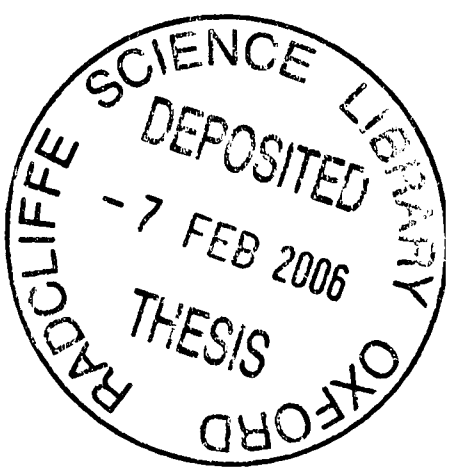
Tracking Homing Pigeons by GPS

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ABSTRACT

Tracking homing pigeons using GPS technology

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The present thesis utilises recently developed miniature GPS loggers to track homing pigeons (*Columba livia)* navigating within their familiar area. This technology allows tracks of extremely high spatial and temporal resolution to be recorded providing a unique opportunity for novel data analysis.

The thesis focuses on the development of pigeons' tracks as they become increasingly experienced with a homing task. Birds' routes became increasingly stereotyped over time, were individually distinctive, and remained substantially longer than the beeline. This was demonstrated at short distances (~5 km) and at 25 km from home. Pigeons seem to use a similar strategy when homing from the longer distance site as at shorter distances, although the distance beyond which this strategy may become inefficient remains to be elucidated.

It seems likely that the cues involved in performing detailed stereotyped routes are familiar visual landmarks, as birds' routes remain stable over varying wind conditions and are resistant to a magnetic disruption treatment. Furthermore, birds released at novel sites perpendicularly displaced along their homeward routes are attracted back to and rejoin their established routes. This demonstrates that the route cues used can be detected and accurately assessed from distances of several kilometres, again suggesting that these route cues are visual.

Birds released at sites they had flown over as part of their stereotyped routes appear unable to recognise their routes until airborne which, along with previous experiments, suggests that certain limitations apply to visual recognition, which could have profound effects on the way visual landmarks are remembered and subsequently recognised. This, in addition to the similarity between the stereotyped routes performed by pigeons and the foraging routes performed by some insects (ants, bees and wasps) allows novel parallels to be drawn between pigeon and insect navigation.

The ability of birds to detect and accurately assess route cues from distances of several kilometres suggests that pigeons may be able to perform detailed stereotyped routes via visual attraction between successive landmarks without reference to a compass system. This hypothesis is tested in the final experimental chapter which incorporates artificial manipulation of the birds' sense of compass direction through a clock-shift treatment. The results show that while some birds are able to perform their stereotyped routes without the aid of the sun compass, in others the sun-compass may have a role to play even after they have become extremely familiar with a local homing task.

The combined results demonstrate an extremely important role for visual landmarks in familiar area navigation, and provide evidence as to how familiar visual landmarks are remembered, recognised, and encoded by homing pigeons.

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CHAPTER 1

Introduction

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1.1 SETTING THE CONTEXT FOR THIS THESIS

The current thesis utilises recently miniaturised GPS technology (von Hünerbein et al., 2000; Steiner et al., 2000) in order to track pigeons navigating homeward from release sites close to the home loft. This technology represents an important advance on previous methods of studying avian orientation (see section 1.4 for a review), and allows experimenters to record the homeward paths taken by pigeons in unprecedented detail.

The main focus of this thesis is the question of whether pigeons utilise familiar visual landmarks when performing local homing tasks. The role of familiar visual landmarks in pigeon homing has been a controversial issue since experiments performed in the 1970's demonstrated that pigeons released wearing frosted contact lenses, restricting their vision such that they were able to view the sun but no detailed visual features, were able to reach to within a few hundred metres of home (Schmidt-Koenig & Schlichte, 1972, Schlichte, 1973; Schmidt-Koenig & Walcott, 1978). These experiments were taken to indicate that vision was not an important cue for pigeon homing, and much of the following experimentation concentrated on other senses which could provide pigeons with enough information to return to their home lofts, often over great distances from unfamiliar sites (see section 1.2.1).

It has since been demonstrated that when familiar visual cues are available at release sites, birds are able to utilise this information to home more quickly than when denied familiar visual cues (Braithwaite & Guilford, 1991; Burt et al., 1997). These experiments involved manipulating the visual input available to the pigeon before release. It was shown that birds given a 5 min view of a familiar site before release were able to home significantly faster than birds not given such a preview. The effect

was lost when birds were released at unfamiliar sites (Braithwaite & Newman, 1994). These results suggest that, although non-essential due to redundancy in the pigeon's navigational system, when available familiar visual landmarks are used, and significantly enhance homing performance (these experiments are reviewed more fully in section 1.3.1 and the preview paradigm is revisited in Chapter 4).

These "preview" experiments provided a tantalising insight into the way in which familiar visual landmarks may be represented by the homing pigeon, but the experiments were limited to a small area surrounding the release site, and homing times were the only way to characterise the remainder of the homeward journey. Several attempts were made to track pigeons (reviewed in section 1.4) but it is only recently, with the development of GPS loggers small enough to be carried by pigeons (Steiner et al., 2000; von Hünerbein et al., 2000), that the full homeward journeys of pigeons could be reproduced in sufficient detail to allow detailed analysis of flight paths to be performed.

In the next sections I first summarise the sensory modalities that pigeons use to navigate from distant unfamiliar sites, and the theoretical basis of much of the research carried out on pigeon navigation, before reviewing what is currently known about the use of visual landmarks at various stages along the homeward journey. I shall then review methods of avian tracking, before describing the structure of the thesis.

1.2 PIGEONS' MAPS AND COMPASSES

In 1953 one of the first models to explain pigeon homing was proposed (Kramer, 1953b). Kramer's model consisted of a two-step homing system, the Map-and-Compass model. In the first stage, the "map step", a displaced bird determines its position with respect to home, and thus the theoretical direction in which to fly in order to reach home. In the second stage of the process, the "compass step", this homeward direction is selected by means of a compass. This model is widely accepted and much of the research in the field has focussed on the nature of the map and compass systems. The environmental cues which are used to determine position with respect to home, and the subsequent homeward direction, are discussed in the following two sections.

1.2.1 THE MAP SYSTEM

Though initially treated with scepticism, the most widely accepted navigational map system, allowing pigeons to home from distant unfamiliar release sites, is one based on environmental odours (reviewed extensively by Papi, 1991; Wallraff, 2004). Pigeons allowed free access to winds at the home loft are thought to develop a representation of the odours in the surrounding area, by learning the composition of atmospheric odours arriving on winds from different directions. When birds are subsequently displaced, by comparing the relative change in composition of atmospheric particles at the release site to the composition of the air at the home loft, the direction of the release site relative to home can be calculated.

A large body of experimental evidence supports this model. Experiments involving anosmia brought about by a variety of techniques (olfactory nerve sectioning, e.g. Papi, 1971; nerve sectioning associated with nostril plugging, e.g. Papi, 1972; Irrigation with zinc sulphate solution: e.g. Benvenuti et al., 1992) have demonstrated that anosmic pigeons perform consistently poorly in comparison to controls. The latter method has been utilised in several different parts of the world (Italy; Benvenuti & Gagliardo, 1996, Morocco; Gagliardo et al., 2000, USA; Bingman et al., 1998; Bingman & Benvenuti, 1996, Brazil; Ranvaud et al. 2001, Germany; Schlund, 1992, & England; Guilford et al., 1998), and in every case experimental birds performed worse than control birds, though the performance varied across the different locations.

Further experiments manipulating the composition of air available to birds upon release were performed. First, larger atmospheric molecules were filtered out of air available to birds before release (followed by anaesthetic applied to nostrils). Unlike control birds, birds which had breathed filtered air were not significantly homeward oriented (Wallraff & Foà, 1981). It was subsequently demonstrated that if birds were allowed to breathe ambient air at one site, and were subsequently transported to a second site (their sense of smell having been disrupted using anaesthetic), upon release birds flew in the direction that would have been appropriate for the first site (Benvenuti & Wallraff, 1985; Kiepenheuer, 1985).

The importance of access to winds at the home loft in the development of a pigeon's navigational map was demonstrated in several experiments using shields to deflect the direction of winds entering aviaries (e.g. Baldaccini et al., 1975; Ioalè et al., 1978). The screens deflected the wind by ~ 90° to the left or right of their natural direction. When these birds were released their orientation was shifted by the

corresponding amount when compared to control birds (although see Waldvogel & Phillips, 1991 for alternative explanation for results).

The question of how a navigational map based on atmospheric odours is structured remains unanswered, though the discussion is dominated by two hypotheses. The first was proposed by Papi et al. (1972) and later discussed by Wallraff (1991), and suggests that the map is based on a patchwork of irregularly changing odours referred to as an "Olfactory Mosaic Map" (Bingman, 1998). Pigeons would learn to associate varying atmospheric odours with different directions around the loft, either by memorising direction of wind-borne odours, or by flying around the loft, or a combination of both methods. When a bird is subsequently displaced to a distant area, by sampling the atmospheric odours at the new site and comparing the odours present with the learnt pattern of odours around the home loft, it would be able to determine its position with respect to home, and the direction in which it should fly to return to it.

The second hypothesis of how an olfactory navigational map might be structured is referred to as an olfactory gradient map (Papi & Wallraff, 1992). It is hypothesised that odours may vary consistently along two non-parallel axes, which can therefore provide coordinates of both the position of the home loft and the position of any point that a pigeon is taken to. A displaced pigeon could therefore determine its position with respect to home

It is not yet known which of these two differing hypotheses best matches the system which homing pigeons use, but atmospheric trace gases that remain in fairly constant ratios despite changes in wind direction have been identified (Wallraff & Andreae, 2000), though whether it is these particular trace gases that are used by the homing pigeon has not been confirmed.

Though there is much evidence in favour of a pigeon's navigational map being odour based, there are alternatives. Some, such as navigation based upon the position of the sun (Matthews, 1953), and grids based on the earth's magnetic field coupled with the Coriolis force (Yeagley, 1974) though theoretically possible, have received little experimental support and have therefore been abandoned. A further mechanism by which it has been suggested that pigeons gain position information is by detection of low-frequency infrasound, generated by infrasonic cues emanating from steep sided topographical features such as mountain ranges. Though pigeons have been shown to be able to detect infrasound (Kreithen & Quine, 1979), there is little evidence supporting the possibility of such a map, and much speculation on such a map being used is based on the disruption of pigeon races coinciding with infrasonic cues caused by Concorde flights (Hagstrum, 2000; 2001).

