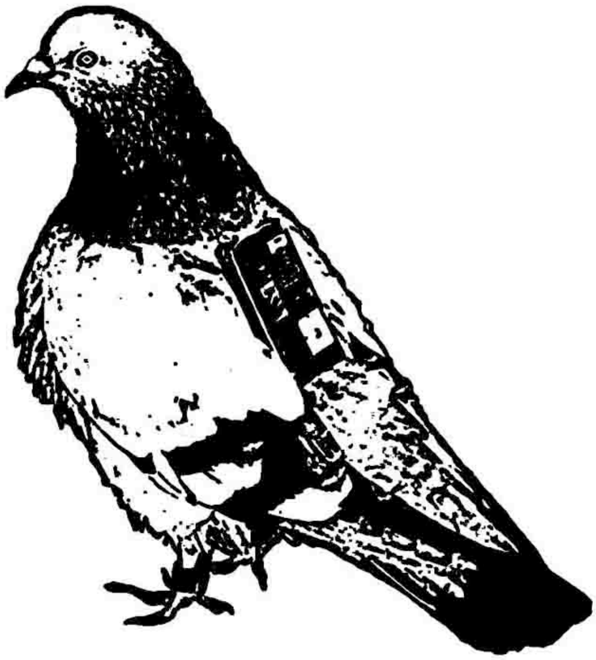
Spatio-temporal Use of the Urban Habitat by Feral Pigeons (*Columba livia*)



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Abstract

Despite the large number of feral pigeons and their proximity to humans, their use of the urban habitat is not entirely understood. Previous studies have given various results about the home range of feral pigeons and their temporal activity patterns. The aim of our study is to clarify the situation for Basel and to compare it to other cities. For this purpose, we adapted the global positioning system (GPS) to use it for the first time with feral pigeons.

In a first step, we tested the suitability of this method for studying the spatio-temporal use of the urban habitat by feral pigeons. Despite some problems due to the highly structured urban habitat such as poor satellite signal reception in the street canyons, and technical limitations such as short battery life, the method revealed itself to be very suitable.

In a second step, we studied the behaviour of 80 free-ranging feral pigeons living in three lofts situated in the city of Basel.

In our study, we could prove that pigeons follow individual strategies in using the urban habitat. Some birds covered only short distances (300–500 m), others flew to surrounding agricultural areas 5 km away from the loft. On average, pigeons in Basel covered longer distances than pigeons in many other cities. These differences may partially be due to the method applied. Contrary to other methods, GPS-tracking records all displacements. The differences probably also depend on the availability and distribution of food resources in the cities. The pigeons of each loft visited one or two principal feeding places, but used also other places on a less regularly basis. The pigeons showed flexible behaviour that enables them to adapt to different situations. Pigeons are not dependent on feeding in the vicinity of their sleeping or breeding places, as stated by some authors. Our results show that they are able to fly a few kilometres to search for food. Death from starvation is, therefore, not a valuable argument against pigeon control campaigns which are based on reduction of intentional feeding. Our findings are also important for biomonitoring projects using feral pigeons. For statements about pollution indicated by this species, it is generally assumed that they show a limited mobility in the city. Our results prove that this is not always the case and that the use of the urban habitat must be verified for each project.

In our study, females covered longer distances than males. Reproduction is much more energy consuming for females than for males. Females also have problems competing for food with the stronger males. We therefore believe that females preferred flying longer distances to reach more abundant and reliable food sources.

The home ranges differed between the lofts but showed an overlap at some feeding places. Diseases and parasites can therefore be transmitted from one subpopulation to another and spread over the entire city. This is of human concern, since at least seven infectious diseases can be transmitted from pigeons to humans.

On average, pigeons spent 31.3% of the day outside the lofts. This percentage varied according to breeding state and season. Breeding pigeons spent less time outside than non-breeding pigeons or pigeons rearing young and had a different temporal activity pattern. Breeding is a constraint to pigeon life, not only because it is time consuming, but also because temporarily restricted food resources can no longer be exploited by one pigeon of the breeding pair.

Even during short winter days, pigeons spent on average only 28.5% of the day outside. Day length is therefore not a limitation to finding enough food. In autumn, the pigeons spent more time outside than in any other season. We found no correlation with the day length or the percentage of breeding birds. We suppose that the pigeons must replenish their fat reserves after the energy consuming breeding season, as well as moult, and that they therefore spend more time foraging. The evolution of pigeons' weight over the seasons reinforces this hypothesis. The weight was highest in winter, decreased during spring and summer and increased again in autumn.

During this study, females spent more time outside the lofts than males. We suppose that males must spend more time in the lofts to defend their territories. As stated above, females

also have problems competing with the stronger males for food at unnaturally concentrated food sources that are typical for cities. The longer periods of time spent outside may reflect their difficulty to gain access to food.

Before starting pigeon control campaigns, it is important to know the size of the population. Census counts are best undertaken when most pigeons have left their sleeping or breeding places. Our results show that, in Basel, the best time for counts is in the early afternoon, between 12:00 and 14:00, when, on average, 60–70% of the pigeons are outside.

To sum up, the GPS method allowed us to gather detailed information on the individual use of the urban habitat by feral pigeons. These findings are important for the three practical applications: biomonitoring with feral pigeons, understanding of transmission of diseases, and pigeon control campaigns.

Zusammenfassung

Tauben gehören zum Strassenbild jeder grösseren Stadt. Dennoch ist längst nicht alles über ihre Nutzung des urbanen Lebensraumes bekannt. Bisherige Studien haben recht unterschiedliche Ergebnisse hervorgebracht, vor allem bezüglich der Aktionsradien der Tauben und der zeitlichen Verteilung ihrer Aktivitäten.
Unsere Studie verfolgte das Ziel, die Situation in Basel abzuklären und mit derjenigen in anderen Städten zu vergleichen. Wir haben dafür zum ersten Mal bei der Strassentaube das *global positioning system* (GPS) eingesetzt.
In einer ersten Phase unserer Untersuchungen haben wir die Eignung dieser Methode zur Erforschung der Aktionsradien von Strassentauben im urbanen Lebensraum getestet. Wir konnten die GPS-Technologie an unser Forschungsprojekt anpassen, so dass wir trotz kleiner Probleme wie schlechtem Empfang in engen Strassenschluchten und technischen Grenzen (z.B. begrenzter Batteriedauer) eine detaillierte Erfassung der Nutzung des städtischen Lebensraumes durch die Taube durchführen konnten. Die GPS-Methode hat sich damit für unser Erkenntnisinteresse als geeignet erwiesen.
In der zweiten Phase haben wir das Verhalten von 80 Tauben aus drei Taubenschlägen der Stadt Basel erfasst. Die gleiche Taube wurde jeweils bis zu 15-mal einen Tag lang mit dem GPS beobachtet.
Die Basler Strassentauben nutzen ihren urbanen Lebensraum sehr individuell. Manche Tiere legten nur relativ kurze Strecken zurück (300–500 m), andere flogen auf 5 km entfernte landwirtschaftliche Flächen. Im Vergleich mit anderen Städten legten die Tauben in Basel durchschnittlich grössere Strecken zurück. Diese Unterschiede könnten einerseits durch die Methode bedingt sein, da GPS im Gegensatz zu anderen Methoden alle Flüge und Aufenthaltsorte erfasst. Andererseits könnte aber auch ein unterschiedliches Nahrungsangebot und dessen Verteilung dafür verantwortlich sein. Die Tauben aus den verschiedenen Taubenschlägen haben ein bis zwei Stammplätze, wo sie zum Fressen hinfliegen, und suchen unregelmässig auch noch andere Orte auf. Ihr Verhalten passte sich den verschiedenen Situationen sehr flexibel an und widerlegt das häufig geäusserte Vorurteil, dass Tauben von Futterquellen in unmittelbarer Nähe ihres Schlafplatzes abhängig seien. Unsere Resultate zeigen, dass sich ihre Futtersuche sogar über mehrere Kilometer erstrecken kann. Wir konnten somit wissenschaftlich eindeutig beweisen, dass eine Reduktion der Fütterung in der Stadt keineswegs zum Hungertod von Tauben führt. Derartige Behauptungen, die von Taubenfütteren vorgebracht werden, erwiesen sich als unhaltbar.
Unsere Resultate liefern auch einen wichtigen Beitrag für Biomonitoring-Studien, in denen Tauben oder deren Eier als Schadstoffindikatoren verwendet werden. Dabei wird in der Regel angenommen, dass sich Tauben wegen ihrer limitierten Aktionsradien für die Beurteilung von lokalen Schadstoffbelastungen eignen. Wie unsere Resultate aber zeigen, ist der Aktionsradius nicht immer beschränkt. Deshalb muss für jedes Biomonitoring-Projekt abgeklärt werden, welche Schadstoffbelastung die Tiere je nach frequentierter Fläche anzeigen können.
Gemäss unserer Untersuchungen fliegen Weibchen im Durchschnitt längere Strecken als Männchen. Sie verbrauchen während der Fortpflanzung mehr Energie als die Männchen. Ausserdem können sie sich bei konzentriert auftretendem Futter gegenüber kräftigeren Täubern schlechter durchsetzen. Wir vermuten deshalb, dass Weibchen weitere Flüge in Kauf nehmen, um an zuverlässige Nahrungsquellen heranzukommen.
Die Tauben aus den drei Schlägen nutzen unterschiedlich grosse Gebiete der Stadt. Die Flächen weisen eine Überlappung an einigen Futterplätzen auf. Das hat zur Folge, dass Infektionskrankheiten über das gesamte Stadtgebiet verbreitet werden können. Da nachweislich sieben davon auf den Menschen übertragen werden können, ist diese Erkenntnis über den Aktionsradius und das Flugverhalten der Strassentauben sehr wichtig.
Im Durchschnitt verbrachten die Tauben 31.3% der Hellzeit ausserhalb ihres Schlages. Diese Zeit variierte je nach Jahreszeit und Brutstatus der Tiere. Brütende Tauben

verbrachten weniger Zeit ausserhalb des Schlages und teilten sich den Tag zeitlich anders ein als nichtbrütende Tiere. Die Brut ist mit einer hohen zeitlichen und energetischen Investition für die Strassentauben verbunden, da sie in diesem Zusammenhang nicht nur viel Zeit zum Brüten aufwenden müssen, sondern durch die veränderte Zeiteinteilung den Tag auch anders nutzen müssen. Zeitlich beschränkt auftretende Futtervorkommen sind dem brütenden Partner nicht mehr zugänglich, wenn er den Zeitpunkt verpasst.

Auch während der kurzen Wintertage hielten sich die Tauben im Durchschnitt nur 28.5% des Tages ausserhalb des Schlages auf. Die verkürzte Helligkeitsdauer war somit kein limitierender Faktor für die Futtersuche. Im Herbst verbrachten die Tauben deutlich mehr Zeit ausserhalb des Schlages als in den anderen Jahreszeiten. Wir konnten keine Korrelation mit der Helligkeitsdauer oder der Anzahl nichtbrütender Tauben nachweisen. Wir vermuten, dass die Tiere nach der Hauptbrutsaison und der Mauser ihre Fettreserven wieder aufbauen und deshalb mehr Zeit für die Futtersuche investieren müssen. Die Analyse des saisonal schwankenden Körpergewichts ergab, dass die Tauben im Winter am meisten wogen. Bis zum Ende des Sommers verloren sie an Gewicht und nahmen im Herbst wieder zu.

In der vorliegenden Untersuchung hielten sich Weibchen länger ausserhalb der Schläge auf als die Männchen. Wir vermuten, dass die Männchen mehr Zeit im Schlag verbringen, um ihre Brutterritorien besser zu verteidigen. Da sich Täubinnen ausserdem an konzentriert auftretendem Futter weniger gut gegen die kräftigeren Männchen durchsetzen können, müssen sie auch mehr Zeit für die Futtersuche aufwenden als die Männchen. Die längeren Zeiten ausserhalb der Schläge werten wir auch als Zeichen dafür, dass die Weibchen grössere Schwierigkeiten bei der Futtersuche haben.

Zwischen 12:00 und 14:00 Uhr werden zur Ermittlung der Populationsgrösse von Taubenbeständen am meisten Exemplare erfasst, da sich in diesem Zeitraum gemäss unserer Resultate mit 60–70% die Mehrheit der Tauben ausserhalb der Schläge aufhält.

Zusammenfassend lässt sich festhalten, dass die GPS-Methode die Erfassung sehr genauer Daten über die individuelle Nutzung der Stadt durch die Strassentaube erlaubt. Die gewonnenen Resultate sind vor allem für das Biomonitoring mit Strassentauben, die Epidemiologie von Infektionskrankheiten, die Bestandesaufnahme und Kontrollstrategien bedeutsam.

Résumé

Malgré l'omniprésence des pigeons en ville, tout n'est pas encore connu sur l'utilisation qu'ils font du milieu urbain. Les opinions divergent quant à leurs rayons d'action et au timing de leurs activités.
Le but de notre étude est de clarifier la situation pour la ville de Bâle en utilisant pour la première fois avec les pigeons urbains la technologie du GPS (Global Positioning System).
Lors d'une première étape, nous avons testé l'efficacité de cette technologie pour l'étude des pigeons en ville. Malgré quelques problèmes liés à la structure de l'habitat urbain, comme la mauvaise réception du signal des satellites dans les rues étroites, et quelques limitations technologiques (durée des accus), le système s'est révélé très efficace pour une étude détaillée de l'utilisation du milieu urbain par les pigeons.
Nous avons étudié en détail 80 pigeons de trois pigeonniers de la ville de Bâle.
Les pigeons ont montré une utilisation très individuelle de la ville. Certains n'ont parcouru que de petits trajets (300–500 m), d'autres sont sortis de la ville pour se nourrir en milieu agricole (5 km). Dans l'ensemble, les pigeons de Bâle se sont révélés plus mobiles que dans de nombreuses autres villes. Ces différences peuvent être dues à la méthode employée, le GPS permettant d'enregistrer tous les déplacements contrairement aux techniques utilisées précédemment. Mais ces différences peuvent aussi provenir de la quantité de nourriture en ville ainsi que de sa distribution. Les pigeons d'un même pigeonnier ont une ou deux places de nourrissage principales. Ils connaissent et visitent encore d'autres endroits, mais moins régulièrement. Les pigeons ont montré un comportement très flexible qui leur permet de s'adapter aux différentes conditions. Contrairement à une opinion répandue, ils ne sont pas dépendants du nourrissage à proximité de leurs gîtes, car ils sont capables de chercher leur nourriture à une distance de plusieurs kilomètres. Ce résultat permet de contrer les arguments de quelques amis des pigeons qui prétendent que la réduction du nourrissage en ville condamne les pigeons à mourir de faim. Nos données sont également importantes pour les projets de biomonitoring, utilisant les pigeons ou leurs œufs comme indicateurs de pollution. Dans ces études, on admet en général que les pigeons sont peu mobiles et que les résultats du biomonitoring reflètent donc la pollution locale. Nos données indiquent cependant que les rayons d'action des pigeons peuvent être relativement grands et qu'il faut donc les vérifier avant chaque projet de biomonitoring.
Dans notre étude, les femelles ont parcouru de plus grandes distances que les mâles. Nous supposons que les femelles acceptent de voler de plus grandes distances pour visiter des sources de nourriture sûres et abondantes, car elles ont de plus grands besoins énergétiques pour la reproduction comparé aux mâles. En outres, elles ont de la peine à s'imposer face aux mâles à des sources de nourriture concentrées.
Les surfaces utilisées par les pigeons des différents pigeonniers sont de tailles variables et partiellement superposées. Cela rend les transmissions de maladies possibles à travers tout le territoire de la ville. Cet aspect est important pour l'homme, puisque sept maladies infectieuses peuvent être transmis des pigeons aux humains.
En moyenne, les pigeons ont passé 31.3% de la durée du jour en-dehors du pigeonnier. L'utilisation temporelle de la ville varie essentiellement en fonction de la reproduction et des saisons. Les pigeons qui couvent passent moins de temps hors du pigeonnier et ont une répartition temporelle bien précise contrairement aux non reproducteurs.
Même pendant les courtes journées hivernales, les pigeons n'ont passé en moyenne que 28.5% du jour dehors. La longueur du jour n'est donc pas un facteur limitant pour trouver assez de nourriture. En automne, les pigeons ont passé plus de temps dehors que pendant les autres saisons. Ce n'est lié ni à la durée du jour, ni au nombre de pigeons non reproducteurs. Nous supposons qu'en automne, après la saison principale de reproduction et la mue, les pigeons doivent reconstituer leurs réserves de graisse et passent ainsi plus de temps à chercher de la nourriture. L'évolution du poids des pigeons de Bâle renforce cette

hypothèse. Les pigeons pèsent le plus en hiver, le poids diminue ensuite jusqu'en été et augmente à nouveau en automne.
Les femelles ont passé en moyenne plus de temps en dehors des pigeonniers que les mâles. Nous supposons que ces derniers restent plus de temps à l'intérieur pour défendre leurs territoires. Mais le temps plus long passé dehors par les femelles peut aussi refléter leur peine à s'imposer face au sexe « fort » aux sources de nourriture concentrées.
Beaucoup de villes entreprennent des mesures pour réduire les populations de pigeons. Avant de lancer de telles campagnes, il est important de compter les pigeons. Les heures du jour les plus favorables au comptage des populations de pigeons sont celles durant lesquelles le plus d'oiseaux sont en dehors de leurs sites de repos ou de reproduction. Notre étude montre que pour Bâle, les heures les plus favorables se situent entre 12 et 14 heures, où 60 à 70% des pigeons se trouvent dehors.
En conclusion, ce travail a permis d'obtenir plus de détails sur l'utilisation individuelle de la ville par le pigeon. Nos résultats sont importants pour les trois applications pratiques que sont le biomonitoring avec les pigeons, la transmission de maladies du pigeon à l'homme et le contrôle des populations de pigeons.

