft and 6) records with single positions only that were not analysable. The last two categories were excluded from the statistics. We discussed the technical problems leading to incomplete records and their implications in Rose et al. (2005).

Variables

We used as maximum distance for one record the straight-line distance between the loft and the most remote spot visited by the pigeon on that-day record. The mean distance for a loft was calculated using the mean maximum distances of all pigeons.

The recorded data showed that our GPS-equipped pigeons sometimes flew in and out of the loft several times a day. We summed up the time spent outside without considering the time spent inside the loft between two flights.

We defined the seasons according to day length because our hypothesis was that this factor would have a great influence on the pigeons' behaviour. We took the 92 longest (summer) and the 91 shortest days (winter) of the year and for spring and autumn 91 days of intermediate length each as calculation basis for our statistics.

For all statistical analyses, we used the program SAS statistical software (release 8.2, SAS Institute, Cary, NC, USA). We entered all individual records in the models used (PROC MIXED). The factors "affiliation to a loft", "sex", "breeding state" and "season" were treated as fixed factors. Repeated observations within subjects were modelled using an AR(1) covariance structure. We searched for the factors influencing the distance covered by the pigeons using a mixed linear model and we applied a logarithmic transformation to the variable "distances covered" to approach a normal distribution. For the analysis of distance, we employed all records that ended at the loft (complete records and records that had not started at the loft). We assume that incomplete records of this category show the maximum distance attained on that day.

We tested the influence of "loft", "sex", "breeding state" and "season" on the time spent outside the loft. For these analyses, we employed the complete records only.

For the graphical representation of the day's activity, we divided the day into time intervals of 30 min and for each interval we counted the number of pigeons equipped with a GPS receiver that were outside the loft. Time is given in central European time (CET).

The influence of "loft", "sex", "breeding state" and "season" on the time of departure and arrival and on the time spent outside the lofts was tested with a mixed linear model. For analysis of the time of departure, we employed all records that started at the loft (complete or not) and for the time of arrival, we employed all records that ended at the loft. Data of departure and arrival (calculated in seconds after midnight) were adjusted to attain normal distribution of the residuals. The following transformation was applied to the time of departure: $y'=\ln[(y-6\times3600)/60]$. Time of arrival was adjusted with the following transformation: $y'=\ln[(22\times3600-y)/60]$.

In a second step, we introduced the day length as a supplementary fixed factor into the model to test its influence on the time spent outside and the times of departure and arrival. Day length was calculated on the basis of the effectively measured light intensity on each day. The day began with the beginning of civil twilight at dawn and ended at the end of the civil twilight at dusk (when the solar azimuth was at −12°).

In the subsample of animals with data from different breeding states, we also performed two-way analyses of variance with "average flight characteristics by animal and breeding state" as the dependant variable and "animal" and "breeding state" as explanatory factors. In this way, the influence of time-invariant factors can be automatically controlled and statistical power to detect differences by breeding state may be enhanced, provided that there is a sufficient number of individuals with data from different breeding states.

In all our analyses, we set the level of significance at $\alpha=0.05$.

Results and discussion

We performed 575 records of which 497 stored positions (86.4%). Two hundred fifteen records (43.3%) were complete, 232 records (46.7%) were incomplete (111 missed the beginning of the record, 65 missed the end and 56 missed both), 44 records (8.9%) only remained on the roof of the loft and six records (1.2%) only stored a few isolated positions and could not be analysed. We obtained between 1 and 15 (mean 6.2±3.2) analysable records for each pigeon. One pigeon of the 80 used for the GPS flights performed only one record with no stored positions and was, consequently, not included in the statistics. We also excluded the records from the pigeons with unknown sex. This led to the number of 212 complete records quoted in the results. Other aspects drawn from the same dataset, such as the detailed description of the places visited by the pigeons, are published in Rose et al. (2006).

Maximum distances attained from the loft

The maximum distances attained during the records varied between 0.03 and 5.29 km. The 31 pigeons from the Matthäus loft attained mean distances of 0.70±0.26 km (mean±SD), the 13 pigeons from the Peters loft 0.65±0.53 km and the 23 pigeons from the Stapfelberg loft 0.49±0.62 km. The distances attained by pigeons from the Matthäus loft were significantly longer (mixed linear model, $P=0.0001$, $n=67$ pigeons and 320 records).

The maximum distances covered were due to a small number of the pigeons (Fig. 1). Over 32% of all pigeons equipped with a GPS receiver were never recorded more than 0.3 km away from their loft and only 6.4% flew further than 2 km.

Table 1 compares our results with those of other studies. The maximum distances covered by pigeons in Basel during the present study ranged within the results obtained in Rome, Salzburg and Vienna, but were longer than those measured in Barcelona, Zurich and in towns from other publications stating that feral pigeons covered rarely more than 0.5–0.6 km. The distances covered to reach the fields (max 5.3 km) were shorter than those given by other publications (Table 1). They depend essentially on the size of the city, the spatial distribution of the resources and the food supply in the fields. More information about the food resources available in and outside the cities would be necessary to work out common factors that influence the pigeons' behaviour.

There is no evidence of impact of the weight of the receiver on the distances flown by the pigeons. Observations in the lofts showed no behavioural changes on pigeons equipped with the load. Fielding pigeons (without an artificial load) have never been observed in high numbers. Only isolated flocks of 20–40 birds were sometimes recorded. And finally, a detailed study performed in Basel with ringed pigeons of the same population (Haag 1984) measured shorter maximum distances than in the present study (Table 1). The GPS method allowed to record commuting flights to the fields, which was not possible with the other method.