The most enduring alternative to a map based on odour cues, is one utilising the earth's magnetic field. Because the intensity and direction of the earth's magnetic field varies systematically between the magnetic equator and poles, any point on the earth can be described as unique 3D vector based on these two variables (Walker, 2002). Such a map was initially hypothesised because of effects on initial heading seen at magnetic anomalies (e.g. Walcott, 1978). But as these effects were often inconsistent, the idea that pigeons might use a magnetic map was largely abandoned (e.g. Wallraff, 1983; 1990; Walcott, 1991). Recently the possibility of a magnetic map has generated more interest. Pigeons have been shown to be able to detect the presence or absence of magnetic anomalies in conditioned choice experiments in a laboratory setting (Haugh et al., 2001b, Mora et al., 2004). And there is some evidence that carrying a magnet affects position determination (Haugh et al., 2001a). In the most recent paper (Mora et al., 2004) the authors suggest that some treatments

used to render birds anosmic (such as anaesthetic applied to the beak; nerve sectioning) may also disrupt pigeons' ability to detect magnetic cues. Whether the magnetic information available, and pigeons' sensitivity to the information is fine enough for pigeons to rely upon magnetic information for position determination remains to be resolved.

1.2.2 THE COMPASS SYSTEM

The compass system used by homing pigeons is better understood and more widely agreed upon than the map system discussed in the above section. In 1950, Kramer first reported the use of the sun, as a time compensated compass in birds (Kramer, 1950; 1953a). In 1958 pigeons were first subjected to clock-shift manipulation (Schmidt-Koenig, 1958). It was shown that pigeons' heading directions could be predictably deflected by maintaining birds under an artificial light-dark cycle, and shifting their internal clocks by turning lights on and off a certain number of hours before or after natural sunrise and sunset. On subsequent release birds were shown to move off in a direction deflected by the degree of compensation made for the movement of the sun across the sky, between the actual time of day and the birds' subjective time of day, given their shifted circadian cycle (birds were shown to attend only to the sun's azimuth, not the sun's altitude; Papi et al., 1992). On average, each hour that a bird's circadian clock is shifted results in an approximate 15° deflection in heading in comparison to control birds (Schmidt-Koenig et al., 1991), though this varies with time of day, time of year and latitude. The deflection can be set in the anticlockwise direction by waking the birds up artificially early, or in the clockwise direction by waking the birds up late. This apparent independence of the compass step

from the map step reinforces the idea that pigeon homing is a two-part process. Clock-shifting as an experimental manipulation in pigeon navigation research has been used extremely widely and has produced very robust results, though the amount of deflection seen is not always as great as theoretically expected (see Chappell, 1997; Wiltschko et al., 1994 for reviews; see also section 5.1).

As pigeons are still able to orient homeward under overcast conditions, it seems that pigeons also have a second compass system available to them, that of the magnetic compass. Various experiments have demonstrated that very young pigeons without free-flight experience, rely on magnetic compass information before they have the opportunity to develop their sun compass (Wiltschko & Wiltschko, 1981; Keeton, 1971; Wiltschko et al., 1987). Keeton (1972) demonstrated that experienced birds released under sunny conditions, with bar magnets attached to their backs were as well orientated as controls, but when released under total overcast the magnets disrupted their orientation, and random homeward bearings were recorded. Several further experiments have confirmed these results (e.g. Walcott & Green, 1974; Ioalè, 1984; Wiltschko et al., 2001). Pigeons' upper beak skin has been shown to contain aggregates of magnetite crystals, adjacent to nervous material, which change shape as magnetic fields vary (Shcherbakov & Winklhofer, 1999; Winklhofer et al., 2001). It is thought that these crystals potentially serve as the basis to birds' inclination compass.

The robustness of clock-shift experiments, the observation that return rates are lower when birds are released under overcast conditions than when the sun's disc is visible (Benvenuti et al., 1996), and the result that magnets do not cause disorientation to experienced birds when the sun's disc is visible, all strongly suggest that the magnetic compass acts as a back-up system to the more dominant sun compass.

1.3 THE ROLE OF VISUAL LANDMARKS WITHIN A FAMILIAR AREA

The map systems described above are navigational maps, which spread far beyond the range of a bird's own experience and can be used to navigate homeward from distant unfamiliar release sites. Once a bird becomes familiar with an area around the home loft, in addition to a navigational map, the bird gains access to a further set of cues; familiar visual landmarks. Pigeons are highly visual animals and vision has been shown to be their most dominant sense (Randich et al., 1978). Many experiments have investigated the avian visual system within a laboratory setting (see Cook, 2001 for a review), but far fewer have explored avian visual cognition in more naturalistic settings. The following sections review what is now known about the use of visual landmarks within a pigeon's "familiar area", defined as an area with which a bird has had direct sensory contact, though which might extend beyond areas actually visited by the bird (Wallraff, 2001).

1.3.1 VISUAL LANDMARKS AT THE RELEASE SITE

In 1991 the first of several experiments manipulating the view available to pigeons before release was performed (Braithwaite & Guilford, 1991). In this experiment birds were released at familiar sites, out of visual range of the home loft, with and without a preview before release. Birds were released from a box which could be made clear or opaque, thus controlling the visual input, but allowing birds access to olfactory cues and a view of the sun's disc. Birds homed on average 18 % faster when allowed to observe the visual landscape before release. These results were investigated further in similar experiments allowing greater access to olfactory cues (Burt et al., 1997) and

observing birds' orientation within a circular arena (Gagliardo et al., 2001). Since no advantage of a preview was found when birds were released from unfamiliar sites (Braithwaite & Newman, 1994), this confirmed the result that visual cues are used to recognise familiar release sites, allowing birds to determine their location more quickly than birds denied a view of the landscape, and that this earlier position recognition significantly improves homing speeds. In 2002 the "preview effect" was examined in greater detail because the advent of GPS loggers small enough to be carried by homing pigeons (Steiner et al., 2000; von Hünerbein et al., 2000; see section 1.4), allowed pigeons' entire homeward flight to be recorded (Biro et al., 2002). This experiment adopted the same preview paradigm as explained above. Analysis of tracks of birds released with and without a preview of the landscape revealed that the preview effect was limited to the 1000 m radius surrounding the release site. Birds denied a preview before release took paths that were initially more tortuous and included more circling behaviour. This suggested that birds denied a preview carried out these behaviours as part of an information gathering strategy, which was unnecessary if birds had been able to view the landscape before release.

Recently, the mechanisms allowing recognition from a familiar site were further probed by controlling more precisely the visual cues available before release (Biro et al., 2003). It was shown that birds released from a box with one clear side and three opaque sides were able to home faster than birds denied any view of the landscape, thus indicating that an ~ 140° view of the landscape was enough to facilitate site recognition. In a further experiment, birds were given a single training release with a 140° view of a release site and were subsequently released either with the same view available, or with a non-overlapping view out of the other side of the box. Birds that received the same view as in training homed more quickly than birds

that received a "novel" view. This suggests that birds did not recognise the non-overlapping viewpoint, despite having been able to view the set of landmarks during the training flight. It is possible that pigeons' ability to recognise visual landmarks is limited by their visual system, the possible implications of which are discussed further in section 1.3.2.

Other experiments where the pigeon's visual sense was not directly manipulated also imply an important role for visual landmarks when homing in the familiar area. Experiments involving releasing birds under clock-shift conditions from familiar areas often result in a reduced deflection (e.g. Foà & Albonetti, 1980; Bingman & Ioalè, 1989), although some findings contradict these results (Füller et al., 1983; Luschi & Dall'Antonia, 1993). Pigeons released under anosmic conditions in a familiar area are able to home almost as well as control birds, whereas anosmic pigeons released from unfamiliar locations are severely impaired in their homing abilities (Benvenuti et al., 1992; Wallraff & Neumann, 1989; Wallraff et al., 1993). This suggests that the presence of familiar visual landmarks cause olfactory cues to become redundant within a familiar area.

The experiments reported above demonstrate that at familiar release sites visual landmarks play an important role in site recognition. The question of how visual landmarks are encoded into a pigeon's representation of space then arises. This question is complicated by the nature of a map based on familiar visual landmarks, as opposed to a map based on olfactory or magnetic cues. Unlike magnetic or olfactory cues, visual landmarks cues can be detected at a distance, providing information not only about the particular point in space that the bird currently occupies, but also distant locations. This has led to a map based on visual landmarks being described as a "pattern map", in comparison to a map based on olfactory or magnetic cues, which

is described as a "point map" (Wallraff, 1991). A point map, as it is based on cues which can only be detected at the bird's current position, not at some distance away, provides no directional information in itself, and is therefore "freely rotatable" (Wallraff, 1991). Birds relying on such a map, when released under clock-shift conditions, should experience no conflict between the homeward direction as indicated by the shifted sun compass, and the true homeward direction. In contrast, a map based on visual landmarks includes a pattern of features visible from a distance, which are fixed in relation to each other as well as the sun, and therefore include directional information. A bird released under clock-shift using a map based on the relationship between familiar visual landmarks, should immediately experience conflict between the homeward direction as indicated by the sun compass, and the homeward direction as indicated by visual landmarks.

Because birds released under clock-shift conditions from familiar sites are usually deflected in the expected direction (Füller et al., 1983), but are able to travel homeward accurately when released under anosmic conditions from familiar sites (Bingman & Ioalè, 1989), this suggests that birds are able to use familiar visual landmarks at a release site in two ways. The first is analogous to the "point map" described above, where birds would use a familiar array of landmarks at a release site for site recognition, and then assume the homeward direction by means of a compass, without using the directional information included in the landmark array. Secondly birds could utilise the directional component of a landmark array, and orient homeward, referring to remembered relationships between visual landmarks without reference to a compass system. This mechanism of navigation using familiar visual landmarks without reference to a compass system is usually referred to as "Pilotage" (Papi, 1992).