Chapter 1

General Introduction

GENERAL INTRODUCTION

Feral pigeons are one of the most popular appearances in our cities. They have optimally adapted to their new environment. The relief of urban areas with high buildings and street canyons offers a structure similar to the original habitat of the rocky coast (Haag-Wackernagel 1998). When pigeons first settled in cities, they needed the urban habitat primarily for nesting. Food was available in small quantities only and the pigeons flew to forage in the surrounding agricultural areas (Haag-Wackernagel 2003). In most European cities, the feral pigeon populations increased after the Second World War when foodstuffs became cheaper compared to wages (Cramp & Tomlins 1966). A lot of food remainders were carelessly thrown away and people had enough money to buy extra food for pigeons. The pigeons were able to feed more and more directly in the towns. They no longer had to undertake long and dangerous foraging flights to surrounding agricultural areas. Pigeons that lived in the cities had become almost totally independent from natural selection through predation and starvation in winter. On the contrary, Johnston & Janiga (1995) suppose that the increase in pigeon populations was primarily influenced by changes in agricultural practice that made more food available for pigeons. At this point in time, the feral pigeon population is estimated at 500 millions worldwide (Simms 1979).

Several studies have been performed to analyse how feral pigeons use their urban habitat. Different methods were used for this purpose: (1) observations and counts of flying pigeons (Havlin 1979, Janiga 1987, Ragionieri et al. 1992), (2) observation of individually marked birds in town (Lefebvre & Giraldeau 1984, Lévesque & McNeil 1986, Bauer et al. 1990, Steiner & Zahner 1994, Slotta-Bachmyr et al. 1995, Sol & Senar 1995), (3) use of electronic rings detected by an antenna at feeding places (Dell'Omo 1997), and (4) telemetry (Scholl & Häberling 1995, unpublished report). All of these methods have limitations due to the time needed for observation, the impossibility of searching the entire town and its surroundings for marked pigeons, the difficulty of recognizing the rings, or the unknown provenance of the pigeons observed.

Different authors obtained varying results concerning the foraging strategies and the distances covered by pigeons from different cities. Havlin (1979) and Janiga (1983) found that a majority of pigeons fed in agricultural areas surrounding the cities. Johnston & Janiga (1995) suppose that this is the principal foraging strategy for most pigeon populations. They state that intentional public feeding is unlikely to influence urban pigeon numbers, at least in many localities. In Zurich (Bauer et al. 1990), Rome (Dell'Omo 1997), Barcelona (Sol & Senar 1995), Salzburg (Slotta-Bachmayr et al. 1995), and London (Gompertz 1957) no commuting flights could be proved. The feral pigeons in these cities seem to feed within the city. Sacchi et al. (2002) found an intermediate situation in Milan, with around 50% of the pigeons flying to fields and the others feeding in the city. In a few cities, e.g. London, Vienna, Klagenfurt, flying pigeons were observed or pigeons were recorded in fields in the surroundings of the city, but the exact provenance could not be determined (Goodwin 1960, Steiner & Zahner 1994, Schneditz 1996). Previous studies in Basel (Haag 1984) showed that a majority of pigeons feed in town, but observations of pigeons in the surrounding fields let the authors suppose that commuting flights could occur in Basel. With the methods employed previously, the origin of the pigeons foraging in fields could not be determined.

These thesis searched for answers to the following problems:

- How long are the maximum distances covered and what are the dimensions of the total ranges?
- What factors influence the distances covered?
- Do the individual feral pigeons follow different foraging strategies?
- How stable are feeding flocks?
- Are the urban areas covered by the different breeding flocks overlapping?
- What are the patterns of the temporal use of the city?
- Is the temporal use of the city constant?

This thesis consists of three manuscripts to be published independently one from each other. They are hereafter referred to as Chapters 2–4.

In **Chapter 2,** we show how we used the global positioning system (GPS) to study the spatio-temporal use of the urban habitat by feral pigeons. This method has been successfully used to monitor flight tracks of albatrosses (Weimerskirch et al. 2002) and homing pigeons (Von Hünerbein et al. 2000, Lipp et al. 2004). We show that this method is also suitable for the monitoring of feral pigeons in the urban habitat. GPS was previously used under good signal reception conditions (birds flying over the open sea or over obstacles) or for long term displacement studies of tall mammals (e.g. Blake et al. 2001, Chadwick & Garner 2002). We investigated the suitability of this method in town under suboptimal conditions. For our study, we needed to be able to record precise locations, since we also wanted to show displacements of less than 100 m. In the first phase of our study, we tested the accuracy of GPS locations in town. We placed stationary GPS receivers for this purpose at different places in the city and compared the stored positions with the real positions.

In the second part of the study, we equipped pigeons with GPS receivers to gather precise information about their spatio-temporal use of the city of Basel, and to subsequentially search for factors influencing this behavioural patterns.

Chapter 3 presents the main results of our observations of the spatio-temporal use of the urban habitat by feral pigeons. We indicate the maximum and mean distances travelled by the pigeons from the three lofts used for this study as well as the time spent outside the lofts. Previous studies of the temporal activity of feral pigeons analysed their presence at feeding places (Murton et al. 1972, Lefebvre and Giraldeau 1984) or the timing of foraging flights out of the city (Havlin 1979, Janiga 1987, Ragionieri et al. 1992). In our study, the temporal activity is the entire time spent in the urban habitat, i.e. outside the lofts. We tested the influence of the factors “sex”, “breeding state”, “affiliation to a loft” and “season” on the distances covered by feral pigeons and on the temporal use of the city. We comment on the different foraging strategies employed by the pigeons and compare them to the strategies found in other feral pigeon populations and in wild rock dove populations.

In **Chapter 4,** we show supplementary results of the spatial use of the urban habitat by feral pigeons. We give a detailed analysis of the areas of the city used by the pigeons from the three lofts. We analysed the use of the city for groups constituting of pigeons from the same loft, and for individuals. We recorded the number of different spots visited by the pigeons and describe the most important ones. We discuss the importance of our findings for three practical applications: (1) biomonitoring with feral pigeons as an indication of pollution levels, (2) transmission of diseases and parasites between pigeon flocks and from pigeons to humans, and (3) pigeon population control strategies.

In **Chapter 5,** we summarize and discuss the main results of the three publications, give an answer to the main research questions, and present our general conclusions.

METHODS

The methods are described in detail in **Chapter 2**. In the following paragraphs we will summarize the methods and show some figures that are not included in the manuscripts.

The Study Species, *Columba livia*

The pigeons used in this study were living in three lofts situated in public buildings in Basel. These lofts were built in relation to the “Basler Taubenaktion”, a pigeon control campaign which was started in 1988 (Haag-Wackernagel 1995). Figure 1 shows the Matthäus-loft with its breeding boxes. The birds use the lofts as roosting and/or breeding places but have no food or water supply therein and must search themselves for food in the city. The pigeons, therefore, show normal behaviour and activity patterns of free living urban feral pigeons.

Figure 1: Breeding boxes in the Matthäus-loft.

We marked all pigeons of the three lofts with coloured rings. Every pigeon was individually recognisable by a colour-ring code and its plumage coloration (Leiss & Haag-Wackernagel 1999). Before the start of and during the experiment, we observed the pigeons in the lofts weekly to identify the pairs and to control 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 experiment. For the GPS study, we selected 35 females, 44 males, and one pigeon of which we could not determine the sex. All birds were in good physical condition, i.e. they weighed over 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.

Before equipping the pigeons with GPS receivers, we trained them with dummies of the same size and weight as the receivers. Dummies and receivers were fixed on the pigeons' back with velcro tape (fig 2) and with a harness consisting of two loops passing around the body and joined at the breast.

Figure 2: Pigeon equipped with Velcro tape glued onto the feathers. The counterpart of the Velcro tape is glued onto the back side of the dummy or the GPS receiver.

For the experiment, we caught the pigeons in the morning to fix the GPS receivers on their backs and released them immediately in the loft (fig 3). The records started as soon as the pigeons flew out of the loft. Inside buildings, there is no reception of satellite signals.

Figure 3: Pigeon equipped with a GPS receiver after release in the loft. It is now free to fly out at will.

After dark, we removed the GPS from the homed birds to download the data onto a PC and to charge the battery. For each daily record, we obtained the locations visited by the respective pigeon and the flight tracks, as illustrated in fig 4 with a record performed on 25 March 2003 with pigeon A377.

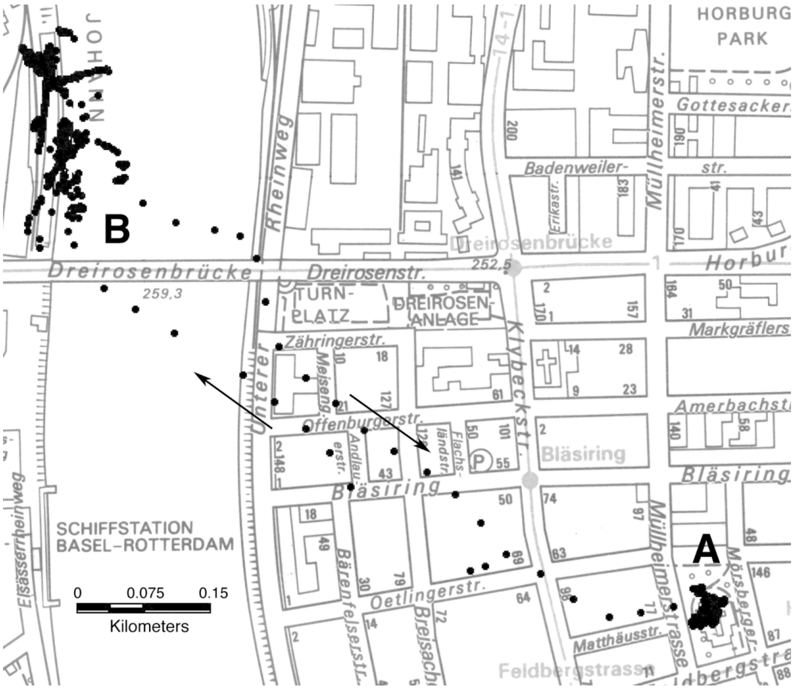

Figure 4: Flight path of feral pigeon A377 recorded on 25 March 2003. Each dot represents the position of the pigeon at a certain time. The pigeon stayed from 11:58 to 12:50 on the roof of the Matthäus-loft (A). From 12:51 to 15:21 it returned inside the loft (no stored positions). At 15:21 it flew to the Rhine harbour St Johann (B) and remained there until 17:28. Then the pigeon returned directly to the loft. Our tracking shows clearly the two flight paths between the harbour and the loft.

Between July 2002 and November 2003, we performed a total of 575 records with 80 pigeons.

The Global Positioning System

The GPS-technology is based on a network of 28 satellites circling the earth and continuously transmitting signals. This coded information allows GPS receivers on earth to calculate their 3-D position using the known distances to at least four satellites. The receiver stores its position every second (continuous mode) or at another time interval chosen by the user (low-power mode). After downloading of the stored data onto a PC, the positions are analysed and represented graphically on a map.

For our study, we first used three GPS-MS1 receivers (Steiner et al. 2000) from July 2002 to February 2003 and from February 2003 to November 2003, we used ten SAM receivers

(GPS smart antenna module, basing 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 about 36 g, depending on the size of the battery. The GPS receiver represented 10–15% of a feral pigeon's body weight. When equipped with a 960-mA battery, recording lasted about 54 h in low-power mode (with the setting of one position every 5 s).

Accuracy Tests

To assess the suitability of GPS-tracking in the urban habitat, we tested the accuracy of GPS positions obtained in streets, in parks, on bridges and on buildings in Basel. We placed stationary GPS receivers at eight locations with varying amounts of open sky (for details see table 1, **Chapter 2**). The amount of open sky accessible to the receiver can greatly influence the reception and precision of GPS-positions (Dussault et al. 2001).

We compared the positions stored by the GPS receivers to the real positions using the electronic map of Basel. We also measured other indicators of data quality: the time-to-first-fix, i.e. the time between the onset of receiver operation and the time of the first recorded position, the number of interruptions, the maximum duration of interruption, and the rate of failure (no stored positions during the record).

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Chapter 2

Suitability of Using the Global Positioning System (GPS) for Studying Feral Pigeons *Columba livia* in the Urban Habitat

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ABSTRACT

Capsule GPS-tracking gives very precise information about Feral Pigeons' spatio-temporal behaviour in the urban habitat.

Aims To test the suitability and the limits of GPS-tracking in the urban habitat for a detailed analysis of Feral Pigeons' spatio-temporal behaviour.

Methods We placed ten receivers in eight different locations in the city of Basel, Switzerland. Between 1 and 23 April 2003, we performed 166 recordings and compared the stored positions with the real location. We also tested the GPS receivers on 29 free-living Feral Pigeons.

Results Almost 82% of the positions obtained with the GPS receivers were within 25 m and 96% within 100 m of the real location. The accuracy varied between locations, depending on the proportion of open sky. In 38% of the tests, no positions were stored. We performed 143 test flights with 29 Feral Pigeons (18 males and 11 females). A total of 118 flights produced "storable" position information, 25 flights (17.5%) produced no storable data. Over 47% of the flights were complete (beginning and ending at loft), the others began or ended elsewhere. We encountered some difficulties: delays to get the first fix; reflection of the satellite signal on tall buildings; and limited battery life.

Conclusion Despite some difficulties related to the urban habitat and the technical features of the GPS receivers, we recommend the GPS-based tracking method for studying the spatio-temporal behaviour of Feral Pigeons and other birds weighing over 300 g and which are easy to capture.

INTRODUCTION

The daily activity rhythms and the home range of Feral Pigeons are not well understood, despite a great number of studies, involving a variety of methods. Methods used include: (a) direct observation of pigeons commuting to the surroundings or flying within the city (Janiga 1987), (b) observation of individually marked birds at different places in town (Sol & Senar 1995), (c) use of an automated system based on electronic rings detected by an antenna at feeding places (Dell'Omo 1997), and (d) telemetry (Scholl & Häberling unpubl. data). Each method is limited, leading to sampling bias dictated by the observation points and time needed for observation. Direct observation gives a first indication where feeding occurs, but it is difficult to make statements about the individual foraging strategies. Marked individuals are sometimes difficult to locate, because pigeons can fly to places where recording is not possible (e.g. inner courts of private buildings). Sometimes the markings are difficult to recognize, e.g. when the birds are sitting too far away or because they escaped when the observer came too close. With an automated system the pigeon is registered only in places where the antennae are placed. Telemetry needs to follow the bird during observation and this can be difficult in towns because of the complex spatial structure.

A GPS (Global Positioning System) has been used successfully to monitor the flight of homing pigeons from the release point to the home loft (Von Hünerbein et al. 2000). The results of these studies were gathered under optimal conditions: in open field habitat without disturbance by high buildings and trees; easy handling by using tame homing pigeons; the pigeons flew directly back to their home loft, so the battery life in the GPS receivers was not a constraint. Weimerskirch et al. (2002) tracked foraging Wandering Albatrosses *Diomedea exulans* using GPS under good receiving conditions in open sea.

We set out to test the suitability and limits of GPS tracking in the urban habitat to perform detailed tracking of bird movements. We expected to encounter two main problems (Garmin Corporation 2000a): (a) reflection of the signals on buildings and (b) insufficient satellite signals, when the proportion of open sky is too restricted. Reflection can result in recording of shifted positions that are several hundred meters away from the real position. Limited reception of signals can lead to interruptions in the record, if there are not enough satellites available to calculate the position.

MATERIAL AND METHODS

GPS Receivers

The GPS system is based on a network of satellites that continuously transmit coded information. It allows precise location information to be gained by measuring the distances from the earth to the satellites (Mehl 1996). A GPS receiver stores its own position calculated from its distance to at least four satellites every second (continuous mode) or at another time interval chosen by the user (low-power mode). The stored data are downloaded from the GPS receiver to a PC where the positions are analysed and represented graphically on a map.

For our tests, we used ten GPS receivers (SAM, GPS Smart Antenna Module, basing 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 between 29 and 36 g, depending on the size of the battery. The GPS receiver is 10–15% of a Feral Pigeon's body weight. When equipped with a 960-mA battery (Li-poly accu SLPB523462 with PCM, Worley, Australia), recording lasted about 5 h in continuous mode or at least 54 h in low-power mode (with the setting of one position every 5 seconds). Steiner et al. (2000) discuss technical considerations and limitations of GPS tracking.

There are three options for data storage and retrieval (Rodgers et al. 1996): (a) storage of all data onboard, with retrieval upon recapture of the animal, (b) storage of data and transmission for retrieval by secondary low earth orbit satellite link or (c) storage of data and transmission to a local computer by radio link. We chose option (a), because the other two need supplementary modems for communication, which would increase the weight of the GPS receivers.

We used the software μ-logger (u-blox AG, Thalwil, Switzerland) for downloading. Positions from the GPS system are given in WGS-84 coordinates (World Geodetic System 1984, an earth-fixed global reference frame). We transformed these into CH-1903 coordinates (Swiss geodetic coordinates) and projected them on the electronic map of Basel (from the Grundbuch- und Vermessungsamt, Justizdepartement des Kantons Basel-Stadt), to show each position of the pigeons. The stored positions were represented on the electronic map by the software MapInfo Professional (MapInfo Corporation Troy, New York).

Accuracy Tests

To test the accuracy of the GPS positions obtained in an urban area, we placed stationary GPS receivers at different locations in the city of Basel, Switzerland (see table 1). The satellite geometry (the satellites' positions in three-dimensional space) greatly influences the location accuracy of GPS positions (Dussault et al. 2001). The ability to determine a position deteriorates if the four satellites used to take measurements are close together (Zogg 2002). If there are more than four satellites available, the GPS receiver chooses those that give the best satellite geometry. In urban areas, access to open sky is restricted and this often results in poor satellite geometry. Our GPS receivers do not indicate the satellite geometry they used to calculate the positions. We therefore tested the reliability of GPS position recording at least twice at exactly the same location at different times so as to receive different satellite geometries (the satellites are not stationary). Eight different locations with a different amount of open sky space were determined for that purpose. The locations were classified in categories according to the proportion of open sky.