Figure 1 additionally shows a large variation in the covered distances between the lofts. These differences are

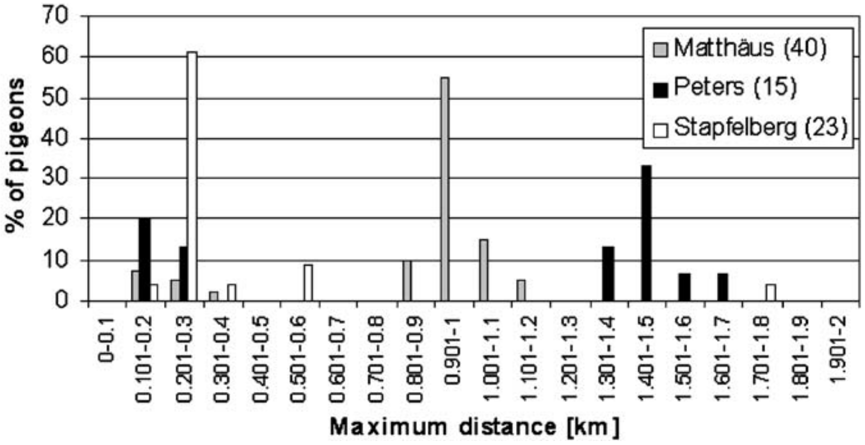


Fig. 1 Percentage of pigeons that had their maximum distances in the different categories of distances. The numbers in *brackets* following the name of the lofts indicate the number of pigeons studied. Flights longer than 2 km are not represented on the *graph*. It concerns five flights, one of 4.53 km performed by a pigeon from the Peters loft and four flights of pigeons from the Stapfelberg loft (3.94 km, 2×3.95 km, and 5.29 km)

Table 1 Comparison of maximum and mean straight-line distances of feral pigeons

Maximum distance (km)	Mean distance	City	Method	References
0.34		Barcelona, Spain	Marked pigeons	Sol and Senar (1995)
0.5		Hamburg, Germany	Marked pigeons	Reinke (1959)
0.5 (rarely more)		Essen, Germany	Observations	Eber (1962)
0.5–0.6 (rarely more)		Vienna, Austria	Observation of obviously coloured plumage	Friedl (1938)
0.6		Zurich, Switzerland	Marked pigeons	Bauer et al. (1990)
0.8 (0.5 mi)		London, England	Marked pigeons	Gompertz (1957)
1		Rome, Italy	Marked pigeons and automated system with eletronic rings	Dell'Omo (1997)
1.3	0.11 km (inner part of city) 0.19 km (outer part of city) 96% (inner part) and 60% (outer part) within 0.2 km	Salzburg, Austria	Marked pigeons	Slotta-Bachmayr et al. (1995)
1.3		Geneva, Switzerland	Marked pigeons	Nötzli (1991)
1.4		Vienna, Austria	Marked pigeons	Steiner and Zahner (1994)
1.75 (in the city) 5.29 (to surroundings)	0.56 km (complete records) 0.59 km (all records) 32.1% within 0.3 km 34.7% within 0.5 km	Basel, Switzerland	GPS	present study
1.9		Basel, Switzerland	Marked pigeons	Haag (1984)
3–25 (flights to fields)		Bratislava, Slovakia	Visual observation of commuting pigeons	Janiga (1983)
6	95.6% within 0.5 km	Montréal, Canada	Marked pigeons	Lévesque and McNeil (1986)
6.4 (4 miles)	85% within 0.09 km (100 yards)	Manchester, England	Marked pigeons	Murton et al. (1972b)
6–8 (flights to fields)		Parma, Italy	Visual observation of commuting pigeons	Baldaccini and Ragionieri (1993)
6–11 (flights to fields)		Reggio Emilia, Italy	Visual observation of commuting pigeons	Ragionieri et al. (1992)
6–18 (flights to fields)		Brno, Czech Republic	Visual observation of commuting pigeons	Havlin (1979)
15–20 (flights to fields)		Cape Town, South Africa	Observation of commuting pigeons	Little (1994)

related to the strategies employed by the pigeons from the three lofts and are discussed in Foraging strategies.

The GPS records showed that females had longer maximum distances than the males and, on average, flew significantly longer distances (mixed linear model, *P*=0.04, *n*=67 pigeons and 320 records, including all records that ended at the loft). Table S1 in the electronic supplementary material indicates the distances attained by males and females of the three lofts. The long-distance flights to the surroundings of the city belonged to four females and only one male that was not mated to one of these females. Two studies revealed similar observations. Eber (1962) recorded more flights to agricultural areas for female homing pigeons than for males, i.e. the females flew longer distances than males. Johnston and Janiga (1995) remarked that females tended to be more conservative commuters to the agricultural surroundings, preferring to fly to predictable food sources. A possible explanation is that at less abundant or concentrated food resources, the weaker females have problems competing for food with the males (Haag 1984). Females also have higher energetic costs for reproduction. They expend 15–85% more energy than males during the egg-laying period (Walsberg 1983). Egg production is particularly sensitive to caloric deficien-

Table 2 Number of records showing the different foraging strategies, both alone and in combination

Foraging strategy	All records		Complete records	
	Number	Percent	Number	Percent
Streets/squares	252	56.4	124	57.7
Parks	4	0.9	2	0.9
Harbour	62	13.9	23	10.7
Streets/squares+fields	9	2.0	5	2.3
Streets/squares+harbour	89	19.9	46	21.4
Streets/squares+parks	27	6.0	13	6.1
Streets/squares+parks+harbour	3	0.7	1	0.5
Streets/squares+parks+fields	1	0.2	1	0.5

The combinations that are not in the table did not occur during the records (e.g., no record showed a direct flight to the fields followed by a direct return to the loft)

cy, as ovulation stops within 48 h or less in response to complete starvation (King 1973). Therefore, females are more dependent on reliable food sources than males. This could be an explanation for the observed differences.