Experiments performed using hippocampal-ablated homing pigeons (Gagliardo et al., 1999; 2002) support the existence of both strategies. Anosmic pigeons released under clock-shift from familiar sites were homeward oriented (presumably using landscape features without reference to a compass), but when hippocampal-ablated birds were released under the same conditions, they were deflected in the clock-shift direction. This indicated that, though a topographical map based on the relationship between landmarks became unavailable to the hippocampal-ablated birds, they were able to associate the array of landmarks at the release site with a (shifted) homeward compass bearing. A further experiment by some of the same authors (Gagliardo et al., 2004) was designed to induce conflict between the topographical and compass information available to pigeons, by releasing clock-shifted birds at familiar sites. Birds were released under clock-shift and no shift conditions, at familiar and unfamiliar sites, under unmanipulated and anosmic conditions. The results showed a general dominance in reliance on using the sun compass, rather than a pilotage strategy, but demonstrated a reduction in deflection at familiar release sites, which was further enhanced when birds were released under anosmic conditions. The authors suggest that when an olfactory map is unavailable to pigeons, it leads the birds to use topographical information in a way more consistent with pilotage than a map and compass strategy.

1.3.2 VISUAL LANDMARKS ALONG THE HOMEWARD JOURNEY

Until recently the study of the role of visual landmarks in homing pigeon navigation has essentially been limited to the effects of landmarks at the release site. Early attempts at tracking pigeons (reviewed in section 1.4) attempted to correlate birds'

movements and behaviour with the topographical landscape. Dornfeldt (1982) investigated the influence of various visual features around release sites on pigeons' vanishing bearings and found that birds were attracted to visual features such as railway lines and settlements. Kiepenheuer (1993) also noted that pigeons' vanishing bearings seemed to be affected by the presence of settlements near the release site; birds were attracted to larger settlements, closer to the release site. These influences of the topographical landscape on pigeon homing were initially thought to be distracting, but in 1993 Guilford proposed that attraction to various landscape features might have an important role in familiar area navigation. These studies are limited to a fairly small area around the release site; due to methodological limitations few experiments have been carried out which directly address the use of familiar landmarks along the homing route.

In 1993 Braithwaite published a paper which included one such experiment, adopting the preview paradigm described in the section 1.3.1. Birds were released from boxes part way along a route they were assumed to have flown, under preview and no-preview conditions, and the homing times under the two treatments were compared. A preview of the landscape before release was not found to provide a homing speed advantage. These results could be interpreted in three ways. First, birds may not have flown over the areas they were assumed to have done, and therefore the previews given may have been at unfamiliar sites, where a homing speed advantage would not be expected. Second, birds may not have recognised the sites they had viewed from the air because of the substantially different viewpoint found at ground level. Finally, birds may pay no attention to visual landmarks along the homeward route. In Chapter 4 I reproduce the main elements of this experiment, with the aid of GPS tracking, in an attempt to determine which of the above three possibilities best

explains the results, and to further investigate the role of visual features along the homeward journey.

The development of GPS trackers small enough to be carried by pigeons has revolutionised the ability of researchers to investigate topographical cues attended to by homing pigeons through their homeward journeys. Pilot trials of the technology, reported by Biro (2002), show evidence of linear landmark following, where birds flew along roads, rivers and railway lines (further experiments utilising GPS technology have also shown evidence of such linear landmark following; Guilford et al., 2004; Lipp et al., 2004). Biro also noted that linear landmarks were often associated with incidences of circling and marked changes in direction. Another striking feature reported was that birds often returned to the same landscape features, in flights from various locations, and again these features coincided with marked changes in direction. These points of "re-evaluation" were often found to be similar across different subjects. Biro suggested that these landscape features served as "waypoints"; intermediate goals from which the homeward orientation is known.

Another interesting phenomenon observed was that birds tended to approach these "waypoints" from consistent directions, and that individual birds released several times from the same site would take similar paths on subsequent releases. These observations, coupled with the results investigating familiar release site recognition (Biro et al., 2003), suggest that certain limitations may apply to pigeons' visual recognition abilities, which are possibly analogous to those found in insect visual cognition. Honeybees remember retinal "snapshots" of an array of visual landmarks as seen from a target and to return to their goal they position themselves so as to reduce the discrepancy between the current retinal image and their stored snapshot (Cartwright & Collett, 1982). Ants (Wehner & Raber, 1979), bees

(Cartwright & Collett, 1983), Wasps (Collett & Rees, 1997), and Water striders (Junger, 1991) have all been shown to use this technique of "image matching". To make it easier for learnt snapshots to be recalled, many animals maintain the consistency of their viewing angles over many trips, by following a set route (ants: Rosengren, 1971; Rosengren & Pamilo, 1978; Collett et al., 1992 and bees: Chittka et al., 1995; Dyer, 1991; Dyer et al., 1993). This type of image matching has also been shown more recently to facilitate object recognition in chickens (Dawkins & Woodington, 2000).

The idea of pigeons repeatedly following similar routes, possibly including a certain number of waypoints viewed from similar angles, over successive releases is a recurring theme of this thesis and is discussed in chapters 2, 3, 5 and 6.

1.3.3 VISUAL LANDMARKS AT THE END OF THE HOMEWARD JOURNEY

The use of visual landmarks at the final stage of the homing journey has not led to the same debate as the use of visual landmarks in the preceding stages. Even in Schmidt-Koenig and Schlichte's (1972) experiment releasing birds wearing frosted contact lenses, a role for vision was identified. Some birds were able to reach within a few hundred metres of their home loft, but the birds were unable to complete their journeys, presumably because they were unable to see the loft buildings.

The importance of a view of the home loft was also highlighted in Graue's (1963) experiments, releasing birds under clock-shift conditions < 1 mile from the loft. In all cases the birds were deflected in the correct direction, except when the loft could be directly perceived at the release site. From this site, birds returned directly to the loft without being influenced by the clock-shift treatment.

Many of the experiments described in the previous sections, though providing valuable information of the importance of visual landmarks at various stages in the homing task, are limited by various methodological constraints. In the following sections I summarise previous attempts at reproducing pigeons' homeward journeys, before describing the technology which is utilised to track homing pigeons in the experimental chapters of the current thesis.

1.4 METHODS OF AVIAN TRACKING

To answer some of the most fundamental questions about bird navigation it is important to accurately determine the route taken by birds. This is true over both long and short distances. Over long distances migratory routes and destinations can be determined. Over short distances, birds such as homing pigeons can be experimentally manipulated to test theories about their navigation that cannot be examined using traditional measurements. For example, vanishing bearings only give information about the initial stages of homing, and homing times do not distinguish whether a bird has taken a long homeward route, or simply landed along the way. In the next sections I review the development of different types of systems used to track birds over several decades, and finish with a description of the technology utilised throughout the current thesis.

1.4.1 AEROPLANE AND HELICOPTER TRACKING

The first attempts to gain full flight information of birds' routes were by Hitchcock (1952) and Griffin (1952) where small flocks of pigeons were followed in an aeroplane. The birds were followed visually by an experimenter within the plane. In 1955 Hitchcock repeated the procedure, again tracking small flocks but also following individual birds. The author reported difficulty in tracking individual birds, with many landing soon after release, and none followed for more than an hour at distances of > 80 km, therefore no complete flights of individual birds were recorded. Helicopters were also used slightly later to track pigeons (Talkington, 1967; Fiaschi et al., 1981). These studies have obvious disadvantages. They are extremely costly, labour intensive, and may also have substantial effects on the birds' behaviour, and because of these factors relatively few studies have been carried out.

1.4.2 RADIO TRACKING

In contrast to the above method of tracking birds visually, in the 1960s the technique of VHF (very high frequency) radio-tracking was developed (Cochran & Lord, 1963), and used to follow bird movements (Marshall & Kupa, 1963). Birds were fitted with radio transmitters, which gave out radio pulses of a certain frequency that could be detected by experimenters using receivers set to the same frequency. The direction of the transmitter from the receiver can be determined by measuring the relative strength of the signal (i.e. strength is greatest when the receiver is pointing directly at the transmitter). The distance of the transmitter from the receiver must be determined by means of triangulation. If at least two receivers are used, the point where the two

bearings intersect gives the theoretical position of the animal. In practise three or more bearings are required due to the imprecise nature of the directional signal. When more than two bearings are plotted on a map they form an "error polygon" (Heezon & Tester, 1967) which contains the animal's position.

The technique of radio-tracking is useful for studies of long-range animal movements. The transmitters carried by subjects weigh as little as 0.8 g (Samuel & Fuller, 1996), and can operate for several years, over distances of 15-25 km (Rodgers et al., 1996), and the technique has been used on many different species.

Radio-tracking has been used in conjunction with aeroplanes for recording the paths of homing pigeons. Michener and Walcott (1967) used the technology to track single pigeons, and found the combination of technology more effective than tracking birds by sight, as birds could be followed from a greater distance, reducing the possible effects of the presence of an aeroplane on the birds' behaviour. The technique was also used by Schmidt-Koenig and Walcott (1978) to compare the flight paths of control birds, and birds released wearing frosted contact lenses. The results showed that both groups were fairly well homeward orientated, though birds wearing frosted lenses had a more scattered distribution.

Although more effective than aeroplane tracking alone, the use of radio-tracking to follow pigeons from aircraft is still an expensive, labour intensive exercise producing flight paths of relatively low resolution. More recently, Wolff (1997) used a series of four ground-based radio stations to monitor the flight paths of clock-shifted pigeons wearing radio transmitters. Despite providing some information of birds' positions after vanishing, the results did not provide accurate information of a pigeon's entire homeward flight.

1.4.3 SATELLITE TRACKING

A less labour intensive method of tracking birds is by use of satellite telemetry. The ARGOS (Advanced Research and Global Observation Satellite) system became operational in 1978 and the first bird successfully tracked using this technology was a bald eagle in 1984 (reported in Fuller et al., 1995). The system was set up by the French Space Agency (CNES), with the US National Oceanic and Atmospheric Administration (NOAA) and the US National Aeronautic and Space Administration (NASA). The system works on the basis of Doppler shift. Transmitters carried by animals send out radio-waves of constant frequency which are received by satellites. The frequency received by the satellite peaks as it passes closest to the transmitter, and this frequency is recorded and time tagged. The position of a transmitter can be calculated if the frequency transmitted, frequency received, and the time the signal is received are known. The positional data are sent to ground stations, where they are made available to researchers.