We placed between six and ten GPS receivers simultaneously at one location and left them stationary for at least 32 min (maximum 101 min). Half of the GPS receivers were running in continuous mode (79 records), the others (87 records) in low-power mode set on one fix every 3 s. We configured the GPS receivers to store only positions calculated with four or more satellites. When navigating with less than four satellites the GPS utilizes the last computed altitude (Garmin Corporation 2000b). With stationary GPS receivers this can achieve good results (u-blox AG 2002). But with pigeons that rapidly change altitude the positions would be less accurate.

We compared the positions stored by the GPS receivers to the real positions using the electronic map of Basel. We observed that some stored positions were on altitudes that are not possible in Basel (e.g. below the lowest altitude of Basel). In such cases, the horizontal position error may be as large as the altitude error, e.g. when calculations are based on bad satellite geometry. Subsequently, we developed a filter to reject all non-sense positions (altitudes below 250 m and above 390 m)[a]. We compared this new set of data with the real positions to verify the reliability of our altitude filter.

We also measured other indicators of data quality: the time-to-first-fix, i.e. the time between the onset of receiver operation and the time of the first recorded position; the number of interruptions lasting longer than 1 min and longer than 5 min; the maximum duration of interruption; and the rate of failure (no stored positions during the record). We tested the differences between the receivers, the test locations and the operating modes using these indicators of data quality (see table 2).

Test with the Pigeons

The pigeons used for this study were living in three lofts situated in public buildings in Basel, Switzerland. The loft of the Matthäus church has a surface of 27.8 m^2 and contains 39 breeding boxes. Around 90 pigeons were resident in this loft. The Stapfelberg loft is 22 m^2 and was used by around 35 pigeons. The loft of the St Peter’s church is 11 m^2 and around 15 pigeons were resident there. The birds foraged in the city without any supporting food or water in the loft. The pigeons, therefore, show behaviour and activity patterns typical of free-living urban Feral Pigeons. We studied 11 females (average weight 339 ± 22 g) and 18 males (average weight 354 ± 25 g) known to be closely attached to the lofts, since they were breeding during the experiment or had bred a few weeks before. We studied only subjects in good body condition (birds that weighed over 300 g). We checked their weight repeatedly during the training and the subsequent GPS experiment.

In the Matthäus loft, we constructed special breeding boxes that can be closed from outside the loft to catch the breeding birds. Pigeons sitting outside the boxes and those in the other lofts were caught in the lofts with a net.

Before releasing the pigeons equipped with GPS receivers, they were accustomed to carry dummies of the same size and weight as the receivers for four to nine days. None of the birds seemed to be handicapped by the dummies, so all trained pigeons were used for the experiment. Only immediately after fixing the dummy on the birds, did we observe intensified preening, which stopped after a few minutes. Consequently, we believe that the GPS receivers do not irritate the pigeons or significantly influence their behaviour.

Both the dummies and the GPS units were fixed on the pigeons' back with Velcro tape glued to the feathers with cyanoacrylate (power-glue). To ensure a good fixation of the Velcro, the feathers were cut down to approximately 3 mm. Since some pigeons lost their dummies at the beginning of the study, we developed a supplementary fixation with a lightweight harness of elastic ribbon. Two loops of the ribbon passed around the pigeon's body, one anterior to the wings, the other between the cloaca and the legs. The two loops were connected on the abdomen with a strip that was sewn directly with silk to adapt it individually to the size of each pigeon. The GPS receivers were covered with a plastic film during the flights to protect them from precipitation and soiling.

We caught the pigeons in the morning to fix the GPS receivers onto their backs and released them immediately in the loft. The records started when the pigeons flew out of the loft, since there is no reception of satellite signals inside buildings. There was always a delay between leaving the loft and starting the record, due to the acquisition time of the GPS receiver (typically 45 s, u-blox AG 2003). In the evening, we removed the GPS from the homed birds to charge the battery and download the data to the PC. Between 12 February and 31 March 2003, we performed 143 test flights in low-power mode with 29 Feral Pigeons (18 males and 11 females).

RESULTS

Accuracy Tests

We obtained 166 records from ten unmounted GPS receivers at eight different places in the city of Basel. One receiver gave poor results due to problems with the battery so we eliminated this from the study. For 96 (61.9%) of the remaining 155 records, the GPS receivers successfully stored data.

Horizontal Accuracy

Over 81% of all stored positions were within 25 m of the real location and 96.3% within 100 m. The accuracy of the GPS positions varied between the different test locations (table 1). The mean percentage of positions within 25 m of the real location differed between the test locations (minimum 42.0% and maximum 95.3%). The mean percentage of positions within 100 m varied between 85.9% and 100%. We measured horizontal location errors (i.e. the distance between the real location and the measured position) up to 630 m.

After the elimination of positions with large altitude errors (under 250 m and over 390 m asl), the mean percentage of positions within 25 m of the real location increased from 81.8% to 86.6% (table 1). The mean percentage of positions within 100 m was also higher: > 99.9% instead of 96.3%. The maximum horizontal location error was reduced to 207 m after the data were corrected.

Table 1: Accuracy of the recorded positions at each test location (category 1: 76–100% of open sky; category 2: 51–75%; category 3: 26–50%). For each location, we give the total number of records performed, the number of successful records (with positions), the mean percentage of positions within 25 m and 100 m of the real position, the maximum distance error (both for uncorrected and corrected data set), and the vertical location error.

Location	Proportion of open sky, category	Number of records			Mean % of fixes				Max horizontal location error [m]		Mean vertical location error [m]
		Total	With positions	No of positions	Within 25 m	Corrected data set	Within 100 m	Corrected data set	Uncorrected data set	Corrected data set	
Mittlere Rheinbrücke	1	14	12	13 070	95.33	95.33	100	100	86	86	45
Johanniter-brücke	1	18	16	26 730	90.32	94.65	95.48	99.7	564	207	52.9
Matthäuskirche	1	18	11	35 198	86.63	88.17	99.53	100	198	77	57.8
Dreirosen-brücke	1	18	14	18 011	86.83	92.47	95.88	100	280	96	-
Stapfelberg	2	14	11	24 180	85.81	89.43	100	100	85	72	46.3
Rhine harbour St Johann	3	18	11	7022	41.97	52.37	85.94	100	252	64	96.8
Marktplatz	3	32	12	21 131	79.57	90.24	96.61	99.99	199	103	44.2
Petersplatz	3	23	9	9661	87.7	90.08	96.71	99.87	630	113	52.4
Total or mean		**155**	**96**	**155 003**	**81.77**	**86.59**	**96.27**	**99.95**	**286.75**	**102.25**	**56.49**

There was no statistically significant difference in the horizontal accuracy (percentage of positions within 25 m of the real location) between the receivers (three-way-ANOVA, $P = 0.34$, $n = 96$). The records in continuous mode gave slightly more accurate positions and approached significance ($P = 0.06$). There was a significant difference between the categories of locations ($P = 0.0009$), but this difference was only due to one test site, the harbour St Johann that differed considerably from the other locations ($P < 0.0001$). When testing the difference between the categories of locations excluding this problematic test site, the results were still slightly better in category 1, which had the more accurate positions, and category 2 compared with category 3, but the difference is not significant (three-way-ANOVA, P = 0.34, n = 85).

Vertical Accuracy

The mean difference between the altitudes calculated by the GPS and the real altitudes was 56.5 m (table 1). The smallest difference was 44.2 m and the greatest difference 96.8 m. We made no further analysis on the vertical accuracy, since the height calculated by GPS receivers is not directly comparable to altitudes above sea level.

Table 2: The ease of obtaining positions at each location, expressed as the time needed to get the first position (time-to-first-fix) and the number of interruptions that occurred during the test. The total operating time is the number of minutes between the first fix and the end of each test summed up for all tests in each location.

Location	Time-to-first-fix [min]			No of interruptions > 1 min	No of interruptions > 5 min	Max interruption [s]	Total operating time [min]
	Mean	Min	Max				
Mittlere Rheinbrücke	4.5	< 1	19	0	0	19	359
Johanniterbrücke	5.75	< 1	25	4	0	124	678
Dreirosenbrücke	5.5	1	26	11	2	300	516
Stapfelberg	5.3	< 1	33	6	1	485	628
Harbour St Johann	16.5	< 1	38	30	13	2340	480
Marktplatz	9.5	< 1	29	9	0	223	556
Matthäuskirche	7.2	< 1	29	44	11	2410	1019
Petersplatz	34	16	55	16	1	636	245
Mean	**11.0**	**8.5**	**31.75**	**15.0**	**3.5**		**4481**

Other Indicators of Good Quality Data

Table 2 shows the values obtained for each indicator of data quality at the different test locations. The interruptions and the long duration of time-to-first-fix occurred when the GPS receiver was unable to get signals from at least four satellites.

The statistical tests (three-way-ANOVA, logistic regression, and Poisson regression for the different indicators of data quality) showed no significant differences between the receivers.

The recordings in continuous mode gave significantly shorter interruptions than in low-power mode (three-way-ANOVA, P = 0.01, n = 96). The continuous mode also had fewer interruptions. The difference was statistically significant for the number of interruptions > 1 min (Poisson regression, P = 0.02, *n* = 96) but not for the interruptions > 5 min (P = 0.54). In those cases where we included the harbour, the difference in the maximum duration of interruption between the location categories was significant (P = 0.008) but when we excluded the harbour the maximum interruption was no longer significantly shorter in categories 1 and 2 compared with category 3 (P = 0.75, *n* = 85). The rate of failure was also significantly greater in location category 3 (with or without the harbour) compared to location-category 2 (with harbour P = 0.013, n = 155, without harbour P = 0.004, n = 137) and to category 1 (P < 0.0001 with or without the harbour). The other indicators of quality data gave no significant differences between the location categories or between the operating modes.

Table 3: Flights performed by male and female Feral Pigeons carrying GPS receivers. Flights of less than one hour were not included in the analysis.

	Number of flights (%)							Flight duration [min]	
Sex	**No**	**With data**	**Complete**	**Beginning at loft**	**Ending at loft**	**Neither beginning nor ending at loft**	**Lasting < 1 hr**	**Mean**	**Range**
Male	82	70 (85.4)	34 (48.6)	4 (5.7)	18 (25.7)	5 (7.1)	9 (12.9)	286	75–522
Female	61	48 (78.7)	22 (45.8)	7 (14.6)	11 (22.9)	3 (6.3)	5 (10.4)	336	62–566
Total	**143**	**118 (82.5)**	**56 (47.5)**	**11 (9.3)**	**29 (24.6)**	**8 (6.8)**	**14 (11.9)**	**307**	

Tests with Pigeons

Of the test flights with pigeons, 118 produced storable position information and 25 flights (17.5%) produced no stored data (table 3). There were 56 (47.5%) complete flights and the others were incomplete (table 3); 14 flights (11.9%) had a record duration of less than 1 h. There were no significant differences between the number of successful flights obtained with males or with females (Fisher's exact test, P = 0.37, n = 143), the number of complete flights (P = 0.61), the number of flights beginning at the loft (P = 0.21), ending at the loft (P = 0.68), neither beginning nor ending at the loft (P = 1.0), and the number of flights lasting less than one hour (P = 0.78).

The pigeons always returned to the lofts in the evening except for three flights: two pigeons returned the next day and one pigeon returned two days later.

We monitored the pigeons' body weight during the entire experiment. After the training with the dummies (4–9 days), the pigeons had significantly lost weight (one-sample-t-test, P = 0.003, n = 29). The mean loss was 2.6% of the body weight. The females showed a significantly greater weight loss (4.6%) than the males (1.5%, Wilcoxon-Mann-Whitney-Test, P = 0.04, n = 29). We employed mixed linear models to examine if there were changes in body weight after the training, but there were no more significant changes.

DISCUSSION

Accuracy Test

In our tests, 81.8% of the positions were within 25 m of the real location and 96.3% within 100 m. Elimination of obviously false positions by altitude resulted in higher percentages (86.59% and 99.95% respectively). Theoretically, 95% of the time an accuracy of ≤13 m in the horizontal and ≤22 m in the vertical plane is attained (Zogg 2002), assuming optimal conditions with completely open sky and good satellite geometry. Dussault et al. (2001) performed tests in open areas: 95% of the positions were within 250 m and 50% within 160 m. They performed their study before removal of the selective availability (the United States Department of Defense previously intentionally degraded the signals transmitted by the GPS satellites for civilian users). Dussault et al. (2001) applied a data correction eliminating positions obtained with bad satellite geometry, increasing the accuracy to 95% within 75 m and 50% within 15 m. The accuracy of the GPS positions in our tests is comparable to the results obtained by Dussault et al (2001).

The maximal horizontal location error we measured was 630 m. It is in the same range as the 650 m obtained by Rempel et al. (1995) under boreal forest canopy.

The accuracy of positions obtained during the flights with pigeons can hardly be verified. We expect the positions to be more accurate since pigeons spend a lot of time on the roofs of buildings, where the proportion of open sky is nearly unrestricted. But gaps in the record are inevitable when the pigeons fly down to the streets to feed or when sitting on the walls of buildings.

We made no further analysis of the vertical accuracy, since the height calculated by GPS receivers is not directly comparable to altitudes above sea level (see section “Accuracy tests” in Material and methods).

We found no statistically significant differences in the quality of data obtained with the different receivers. Therefore, we conclude that the differences that occurred are due to the operating mode and the locations. We obtained more accurate positions and less interruptions with receivers operating in continuous mode. Since we intended to record the pigeons’ flight activity of the entire day, we had to set the receivers in low-power mode. The accuracy of GPS positions in this operating mode could be further improved with the use of differential GPS (a costly system that uses the known position of a local reference station to correct the obtained GPS positions).

Problems with the Urban Habitat

We expected to encounter two problems connected to the structure of the urban habitat: reflection of the satellite signals on high buildings and insufficient satellite signals. During the accuracy tests, at the harbour St Johann location (characterized by high grain storage buildings) we achieved significantly less precise data than at all other locations. Without this problematic location, the categories of locations differed significantly only in the rate of failure. Generally, the accuracy of the results depended on the degree of open sky, but the differences were not statistically significant.

Some flight paths of pigeons showed positions that we interpreted as shifted positions because of the reflection of satellite signals. With the accuracy tests we proved that reflection had occurred.

The lack of sufficient satellite signals occurred when the records had interruptions or if there were long times-to-first-fix. Rempel et al. (1995) had similar problems under forest canopy (at some locations only 10% of the attempts to get a position were successful). We had comparable results in our tests: the time-to-first-fix varied among the different locations, being shorter at open locations than on narrow public squares. The interruptions during the records were also more frequent at locations with a smaller percentage of open sky. The positions stored immediately before and after interruption indicate where these interruptions occurred and if the pigeon moved during the gap. During flights, the access to open sky is better, so we expect the record to restart quickly if the pigeon flies during a gap.

Problems with the Behaviour of Feral Pigeons

Feral Pigeons are not really used to handling by man and they are free-ranging (Haag-Wackernagel 2000), so their behaviour is unpredictable. The GPS-based method requires the return of the carrier bird to the loft or to a site where the receiver can be removed. Our tests showed that the trained pigeons always returned to the loft in the evening or the following day, even after some weeks of daily disturbance by human activity in the loft. Handling, and especially capturing, represents stress for a wild bird. This might influence normal behaviour. After handling, however, the Feral Pigeons from our lofts returned rapidly to their normal activity, e.g. breeding birds returned to their eggs, as we observed in the loft. Consequently, we believe that the GPS receiver does not irritate or disturb the pigeons significantly.

The pigeons showed an average weight loss of 2.6% at the beginning of the tests during the training with the dummies, but afterwards the weight stabilized. For comparison, we calculated an intraindividual standard deviation of 8% in the weight variation in a data set obtained over a few years with undisturbed Feral Pigeons in Basel (n = 28). During training, females showed a significantly greater weight loss than males. Despite this, females didn't behave differently during the flights with the receiver (no significant differences in the numbers of successful flights, complete flights, or incomplete flights).

Technical Problems

The GPS receivers needed a few minutes to store their first position (time-to-first-fix), especially when the receivers were at a location with poor satellite reception. Even under optimal conditions the delay due to the acquisition time required by the receiver is of around 45 s. This can lead to incomplete records.

The battery life may be insufficient to record the entire day's activity if the pigeons are equipped with the device in the morning but fly out to forage only in the late afternoon. During their stay in the loft, the GPS receiver continuously tries to get satellite signals. This energy-consuming process has limiting effects similar to using continuous working mode. The capacity can be increased only by adding a heavier battery or by lowering the sampling frequency (low-power mode). A weight increase would however, be problematic. We think that the present weight already represents the maximum a pigeon can carry without influencing normal behaviour. Kenward (2001) indicates that adverse effects tend to emerge in the long-term for harness-mounted tags weighing more than 4–5% of body mass. Gessaman & Nagy (1988) and Gessaman et al. (1991) tested the flight performances of homing pigeons and tippler pigeons with a load of 5% of the body mass. The load decreased the speed and increased the intensity of the pigeons' metabolism during long flights, but the pigeons nevertheless remained able to perform long flights (320 km). In our tests, the pigeons carried GPS receivers representing 10–15% of their body mass, but they did not have to fly over long distances and did not carry the receivers for a long time.

The sampling frequency can be lowered to save power, but the accuracy of the positions consequently decreases (u-blox AG 2002). Another way to save power is to set longer standby phases when the receivers can't get satellite signals. But the resulting information loss may be crucial.

The results show that 17.5% of the flights had no stored position. The failures can be explained in three ways: either the pigeon leaves the loft with an empty battery, the pigeon does not leave the loft at all or the pigeon flies out and spends all the time at a place where the satellite signals cannot be recorded (not enough open sky, poor satellite geometry).

Our tests with GPS receivers confirm that GPS-tracking is an appropriate method for studying Feral Pigeons, despite some problems due to the structure of the urban habitat, the technical features of GPS receivers and the unpredictable behaviour of wild birds. The stored data can be filtered (e.g. according to altitude) to eliminate inexact positions. Therefore, very precise information about a bird's spatio-temporal use of a habitat can be supplied. Some elements of a species' lifestyle are required to render it suitable for GPS tracking: with the actual weight of the GPS receivers, the animal's body weight should be over 300 g, and they must be easy to capture and recapture. In the urban habitat, recording is difficult on the ground of the street canyons. Therefore, GPS-tracking is unsuitable for animals staying only at ground level.