The breeding state and the season had no significant influence on the distance covered (mixed linear model, P=0.85 and P=0.57, respectively, n=67 pigeons and 320 records).

Foraging strategies

Table 2 shows the number and the percentage of records that exhibited the various foraging strategies or combinations of them. Foraging near the loft in streets, squares and parks was the principal strategy, as it occurred in 63.3% of all records. Flying to surrounding agricultural areas was never found alone: All these records started with a stay in streets or squares. Table 3 shows the foraging strategies employed by the studied individuals. More than 37% of the pigeons foraged only near the loft (streets/squares and parks). More than 47% showed a combination between foraging near the loft and flying to the harbour ("streets/squares+harbour" and "streets/squares+park+harbour"). Only 6.4% showed flights to agricultural areas in combination with foraging near the loft ("streets/squares+field" and "streets/squares+park+field").

Figures 2, 3, 4, 5 and 6 show examples of day records illustrating the different foraging strategies. These are only five examples of strategies employed by the individuals. All combinations occurred: first, a stay in the streets near the loft and after a flight to a remote place with a direct return to the loft (not illustrated); first, a flight to a remote place and then a stay in the streets near the loft (Fig. 2); a direct flight to a remote place and a direct return to the loft (Fig. 5), a stay in the streets near the loft before and after a flight to a remote place (Fig. 6), or no flight to a remote place (Fig. 3). Some individuals searched several places during a day record (Fig. 3), others visited only one place (Fig. 4). Foraging strategies seem to vary individually, according to our limited data. Some pigeons apparently preferred flying longer distances to reach a predictable food source (e.g. the harbour), others searched many spots at shorter distances from the loft and exploited less predictable food sources, e.g. spilled food in the streets or at school buildings. Descriptions and details about the different places visited by the pigeons from the three lofts are given in Rose et al. (2006). Some pigeons employed only one strategy as pigeon "B+C+lw/or" from the Stapfelberg loft that visited the streets and squares near the loft in the 9 day records it performed (numbers are given in Table 3). Other pigeons employed different strategies on different days. For example, pigeon "A635" from the Peters loft remained in streets and squares near the loft in one record. On another day, it only visited the harbour. During five other day records, it stayed in streets and squares near the loft, but also flew to the harbour. And finally, it visited streets/squares, the harbour and, additionally, a park during one day record. We agree with Lefebvre and Giraldeau (1984), that changes in the foraging strategy may occur if a pigeon is less successful at obtaining food in an area it normally selects. It may follow other birds to their preferred areas from a common feeding ground. As our GPS records give no indications about the quantity of food taken at each visited place, other methods are required to analyse this interesting hypothesis.

Table 3 Foraging strategies of the studied individuals

Loft (n pigeons)	Streets/squares	Harbour	Streets/ squares+parks	Streets/ squares+fields	Streets/ squares+ harbour	Park+ harbour	Streets/ squares+ park+harbour	Streets/ squares+ park+field
Matthäus (40)	6 (15%)	5 (12.5%)	0	0	29 (72.5%)	0	0	0
Peters (15)	3 (20%)	1 (6.7%)	2 (13.3%)	0	6 (40%)	1 (6.7%)	1 (6.7%)	1 (6.7%)
Stapfel (23)	16 (69.6%)	0	2 (8.7%)	4 (17.4%)	0	0	1 (4.3%)	0
Total (78)	25 (32.1%)	6 (7.7%)	4 (5.1%)	4 (5.1%)	35 (44.9%)	1 (1.3%)	2 (2.6%)	1 (1.3%)

The combinations that are not shown in the table did not occur (e.g., no pigeon relied only on the strategy of visiting parks). Indications to the spatial distribution of the resources: The harbour is 1 km away from the Matthäus loft, 1.4 km from the Peters loft, and 1.6 km from the Stapfelberg loft. Fields could be attained within 3 km from all lofts