The advantage of the ARGOS system is that the PTTs (platform transmitter terminals) carried by the birds weigh as little as 4 g, and use fairly small amounts of power, as they transmit to highly sensitive low orbiting satellites, so batteries can last up to 1 year. Because the PTTs transmit rather than receive data, route information can be obtained without recovering the transmitter attached to the bird. This can be very useful, as many wild birds are difficult to locate and re-catch, particularly if the battery has run out and the position of the bird is no longer known. As the equipment is expensive (typically $3000 - $4500) it is preferable to recover the devices, but if this is not possible then the data for the experiment is still available. The system has proved an important tool for tracking birds on a large scale and has been used on a

wide variety of wide-ranging birds such as Swans (Nowak et al., 1990), Albatrosses (Jouventin & Weimerskirch, 1990), Vultures (Berthold et al., 1991), Thick billed Murres (Falk et al., 2001), Petrels (Benhamou et al., 2001), Storks (Berthold et al., 2004) and Flamingos (Childress et al., 2004), as well as on Flying Foxes (Tidemann & Nelson, 2004).

The technology is less useful for tracking the local movements of birds on a smaller scale. Because only a few satellites are operational at any one time, complete global coverage only occurs a few times a day. The satellites pass over the poles in every rotation, but pass the equator at points fixed in time. When two satellites are operational a satellite will pass over a transmitter at one of the poles on average 28 times a day, whereas a satellite will only pass over a transmitter at a certain point on the equator approximately 6-7 times a day. Transmitters can be programmed to broadcast for a limited number of hours per day, in order to conserve battery power. A satellite receives messages from transmitters within a 5000 km diameter circle beneath it, and a satellite can receive signals from a transmitter as it passes over for 8-15 minutes. Within a pass over a transmitter the satellite must receive at least four signals. At least one signal must be received from each side of the inflection point, which is the point where the satellite is closest to the transmitter. Thus the ARGOS system provides low spatial resolution (accurate to between 150 -1000 m), with low sampling frequency and is therefore only suitable for tracking birds that cover very long distances, and is unsuitable for the short distance, high resolution tracks that are essential in studies of pigeon homing.

1.4.4 ON BOARD ROUTE RECORDERS

In 1988 a system much more suitable for obtaining short distance, high resolution, tracks of birds was developed by Bramanti and Dall'Antonia. The trackers, known as "route recorders", were dead reckoning devices, and recorded the angle between the heading of the main axis of the bird's body and magnetic north at set intervals as frequently as 2 s. The devices were designed for use on homing pigeons and weighed 30 g including a battery (second and third generation devices were developed that weighed as little as 13 g; Holland et al., 2000). On recovery of the bird and device, the route taken could be reconstructed using the coordinates of the start and end point, and some assumptions of flight speed, along with wind data recorded at various points between the release site and home loft.

This constituted a large technical advance, as no direct following of the birds was necessary and fairly high-resolution tracks resulted which could be plotted on a map, relating the tracks to ground features. This system was used initially on pigeons (Bramanti & Dall'Antonia, 1988) to successfully record repeated flights of birds over distances of up to 60 km, providing detailed route information (Bonadonna et al., 1997). The loggers made it possible to record detailed homeward paths of clock-shifted birds (Bonadonna et al., 2000; Holland et al., 2000). These experiments provided evidence of differing navigational strategies, with some birds relying more heavily on sun-compass information at some sites than at others. The route recorders were also adapted for use on Cory's Shearwaters (Dall'Antonia et al., 1995), Thick-billed Murres (Benvenuti et al., 1998) and Razorbills (Dall'Antonia et al., 2001).

The disadvantages to this type of route recorder stem from the fact that only heading is recorded; errors included in tracks would result in discrepancies between

the end point as recorded by the logger, and the actual position of the loft. Assumptions also had to be made about the speed a bird travelled (a constant speed of 60 km/h assumed; Holland et al., 2000) and the device could only be used on relatively calm days as wind drift affected reconstruction of the tracks. These problems were partially solved by recording wind speed information at various points between the release site and home, and by rejecting tracks where the angular difference between the position of the loft and the final point of the track exceeded 10° (Holland et al., 2000). It was also possible to tell if a bird had landed due to lack of noise in the recording of direction, but, without direct positional information, the system remained a less than perfect method of tracking birds.

1.4.5 GLOBAL POSITIONING SYSTEM (GPS) TECHNOLOGY

GPS (Global Positioning System) loggers utilise information sent from satellites to determine accurate, time-stamped, positional information, which is recorded by the receiver and can be downloaded on recovery of the device. GPS technology was developed by the American Ministry of Defence, but has since been made available for civilian use. GPS devices can receive signals at < 1 s intervals, and initially provided positional information accurate to within 100 m. GPS technology therefore provided one of the most accurate ways to study animal movement and has been used on large animals such as sheep, deer, and wolves since the early 1990s (Rutter et al., 1997; Bowman et al., 2000; Frame et al., 2004). Initially the size and weight of GPS devices (weighing as much as 3.4 kg (Blanc & Brelurut, 1997)) made them practical for use only on large mammals, but in 2000 two groups published papers detailing

GPS loggers small enough for use on homing pigeons (von Hünerbein et al., 2000; Steiner et al., 2000).

The development of this technology suitable for use on homing pigeons coincided with the US Government lifting "selective availability" which distorted the satellite transmissions and reduced the accuracy of positional fixes. Resolution of fixes increased from within ~100 m to ± 4 m in the horizontal plane (Weimerskirch, 2002). Thus, in 2000 loggers weighing as little as 33 g, with battery lives of up to 3 hours (with a 1 Hz sampling rate) were available for use on the homing pigeon, providing tracks of unparalleled resolution.

The GPS system consists of 24 satellites moving in orbits arranged such that, at any point on the earth, at least four satellites are visible 95 % of the time. Each satellite transmits unique codes as radio-waves so GPS receivers can identify which satellite a signal is from. The GPS receiver plays the same code as the satellite and measures the amount that it must delay its code to match it to the code that the satellite sends. This amount of time multiplied by the speed of light (the speed radio-waves travel), gives the distance from the receiver to the satellite. When at least four satellites are visible to a GPS receiver, its position in space can be accurately calculated by computing the distance from each of the satellites to the receiver, as a sphere with the satellite in the centre. Where the four spheres intersect indicates the position of the receiver.

It is possible for GPS loggers to transmit data via satellites to ground stations which can be forwarded on to researchers, but this extra transmitter would, with current technology, make the GPS system too heavy to be carried by homing pigeons. Because of the very high return rates and easy recapture of homing pigeons this does not reduce the suitability of GPS loggers for recording the flight paths of pigeons. The

detailed tracks obtained via GPS technology are very important for experiments designed to investigate navigation over small distances. Once the loggers are recovered tracks can be downloaded onto topographical maps, which makes it possible for birds' tracks to be related to physical features of the environment, as well as recording time and distance.

The disadvantages of the GPS system include relatively weak satellite signals, which can be disrupted if the logger does not receive an uncluttered view of the sky. This is more of a problem for studies involving ground-based mammals however, than studies involving pigeons where during flight an uncluttered sky view is almost always available. A second limitation to GPS technology is the relatively poorer altitude resolution than position resolution in the horizontal plane. GPS position fixing works on the basis of measuring distances from at least four known points (satellites), to the GPS receiver. The estimated position of the GPS receiver therefore becomes more accurate when the satellites it receives signals from are widely distributed in the sky. The distribution of satellites is usually sufficient to allow an accurate positional fix in the horizontal plane, but because satellites are rarely positioned directly above a receiver and never below, altitude estimates are less accurate than estimates of horizontal position. This relatively poor altitude information remains an advance in comparison to the tracking techniques mentioned above, none of which provide altitude information, except visual following of pigeons from aircraft. A third disadvantage to GPS technology is its weight in comparison to the above tracking devices. As technology improves however, the weight of GPS devices is continually being reduced (see Appendix 1 for details), and this weight reduction may well facilitate the addition of devices such as altimeters (Weimerskirch et al., 2005) to provide more accurate altitude information to complement the GPS technology.

1.5 STRUCTURE OF THE THESIS

The following four experimental chapters all involve using GPS tracking as a tool to investigate pigeons' use of familiar visual landmarks, whilst navigating homeward under various experimental conditions.

In Chapter 2 I used GPS technology to track the paths of pigeons as they became increasingly familiar with a homing task. Pigeons were released > 20 times from the same site and each of their homeward paths were recorded. I used a novel method of measuring track similarity to investigate how birds' flight paths changed as subjects became increasingly experienced with a local homing task. I repeated the procedure with new subjects from a new site, with the additional factor of a magnetic disruption treatment (Haugh et al., 2001a). The results show striking degrees of route stereotypy, which strongly suggests the use of visual landmarks to mediate these established routes.

In Chapter 3 I investigate how far the route-recapitulation effect extends away from home, by repeatedly releasing birds from a release site 25 km from the home loft. The technique of releasing birds from novel sites perpendicular to their stereotyped routes (Biro et al., 2004), was introduced to investigate whether birds return to their established routes, and what cues they may be attending to in order to do so. A system of yoked controls was included, so that homeward flights of route-recapitulating birds could be objectively compared to tracks of birds that had not been allowed extensive experience of the landscape, to control for factors such as possible constraints caused by terrain features. Releases in this chapter were performed jointly by myself and Dora Biro.

Chapter 4 reproduces the main elements of Braithwaite's 1993 experiment (see section 1.3.2). I used GPS trackers to pinpoint areas that birds had flown over and then released these "aerially familiar" birds, with naïve partners, from the chosen sites, under preview and non-preview conditions. This was carried out to investigate whether "aerial familiarity" with a release site allowed birds to home more efficiently, and also whether a ground-level preview of a site allowed aerially familiar birds to recognise the site before release, and translate this recognition into a homing speed advantage. In the first experiment birds were released from a site they were known to have flown over at least once, and in the second experiment birds were released from sites which made up part of the stereotyped homeward routes developed in experiment 2.2.

Chapter 5 reports one of the first instances of GPS tracking birds released under clock-shift conditions. In the first experiment birds that had been phase shifted by one hour were tracked from two release sites. In the second experiment birds that had developed stereotyped routes were released from four release sites under clock-shift conditions. Tracks performed by highly experienced birds were compared to tracks performed by birds that had not been allowed to develop stereotyped routes, resulting in a fascinating insight into the way in which familiar cues are encoded into stereotyped routes developed by homing pigeons. Releases in the first experiment were carried out in collaboration with Jennifer Harcourt as part of an undergraduate project, and releases in the second experiment of this chapter were performed jointly with Dora Biro.

Chapter 6 summarises the results of the five experimental chapters of the thesis, and attempts to draw together the results to give an overview of the

navigational strategies used by birds extremely familiar with a homing task. The chapter also suggests areas for further research utilising GPS technology.