ENDNOTES

a. To develop the altitude filter we determined the altitude range within which the pigeons were expected to stay. The lowest altitude in Basel is the Rhine river (240 m asl). We recorded pigeons on the top of the highest buildings (grain storage building in the harbour St Johann, 315 m), but they never flew at high altitudes above these high buildings. Our accuracy tests revealed that the altitudes calculated by the GPS receivers are always higher than the real altitudes (mean 56 m, see results). The real altitudes are defined here as altitudes in Switzerland measured on sea-level of the Mediterranean Sea. The height determined by GPS measurements relates to the perpendicular distance above the reference ellipsoid and therefore differs from the height datum Mean Sea Level (MSL). The difference between altitudes approximated by the WGS-84 ellipsoid and the MSL measurements can come up to 100 m (u-blox AG 1999). To avoid excessive information loss, we set an altitude filter to reject GPS altitudes below 250 m and above 390 m, including margins above and below the pigeons' normal altitude range and also the difference between GPS height and altitude above sea level.

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Chapter 3

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 and have optimally 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 differed between 300–500 m 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 and places near the home loft, (2) in agricultural areas surrounding the city, (3) on docks and railway lines in harbours. The maximum distance covered was 5287 m. More than 32% of the pigeons remained within 300 m of the home lofts and only 7.5% flew distances of more than 2000 m. 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, since 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.

INTRODUCTION

Feral pigeons are descendants of wild and domesticated rock pigeons (Johnston and Janiga 1995) and have optimally adapted to the urban habitat (Haag-Wackernagel 1998). 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. 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). Johnston and Janiga (1995) define two principal foraging strategies for feral pigeons: (1) foraging in the streets and places 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 commuting flights were recorded, and the pigeons fed in the streets and places (e.g. Gompertz 1957; Sol and Senar 1995; Slotta-Bachmayr et al. 1995). This contradictory situation indicates that the foraging habits of feral pigeons may greatly vary between cities.

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, 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. This method was successfully used to monitor flight tracks of albatross (Weimerskirch et al. 2002) and homing pigeons (Von Hünerbein et al. 2000; 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, since 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.

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 seconds). 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. 86–100% of the positions are expected to lie within 100 m of the real location (Rose et al. 2005).

We set the GPS-receivers to store their position every three seconds. 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 weekly to identify the sex of the birds (through their behaviour), the pairs, and to control 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). 42 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 over 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 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 four to nine 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, since 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, since 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. 266 records were performed with pigeons from the Matthäus-loft, 104 from the Peters-loft, and 205 from the Stapfelberg-loft. 87 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 3631±3036).

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

Statistical Tests

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, 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 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 a calculation basis for our statistics.

For all statistical analyses, we used the program SAS statistical software (release 8.2, SAS Institute Inc., Cary, 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 record and records that had not started at the loft). We assume that incomplete records of his 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 the 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 were adjusted to attain normal distribution of the residuals.

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°).

Some pigeons presented all three breeding states (non-breeding, breeding, and rearing juveniles) in their records. For these birds, we tested the intraindividual influence of the breeding state on the time spent outside using a Signed Rank test. We chose this simple test to exclude the influence of other factors that are present in the mixed model and to increase the statistical efficiency.

In all our analyses, we set the level of significance at P=0.05.

RESULTS

We performed 575 records of which 497 stored positions (86.4%). 215 records (43.3%) were complete, 232 records (46.7%) were incomplete, 44 records (8.9%) only remained on the roof of the loft, and 6 records (1.2%) only stored a few isolated positions and were not analysable. 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.

Covered Distances

The maximum distances attained during the records varied between 26 m and 5287 m. Table 1 shows the covered distances (mean and range) of the pigeons from the three lofts.

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 300 m away from their loft, and only 7.5% flew further than 2000 m. Figure 1 additionally shows a large variation in the covered distances between the lofts. Long distances (more than 2 km) were covered by five pigeons, four from the Stapfelberg-loft and one from the Peters-loft, commuting to the agricultural areas in the surroundings of Basel.

Table 1: Maximum distances attained by the pigeons of the three lofts. The basis for the analysis are the mean values calculated for each pigeon. We included all records that ended at the loft.
[a] Pigeons from this loft had significantly longer maximum distances (mixed linear model, P = 0.0001, n = 67 pigeons and 320 records), [b] There was no significant difference between the pigeons of these two lofts.

Lofts	Mean±SD [m]	n pigeons	Range of the max distance in all records [m]
Matthäus	703±263[a]	31	40–1180
Peters	654±528[b]	13	26–4530
Stapfelberg	491±619[b]	23	70–5287
Total	621±476	67	

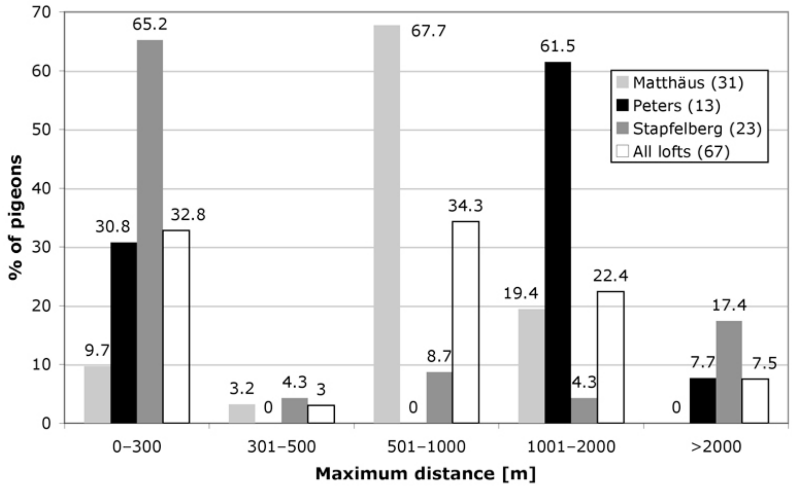

Figure 1: Percentage of pigeons that had their maximum distances in the different categories of distances. The maximum distance covered for each loft was 1180 m for Matthäus, 4530 m for Peters, and 5287 m for Stapfelberg. The numbers in brackets beside the names of the lofts indicate the number of pigeons included in the statistics. On average, pigeons from the Matthäus-loft covered significantly longer distances than those from the other lofts (mixed linear model, P = 0.0003, n = 67 pigeons and 320 records).

Table 2 shows the differences in the distances covered by male and female pigeons of the three lofts. The 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 the records that ended at the loft). The long distances to the surroundings of the city belonged to four females and only one male that was not mated to one of these females.
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).

Table 2: Maximum distances attained by female and male pigeons on their day-records. The mean value for the lofts is calculated on the base of the mean values of all pigeons. We included all records that ended at the loft. On average females covered significantly longer distances than males (mixed linear model, *P*=0.04, *n*=67 pigeons, 320 records).

Lofts	Sex (n pigeons)	Mean distance [m] ±SD	Range [m]
Matthäus	F (14)	763±248	250–980
	M (17)	653±280	74–967
Peters	F (5)	917±546	138–1445
	M (8)	490±517	90–1443
Stapfelberg	F (11)	580±742	193–2653
	M (12)	408±536	189–2069

Foraging Strategies

Table 3 shows the number and the percentage of records that exhibited the various foraging strategies or combinations of them. Foraging in streets and places was the principal strategy, since it occurred in 63.1% of all records. Flying to surrounding agricultural areas was never found alone. All records started with a stay in streets or squares.

Table 3: Number of records showing the different foraging strategies, both alone and in combination. The combinations that are not in the table did not occur during the records.

Foraging strategy	All records		Complete records	
	Number	%	Number	%
streets/places	282	63.1	136	64.2
fields	0	0	0	0
harbour	62	13.8	25	11.8
streets/places + fields	10	2.2	7	3.3
streets/places + harbour	93	20.8	44	20.8

Table 4 shows the foraging strategies employed by the studied individuals. More than 45% of the pigeons had only one strategy, i.e. foraging in streets and squares. The same percentage showed a combination between streets/squares and harbour. Only 8.3% showed commuting flights in combination with foraging near the loft.

Table 4: Foraging strategies of the studied individuals (pigeons with >4 records). The combinations that are not shown in the table did not occur. 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.

Loft (n pigeons)	**Streets/ places**	**Fields**	**Harbour**	**Streets/ places + fields**	**Streets/places + harbour**
Matthäus (18)	2 (11.1%)	0	0	0	16 (88.9%)
Peters (10)	4 (40%)	0	0	1 (10%)	5 (50%)
Stapfel (20)	16 (80%)	0	0	3 (15%)	1 (5%)
Total (48)	22 (45.8%)	0	0	4 (8.3%)	22 (45.8%)

Temporal Use of the City

Figure 2 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 (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.

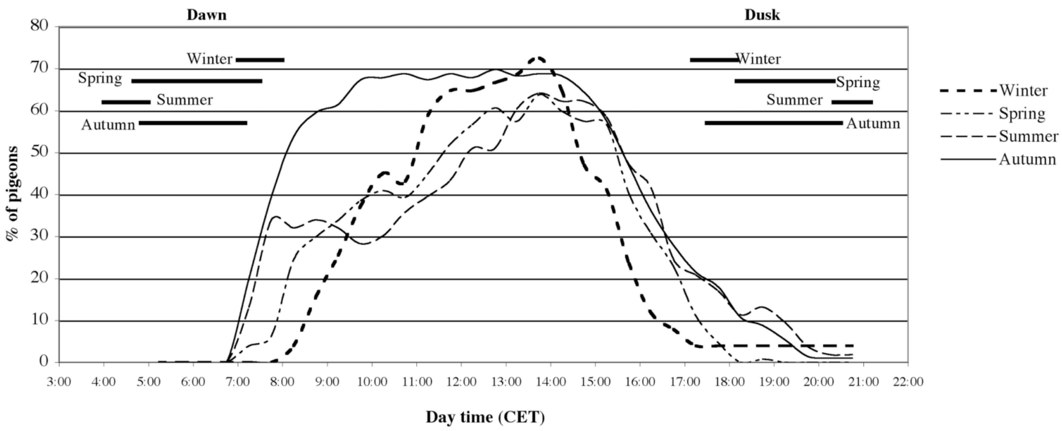

Figure 2: Seasonal variations in the percentage of pigeons outside. Winter = 6 November – 4 February, spring = 5 February – 6 May, summer = 7 May – 6 August, autumn = 7 August – 5 November. The black lines on the left and the right of the curves represent the hours of dawn and dusk for each season. Pigeons left the lofts significantly later in winter and spring (mixed linear model, P = 0.002 and P = 0.003, n = 68 pigeons and 263 records, including all records that started at the loft). In winter they came back significantly sooner than in the other seasons (P = 0.04, n = 67 pigeons and 300 records, including all records that ended at the loft).

Non-breeding males and females showed a similar temporal use of the city (Fig. 3A). The temporal distribution of breeding pigeons reveals a bimodal use of the urban habitat (Fig. 3B). Males predominantly stayed outside between 7:00 and 11:30, females between 11:31 and 17:00. 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 later 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.

On average, the pigeons spent 29.4% of day length outside (226 min). The maximum time spent outside was 681 min (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. There was no significant difference between the lofts in the average time spent outside.

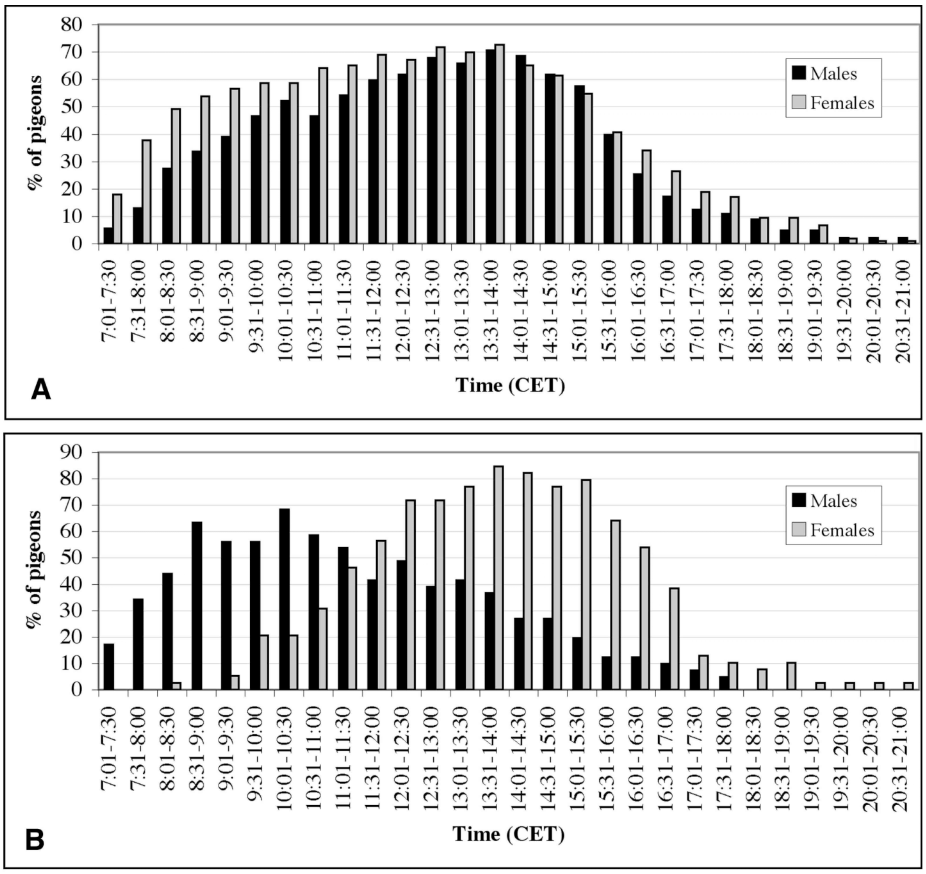

Figure 3: Differences in the activity patterns of males and females between non-breeding (A) and breeding pigeons (B). Breeding females left the lofts significantly later than non-breeding females or those rearing young (mixed linear model, $P = 0.04$, $n = 33$ females and 130 records, including all records that started at the loft). They also returned significantly later ($P = 0.003$, $n = 30$ females and 141 records, including all records that ended at the loft). Breeding males returned significantly sooner than non-breeding males or those rearing young ($P = 0.02$, $n = 37$ males and 159 records, including all records that ended at the loft), but the beginning of their external activity didn't shift significantly during breeding.

Figure 4 shows the time spent outside for males and females of the three lofts. Females spent on average 258±135 min outside, males 196±106 min. This difference was statistically significant (mixed linear model, P=0.01, n=62 pigeons and 212 complete records).

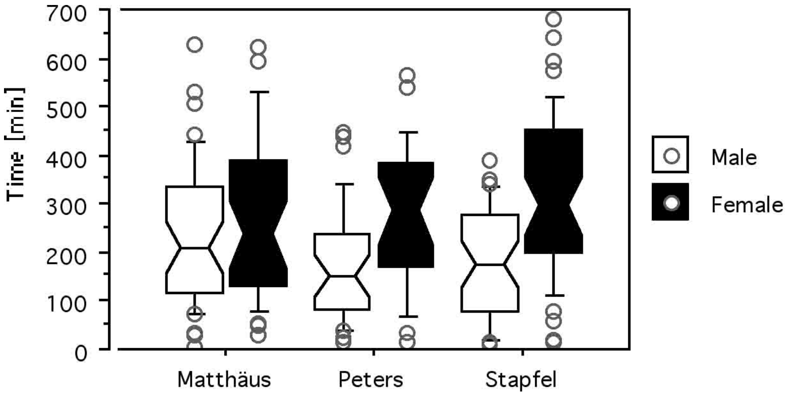

Figure 4: Box plot of the mean time spent outside the lofts by males and females of the three lofts. Females spent significantly longer times outside than males (mixed linear model, $P = 0.01$, $n = 62$ pigeons and 212 complete records).

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 (Signed Rank test, P=0.04, 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.

Pigeons spent more time outside in autumn (Table 5) compared to the other seasons and this difference was significant (mixed linear model, P=0.002, n=62 pigeons and 212 complete records). In autumn, pigeons spent a significantly longer proportion of the day outside compared to the other seasons (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).

Table 5: Mean and maximum time spent outside the loft by the pigeons during the different seasons. The last row indicates the mean percentage of day length spent outside in each season. [a] differed significantly from the other seasons (mixed linear model, P=0.002, n=62 pigeons and 212 complete records). [b] differed significantly from the other seasons (P=0.04, n=62 pigeons and 212 complete records). Some pigeons performed records in more than one season. In these cases, we calculated their mean time spent outside in the different seasons. The total number of pigeons included is 62.

Season (n pigeons)	Mean time [min ±sd]	Maximum time [min]	% of the day outside
Winter (11)	159±103	445	26.9
Spring (25)	201±90	442	26.2
Summer (10)	204±129	515	20.4
Autumn (29)	285±161[a]	681	37.5[b]

DISCUSSION

Distances

Table 6 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 500–600 m. The mean distances were longer for pigeons in Basel, except for commuting flights.

The distances covered to reach the fields (max 5.2 km) were shorter than those given by other publications (Table 6). These studies did not indicate the exact distances covered, since the starting point of the pigeons commuting to the fields was unknown. The distances covered depend essentially on the size of the city, the spatial distribution of the resources, and the food supply in the fields.

There is no evidence for an 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. 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 6). The GPS-method allowed to record commuting flights to the fields, which was not possible with the other method. The few studies that measured longer flights (Murton et al. 1972b; Lévesque and McNeil 1986) obtained distances comparable to those recorded in the present GPS-study.

The factors “sex” and “loft” significantly influenced the distances covered during the records. Female pigeons were recorded at significantly longer distances from the loft than males. Two studies revealed similar observations. Eber (1962) recorded more commuting flights 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 deficiency, since 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.

Table 6: Comparison of maximum and mean distances of feral pigeons.