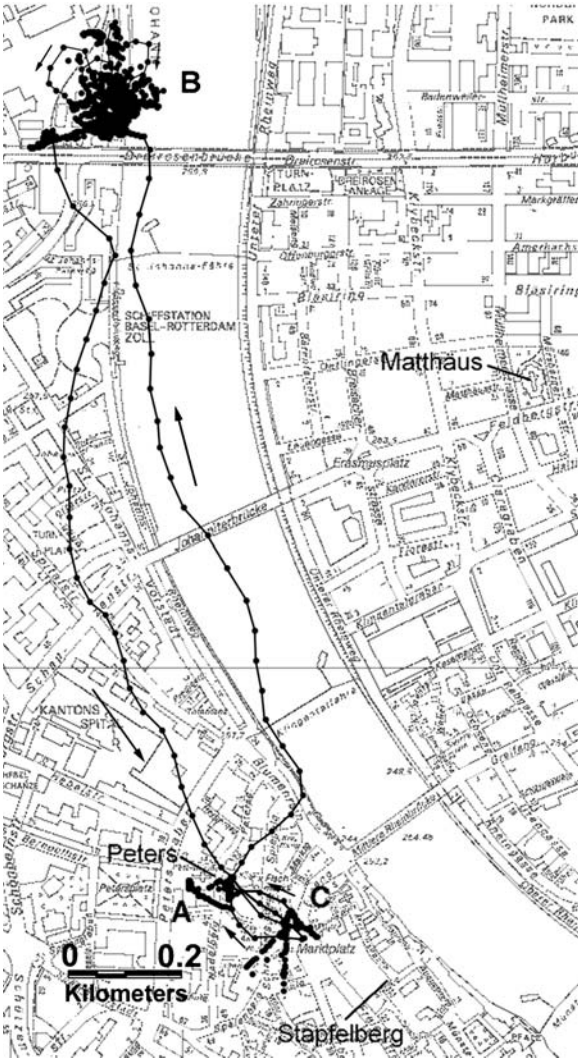


Fig. 2 Example of a day record illustrating the strategy “streets/squares+harbour” (see Tables 2 and 3). Pigeon “A488” from the Peters loft on 13 February 2003. From 8:22 to 8:47 (local time), the pigeon stayed on the roof of the house facing the entrance of the loft (**a**) and then returned in the loft (no positions recorded). At 12:27 it left the loft again, flew to the harbour (**b**), and remained there until 15:24. Afterwards, it flew to the market place (**c**). The return to the loft occurred at 15:35. The positions recorded during the flights are joined by *lines* and flight directions are indicated with *arrows*. The *isolated dots* that are not connected with lines are shifted positions (due to reflection of satellite signals on buildings)

The strategies also differed between the lofts. Pigeons from the Matthäus loft preferred to forage in the harbour and never commuted to fields (Table 3). The pigeons in the other two lofts used all strategies in variable percentages. It is known that young feral pigeons follow their parents, especially their fathers, to the feeding places (Goodwin 1983, own observations). This social learning is probably responsible for the differences between the lofts. Adult pigeons may also follow each other, as proposed by Lefebvre and Giraldeau (1984). Details about pigeons flying together are given in Common flights.

We recorded the two foraging strategies listed in the Introduction and also the intermediate one. We think that

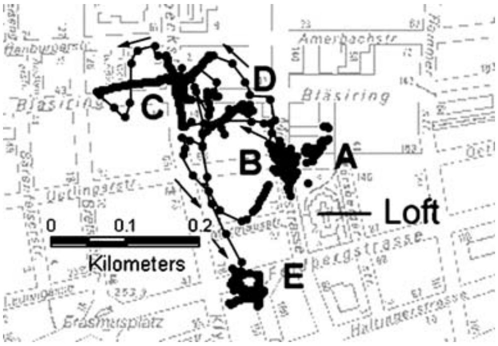


Fig. 3 Strategy “streets/squares”. Pigeon “A446” from the Matthäus loft on 23 September 2003. The record began at 8:19 at a school building (**a**). At 8:48 the pigeon flew to an adjacent street (**b**), stayed there until 10:37, and then flew to another street (**c**). The next flight, back to place **b**, occurred at 11:16. At 11:24 the pigeon returned to **c** and stayed there until 11:45. Then it moved to **d** and stayed there for 18 min. Between 12:04 and 14:46 it moved twice between **c** and **b** and back. Finally at 14:46 the bird flew to point **e**. The record ended there at 16:21

we are faced with three clearly separated strategies in Basel. They have different implications concerning the distance that must be travelled, reliability of the food source and predation risk. Streets, squares and parks near the loft present no predation risk, but they are not very reliable as food sources. The pigeons must search for leftover or spilled food, wait for pigeon feeders, or beg for food (Weber et al. 1994). Foraging in agricultural areas implies long flights and a high predation risk. Reliability of food sources varies seasonally (e.g. very reliable after harvest, food shortage in May–June). The third strategy, foraging on docks and railway lines in the harbour, requires travelling intermediate distances and, in Basel, it presents a predation risk, as peregrine falcons (*Falco peregrinus*) hunt in this area. At such a location, pigeons feed on grain spilled during transhipping that is available all around the year and on wild seeds growing between the railway lines. Additional studies are required to determine the energetic costs and benefits of the observed strategies.

In our GPS records, five pigeons performed flights to more distant agricultural areas. Additionally, we made visual observations in the agricultural areas and sporadically observed larger flocks of feral pigeons in the fields surrounding the city. Commuting flights to agricultural

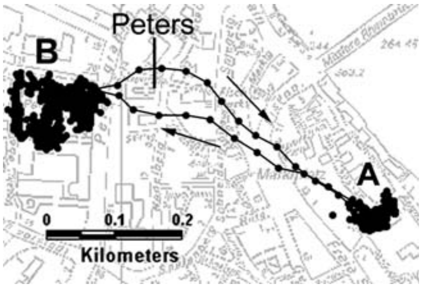


Fig. 4 Strategy “park”. Pigeon “B+C+gr/bl” (marking *green*/*blue*) from the Stapfelberg loft on 8 September 2003. The bird stayed from 8:45 to 10:16 on the roof of the loft (**a**). After a stay in the loft, the pigeon flew out again on the roof at 11:12 and moved to a park at 11:35 (**b**). At 16:55, it returned to the loft