CHAPTER 2

Route Recapitulation by the homing pigeon

2.1 INTRODUCTION

2.2 EXPERIMENT 2.1:

2.2.1 Methods

2.2.1.1 Subjects and Materials

2.2.1.2 Procedure

2.2.1.3 Analysis

2.2.2 Results and Discussion

2.3 EXPERIMENT 2.2:

2.3.1 Methods

2.3.2 Results and Discussion

2.3 GENERAL DISCUSSION

N.B. Experiments 2.1 & 2.2 have been published as: Meade, J., Biro, D. & Guilford, T. (2005). Homing pigeons develop local route stereotypy, *Proceedings of the Royal Society, B,* 272, 17-23.

2.1 INTRODUCTION

It is now well established that familiar visual landmarks are important for homing pigeons, both at the beginning and at the end of a homing flight. The question as to whether, and how, pigeons utilize familiar visual landmarks throughout the length of a homeward journey remains largely unanswered. A 5 min view of a site before release significantly improves homing speeds at familiar sites (Braithwaite & Guilford, 1991; Burt et al., 1997; Gagliardo et al., 2001; Biro et al., 2002), but not unfamiliar sites (Braithwaite and Newman, 1994). This difference in homing speed is attributed to improved recognition of the release site using familiar visual cues during the preview stage. Schmidt-Koenig and Schlichte's experiment (1972) where birds were released wearing frosted contact lenses, allowing a view of the sun but no detailed visual features, illustrated that a view of the home loft was important for the final stage of homing as, though many birds reached within a few hundred metres of home, few managed to alight on the loft building.

Though it has been demonstrated that familiar visual landmarks are utilised by pigeons to aid homing, it has also been shown that there are certain limitations to pigeons' visual recognition. Biro et al. (2001, 2002) showed that in order for a view to be useful to a bird (i.e. to facilitate site recognition) it must be similar to one viewed previously. In these experiments pigeons were placed in a Perspex box, and before release subjects were provided either with a 140° view of an array of landmarks at the same distance and angle as they had viewed in previous training flights, or they were given the non-overlapping 140° view of the landscape in the other direction. Homing performance was better when subjects were given a preview that matched the one they had experienced in training.

This apparent lack of recognition of landmark arrays from novel viewpoints is reminiscent of the visual strategy that has been demonstrated over many years in insects (Collett & Land, 1975; Cartwright & Collett, 1982, 1983). It was shown that insects such as honey bees remember retinal "snapshots" of an array of visual landmarks as seen from a goal. To later return to the goal they position themselves so as to reduce the discrepancy between their current retinal image and their stored snapshot. Remembering all the possible views of a 3D landmark is likely to require a high memory load because of the wide range of angles and distances that 3D landmarks can be viewed from (Ullman, 1996). One way of minimizing the number of images that must be stored, but still facilitating recognition, is by following a stereotyped route, thus approaching landmark arrays from consistent positions. In this way landmarks can only be recognized from the set route, but the number of images that must be remembered is greatly reduced. This strategy of "image matching" has recently been demonstrated for the first time in vertebrates (Dawkins & Woodington, 2000). Chickens were shown to follow set routes, and use patterns of stereotyped head movements to fixate objects, in order to identify and approach a food goal. If their way was blocked so that they could not follow their route, their ability to find the food reward was reduced.

It is possible that, if visual landmarks are utilised by homing pigeons throughout the homeward route, a similar strategy might be employed in order to reduce the large cognitive load that would be incurred if landmark arrays must be memorised from every viewing angle. Biro (2002) investigated the possible use of visual landmarks along the length of the homeward route by tracking birds on three consecutive flights from a number of sites up to 7 km from the home loft, and found evidence of some birds performing very similar routes on successive flights.

The following pair of experiments were designed to further investigate the possibility of pigeons adopting a strategy of familiar route following, in order to approach visual landmarks from consistent angles across successive flights. I used high-resolution GPS loggers to track pigeons as they homed up to 24 times from two sites close to the loft, to examine the development of birds' flight paths as they become increasingly familiar with a local homing task.

2.2 EXPERIMENT 2.1:

2.2.1 METHODS

2.2.1.1 *Subjects and Materials*

Seven homing pigeons (*Columba livia* L), hatched and raised at the University Field Station, Wytham, Oxford were selected as subjects. All were successful homers and had been used in previous experiments. All birds were > 2 years old and at least 450 g in weight. Feather condition and body weight were monitored throughout the study.

In order for the GPS trackers to be attached to the birds, a Velcro strip (30 mm x 70 mm) was fitted to the subjects. Feathers were trimmed to ~ 5 mm in length over a patch slightly larger than the Velcro strip, between the bird's wings. The strip was attached to the feathers using flexible leather glue. Following this procedure, the birds were left for one day and checked to make sure the Velcro was securely attached to the feathers, allowing no sideways movement. Birds were then fitted with plasticine dummy weights measuring 30 mm (w) x 50 mm (l) x 15 mm (h) and weighing 25 g including a Velcro strip for attachment to the bird. The birds were then monitored for a further day, to ensure that they seemed comfortable carrying the weights, and that

body movement was not affected in the air or on the ground (see Biro et al., 2002 for details). The Velcro strip remained attached to the birds throughout the experiment, and if necessary the attachment was reinforced by addition of extra glue.

During each test release the birds carried GPS logging devices (see Appendix 1 for technical description) attached to the back by Velcro and weighing 28-32 g. Time stamped positional fixes (accurate to ± 4 m in horizontal plane; Weimerskirch et al., 2002) were logged every second and were downloaded on recovery of the device. The positional data was overlaid onto Ordnance Survey maps using Fugawi™ mapping software (copyright 2000-2002 Northport Systems Inc.), see appendix 1 for more details.

2.2.1.2 *Procedure*

(a) Training

Once birds had carried the dummy weights for at least a day and showed no discomfort either in the air on the ground, they were released from short distances (< 2 km) around the home loft, both in flocks and singly. Birds were transported to the release sites by car in aluminium carrying boxes and released by careful tossing into the air. As birds became more used to carrying the weights the distances were gradually increased to 7 km from a variety of directions to the home loft (see appendix 2 for details).

(b) Test releases

The chosen test release site was Bladon Heath (distance to home: 5 km, direction to home 153°; see appendix 2 for more details). The subjects had never before been released from this site. Each bird was released 24 times consecutively from the chosen

site, with a maximum of four releases in a day. All birds were released singly and watched with binoculars (magnification 10 x 40) until they disappeared from view. The next bird was not released until at least 5 minutes had elapsed, to reduce the possibility of birds joining each other in flight. All 24 tracks for each bird were collected over a period of two months.

2.2.1.3 *Analysis*

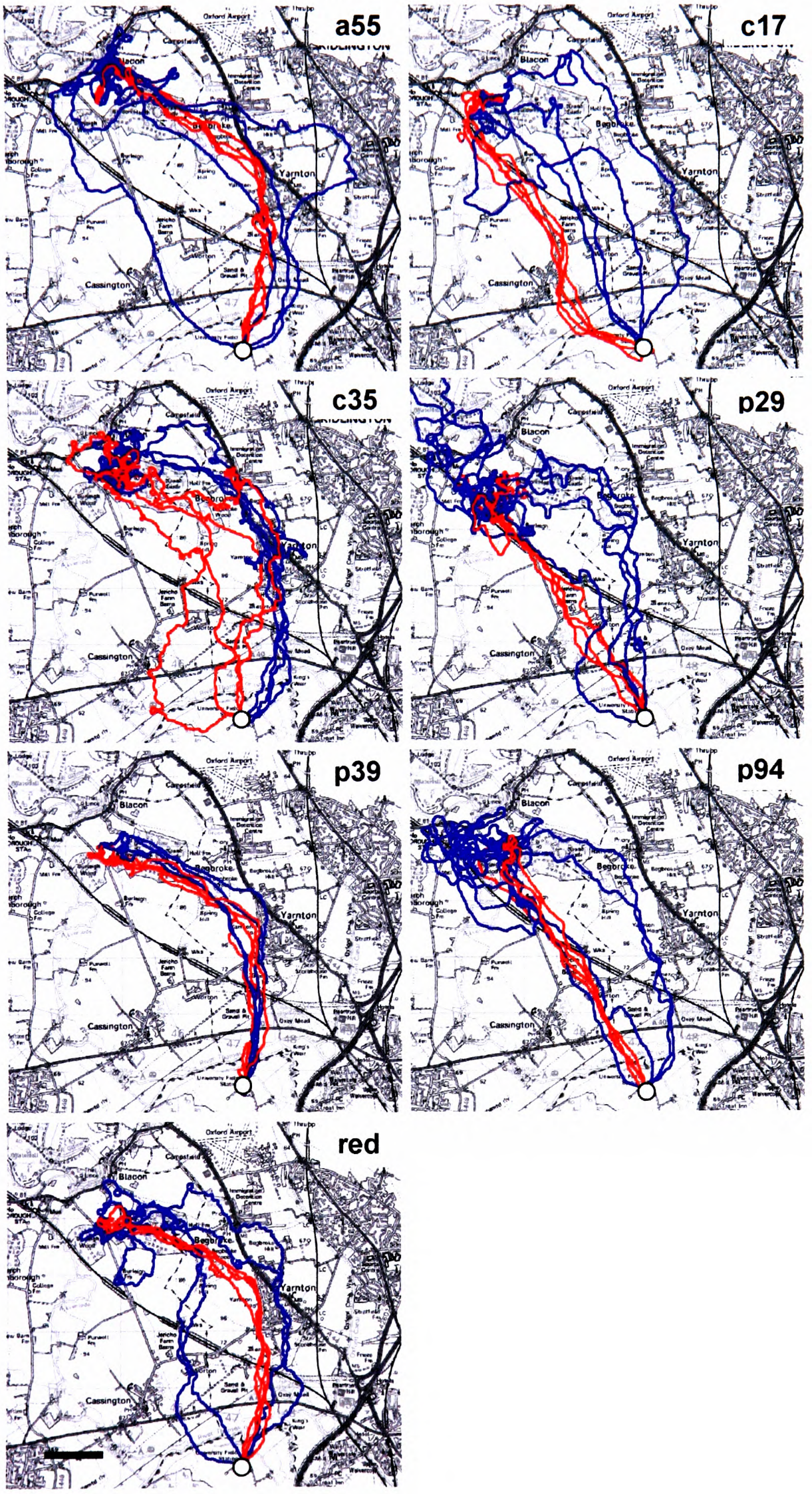
A specially written Fortran program was used to assess track similarity (see appendix 3 for details). The program measured the area between each pair of tracks to be compared. The total area between two tracks was used as a measure of track similarity, with small areas indicating very similar routes and large areas indicating highly dissimilar routes.