Maximum distance	Mean distance	City	Method	References
5287 m (to surroundings) 1746 m (in the city)	560 m (complete records) 585 m (all records) 32.1% within 300 m 34.7% within 500 m	Basel, Switzerland	GPS	Present study
1900 m		Base, Switzerland	marked pigeons	Haag (1984)
340 m		Barcelona, Spain	marked pigeons	Sol and Senar (1995)
500 m		Hamburg, Germany	marked pigeons	Reinke (1959)
Rarely more than 500–600 m		Vienna, Austria	observation of obviously coloured plumage	Friedl (1938)
0.5 miles		London, England	marked pigeons	Gompertz (1957)
Rarely more than 500 m		Essen, Germany	observations	Eber (1962)
600 m		Zurich, Switzerland	marked pigeons	Bauer et al, (1990)
1 km		Rome, Italy	marked pigeons and automated system with eletronic rings	Dell'Omo (1997)
1.3 km	107 m (inner part of city) 194 m (outer part of city) 96% (inner part) and 60% (outer part) within 200m	Salzburg, Austria	marked pigeons	Slotta-Bachmayr et al. (1995)
1.3 km		Geneva, Switzerland	marked pigeons	Nötzli (1991)
1.4 km		Vienna, Austria	marked pigeons	Steiner and Zahner (1994)
6 km	95.6% within 500 m	Montréal, Canada	marked pigeons	Lévesque and McNeil (1986)
4 miles = 6.4 km	85% within 100 yards (91 m)	Manchester, England	marked pigeons	Murton et al. (1972)
6–8 km (commuting flights)		Parma, Italy	visual observation of commuting pigeons	Baldaccini and Ragionieri (1993)
6–11 km (commuting flights)		Reggio Emilia, Italy	visual observation of commuting pigeons	Ragionieri et al. (1992)
6–18 km (commuting flights)		Brno, Czech Republic	visual observation of commuting pigeons	Havlin (1979)
15–20 km (commuting flights)		Cape Town, South Africa	observation of commuting pigeons	Little (1994)
3–25 km (commuting flights)		Bratislava, Slovakia	visual observation of commuting pigeons	Janiga (1983)

Foraging Strategies

We recorded the two foraging strategies and also the intermediate one (see introduction). We think that 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 and places 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.

The most important strategy in Basel is foraging in streets and places near the home loft. There were differences between the lofts. Pigeons from the Matthäus-loft preferred to forage in the harbour and they never commuted to fields. The pigeons in the other two lofts used all three strategies in variable percentages. In our study, five pigeons performed commuting flights. Additionally, we made visual observations in the agricultural areas and never observed large flocks of feral pigeons in the fields in the surrounding of the city. Commuting flights to agricultural 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. Other studies recorded no commuting flights. Eber (1962) found that flights to fields varied between individual homing pigeons. She proposes that pigeons have a variable innate tendency to show this commuting behaviour. Adult pigeons transmit it to their offspring. Brehm (1857) describes how commuting flights 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. Commuting flights are 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). In many studies undertaken in different cities, no commuting flights 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 in the surroundings of the city but their exact provenance could not be determined (Goodwin 1960; Steiner and Zahner 1994; Schneditz 1996). The GPS-method used in this study has the advantage of recording all flights and yielding very precise information about commuting flights.

Foraging strategies varied individually. 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.

Temporal Use of the City

The results of our study are not directly comparable to those of other authors since we did not record the same activity of pigeons. We recorded the absence from the loft, other studies recorded the presence at feeding places (Lefebvre and Giraldeau 1984) or the departure from and arrival at the city (Havlin 1979; Janiga 1987; Ragionieri et al. 1992; Baldaccini and Ragionieri 1993). 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). 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.

Timing of activity was also different for pigeons in Basel. They left the roosting places later in the morning compared to wild rock pigeons (Baldaccini et al. 2000) and to feral pigeons in Montréal (Lefebvre and Giraldeau 1984), Bratislava (Janiga 1987), Brno (Havlin 1979), Reggio Emilia (Ragionieri et al. 1992), and Parma (Baldaccini and Ragionieri 1993). The return of our birds to the lofts also occurred later than reported by Janiga (1987). We closed the Peters-loft and the Stapfelberg-loft in the evening on the day before GPS-records were performed. This might have slightly delayed the departure time of some individuals, but there is no evidence that the global results for these lofts were influenced. 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.

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 found by Havlin (1979) and Reinke (1959).
In winter and spring, the pigeons left the loft significantly later in the morning. As expected, the time of departure was significantly influenced by day length defined by the light intensity.
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

Between winter and summer, the pigeons spent an increasing amount of time outside the loft, but a decreasing percentage of the day, since 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. (1972a) 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.
In autumn, the pigeons spent a greater part of the day outside than during the other seasons. It cannot be explained by the day length which is similar to spring, nor by the percentage of breeding pigeons which is comparable to the winter value. Furthermore, we found no significant effect in the statistical models of these two variables on the amount of time spent outside. Our hypothesis 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. (1972b) 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.

Our results showed that female pigeons spent significantly more time outside the loft than males. 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

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. Our study revealed that breeding pigeons spent less time outside than non-breeding birds or birds rearing juveniles. This shows that breeding is a constraint to pigeons, since it takes them a lot of time that could otherwise be used for other activities. 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.

Pigeons with juveniles spent on average more time outside the loft. Juveniles of one to six or seven 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).

The different results of the various studies show that pigeons have not only 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 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. 1972b). Therefore, in many cities the timing of pigeon activities is due to human influence rather than natural rhythms.

The differences in the results obtained by our study and those of other studies may be due to the method used. GPS-technology allows very precise recordings and cover the pigeons' entire activity, without bias due to observation spots. We were able to show that the pigeons have very individual strategies in using their urban habitat. We found differences between the pigeons of the three lofts, but 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, in order to provide additional statements about the spatial use of the urban habitat by feral pigeons.

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Chapter 4

Practical use of GPS-localisation of Feral Pigeons *(Columba livia)* in the urban environment

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SUMMARY

Feral Pigeons *Columba livia* live in almost every city around the world and often are a problem because of their large numbers. Knowledge of the spatial use of the city by pigeons is important for population control strategies. Previous studies gave contradictory results concerning the urban area used by pigeons and their feeding strategies. We used the Global Positioning System (GPS) to investigate the spatial use of urban habitats by Feral Pigeons in Basel, Switzerland. The total ranges of the subpopulations varied between 32.9 and 306.3 ha and overlapped partially. The total ranges of individual Feral Pigeons varied between 2.9 and 150.6 ha. Pigeons from a single loft had one or two main feeding places and up to 33 other places they used for occasional feeding on food remains or for resting. Individual pigeons visited up to ten different locations. Our study shows that Feral Pigeons have individual feeding strategies and are flexible enough to adapt to different urban environments. Therefore, we must contradict the view that Feral Pigeons are dependent on intentional feeding by man and unable to fly more than a few hundred meters. Our results are important for pigeon control strategies, biomonitoring projects using Feral Pigeons as indicators of pollution, and for the study of transmission of diseases. Pigeon control strategies based on killing have only a local and temporary effect, since pigeon subpopulations are interconnected. Pigeons from other areas will replace removed individuals. Biomonitoring projects usually assume that pigeons show a limited mobility. Our study reveals that this is not a generally valid assumption. Since pigeon subpopulations are connected diseases can be spread over an entire urban area. This is of human concern, since seven infectious diseases have been proved to be transmitted from pigeon to man.

INTRODUCTION

Feral Pigeons *Columba livia* live in almost every city around the world (Goodwin 1978). Their large numbers often cause problems, including soiling of buildings and footpaths and transmission of diseases and parasites (Haag-Wackernagel 1998). Knowledge of the spatial use of the city by pigeons is important for population control strategies. Many studies have investigated how pigeons use their urban habitat. Some authors state that pigeons have small home ranges in towns (Friedl 1938, Reinke 1959, Murton *et al.* 1972, Sol & Senar 1995), whereas others found that pigeons travelled long distances (Havlin 1979, Janiga 1983, Little 1994). Scientific investigators used various methods such as (a) observation of directions taken by flying pigeons (Havlin 1979, Janiga 1987), (b) observation of individually marked birds in towns (Lefebvre & Giraldeau 1984, Steiner & Zahner 1994, Sol & Senar

1995), (c) use of electronic rings detected by an antenna at some feeding places (Dell'Omo 1997), and (d) telemetry (Scholl & 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 where pigeons show an increased escape distance.

We employed the Global Positioning System (GPS) to study the spatio-temporal use of urban habitats by Feral Pigeons. This method has previously been used successfully to monitor flight tracks of albatrosses (Weimerskirch *et al.* 2002) and homing pigeons (Von Hünerbein *et al.* 2000, Lipp *et al.* 2004, Meade *et al.* 2005). We show that this method is also suitable for the monitoring of Feral Pigeons in urban habitats (Rose *et al.* 2005). GPS-tracking eliminates the bias due to the practicability of observing pigeons in built-up areas, since all places visited by the pigeons equipped with this device 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 was to gather precise information about the spatial use of the city of Basel by Feral Pigeons and to identify factors influencing their behaviour. We compared the results obtained by GPS-technology to those obtained previously with other methods. Our research group is working on three principal problems concerning Feral Pigeons: the suitability of Feral Pigeons in biomonitoring projects designed to indicate levels of pollutants in the urban habitat (Nagel *et al.* 2001), the regulation mechanisms that limit large Feral Pigeon populations (Haag-Wackernagel 1993), and the public health problems posed by Feral Pigeons (Haag-Wackernagel & Moch 2004, Haag-Wackernagel & Spiewak 2004). All three research domains need an exact understanding of the spatial use of urban habitats by Feral Pigeons, e.g. the linking of the various flocks within a town. Our basic research using the GPS-technology provides us with precise information that can be used to tackle these problems.

MATERIALS AND METHODS

GPS Receivers

From July 2002 to February 2003, we used three GPS-MS1 receivers (Steiner *et al.* 2000) and from February to November 2003 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 represented 10–15% of a Feral Pigeon's body weight. In Rose *et al.* (2005), we show that pigeons are able to carry this weight without being affected in their behaviour or their welfare.

We set the GPS receivers to store their position every three seconds. For downloading, we used the software μ-logger (u-blox AG, Thalwil, Switzerland).

Study Species

We worked with 80 Feral Pigeons living in three different lofts situated in public buildings in Basel, Switzerland (for a description of the lofts see Rose *et al.* 2005). The pigeons use the lofts as breeding and sleeping places, but they are free living and can voluntarily leave and enter the loft at any time. We do not feed them and they forage like other urban Feral Pigeons. The study environment, therefore, represents the situation of wild Feral Pigeons. Before starting our GPS-study, we observed the pigeons in the lofts weekly to identify their sex according to their behaviour and to recognise the pairs. We also controlled their fidelity to the loft and their breeding state. To ensure the return of the pigeons equipped with GPS receivers to the loft, we chose the ones that were closely bound to it. Most of them were 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 which we could not determine the sex (340 g). All subjects were in good health and body condition, i.e. they weighed over 300 g and presented no symptoms of illness like soiled plumage, or grey and soiled nostrils (Vogel *et al.* 1983).

We first trained the pigeons with dummy packages of the same size and weight as the receivers. Before their first GPS-record, the pigeons carried dummies for four to nine days to become used to the weight. This training period allowed us to observe the pigeons' reaction to the load. Dummies and than the receivers were fixed on the pigeons' back with Velcro tape and with a harness consisting of two loops passing around the body and joined at their breast (Rose *et al.* 2005). For the day-records, we caught the pigeons in the morning to fix the GPS receivers on their back. We released them immediately in the loft afterwards. The record did not start before the departure of the pigeon from the loft, since there is no reception of satellite signals inside buildings. After dark, we removed the GPS from all the homed birds to download the data to the PC and to charge the battery. For more details about the method see Rose *et al.* (2005). Between July 2002 and November 2003, we performed a total of 575 day-records. Each bird was equipped with a receiver between 1 and 17 days (mean 7.2±3.3).

The captures and the experiment were performed with the permission of the Cantonal Veterinary Office of Basel Town, Switzerland (authorization no 1859) and were conform to the Swiss law on animal welfare.

Statistical Analysis

For analysis, we divided the day-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 technical delay to get the first position), 3) records that did not end at the loft (due to the empty battery), 4) records that did not start nor end at the loft, 5) records where the pigeon remained all the time on the roof of the loft, 6) records composed of isolated positions that were not analysable. The last two categories were excluded from the statistics. We discuss the technical problems that led to those incomplete records and their implications in Rose *et al.* (2005).

For statistical analyses, we employed the program SAS statistical software, release 8.2 (SAS Institute Inc., Cary, USA). In our models, “loft”, “sex”, “breeding state”, and “season” were treated as fixed factors and an AR(1) covariance structure was assumed for the serial correlation of measurements within birds. We investigated on the influence these factors had on the number of places visited by the pigeons during all their records. We used a classic regression model for that purpose. The number of day-records performed by each pigeon was included as a fixed factor. We also analysed the influences on the number of places the pigeons had visited during each day-record with a mixed linear model. We set the level of significance at $P = 0.05$.

RESULTS

We performed 575 day-records of which 497 stored positions (86.4%). 215 records (43.3%) were complete, 232 records (46.7%) were incomplete, 44 records (8.9%) remained only on the roof of the loft, and 6 records (1.2%) stored only a few isolated positions. The mixed linear model excluded the three records from the bird with unknown sex, so 212 complete day-records were analysed.

Total Ranges

We took all analysable day-records of the pigeons from one loft together to determine the total range of the city used by the subpopulations. The pigeons from the Matthäus loft used an area of 32.9 ha, those from the Peters loft 195 ha and those from the Stapfelberg loft 306.3 ha. Fig. 1 shows the total ranges covered by the subpopulations and indicates the places visited by the pigeons. Table 1 indicates the variation in the individual total ranges of the pigeons.

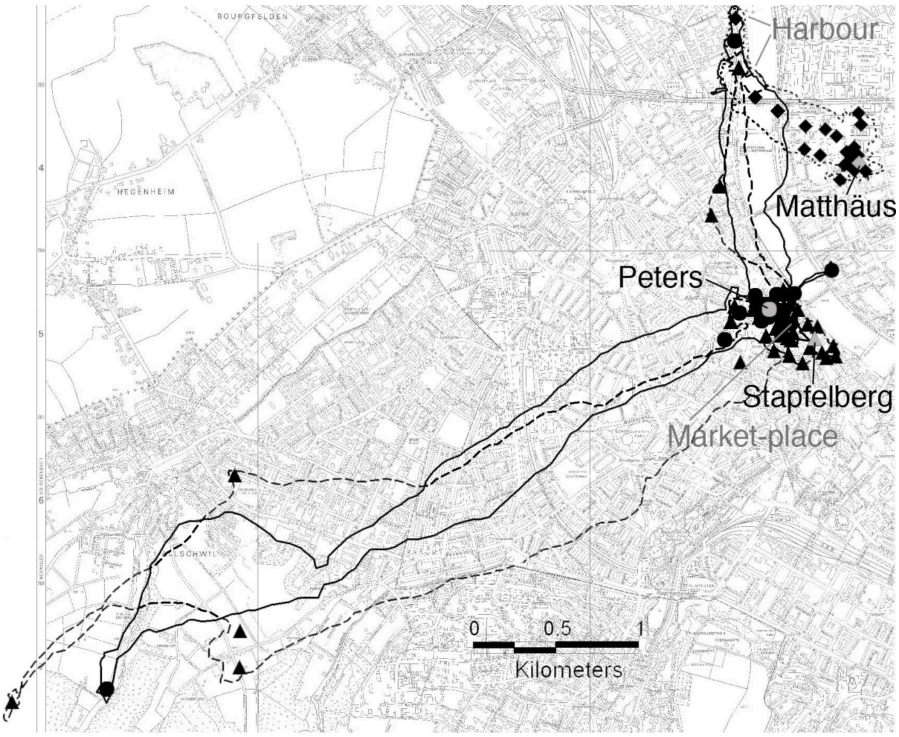

Figure 1: Total ranges covered by the pigeons of each loft. We defined the total range of a loft as the area within which pigeons of a loft could be recorded. We indicate the localisations of the three lofts (Matthäus, Peters, and Stapfelberg, grey symbols) and two important feeding places: the harbour and the market-place. The black symbols represent the places where the pigeons set down (circles for pigeons from the Peters loft, triangles for the Stapfelberg loft, and lozenges for the Matthäus loft). The other parts of the total ranges were only used by flying pigeons.

Table 1: Individual total ranges of pigeons with ten or more day-records.

Pigeon	Sex	Loft	No. of records	Total range [ha]
A 610	M	Peters	10	2.9
BTV 1417	F	Stapfelberg	10	2.9
BTV 53	F	Stapfelberg	10	3.2
B+C+orkg	M	Stapfelberg	10	5.1
B+C+orhw	F	Stapfelberg	15	5.2
A 175	F	Matthäus	10	12.5
A 160	M	Matthäus	10	14.8
A 446	M	Matthäus	10	16.3
STV92H267	M	Stapfelberg	10	24.2
B+C+weor	F	Stapfelberg	10	46.7
A 515	F	Peters	10	144.1
Schecke orwe	F	Stapfelberg	10	150.6

Places Visited

For each loft we recorded one or two principal feeding places visited by a large number of the pigeons from the loft and minor places visited by few individuals only. The Rhine harbour St Johann (Fig. 1), 1 km away from the Matthäus loft, was the main feeding place of the pigeons from this loft. 82.9% of the pigeons flew at least once to this place during all their day-records to feed on grain spilled during transhipping and on seeds of wild plants growing on the railway lines. The harbour was also visited by 60% of the pigeons from the Peters loft (distance 1.4 km), but only by one pigeon from the Stapfelberg loft (distance 1.6 km). The harbour was the only feeding place visited by pigeons from all three lofts and also by a large number of pigeons breeding or roosting in other parts of the city. The harbour is the largest feeding place in Basel. Flocks of 300–500 pigeons were regularly recorded in this area. Another regularly visited place was a school campus 90 m from the Matthäus loft, which was frequented by 56.1% of the birds from this loft. The birds feed on food remains and use the building as resting place. The 17 remaining locations used by birds from this loft were visited on a less regular basis by 2.5–41.5% of the individuals. These locations were situated in the streets and places near the loft. They might be resting places for individual birds or places where spilled food can be found. There never were assemblages of high numbers of pigeons. The market-place is the main feeding place of Feral Pigeons from the Stapfelberg loft. There, the birds find food remains and deliberately distributed grain. At the market-place, all pigeons were recorded at least once and 88.4% of all day-records led there (distance 150 m). 53.3% of the birds from the Peters loft also used that place (distance 150 m). We recorded eight other places visited for feeding or resting by a few individuals from both the Peters loft and the Stapfelberg loft. Nine other places situated in town were visited by 6.7–80% of the birds from the Peters loft only and another 21 places were visited by 4.4–73.9% of the pigeons from the Stapfelberg loft. Those places were visited on a less regular basis and were also used for resting or occasional feeding but they never showed large pigeon flocks.