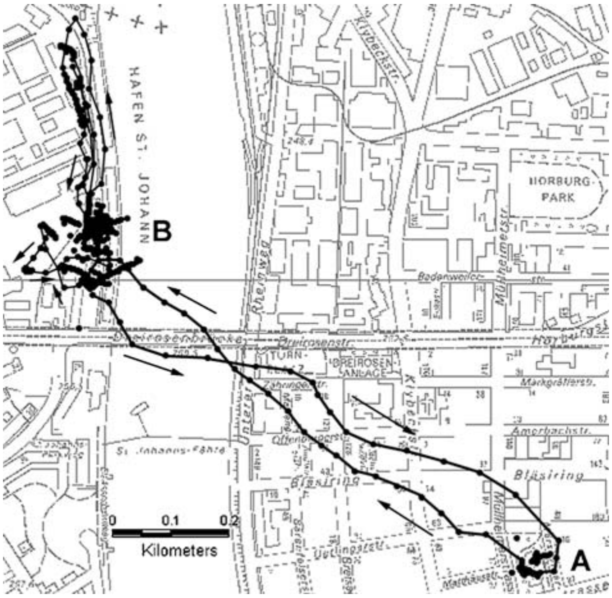


Fig. 5 Strategy “harbour”. Pigeon “A338” from the Matthäus loft on 7 October 2003. At 10:54 and between 12:33 and 12:39, the pigeon stayed on the roof of the loft (**a**). It left the loft again at 12:53, flew to the harbour (**b**) 3 min later, and returned at 14:55

areas are, therefore, not the dominant foraging strategy in Basel. The situation is very different in other cities: In Brno (Havlin 1979) and in Bratislava (Janiga 1983), the majority of pigeons flew into adjacent agricultural areas to find food. In Milan, Sacchi et al. (2002) found that 53.7% of the pigeons fed in urban areas, while 46.3% regularly made foraging flights to the farmsteads. In many studies, no flights to agricultural areas were recorded (Gompertz 1957; Bauer et al. 1990; Sol and Senar 1995; Slotta-Bachmayr et al. 1995). In some cities, flying pigeons were observed or pigeons were recorded in fields surrounding the city but their exact provenance could not be determined (Goodwin 1960; Steiner and Zahner 1994; Schneditz 1996). Eber (1962) found that flights to fields varied between individual homing pigeons. She proposes that pigeons have a variable innate tendency to show this foraging behaviour. Adult pigeons transmit fielding to their offspring. Brehm (1857) describes how commuting flights to the fields can be taught to homing pigeons that previously did not show this kind of behaviour. He demonstrates the importance of the learning component for this behaviour. Flights to agricultural areas seem to be vestiges of the wild origins of feral pigeons: Rock doves travel 4–18.9 km daily from their breeding caves in cliffs to the feeding grounds in fields (Baldaccini et al. 2000).

Common flights

The individual pigeons rarely followed the same time schedule, i.e. they rarely flew together to the foraging places. For the Matthäus loft, we analysed all flights to the harbour made during 66 days while we performed GPS records. In five records, three pairs spent part of the day in common, performing some flights at the same time. The

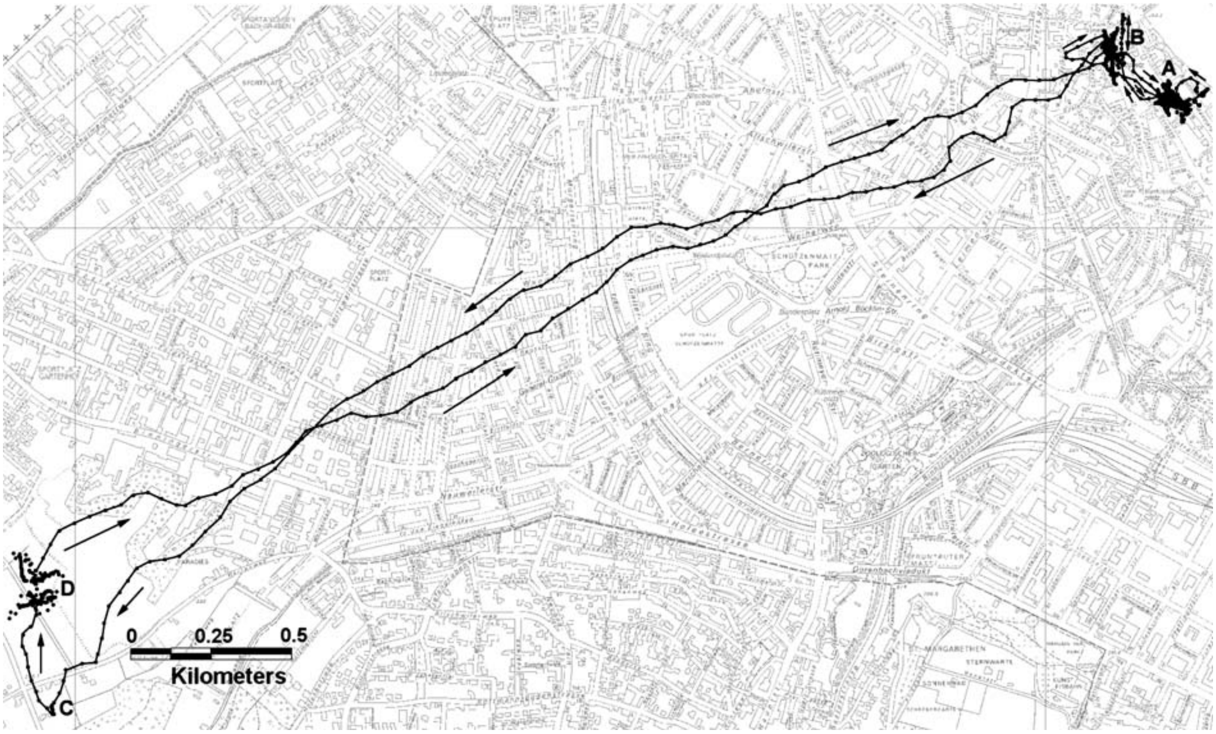


Fig. 6 Strategy “streets/squares+fields”. Pigeon “B+C+we/or” from the Stapfelberg loft on 8 September 2003. From 8:13 to 16:14, the bird visited different streets and squares near the loft (**a**) and also flew twice to the market place (**b**). Then, it flew from this point to a farm outside the urban area (**c**). At 16:23, the pigeon flew from the farm to an adjacent field (**d**). It returned to the market place (**b**) at 16:40. It stayed there a few minutes and then visited other streets/squares near the loft until 19:34, when it returned to the loft

mates of one pair spent an entire day together performing all their flights in common. For this loft, we never recorded common flights to the harbour in unmated pigeons.