2.2.2 RESULTS AND DISCUSSION

Figure 2.1 shows, separately for each bird, the first four and final four tracks recorded for the seven subjects. The difference between the initial and final tracks performed by the subjects is immediately striking. In almost every case the birds initially perform widely dispersed homeward routes, but after becoming very familiar with the homing task almost all the birds develop highly stereotyped routes.

In order to investigate this finding more formally, I used the measure of track similarity described in the section 2.2.1.3 (see appendix 3), to examine whether the pigeons' routes become more stereotyped over time. The tracks for each bird were divided into consecutive groups of four and within these groups the cumulative areas of the four tracks compared to each other were calculated. The cumulative areas were

Figure 2.1 Maps showing the first four (shown in blue) and final four flights (shown in red) performed by each bird. Bird identities are indicated by 3 character labels. Home is indicated by a white circle. A 1km scale bar is shown on the final map.



then plotted against release number (Figure 2.2), and regression lines calculated for each bird.

I found that the area between the pigeons' tracks became smaller over time, indicating a higher degree of stereotypy with an increasing number of releases. Route variability typically decreased progressively, with negative regressions in five out of seven cases (Table 2.1). Of the two exceptions one showed high track similarity from the start (p39) and the cumulative area of the final flights for this bird are comparable to that of the other birds. c35 was the only bird that maintained high track variability throughout the repeated releases. After carrying out the training and initial test flights I noticed that the pupil in this bird's right eye was lighter in colour than the left pupil and the bird did not attempt to move its head when approached from the right side, whereas it did from the left side. Hence it is likely that this bird was blind in its right eye. I continued to use c35 in the experiment as it had already successfully homed a large number of times. Although this does not confirm that the other birds were attending to visual landmarks, it does hint that visual landmarks may play an important role in such high precision route recapitulation.

To assess the level of inter-individual variation in route choice, the final flights performed by each bird were compared to the final flights of all other birds in the experiment. In order to do this, the last three tracks performed by each bird were pooled, creating a set of 21 tracks. These were then randomly reassigned into groups of three, and the area between all possible pairs of tracks within each new group was calculated (again using the similarity program mentioned in section 2.2.1.3) and summed to give a cumulative area. This randomisation procedure was reiterated 10,000 times to provide a test distribution of track similarity. The cumulative areas between the final three tracks performed by individual birds were then compared to

Figure 2.2 The graph shows the cumulative area within blocks of four successive flights plotted against release order. Cumulative area was calculated as the sum of areas enclosed by each possible pair of tracks within a group of four. Each bird is illustrated by a different symbol.

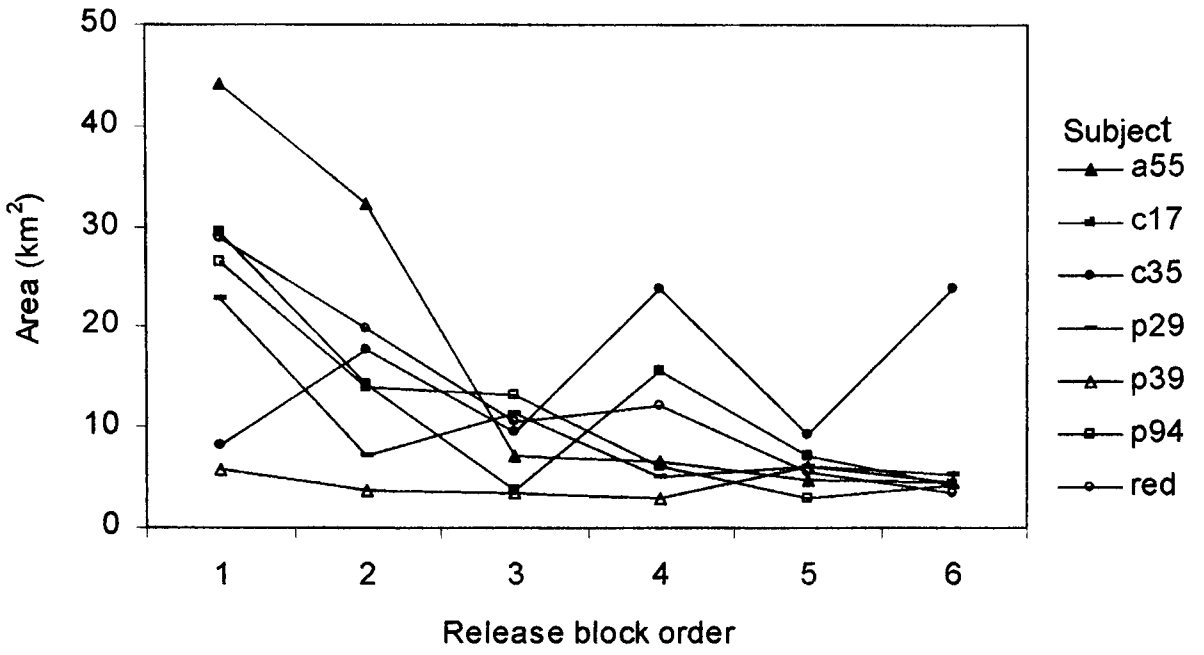
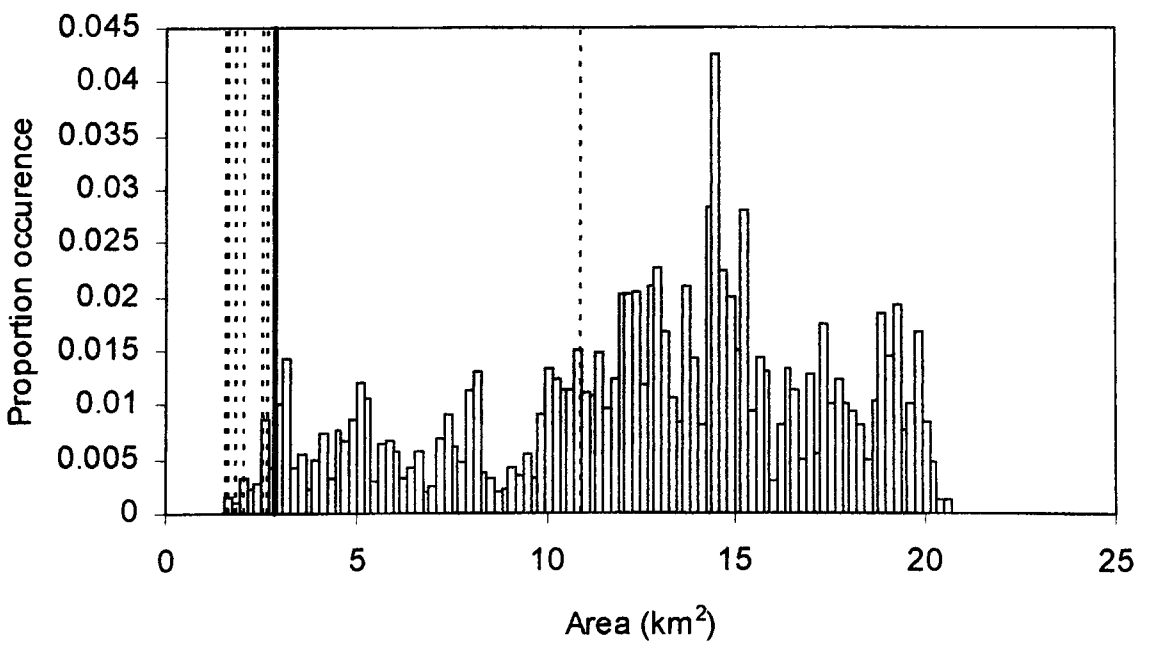


Figure 2.3 Results of the randomisation test for individual variation. The cumulative area for the final three tracks flown by each bird is shown by vertical dotted lines, calculated as the sum of the areas enclosed by each possible pair of tracks within a group of three. The histograms show the distribution of cumulative area when the tracks are assigned randomly into groups of three 10,000 times. The solid line shows the lower 0.025 confidence value.



this distribution. Six of seven birds had a cumulative area smaller than would be expected by chance (Fig. 2.3) and again the exception was c35 (thought to be blind in one eye).

Over a large number of releases, pigeons thus develop tracks that show significantly higher intra- than inter-individual similarity, indicating individual variation in route choice.

I also examined the distance flown by individual birds over successive releases to investigate whether homeward flights became more efficient over time. Distance travelled was plotted against release number (Fig. 2.4). In five of seven cases the regressions were significant and negative (Table 2.1), showing that most birds' routes became shorter with an increasing number of releases. However, track length appeared to asymptote as birds continued to travel substantially longer distances than the bee-line path home. Mean track efficiency (calculated as the straight-line distance home divided by the actual distance travelled) of the final flight performed by each bird was 0.66 ± 0.11, with on average an extra 2.6 km travelled in excess of the 5 km bee-line.

Figure 2.4 Graph showing the distance flown by individual birds on successive flights. Each bird is illustrated by a different symbol.