Table 2: Number of places visited by the pigeons. The table indicates the percentages of pigeons that visited 1–3, 4–6, and 7–10 different locations during all their day-records. These percentages are greatly influenced by the number of day records performed by each pigeon, which makes the comparison difficult. The mean number of different locations visited by the pigeons of each loft was adjusted for differences in number of day-records. [a]Pigeons from this loft visited significantly more places than those from the Stapfelberg loft (classic regression model *P* = 0.03, *n* = 78). [b]Pigeons from this loft visited significantly more places than those from the Stapfelberg loft (classic regression model *P* = 0.002, *n* = 78).

Loft (n pigeons)	% of pigeons that visited			Mean number of different places visited by the pigeons	Max number of different places visited by one pigeon	Number of different places visited by the pigeons of the loft
	1–3 places	4–6 places	7–10 places			
Matthäus (41)	41.5	39.0	19.5	5.0[a]	9	19
Peters (14)	21.4	21.4	57.1	5.9[b]	10	20
Stapfel (23)	39.1	30.4	30.4	3.5	10	34

Table 2 indicates the number of different places visited by each pigeon. This number was significantly influenced by the number of day-records performed by each pigeon (classical regression model, $P < 0.0001$, $n = 78$). Pigeons of the Matthäus loft visited 19 different locations altogether, with an individual maximum of nine different ones. The maximum for one day-record was six different locations. The results were similar for birds from the Peters loft, with 20 places in total and a maximum of 10 for one pigeon. The daily maximum was nine different places visited by the same pigeon. The pigeons of the Stapfelberg loft visited a larger number of locations, 34 in total, but on an individual basis, the maximum number of 10 was not greater than for the two other lofts. The daily maximum was ten different places. Figure 2 illustrates the relation between the number of places visited by each pigeon and the number of day-records performed with them. The probability of recording all places known by a pigeon increases with the number of records. The figure shows the variability in the number of places visited by each pigeon. For example, two individuals from the Stapfelberg loft visited only one location in their ten day-records. Other birds from the same loft visited seven places with the same amount of day-records.

The mixed linear model revealed that birds from the Stapfelberg loft visited significantly fewer different locations on each day-record ($P < 0.0001$, $n = 62$ pigeons and 212 complete day-records) and on average the pigeons from all lofts visited fewer different places on each day-record in summer ($P = 0.0007$, $n = 62$ pigeons and 212 day-records) than at other times of year. Sex and breeding state had no significant effect on the number of different places visited during the day-records.

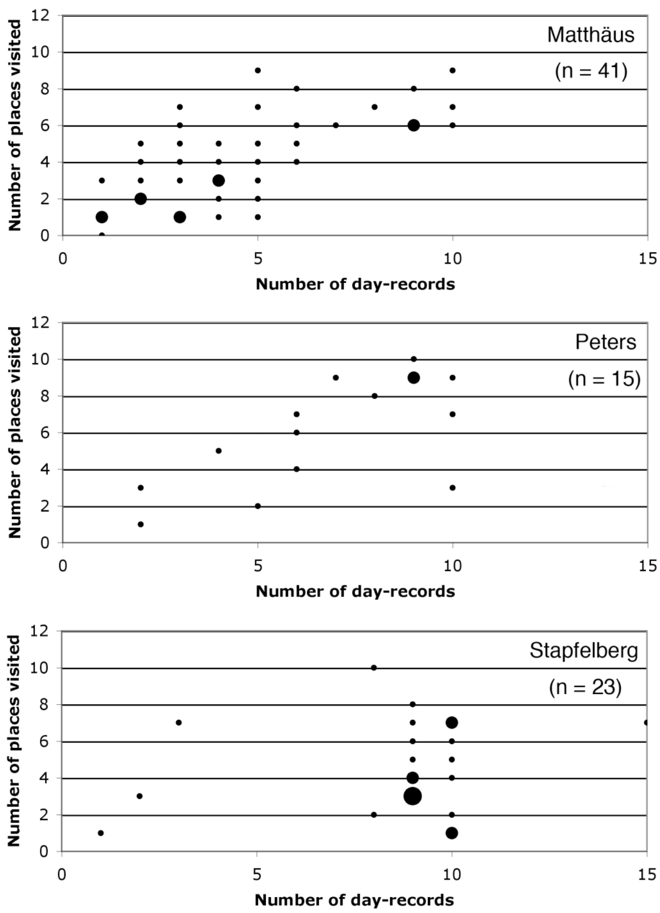

Figure 2: Number of places visited by each pigeon in relation to the number of day-records performed with it. The dimension of the dots indicates the number of birds (1–3).

DISCUSSION

Total Ranges

The urban area used by subpopulations or by individual pigeons in Basel was larger than in other cities. Those investigations, however, used other methodologies (Table 3). The two studies available for comparison (Slotta-Bachmayr *et al.* 1995, Sol & Senar 1995) did not record commuting flights to the surroundings of the city as they occurred in Basel. This may partially explain the larger total ranges measured in Basel.

Table 3: Comparison of the areas of the urban habitat used by Feral Pigeons and number of places visited. The earlier studies that used other methods than GPS may be incomplete due to the difficulties of collecting continuous data on birds' locations.

Area used [ha]	Number of places visited	Technique used	Study season	City	References
Subpopulations: 32.9–306.3 Individuals: 2.9–150.6 (total ranges)	Subpopulation: max 34 Individuals: max 10	GPS	all seasons	Basel, Switzerland	present study
Subpopulations: 3.65 Individuals: 1.34–4.96 (home ranges)		Observation of ringed birds	February to June	Barcelona, Spain	Sol & Senar (1995)
Individuals: 1.6 and 2.7 (total ranges)	1 ind. 4 places and 1 ind. 3 places	Rings and patagial tags	all seasons	Salzburg, Austria	Slotta-Bachmayr, Kössner & Goldschmid(1995)
	Individuals: max 5	Rings and obviously coloured plumage	all seasons	Basel, Switzerland	Haag (1984)
	2 ind. 1 place, 1 ind. 2 places and 2 ind. 3 places (only these 3 locations controlled)	Patagial tags	April, June, August, October, November	Montréal, Canada	Lefebvre & Giraldeau (1984)

Our study recorded differences between the lofts in the spatial use of the city. The members of a certain breeding flock use a restricted number of feeding places and do not forage in other parts of the city, at least not as long as the preferred food resources are available. Juvenile pigeons follow their parents (essentially their fathers) to the feeding places (Goodwin 1960). Doing so, the adults transmit the knowledge about feeding places to their offspring and probably also to pigeons joining the breeding flock from other parts of the city.

Number of Locations Visited

Few studies have recorded the number of locations visited by individual Feral Pigeons (Table 3). Slotta-Bachmayr *et al.* (1995) observed that one individual used at least four and another at least three locations. Lefebvre & Giraldeau (1984) monitored five pigeons: two pigeons used one, one pigeon used two, and two pigeons three places. But they monitored only these three locations. In Basel in a former study, we recorded a pigeon at five different places (Haag 1984). All these studies employed methods that did not allow to monitor the pigeons' locations continuously. In the present study, GPS records showed that Feral Pigeons in Basel used a higher number of different places than the majority of the other studies recorded, with a maximum of ten different places for one pigeon. This may underestimate the real number of different places known and used by one pigeon over its lifetime, since we made a maximum of 15 day-records per pigeon.

Haag (1984) showed slightly different results concerning the places visited by the pigeons from the Peters loft and the Matthäus loft. Table 4 summarises the results of the Peters loft. In 1984, the pigeons from the Matthäus loft fed in the harbour and on a square 500 m from the loft. No other feeding places were found. In the present study, we recorded pigeons at the harbour and at 18 other places but not on the square where they fed in 1984. These differences show that known feeding places can change and that pigeons can adapt to environmental changes and discover new feeding places.

Table 4: Comparison of the places visited by pigeons from Peters loft in 1984 and 2002–2003.
The earlier study that observed ringed pigeons may be incomplete due to the difficulties of collecting continuous data on the birds' locations using this technique. The percentages of [a] and [b] correspond to one pigeon in both studies.

Spots	Distance to loft [m]	% of pigeons recorded there 1984 (Haag, 1984)	2002–2003 (present study)
Peterskirchplatz	10–40	-	13.3
Kellergasse	20–75	-	53.3
Petersgraben	20–170	-	33.3
Petersgasse	25–105	-	80
Totengasse/Nadelberg	30–105	-	60
Petersschule	50	-	66.7
Vor Peterskirche	60	-	33.3
Stiftsgasse	75	-	13.3
Spiegelhof	80	-	6.7[b]
Spiegelgasse	85–100	-	13.3
Peterspark	100–200	100	53.3
Stadthausgasse	110	-	6.7
Fischmarkt	140	25	26.7
Schneidergasse	150–200	-	13.3
Market-place	150–220	10	53.3
Schifflände	215	10	6.7
Totentanz	315	30	-
Spalenvorstadt	320	-	6.7
Rümelinsplatz	325	5[a]	-
Kantonsspital	400	10	-
Sägergasse	460	-	6.7
Harbour St Johann	1280–1900	10	60
Fields Allschwil	4530	-	6.7

Feeding strategies vary individually. Some pigeons apparently preferred flying longer distances to reach a predictable food source (e.g. the Rhine harbour St Johann), whereas others searched many locations at shorter distances from the loft and exploited less predictable food sources, e.g. food remains in the streets or at school buildings.

According to our own results (Haag 1984) and to those of other authors (Gompertz 1957, Lefebvre 1985, Slotta-Bachmayr *et al.* 1995), feeding flocks of Feral Pigeons are unstable units of changing composition, since the pigeons have individual strategies and may at times join different feeding flocks. Lefebvre (1985) states that individual Feral Pigeons sample many feeding sites and may adopt one of them and visit it at regular intervals for a certain time. We confirm this observation. Some feeding places were regularly used, others were visited less frequently. The situation was different in other studies: Lévesque & McNeil (1985) and Murton, *et al.* (1972) found stable feeding flocks. The difference could have occurred through the different food supplies: more predictable and abundant food resources in the studies of Lévesque & McNeil (1985) and Murton *et al.* (1972) and less predictable and patchily distributed food resources in the other studies. The methodology also plays a role: the earlier observations probably are incomplete due to the difficulties of collecting continuous data on the birds' locations.

In summer, the pigeons visited significantly fewer different places than in other seasons. This is not due to the greater proportion of breeding pigeons, since the breeding state had no significant influence on the number of locations visited. A possible explanation could be a more abundant food supply in summer due to more human activity outdoors. Future studies should examine the seasonal variation in availability of food sources and the resulting variation in site use.

Relevance to Conclusions of Applied Studies

Contrary to previously employed methods, the GPS technique allows to monitor the pigeons' locations continuously. With this new method, we obtained more details about the areas of the city used by pigeons. This has direct implications for three practical applications. The first application is biomonitoring that uses eggs, feathers, tissues, or bones of Feral Pigeons to analyse the load of heavy metals or other pollutants in urban habitats (Garcia *et al.* 1988, Altmeyer 1993, Klein & Paulus 1995, Altmeyer & Paulus 1996, Haag-Wackernagel *et al.* 1998, Nagel 1999, Nagel *et al.* 2001, Nam *et al.* 2004). Assessment of results of biomonitoring studies with Feral Pigeons depends on how the pigeons use their urban habitat. Many biomonitoring studies assume that pigeons show a limited home range in cities (Hutton & Goodman 1980, Garcia *et al.* 1988, Nam *et al.* 2004). Our results showed that this is not a generally valid assumption and that home ranges must be verified for each project or city.

The second application are the pigeon control strategies. Our results showed that we must reject the prejudice of Feral Pigeons being totally dependent on intentional feeding by man and unable to fly more than a few hundred metres. These arguments are often used by animal protection societies (e.g. Hess 1998) to argue against pigeon control campaigns based on food restriction. Pigeons are able to adapt to a diminution of food in the surroundings of their roosting places. In doing so, they must search longer for food and, therefore, they have less time to invest in breeding. Murton *et al.* (1972) estimate that only

27% of the pigeon population on his study site in Manchester were breeding. The other birds were able to get sufficient food to survive but had not enough time to successfully manage a breeding routine (Murton *et al.* 1974). Limitation of food resources is an efficient method of long term pigeon control (Haag-Wackernagel 1993) and can not be rejected by animal welfare concerns.

The third application is the transmission of diseases. The total ranges of the lofts showed an existing overlap between the pigeon populations of the lofts (Fig. 1). This overlap explains the occurrence of epidemics in Feral Pigeon populations. Diseases can be transmitted at important feeding places that are meeting points for pigeons from different parts of the city. Details about the transmission of diseases are of human concern, since seven infectious diseases and seven parasites are proved to have been acquired from Feral Pigeons (Haag-Wackernagel & Moch 2004, Haag-Wackernagel & Spiewak 2004).

In conclusion, using GPS allows more precise statements compared to methods used in other studies. Our results show that Feral Pigeons use highly individual foraging strategies and that they are able to adapt to the different food resources available. Feeding strategies vary from one city to another and essentially depend on the quality of the food supply and its abundance. More studies using the GPS-technique should be performed in other cities to see if there are general principles in order to provide additional statements about the spatial use of the urban habitat by Feral Pigeons. Further GPS-receiver development to reduce mass will facilitate GPS-studies also for smaller bird species. We showed the importance of our findings with regard to practical applications such as biomonitoring projects using Feral Pigeons, pigeon control strategies, and the possibilities of disease transmission within the urban habitat.

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Chapter 5

Main Results, Discussion, and Conclusion

AIM OF THE RESEARCH

The aim of this thesis is to gain more precise information about the way feral pigeons use the urban habitat. Feral pigeons are found in almost all major cities, and their high numbers often cause problems. Previous studies performed in other cities provided varying and sometimes contradictory results. Despite the proximity of pigeons to humans, there is a lack of a detailed knowledge of how pigeons use the urban habitat, and which individual foraging strategies are employed. With GPS-tracking, we were able to study the pigeons' spatial use as well as temporal use of their urban habitat with high precision.

ACCURACY TESTS

In Chapter 2, we describe how we tested the accuracy of GPS positions in the urban habitat. We placed stationary receivers at eight different places in Basel and compared the stored positions with the real positions. As expected, the positions were less precise than in theory (Zogg 2002) but comparable to those obtained in studies that took place under forest canopy (Rempel et al. 1995). The accuracy of GPS positions varied between the different test locations. The precision of the records was influenced by two factors common in the urban habitat: (1) reflection of satellite signals on buildings and (2) lack of signals in narrow streets.

Reflection of Signals

The reflection of satellite signals on buildings caused shifted positions. We illustrate this with fig 1 which shows an example of an accuracy test performed with a stationary receiver placed on the bridge Dreirosenbrücke.

Figure 1: On the left, we show an example of a GPS test performed on 22 April 2003 at the bridge Dreirosenbrücke. The star on the map indicates the real position of the stationary GPS receiver during the test. The reflection on the high buildings of the Rhine harbour St Johann (B) caused shifted positions (the points over the river). On the right, we show a view of the high buildings of the harbour.

On records with pigeons, the shifted positions generally showed a characteristic pattern on the map (fig 2) and also in the raw data tables. This allowed us to eliminate these false positions from the analysis.

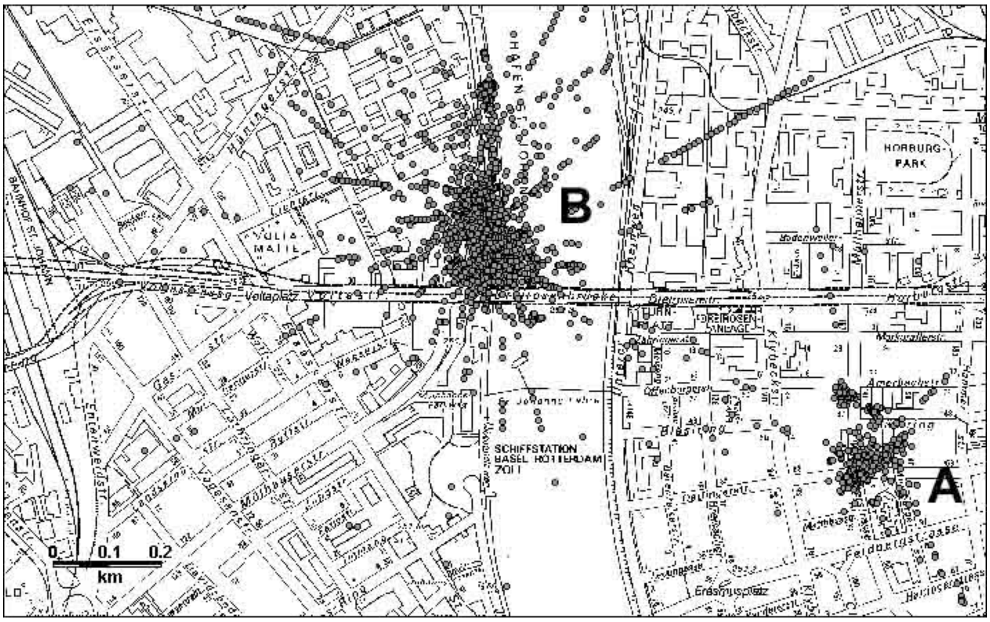

Figure 2: Example of a record with shifted positions (pigeon A026 on 15 July 2002). The straight lines forming the star shape are not due to displacements of the pigeon but to reflected satellite signals. A=Matthäus-loft, B=Rhine harbour St Johann.