For the Peters loft, we analysed the flights to five important feeding places during the 30 days of GPS records. We found only one case where a male and a female that were not mated together performed two common flights on one day. The first flight led to a school building near the loft and the second flight was the return to the loft that took place 2 min later. They spent the rest of the day separately.

For the Stapfelberg loft, we analysed all flights to the different places visited by the pigeons during the 33 days of recording. Four pairs spent a part of the day together during ten day records. For unmated birds, we recorded six common flights of two females, performed by a total of seven different females. One of these flights led from the loft to the market place and five flights led back to the loft. We also recorded seven common flights of two males, performed by ten different males. Two of these flights went from the loft to the market place and five flights went back to the loft.

Finally, we recorded eight common flights of one male and one female not mated together, performed by six females and five males. Two of these flights went to the market place and six returned to the loft. These results show how variable relationships between individuals can be. In total, 0.04% of all analysed flights were common flights. Possibly, more common flights would have been recorded if we would not have been limited to a maximum of ten simultaneous records per day.

Temporal use of the city

Figure 7 shows the seasonal variations in the percentages of pigeons outside. In winter and spring, the pigeons flew out of the loft significantly later than in the other seasons (mixed linear model, P=0.002 and P=0.003, n=68 pigeons and 263 records, including all records that started at the loft). They returned significantly sooner in winter than in the other seasons (mixed linear model, P=0.04, n=67 pigeons and 300 records, including all records that ended at the loft). When including day length into the model, the time of departure was significantly influenced by this factor (mixed linear model, P=0.001, n=68 pigeons and 263 records, including all records beginning at the loft), but the season remains an additional significant factor. On the other hand, day length had no significant influence on the time of return to the loft. In all seasons the pigeons were back before 20:00, except three records where the pigeons spent the night outside. In the summer months, the graph shows a slight bimodal schedule, but not during the other months.

Wild rock pigeons show bimodal foraging activity in the summer months due to reproduction, and a single peak of foraging flights in winter (Baldaccini et al. 2000). The same is reported for feral pigeons flying to agricultural areas (Havlin 1979; Janiga 1987; Ragionieri et al. 1992; Baldaccini and Ragionieri 1993). In Montréal, Lefebvre and Giraldeau (1984) reported a bimodal activity for pigeons feeding in town. In Basel, the absence from the loft showed this clear bimodal activity for breeding pigeons only.

In winter, feral pigeons in Basel showed an activity pattern similar to wild rock doves: a single peak in the early afternoon (Baldaccini et al. 2000).

Pigeons in Basel left the roosting places later in the morning, compared to wild rock pigeons (Baldaccini et al. 2000) and to feral pigeons in other cities (Lefebvre and Giraldeau 1984; Janiga 1987; Havlin 1979; Ragionieri et al. 1992; Baldaccini and Ragionieri 1993). The return of our birds to the lofts also occurred later than reported by Janiga (1987). The results obtained with pigeons from the Matthäus loft that was not closed in the evening show that the pigeons in Basel do not follow natural rhythms depending on sunset. They seem to have their own rhythms to leave the loft. We propose that the differences are essentially due to the food resources. We agree with Lefebvre and Giraldeau (1984) that opportunistic feeding on unpredictable food sources such as irregular human provisioning or garbage may involve searching for food at several sites where the availability may not be compatible with a bimodal foraging schedule.

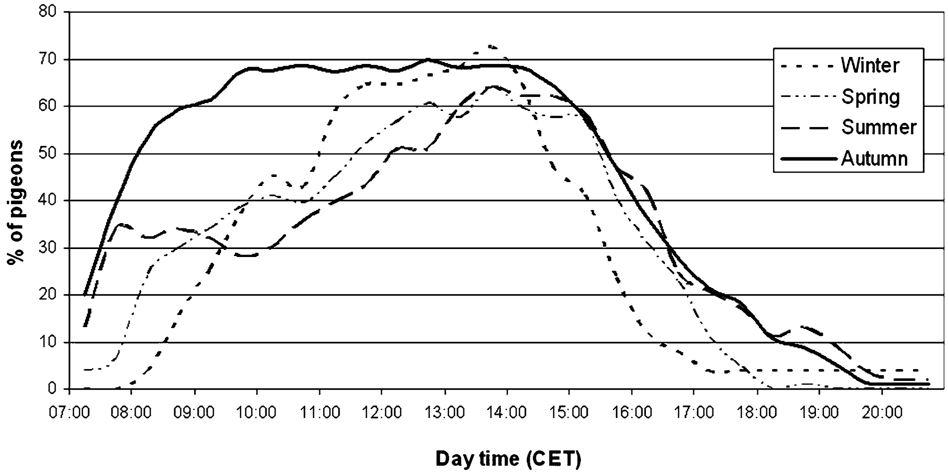


Fig. 7 Seasonal variations in the percentage of pigeons outside. Winter – 6 November to 4 February, spring—5 February to 6 May, summer—7 May to 6 August, autumn—7 August to 5 November