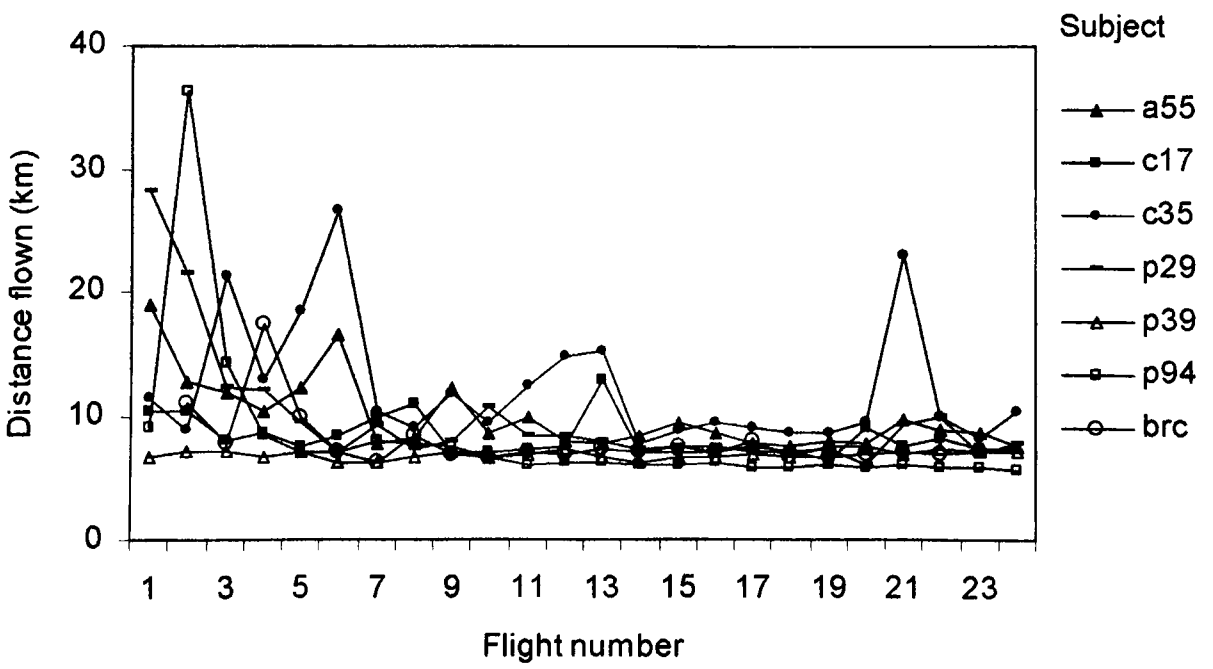
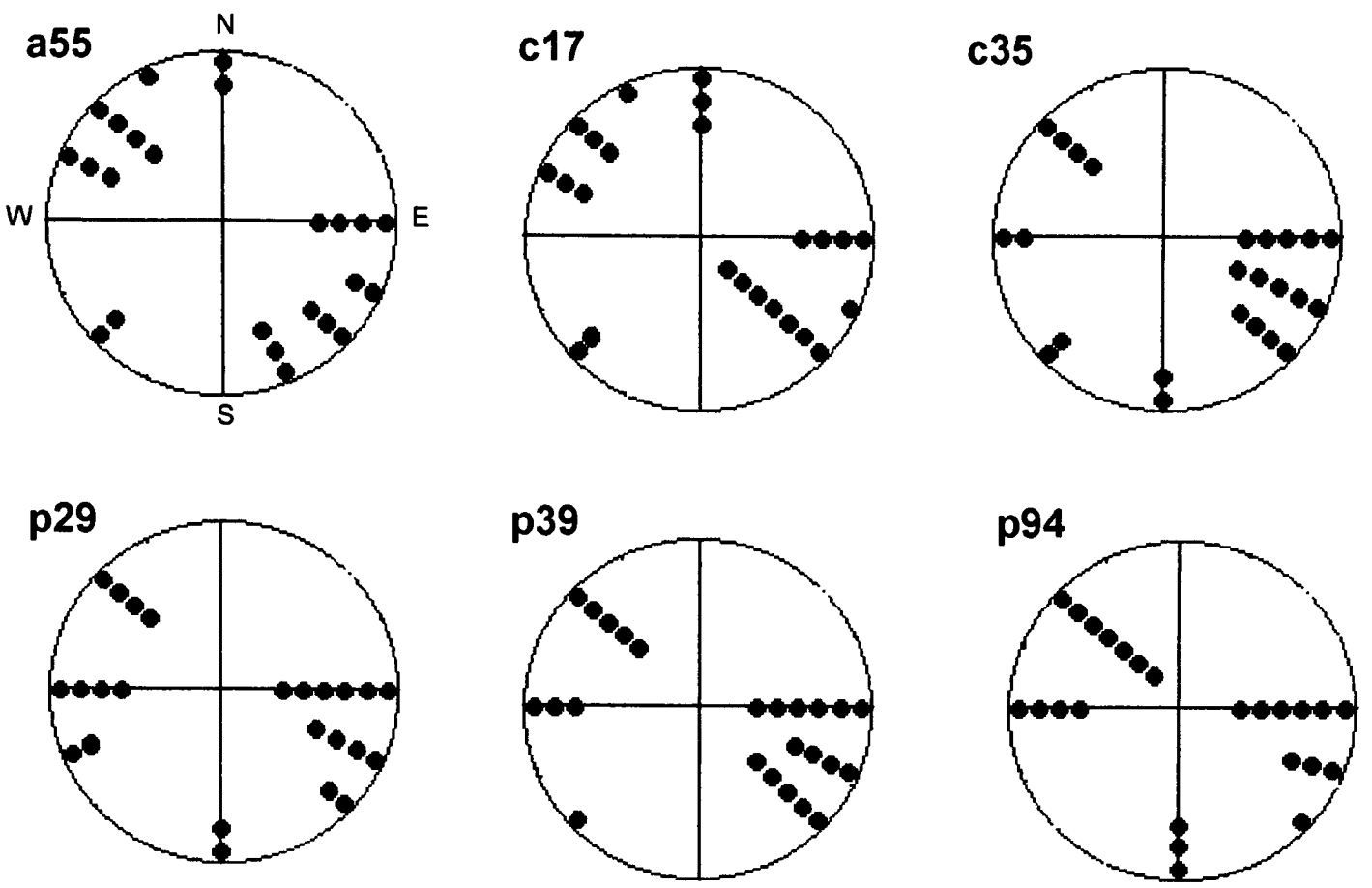


Table 2.1 Regression coefficients for the change in track similarity and track length over the course of repeated releases in Experiment 2.1. Similarity was assessed by calculating the sum of areas enclosed by each possible pair of tracks within a group of four consecutive tracks (see Figure 2.2). The distance travelled on each flight was regressed against release number.

	Cumulative area			Distance travelled		
Bird	Coefficient	F	P	Coefficient	F	P
a55	-0.000262	13.31	0.022*	-0.273957	16.93	0.000*
c17	-0.000115	2.91	0.163	-0.091520	4.49	0.046*
c35	+0.000055	0.87	0.403	-0.218960	2.21	0.151
p29	-0.000089	4.94	0.090	-0.419170	11.96	0.002*
p39	0.000000	0.00	0.978	+0.020782	4.22	0.052
p94	-0.000149	18.87	0.012*	-0.438960	7.16	0.044*
red	-0.000205	28.52	0.006*	-0.179940	6.88	0.016*

This experiment demonstrates that when birds are released many times from the same site, most develop highly stereotyped, individually distinct, homeward routes. The cues used to define the routes with such precision remain to be confirmed, but it is clear that these cues must be present at high resolutions and be relatively immobile. The use of olfactory cues seems unlikely as wind directions varied widely between successive releases (The wind direction for each release was found at http://www.wunderground.com/weatherstation/WXDailyHistory.asp, see Figure 2.5). Visual landmarks seem a likely candidate that would explain the detail of the final stereotyped tracks performed by the birds. It is possible however, that the birds could be using non-visual familiar landmarks such as magnetic anomalies. It has been shown (Walcott, 1989; 1992; 1996; Haugh et al., 2001a) that pigeons are able to detect magnetic anomalies, although there is little discussion of how they would be integrated into a pigeon's familiar area map. I performed a second experiment, following the same procedure, this time attaching small rare earth magnets to the

Figure 2.5 Wind direction on day of release. Circles indicate compass rose, with dots placed in the direction the wind was blowing from on the day of each release. Bird identities are indicated by 3 character labels.



ceres above the pigeon's beak. The skin above a pigeon's beak has been shown to contain aggregates of magnetite crystals, adjacent to nervous material, which change shape as magnetic fields vary (Winklhofer et al., 2001). Application of these rare-earth magnets to the ceres above the beak has been shown to impair detection of magnetic fields (Mora et al., 2004). The aim was not to remove the possibility of using a compass, as use of the sun-compass was available to the birds at all times. In this second experiment I used birds that had less experience of the area surrounding

the release site, as I had noticed that many of the birds seemed to revisit points that they had previously been released from (Hall Farm, Worton, Cassington). I wanted to see how individual birds' routes would develop without the possibility of attraction to familiar release points. In experiment 2.1, two of the birds (a55 and red) joined each other in flight and subsequently flew highly similar routes. I ruled out the possibility of this occurring again by leaving a longer gap between releases, and during this time I placed the birds in a transparent Perspex box to allow them a good view of the site before release. Finally, in the following experiment I reduced the total number of releases from 24 to 20 as in experiment 2.1 all the birds were performing stereotyped routes by this time (excepting c35).

2.3 EXPERIMENT 2.2:

2.3.1 METHODS

Eight new homing pigeons (*Columba livia* L), were selected as subjects. A new test release site was chosen (Church Hanborough: distance to home 5.3 km, direction to home 128.8°). The birds were trained for release from a specially made Perspex release box, mounted on a stepladder of 1.5 m height. Based on the original design of Braithwaite and Guilford (1991), the box had clear Perspex sides, and the base consisted of a wire mesh – allowing access to local odour cues. The box lid was spring-mounted and could be operated remotely by an experimenter pulling on a string. The birds were given successive releases from the box close to the loft until they showed no agitation within the boxes, and no hesitation to fly out when the string was pulled. The purpose of the box was to allow a clear view of the release site for 5

min before release. During the training phase, birds were given no releases from sites with directions to home of 40 - 220° (90° either side of chosen release site) but numerous training releases from various other directions (see appendix 2 for more details). To avoid loss of trackers due to the birds' relative unfamiliarity with the release site, each bird was given one training release from the chosen test site before tracking commenced.