Lack of Signals

The lack of signals in narrow streets resulted in gaps in the records. The interruptions in the accuracy tests lasted exceptionally up to 40 min, but generally they had a duration of a few minutes only. In records performed with pigeons, the positions before and after the gap provide information about the location of the bird during the interruption.

Technical Problems

We also encountered technical problems due to the limited battery life. In some cases, this led to incomplete records finishing elsewhere than at the loft.

The precision of positions obtained with pigeons can not actually be verified. We do assume, however, that the measurements are more precise than those obtained with stationary receivers since pigeons are often sitting on roofs where the open sky is nearly unrestricted. Therefore, we conclude that GPS-tracking is a suitable method to study feral pigeons in cities. It eliminates the bias due to the observation spots, since all places visited by the pigeon equipped with this design are automatically recorded. Using other methods, it is not possible to record pigeons at hidden places like courts or on high buildings where their markings are not visible. GPS-tracking not only provides information about all places visited by the pigeon, but also about the chronological sequence of a daily schedule. The method provides a better insight into the individual strategies of feral pigeons than any of the other methods used previously.

GPS RECORDS WITH PIGEONS

Spatial Use of the Urban Habitat

Previous studies in Basel (Haag 1984) have shown the existence of major feeding places in the city. A majority of the observed pigeons feed there. Observations of pigeons in surrounding fields let us suppose that commuting flights could occur in Basel. The provenance of these pigeons could not be determined with the methods used previously. GPS-tracking allowed us to gain precise information about the spatial use of the city and to answer the related main research questions.

To ensure the return to the loft of the pigeons equipped with GPS receivers, we were forced to make a non-random sampling, choosing pigeons closely attached to the loft. This may have influenced the distances covered and the temporal activity. Pigeons that are less closely attached to the loft (e.g. young birds, non-breeders) may fly longer distances and spend more time outside the lofts. Therefore, our results on distances and times spent outside the loft might be at the lower range.

How long are the maximum distances covered and what are the dimensions of the total ranges?

The maximum distance covered was 5287 m, but distances varied greatly between individuals. Some pigeons remained within 300–500 m of their lofts, others flew out of the city to forage in fields (Chapter 3). Accordingly, the individual total ranges varied between 2.9 and 150.6 ha. The total ranges of the lofts varied between 32.9 ha for the Matthäus-loft with no commuting flights to the fields, and 306.3 ha for the Stapfelberg-loft which harboured the highest number of pigeons flying to agricultural areas. The Peters-loft had an intermediate total range with 195 ha (Chapter 4).

With the GPS records, we verified our hypothesis that pigeons foraging in the city are more mobile than presumed by some authors (Friedl 1938, Reinke 1959, Murton et al. 1972).

What factors influence the distances covered?

The factors influencing the distances covered were the affiliation to a loft and the sex of the pigeon. Birds from the Matthäus-loft covered significantly longer mean distances than those from the other lofts. This is related to the distance between the loft and the main feeding place used by the birds of this loft, the Rhine harbour St Johann. The birds of the other lofts had more possibilities to feed at less remote places.

Females covered longer distances than males (see paragraph "Male/female particularities"). Season and breeding state had no significant effect on the distances covered.

Are the urban areas covered by the different breeding flocks overlapping?

We found an overlap between the total ranges of the lofts (Chapter 4). The overlap occurred at important feeding places, as found by Sol & Senar (1995) in Barcelona. For example, the Rhine harbour St Johann was visited by pigeons from all three lofts, and the market-place was used by pigeons from the Stapfelberg-loft and the Peters-loft.

Do the individual feral pigeons follow different foraging strategies?

We recorded three different foraging strategies for pigeons in Basel (Chapter 3):

1) Foraging directly in the streets around the loft

2) Foraging on docks and railway lines in the harbour (intermediate strategy)

3) Foraging in fields surrounding the city

More than 45% of the pigeons that performed more than four records only foraged in the streets and locations around the lofts. 8.3% were found in the streets and in the fields. The remaining 45.8% fed in the streets and at the Rhine harbour St Johann.

In this GPS study, we recorded ten commuting flights of about 5 km to the surrounding agricultural areas. We therefore could prove that some pigeons of the centre of Basel fly out of the city to forage, but this is not the principal feeding strategy in Basel. Only five pigeons showed this behaviour. The situation seems to differ a lot between one city and another. The differences may partly be due to the method employed, since GPS-tracking allows the recording of all displacements, contrary to other methods. But differences remain which are not method dependent. The abundance and the distribution of food resources in the city are probably the principal factors which explain the existence or absence of commuting flights. The feeding strategies do not differ only between cities. In our study, we recorded differences between the subpopulations (from the various lofts) of the same city. As described in Chapter 4, pigeons from the Matthäus-loft never flew to agricultural areas. Their principal feeding place is the Rhine harbour St Johann where a substantial amount of grain is spilled during transhipping from ship to rail or to grain storage buildings. This feeding place is apparently reliable enough, so that the birds can avoid the long and dangerous flights to the surroundings. Pigeons from the Stapfelberg and the Peters-loft undertook such long flights probably because they were, on some days, unable to get enough food near their lofts.

How stable are feeding flocks?

In our study, the pigeons showed a flexible foraging behaviour, i.e. they did not fly to the same place at the same time every day. Therefore, the composition of the feeding flocks varies throughout the day and the year.

Temporal Use of the Urban Habitat

What are the patterns of the temporal use of the city?

The temporal use of the city is individual and depends on the affiliation to a loft, the sex of the pigeon, the breeding state and the season (Chapter 3). Pigeons from the Matthäus-loft left significantly later in the morning and also came back later than pigeons from the other lofts. Our hypothesis is that the food in the Rhine harbour St Johann, the main feeding place for birds of this loft, is available later in the day than the food source exploited by pigeons from the other lofts. The mean time spent outside did not vary significantly between the lofts. Males were outside on average more often in the morning than in the afternoon. For females the contrary is true. In addition, females spent on average more time outside than males (see paragraph “Male/female particularities”).

In winter, feral pigeons in Basel showed the same activity pattern as wild rock pigeons (Baldaccini et al. 2000): a single peak in the early afternoon. During the other seasons, only breeding pigeons showed the typical bimodal activity (two activity peaks during the day) which was recorded for rock pigeons or feral pigeons commuting to agricultural areas (Havlin 1979, Janiga 1987). The collectivity of non breeding birds showed a single activity peak in the early afternoon. The activity of the pigeons in our study started later compared to those in other cities. In Basel, pigeon activity seems to be essentially dependent on human activity which influences the availability of food, rather than on natural rhythms. Further studies on the availability of food resources are required to research the reasons influencing the later departures of pigeons in Basel compared to other cities.

Is the temporal use of the city constant?

The temporal use is not constant. There are seasonal variations in the start and termination of the outdoor activity of pigeons and also in the amount of time spent outside. Breeding also has an influence on the temporal use.

From winter to summer, pigeons spent an increasing amount of time outside the loft, but a decreasing percentage of the day. This evolution is normal in relation to day length. Even during the short winter days, pigeons spent on average only 28.5% of the day outside the loft, so day length was not a limiting factor in finding enough food. In autumn, the pigeons spent a longer part of the day outside than in all other seasons. This cannot be explained with day length which is similar to the one in spring, nor with the percentage of breeding pigeons which is comparable to the winter value. Our hypothesis is that pigeons must replenish their fat reserves after energy consuming reproduction and moulting. Weight analyses of adult pigeons from Basel (Haag 1984) and London (Murton et al. 1972) support our hypothesis. The pigeons had the highest body weight in winter and then gradually lost weight until the end of summer. In autumn, their weight increased again.

The breeding routine is a constraint in the pigeon's life, not only because breeding birds spend less time outside as our results show, but also because breeding changes the timing of activity. Temporally limited food resources (e.g. food distributed in early morning) can become inaccessible to at least one partner of the breeding pair. Murton et al. (1974) supposed that only pairs with reliable and rapidly accessible food resources are able to rear juveniles. Other birds are able to obtain sufficient food but they spend too much time foraging and cannot manage a breeding routine. The percentage of breeding pigeons in a population will therefore vary from one city to another, depending on the food resources.

Male/Female Particularities

In our study, female pigeons spent more time outside the lofts than males and we recorded females at significantly longer distances away from the lofts than males. We confirmed the findings of Eber (1962) and Johnston & Janiga (1995) concerning the longer distances covered by females. But we found no results in the literature concerning the difference in the time spent away from the sleeping/breeding places by the two sexes. Females bear more energetic costs for reproduction. They expend 15–85% more energy than males during the egg-laying period (Walsberg 1983) and egg production is particularly sensitive to caloric deficiency, since ovulation stops within 48 h or less in response to complete starvation (King 1973). Females therefore are dependent on more reliable food sources than males, which could explain the observed differences. Females are also weaker competitors at concentrated food sources than the stronger males (Haag 1984). The longer time spent outside by females and the longer distances they covered may reflect the need to find more food and the difficulty to gain access to food sources. We suppose that females preferred flying longer distances to reach more reliable food sources. Another hypothesis for the longer times the males spent in the lofts may be their need to defend their territories. Observations showed that regular fighting took place in the breeding boxes and therefore the pressure to maintain a territory seems to be very high. Males are more frequently engaged in territorial conflict than females (Vogel 1992, confirmed with personal observations).

Practical Applications

In Chapter 4, we discuss the importance of our results on spatial and temporal use of the urban habitat by feral pigeons for three practical applications: (1) biomonitoring with feral pigeons, (2) pigeon control strategies, and (3) understanding of transmission of diseases and parasites.

Biomonitoring

Eggs, feathers, tissues or bones of feral pigeons can be used to analyse the load of heavy metals or other pollutants in the urban habitat (Hutton 1980, Hutton & Goodman 1980, Garcia et al. 1988, Altmeyer 1993, Haag-Wackernagel et al. 1998, Nagel et al. 2001, Nam et al. 2004). It is important to examine data on the use of the urban habitat by pigeons in order to make statements about the pollution of the urban habitat. The data provide information on possible local pollution or pollution concerning the entire urban area reflected by the eggs, feathers or tissues. In many biomonitoring studies, it was assumed that pigeons show a limited mobility in the city (Hutton & Goodman 1980, Garcia et al. 1988, Nam et al. 2004). Our results indicate that this is not always true and that the displacements of pigeons must be verified for each project. Further studies are required to assess the pollution levels reflected by pigeons using varying foraging strategies, to confirm whether the differences are significant.

Pigeon Control

Many cities have problems related to high pigeon numbers, with respect to soiling and the destruction of buildings, damage to ornamental plants, noise, and transmission of diseases. Diverse methods are employed to reduce pigeon populations. The most efficient method is the diminution of food resources in the city, at least for those towns where most pigeons feed in the streets (Haag-Wackernagel 1993). Animal protection societies often protest against the reduction of feeding. They claim that this leads to death from starvation because pigeons are not able to fly more than 300–500 m away from their breeding or sleeping place (Havelka & Sabo 1995, Hess 1998). Our results show that pigeons are very well able to fly some kilometres to search for food, if necessary. If less food is available, the pigeons spend more time searching for it and do not have enough time or energy reserves to sustain a breeding routine. Reduction of food sources, therefore, represents a durable control strategy. The pigeon population also becomes healthier. Weak and ill pigeons are unable to survive and the longer flights the birds must undertake reinforce their physical condition.

Determination of the existence of foraging flights to agricultural areas is important with respect to counting pigeon populations (Janiga 1987, Baldaccini & Ragionieri 1993). Data on the time of absence from the breeding or roosting places is also important for census counts. It is not worthwhile counting the population at times where most pigeons are still hidden at their roosting places. Our results show that for Basel the best time for census counts is at midday or in the early afternoon, when a majority of pigeons stay outside throughout the whole year. Counts in the streets are only approximations which need a correction factor in order to estimate the real pigeon population. This factor is very difficult to estimate, since it not only depends on the presence at or absence from the nesting site, but also on the "visibility" of the pigeons in the street. Our GPS study shows that throughout the year, the loft contained at least 30% of the pigeons at any time of the day. But we can give no indication as to the "visibility" factor. Both variables which influence the estimation of the real number will vary between cities, depending on the number of breeding pigeons and the structure of the urban habitat.

The capturing and killing of pigeons is often applied to reduce their high numbers. These methods are criticised because the killing of breeding birds leads to death from starvation of the young. One mate of the breeding pair is not able to rear two young alone (Brehm 1857). Our results show that breeding pairs share the time spent outside during the day, males being preferentially outside in the morning, females in the afternoon. It is therefore not possible to find a time during the day which avoids killing breeding birds. If culling is still the method chosen, it would be best to capture the birds after the principal breeding season, i.e. in autumn and winter. As previously showed, control strategies based on reduction of food supply are more efficient in the long term than removing birds (Haag-Wackernagel 1993). Culling can only have a local short-lived effect and should, therefore, be avoided.

Pigeons in Basel spent more time inside the lofts than outside. This is not surprising, since staying outside always represents a certain predation risk. The positive effect of this behaviour is that pigeons excrete more droppings inside the loft than on the buildings. The lofts therefore contribute to the reduction of pigeon droppings in city.

Transmission of Diseases and Parasites

The urban areas used by the pigeons from each loft (total ranges) showed different sizes according to the distances flown by the members of the loft. The total ranges overlapped partially, especially at important feeding places. The pigeons' subpopulations are connected this way. The overlap can lead to the transmission of diseases and parasites and to their spread over the entire urban area. This is of human concern, since seven infectious diseases and seven parasites have been shown to be transmissible from pigeons to humans (Haag-Wackernagel & Moch 2004, Haag-Wackernagel & Spiewak 2004). The mixing of subpopulations also leads to the inefficiency of control strategies based on culling or removal of individuals. Missing pigeons are rapidly replaced by individuals joining from other parts of the city.

CONCLUSIONS

With this GPS study we obtained a better insight into feral pigeons' use of the urban habitat. This allowed us to make some statements which are important for three practical applications: biomonitoring, pigeon control strategies and transmission of diseases and parasites. Our results differed in many points from those obtained by other studies. These differences may have arisen partly through the different methods employed. With GPS-technology, recordings are very precise and cover the pigeons' entire activity, without bias due to observation spots. Our data show that pigeons have very individual strategies in using their urban habitat. We found differences between the pigeons of the three lofts, but also differences between individuals of the same loft. Therefore, it is only possible to make specific statements about the spatial use of the urban habitat by feral pigeons. Foraging strategies will vary from one city to another and depend essentially on food abundance and distribution. More studies with the GPS-technique should be performed in other cities allowing for the working out of common factors, in order to be able to make further statements about the spatio-temporal use of the urban habitat by feral pigeons.

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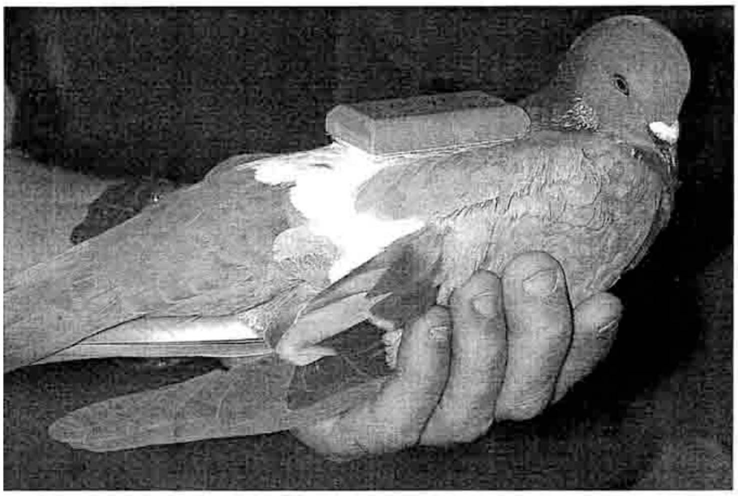
Press Review

Basler Zeitung, 3 June 2002:

Ein Satellit beobachtet die Basler Tauben

Was machen die Tauben den lieben langen Tag? Um das Verhalten dieser Vögel besser kennen zu lernen, werden einige von ihnen mit einem Empfänger bestückt, der ihr Tagesprogramm aufzeichnet: Die Kenntnis ihres Aktionsradius soll verschiedene offene Fragen beantworten.



Global positionierte Basler Tauben. Um das Verhalten der Tauben vertieft studieren zu können, wird einigen Tieren demnächst ein GPS-Empfänger (im Bild eine Testattrappe) auf den Rücken montiert. Das Gerät liefert Daten zu den Flugbewegungen der Tiere.

Foto zVg

Wenn Sie in nächster Zeit eine Taube antreffen, die ein kleines Kästchen auf dem Rücken trägt, dann ist darin kein Diamantring versteckt, sondern wichtige Daten: Das ganze Tagesprogramm des Tiers wird mit dem Kästchen erfasst. Seit etwa 20 Jahren wird in Basel Taubenforschung betrieben. Doch bis heute ist unklar, in welchem Aktionsradius sich die Vögel bewegen. «Wir möchten herausfinden, was eine Taube alles unternimmt, nachdem sie ihren Schlag am Morgen verlassen hat», sagt Daniel Haag-Wackernagel, Leiter der Forschungsgruppe für integrative Biologie des Anatomischen Instituts an der Uni Basel. In Basel leben schätzungsweise 5000 bis 8000 Tauben. «500 davon leben in den acht Schlägen, die von uns betreut und beobachtet werden», so der Autor zahlreicher Fachpublikationen.