Table 4 Mean and maximum time spent outside the loft by the pigeons during the different seasons

Season (*n* pigeons	Mean time (h:min ±sd)	Maximum time (h:min)	Percent of the day outside
Winter (11)	2:39±1:43	7:25	26.9
Spring (25)	3:21±1:30	7:22	26.2
Summer (10)	3:24±2:09	8:35	20.4
Autumn (29)	4:45±2:41	11:21	37.5

The last column indicates the mean percentage of day length spent outside in each season. Day length is given by the light intensity measured each day (see subsection "Variables" in Materials and methods)

On average, the pigeons from the Matthäus loft left significantly later and also returned later. This was probably related to their foraging strategy: The majority fed at the Rhine harbour St. Johann which is a reliable food source that allows feeding without long waiting times.

In winter, the pigeons returned earlier than in other seasons where the pigeons were rarely outside until nightfall. The battery life of the GPS receivers may be insufficient to record all the evening hours, especially when the pigeon remained inside the loft for a large part of the day (Rose et al. 2005). Observations in the lofts showed that the majority of pigeons was back at approximately 18:00, even in summer. Although some evening records may be missing, they concern only a few individuals, and our graphs represent the behaviour of the majority of pigeons.

Time spent outside the loft

On average, the pigeons spent 29.4% of day length outside (3:46 h). The maximum time spent outside was 11:21 h (83% of that day). The maximum time spent outside as a proportion of day length was 84.9%. The longest times were recorded in autumn.

Pigeons spent significantly more time outside in autumn (Table 4), compared to the other seasons (mixed linear model P=0.002, n=62 pigeons and 212 complete records), and the proportion of the day spent outside was also significantly longer (mixed linear model P=0.04, n=62 pigeons and 212 complete records). Day length had no significant influence on the time spent outside (mixed linear model P=0.8, n=62 pigeons and 212 complete records). There was no significant difference between the lofts in the average time spent outside (mixed linear model, P=0.7, n=62 pigeons and 212 complete records).

Our hypothesis explaining the longer outdoor period in autumn is that pigeons must refill their fat reserves after the energy consuming reproduction and moult. Weight analyses of adult pigeons from Basel (Haag 1984) reinforce this hypothesis. The pigeons had the highest body weights in winter and subsequently had lost weight again by the end of summer. In autumn, their weights increased again. Murton et al. (1972a) found a similar pattern: the mean weight of adults was lowest between June and October and there was a considerable increase in weight in November.

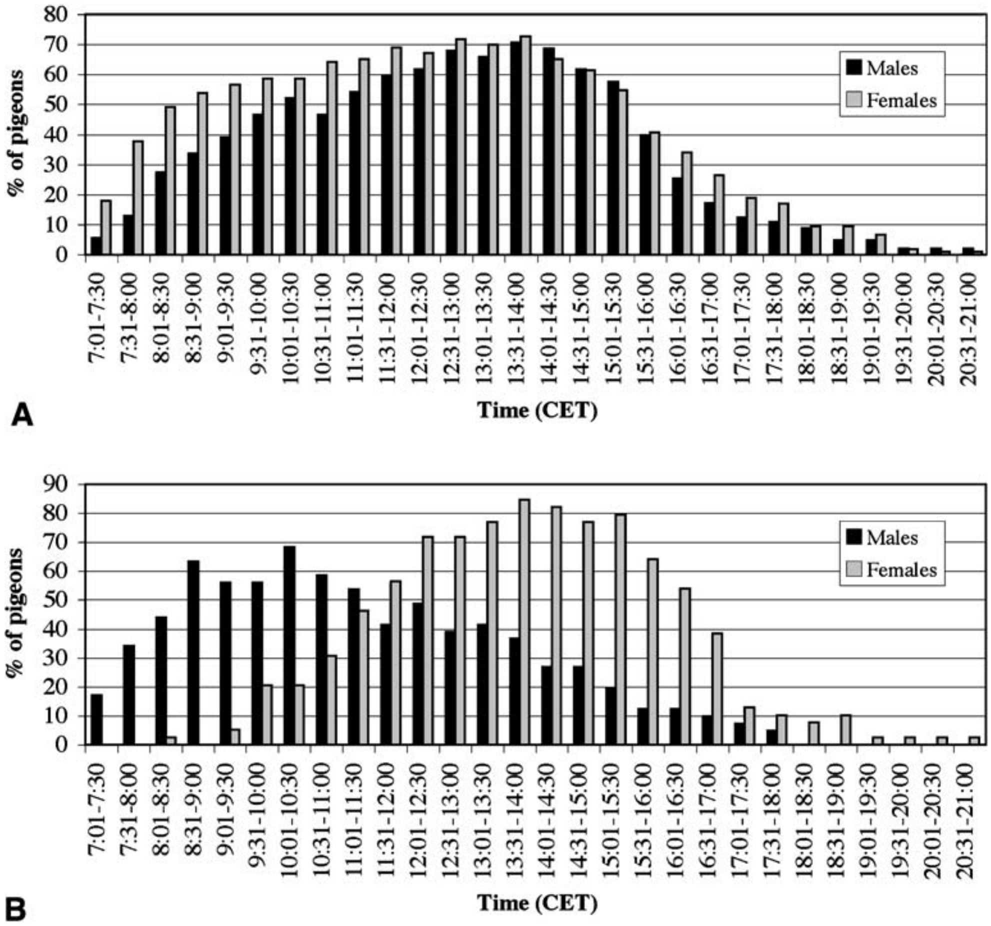
Between winter and summer, the pigeons spent an increasing amount of time outside the loft, but a decreasing percentage of the day, as the days get longer. Even in winter, pigeons spent on average only 26.9% of the day outside, so day length was not a limiting factor in finding enough food. In summer, they spent on average 20.4% of the day outside and did not really profit from the longer days. In September, Murton et al. (1972b) observed some pigeons waiting for 6 h at the feeding place (46% of daytime). In December, this amount increased to 88%. This value is much higher than the values we found with our pigeons. These data most likely represented extreme values.