Tauben mit Satellitenempfänger

Der GPS-Empfänger auf dem Rücken – Global Positioning System: eine Technik, welche die Ortung per Satellit erlaubt – soll Antworten auf diese Fragen liefern. «Vier solche Empfänger werden in den nächsten Tagen bei uns eintreffen», erzählt Haag-Wackernagel. Mehr könne man sich zur Zeit nicht leisten: Die GPS-Empfänger – sechs auf drei Zentimeter gross und 30 Gramm schwer – kosten über 3000 Franken. Die kleinen Wunderboxen, die alle zehn Sekunden die Position des Tiers aufzeichnen, wurden bereits mit Erfolg für die Erforschung von Brieftauben eingesetzt. «Die Kästchen werden auf dem Rücken der Taube montiert und begleiten sie während des Tags.» Am Abend, wenn die Tiere in den Schlag zurückkehren, werden die Empfänger abgenommen und mit Hilfe des Computers ausgewertet. «Wir können die Daten dann auf dem Stadtplan einzeichnen und so den Weg der Tauben mit genauen Zeitangaben nachvollziehen.»

Dieser Versuch werde aufregende Tage und Nächte mit sich bringen: «Wenn eine Taube einmal ausserhalb des Schlags übernachtet, werden wir eine schlaflose Nacht haben und hoffen, dass ihr nichts zugestossen ist», so Haag-Wackernagel. Falls doch ein Tier verunglückt oder der Empfänger vom Rücken fällt, bittet die Forschungsgruppe die Bevölkerung um Mithilfe: «Auf den Sendern wird unsere Telefonnummer stehen. Wer zufällig einen abgefallenen GPS findet, soll uns bitte benachrichtigen.» Die Sender werden längstens zwei Monate auf der gleichen Taube befestigt bleiben. Danach wird ein anderes Tier erfasst. Für die erste Staffel wurden bereits vier Tauben aus dem Matthäusschlag ausgesucht.

Das Taubenprojekt hat verschiedene Ziele: So sollen damit Daten für ein Bio-Monitoring-Projekt des Uni-Instituts für Natur, Landwirtschaft und Umweltschutz (NLU) gewonnen werden. «Das NLU untersucht Basler Stadttauben auf verschiedene Substanzen, welche die Tiere durch die Luft und die direkt vom Boden aufgepickte Nahrung aufnehmen», erklärt Haag-Wackernagel. Mit den so erfassten Verschmutzungswerten könnten Rückschlüsse auf die Ablagerungen im menschlichen Körper gezogen werden. «Ein Baby, dass noch nie Ferien auf dem Land verbracht hat, dürfte ähnliche Belastungswerte aufweisen wie eine Stadttaube.» Allerdings sei es für genaue Vergleiche wichtig, ob die Taube sich nur in einem Quartier oder in der ganzen Stadt bewege. Weiter sollen die Daten Rückschlüsse auf die Übertragung von Krankheiten möglich machen: Auch hier spiele der Aktionsradius eine entscheidende Rolle.

Fütterungsverbot macht Schule

Seit Jahren wird in Basel immer wieder mit Kampagnen und Informationsbroschüren versucht, die Bevölkerung davon abzuhalten, die Tiere zu füttern. «Natürlich verstehen wir, dass es grossen Spass macht, diese intelligenten Vögel zu füttern», räumt Tauben-Fan Haag-Wackernagel ein. Schliesslich würden sie bereits nach einigen Fütterungen ihren Wohltäter erkennen und bei ihm nach Futter betteln. Allerdings schade das übertriebene Nahrungsangebot den Tieren nur. Die Populationen vergrösserten sich so ständig, was zu slumartigen Zuständen und zur Ausbreitung von Epidemien und Parasiten führe. Sei hingegen Futter knapp, müssten die Tiere viel Zeit für die Nahrungssuche aufbringen und hätten weniger Zeit für die Aufzucht.

Tiere besser verstehen

«Militante Tierschützer bezeichnen uns wegen dieser Taktik als Taubenmörder. Sie behaupten, die Tiere bewegten sich täglich nicht weiter als 100 Meter, fänden zu wenig Nahrung und verhungerten deshalb», erzählt der Taubenexperte. Aber das stimme nicht, man müsse nur in den Himmel schauen, dann sehe man Tauben, die weiter als 100 Meter weit flögen. «Damit wir dies wissenschaftlich beweisen können, brauchen wir ebenfalls die Daten der GPS-Empfänger.» So liefert die Aktion die Grundlagen für verschiedene Forschungsgebiete. Aber: «Unser Hauptziel ist und bleibt aber, Tauben besser zu verstehen und mehr über das Leben dieser faszinierenden Tiere zu erfahren.»

Mena Kost

swissinfo, switzerland's news and information platform, 14 August 2002: Ein Satellit beobachtet Basler „Dybli". At www.swissinfo.org/sde/Swissinfo.html?siteSect=41&sid=1274418

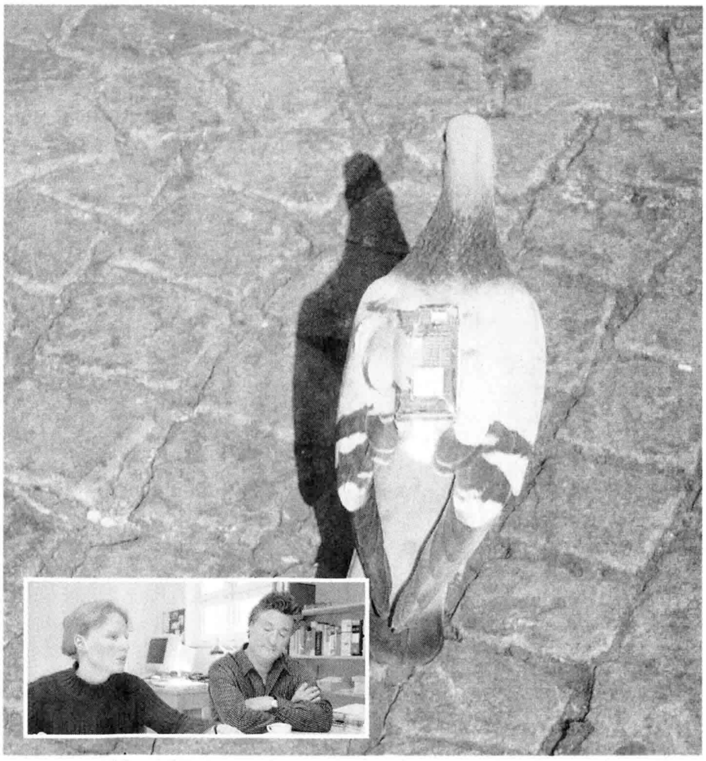
Basler Stab, 27 March 2003:

Basel

Forschungsprojekt der Uni Basel

Tauben sind nicht dumm

Das Leben der Strassentauben wird mit High-Tech beobachtet.



Eva Rose und Daniel Haag-Wackernagel erforschen Strassentauben. Fotos: mo./mat.

Tauben gehören zwar zum Bild jeder grösseren Stadt. In Basel leben über 5000 dieser Vögel. Der Alltag der Tauben ist aber wenig bekannt. Dies soll ein Projekt der Gruppe Integrative Biologie an der Uni Basel ändern. Sie schnallt den Tauben einen Sender auf den Rücken, der alle drei Sekunden mittels Satellit die Position des Tieres bestimmt.

«Erste Resultate zeigen, dass Tauben ihre individuellen Strategien haben, um zum Beispiel zu Futter zu kommen», sagt die Doktorandin und Projektbetreuerin Eva Rose.

Argument widerlegt

Tauben legen im Verlauf eines Tages auch längere Strecken zurück. «Eine ist vom Schlag am Stapfelberg vier Kilometer weit bis nach Allschwil geflogen», verrät Rose. Und Professor Daniel Haag-Wackernagel fügt an, dass «Tauben eben nicht dumm sind und nicht nur auf ihr Futter warten, sondern es aktiv suchen».

Wohlmeinende Tierschützer wenden sich nämlich gegen ein Fütterungsverbot, weil sie vermuten, die Tauben müssten verhungern. «Dieses Argument konnten wir widerlegen», sagt Haag-Wackernagel. «Fütterungsverbote sind also sinnvoll», folgert der Professor: Die Tauben seien länger auf Nahrungssuche und hätten weniger Zeit zur Vermehrung. Eine wichtige Erkenntnis für «taubengeplagte» Städte wie London.

Tauben haben einen schlechten Ruf. Der Volksmund spricht auch von den «Ratten der Lüfte», weil sie Krankheiten übertragen würden. Das können die Forscher aber so nicht stehen lassen: «Die Wahrscheinlichkeit, eine Krankheit von einer Taube zu holen, ist gering», sagt Haag-Wackernagel. «Da liegt eher menschliches Fehlverhalten vor.»

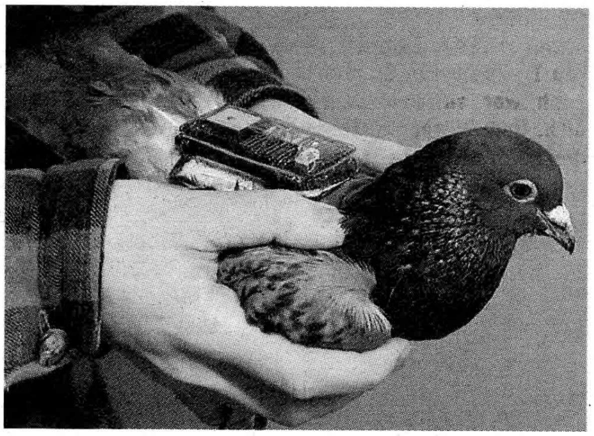
Das Projekt läuft noch zwei Jahre. «Wenn die Tauben abends in den Schlag zurückkommen, wird der Sender abgenommen», erklärt Rose. «Nach der Auswertung wird der Sender wieder einer Taube mitgegeben.» *Ralph Schindel*

20 Minuten, 1 December 2004:

80 Basler Tauben flogen mit GPS durch die Lüfte

BASEL – Die Flüge der Strassentauben wurden in Basel per GPS verfolgt. Erste Resultate des Uni-Forschungsprojekts liegen jetzt vor.

80 der rund 8000 Basler Stadttauben hat Biologin Eva Rose mit 36 Gramm schweren Mini-Empfängern ausgerüstet. «Wir haben die Geräte eigens herstellen lassen, weil diejenigen zur Untersuchung von Brieftauben zu ungenau waren», erklärt die 28-jährige Doktorandin der Forschungsgruppe Integrative Biologie im Anatomischen Institut.



Forschungsprojekt: Tauben wurden mit Mini-Empfängern ausgerüstet.

Über die 28 Satelliten des Global Positioning Systems (GPS) verfolgte Rose danach die Flugbewegungen der Strassentauben. «Die Stadt wird von den Tieren sehr individuell genutzt», gab sie im Wissenschaftsmagazin der Uni Basel «Uni Nova» erste Resultate bekannt. Der Aktionsradius der Tauben sei deutlich grösser als bisher angenommen. Rose: «Sie fliegen zur Futtersuche bis zu fünf Kilometer aus der Stadt hinaus.»

Zudem konnte die Forscherin feststellen, dass die Tauben untereinander «vernetzt» sind. «Wenn an einem Ort der Taubenbestand reduziert wird, füllen sofort andere die Lücke», so Rose. Dies zeige, dass die Taubenpopulation nicht über Fangaktionen reguliert werden kann. Rose: «Das einzige Mittel, um die Anzahl Tauben langfristig zu verringern, ist ein kleineres Nahrungsangebot.»

Christian Degen

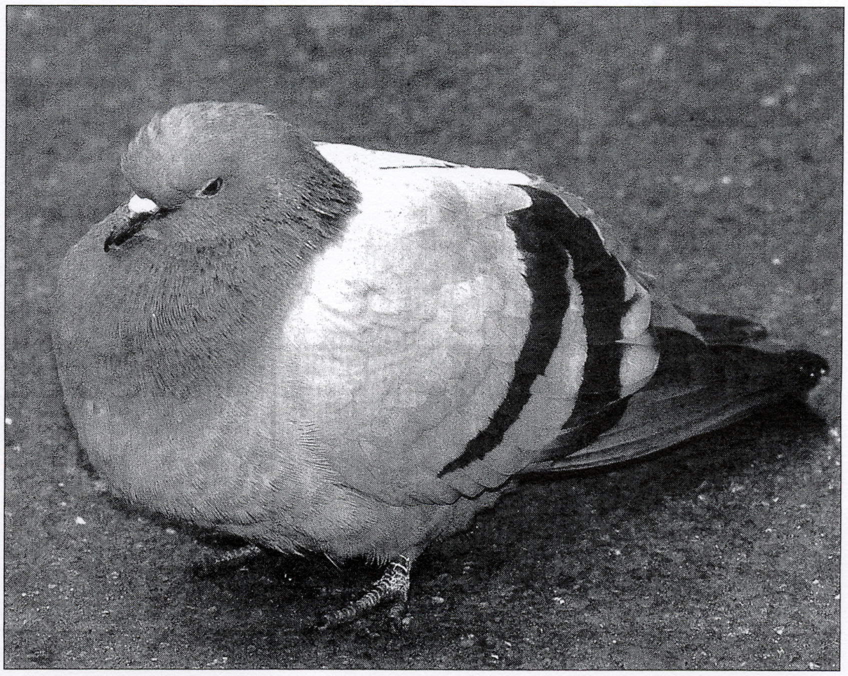
www.20min.ch
Umfrage Sind Ihnen die Tauben in der Stadt lästig?

Basellandschaftliche Zeitung, 14 December 2004:

Tauben navigierten durch Basel

INNOVATIVES PROJEKT / *Die Universität Basel untersuchte mit Hilfe modernster Technik, wie Tauben die Stadt nutzen. Basel ist punkto Kontrolle der Taubenbestände für andere Städte ein Vorbild.*

VON DAVID WEBER



AUFKLÄREN. *Grosse Taubenschwärme verursachen viele Probleme, wissen die Experten der Uni. Ihre Aufklärungsarbeit zeigt Erfolg: In Basel gibt es nur noch halb so viele Tauben wie vor zehn Jahren.* FOTO ZIMMER

BASEL. Tauben polarisieren: Von den einen liebevoll gefüttert, von den anderen als Schmarotzer gehasst. Tauben sind in der Stadt allgegenwärtig, trotzdem ist über ihre Aktivitäten relativ wenig bekannt. Deshalb rüstete Eva Rose insgesamt 80 Basler Strassentauben mit einem Empfänger des Satelliten-Navigationssystems (GPS) aus. Rose ist Doktorandin der Forschungsgruppe Integrative Biologie am Anatomischen Institut der Uni Basel.

Mit dem 36 Gramm schweren Mini-Empfänger flogen die Stadtvögel durch die Strassen und lieferten der Forscherin so exakte Daten über ihre Flugwege und Futterplätze. Das Projekt unter der Leitung des Tauben-Experten und Professors für Integrative Biologie, Daniel Haag-Wackernagel, versucht herauszufinden wie Tauben die Stadt nutzen. Diese Erkenntnisse sind auch für die Kontrolle der Taubenpopulation enorm wichtig.

Taubenschwärme sind untereinander vernetzt

«Grosse Taubenbestände führen zu Problemen wie Verschmutzungen und Schäden an Gebäuden sowie zur Übertragung von Krankheiten und Parasiten», erklärte Rose. Deshalb wurden bis vor kurzer Zeit in Basel pro Jahr etwa tausend Tauben eingefangen oder geschossen, die dann im Basler Zolli als Tierfutter landeten.

«Doch damit löst man das Problem nicht, denn solange es genug Nahrung gibt, werden die Lücken sofort wieder gefüllt», sagte Haag-Wackernagel. Einerseits wegen der hohen Nachwuchsrate der Tauben: «Ein Taubenpaar kann pro Jahr bis zu zwölf Junge produzieren», berichtete Rose. Andererseits – dies zeigten die Flugdaten von Eva Roses Projekt – sind die Taubenschwärme untereinander vernetzt, so dass sich die Schwärme gegenseitig wieder aufstocken.

Laut der 28-jährigen Biologin ist «die einzige Möglichkeit, die Taubenpopulation langfristig zu reduzieren, ein kleineres Futterangebot». Doch dazu braucht es die Mithilfe der ganzen Bevölkerung. «Wir versuchen den Leuten zu zeigen, dass man den Tauben nichts Gutes tut, wenn man sie füttert», erklärte Rose. «Je grösser das Futterangebot, desto häufiger paaren sich die Tauben und desto schlechter werden die hygienischen Bedingungen für die Jungtiere.» Doch einige Menschen sähen das Füttern von Tauben als eine Art Lebensinhalt an und seien nur schwer davon abzubringen.

Zur Futtersuche weit aus der Stadt hinaus

Doch insgesamt hatte die Aufklärungsarbeit der «Basler Taubenaktion» Erfolg. Denn «heute leben in Basel nur noch halb so viele Tauben wie vor zehn Jahren; nämlich acht- bis zehntausend», berichtete Rose. Die «Basler Taubenaktion» wurde 1988 vom Tierschutz beider Basel unter der Leitung von Haag-Wackernagel ins Leben gerufen.

Die GPS-Flugphase der 80 Strassentauben erstreckte sich über eineinhalb Jahre, wobei ein Tier nur zehn bis fünfzehn Tage lang mit dem GPS-Empfänger auf dem Rücken unterwegs war. Neben der Erforschung der Flugwege und Futterplätze der Tauben konnte Rose auch «die verbreitete Annahme widerlegen, dass Tauben nicht weiter als 300 Meter fliegen.

Einige Tiere flogen auf der Futtersuche mehrere Kilometer aus der Stadt hinaus», erzählte Rose. Die Stadt werde von den Tieren in sehr komplexer Weise individuell genutzt. Die endgültige Analyse und Verarbeitung der Daten werde aber noch bis zum nächsten Frühjahr dauern.

«Heute gibt es nur noch an vereinzelten Orten in der Stadt zu grosse Taubenbestände, weil es einige wenige, völlig uneinsichtige Fütterer gibt, zum Beispiel in der Steinen», bilanzierte Haag-Wackernagel. «Aber da das Füttern nicht verboten ist, können wir nichts machen.» Im Vergleich zu anderen Städten steht Basel aber gut da, und das Basler Modell macht Schule. Andere Städte, wie zum Beispiel Luzern, schauen bei den Baslern ab und bemühen sich, das Nahrungsangebot zu reduzieren anstatt jedes Jahr Tauben abzuschiessen.