Females spent on average 4:18±2:15 h outside, males 3:16±1:46 h. This difference was significant (mixed linear model, P=0.01, n=62 pigeons and 212 complete records). We found no comparable results in the literature. We suppose that males spent more time in the loft to defend their territories. Observations showed that many fights took place in the breeding boxes and, therefore, the pressure to defend their territory seems to be very high. In well-bonded pairs, both birds engage in defending nest territory (Johnston and Janiga 1995), but males are much more frequently engaged in territorial conflicts than females (Vogel 1992). In addition, females have more energetic requirements for reproduction (Walsberg 1983) and are weaker competitors at concentrated food resources than the stronger males (Haag 1984). The longer time spent outside by females may reflect the need to find more food and the difficulty in getting access to food resources. Both sexes, therefore, have constraints that influence their use of the urban habitat when they want to breed; for males, it is the need to defend their territories and for females the need to find more food.

Influence of breeding state on the temporal use of the city

Non-breeding males and females showed a similar temporal use of the city (Fig. 8a). The temporal distribution of breeding pigeons reveals a bimodal use of the urban habitat (Fig. 8b). Breeding females left the lofts significantly later than non-breeding females or those rearing young (mixed linear model, P=0.04, n=33 pigeons and 130 records, including all records that started at the loft). They also returned later (P=0.003, n=30 pigeons and 141 records, including all records that ended at the loft). Breeding males returned sooner than non-breeding males or those rearing young (P=0.02, n=37 pigeons and 159 records, including all records that ended at the loft). The departure of males from the loft in the morning was not significantly influenced by the breeding state. Fig. 8b is a good illustration of the breeding pattern of feral pigeons. Females incubate the eggs

Fig. 8 Differences in the activity patterns of males and females between non-breeding (**a**) and breeding pigeons (**b**). Males predominantly stayed outside between 7:00 and 11:30 and females between 11:31 and 17:00



during the night and the morning. They are relieved when the males come back from their foraging. The males then incubate until their mates return in the afternoon. The timing recorded with GPS tracking shows that the males in Basel relieved the breeding females later than in other studies. The time of relief varied, but for the majority of pairs it took place around midday or in the early afternoon. This was late compared to the relief time of 9:00–10:00 A.M. found by Havlin (1979) and Reinke (1959).

Breeding pigeons spent on average 191±104 min outside, non-breeding pigeons 212±129 min and pigeons with juveniles 275±139 min. The effect of the breeding state on the time spent outside was close to the significance limit (mixed linear model, P=0.07, n=62 pigeons and 212 complete records). The search for intraindividual differences in the time spent outside according to breeding state revealed that pigeons spent significantly more time outside the lofts when they were caring for juveniles (up to 36 days old) than when they were breeding (two-way ANOVA, P=0.03, n=8). The other intraindividual differences were not significant. This was probably due to the limited sample size, as in the statistics; we only could include individuals that presented all three breeding states during their GPS records. Juveniles of 1–6 or 7 days are permanently taken into care by their parents (Heinroth and Heinroth 1949). During this period of time, parents behave like incubating birds. After this period, parents spend less time at the nest. They must find an increasing amount of food for their offspring. This can result in longer times outside the loft. Parents might also spend more time outside because they are distressed by the aggressive begging of their older young (Heinroth and Heinroth 1949; Haag-Wackernagel 1991).

Our results confirm that reproduction is not only an energy-consuming activity (Ricklefs 1974), but it is also time-consuming. One parent must always remain at the nest in the earlier breeding stage. The temporal use of the city changed significantly during breeding, not only because pigeons spent less time outside, but also because their timing had changed. This temporal restriction is a great constraint for pigeons. Breeding birds can no longer decide when to fly out and forage. Therefore, some temporally restricted food resources become inaccessible to at least one of the pair of birds.

Conclusion

The differences in the results obtained by our study and those of other studies may be partly due to the method used. Nevertheless, they also show that pigeons do not only have a very flexible behaviour concerning their foraging strategies and maximum distances travelled but, also, the timing of their activity varies greatly. Pigeons that feed in town have adapted and coordinated the timing of their activities to human activity. This is obvious when they wait for pigeon feeders. Spilled food may also become more abundant at certain hours of the day, e.g. after lunch (Lefebvre and Giraldeau 1984). In other areas, like harbours or factories, human activity prevents the pigeons from feeding and they must wait for a break in human activity before they can reach food (Murton et al. 1972a). Therefore, in many cities the timing of pigeon activities is due to human influence rather than natural rhythms.

With the GPS technology, we were able to show that the pigeons have individual strategies in using their urban habitat. We found differences between the pigeons of our three lofts and also interindividual differences within the same loft. Therefore, it is only possible to make individual statements about the spatial use of the urban habitat by feral pigeons. Foraging strategies will probably vary from one city to another and essentially depend on food supply and human activity. More studies with the GPS technique should be performed in other cities, allowing the working out of common factors, to provide additional statements about the spatial use of the urban habitat by feral pigeons.

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