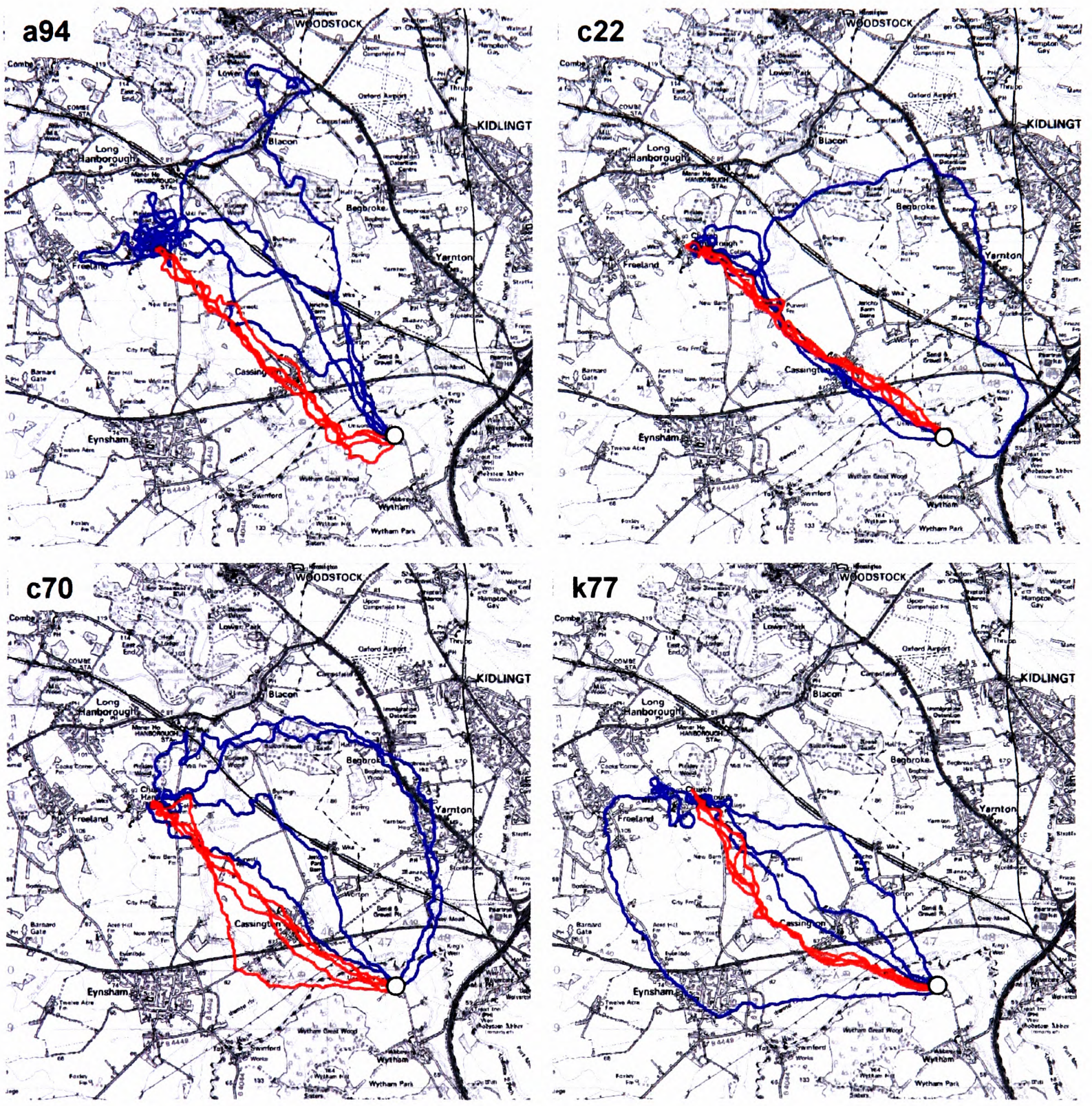
Subjects then received 20 consecutive releases from the test site over the course of 4 weeks. Each test flight was tracked using precision GPS loggers. Immediately before test releases each bird was fitted with a rare earth magnet (Haugh et al., 2001a). The magnets were 2 mm thick and 3 mm in diameter. They were attached using a 3 mm wide strip of adhesive cloth tape approximately 25 mm long, so that the magnet was placed at the base of their ceres (where aggregation of magnetite crystals thought to represent a magnetic-field receptor are found (Winklhofer et al., 2001)) with the tape stuck to the beak and to the feathers above the ceres (see Fig. 2.6 for position of magnet). The nostrils were not obstructed by the tape. The magnet was removed on return to the home loft so that the birds did not have time to become accustomed to the presence of a magnet (Haugh et al., 2001a), as magnetic field impairment is shown to wear off if birds are subjected to presence of the magnets for long periods of time. A maximum of four tracks were taken in a day.



Figure 2.6 A pigeon with a rare earth magnet placed at the base of the ceres. The arrow indicates the position of the magnet. The magnet was secured in position by a length of tape (3mm x 25mm) stuck to the beak and the feathers above the ceres.

2.3.2. RESULTS AND DISCUSSION

Figure 2.7 Maps showing the first four (shown in blue) and final four flights (shown in red) performed by each bird. Bird identities are indicated by 3 character labels. Arrows on map s93 indicate the routes converging in a narrow corridor. Home is indicated by a white circle. The scale bar on the final map indicates 1 km.



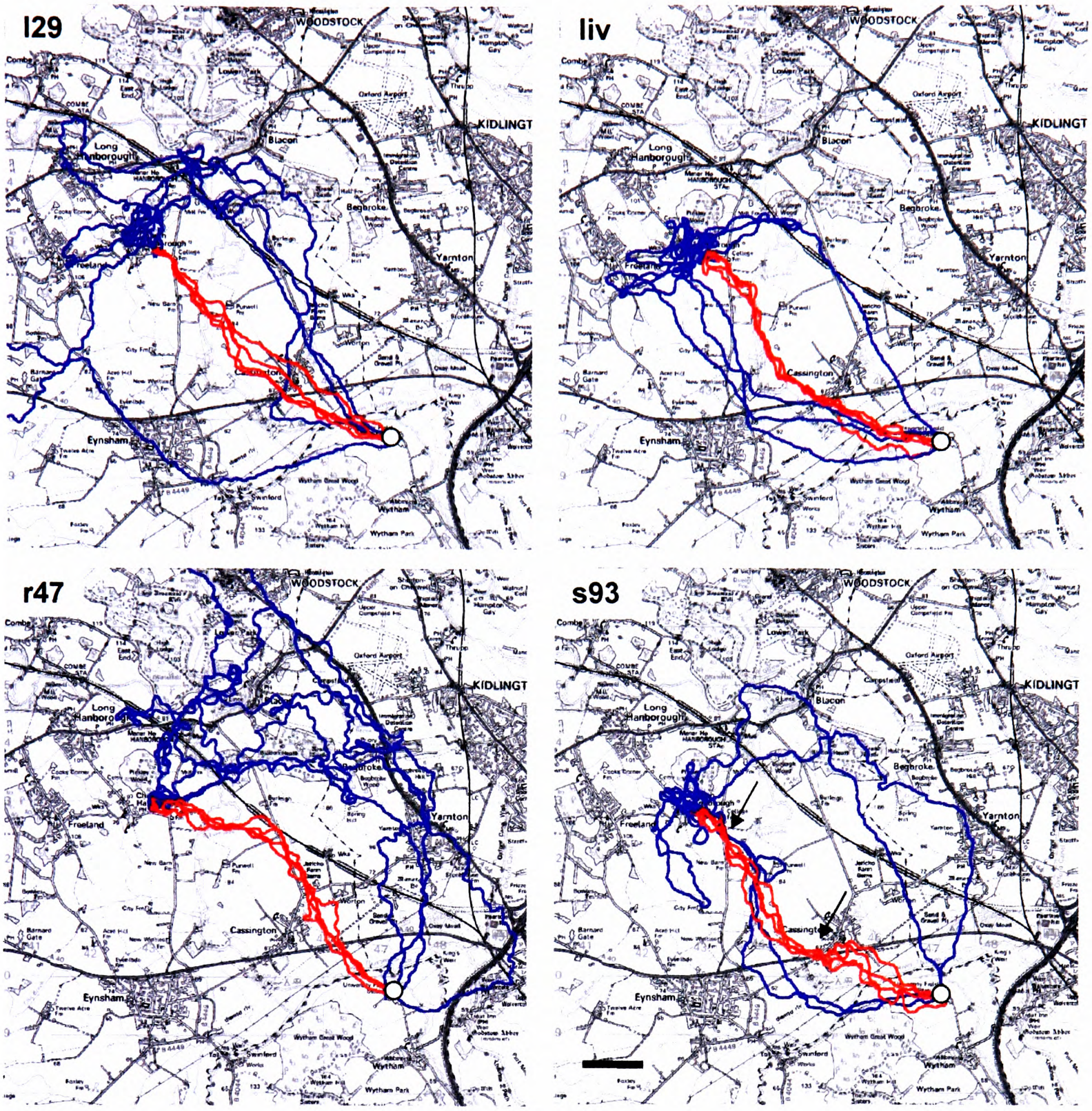
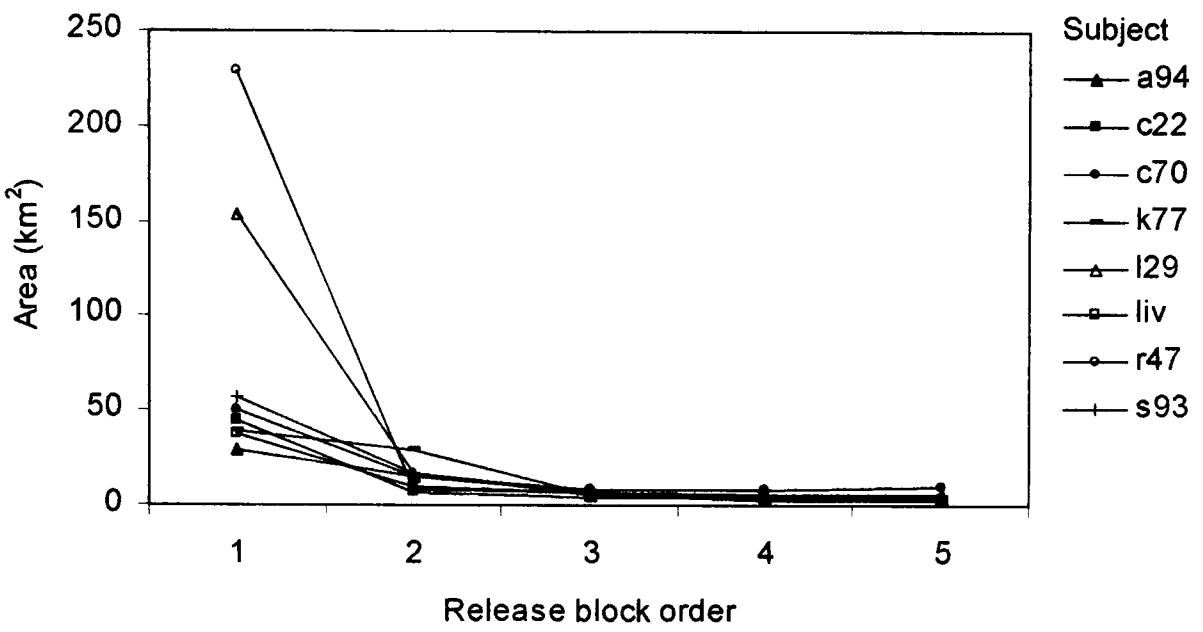


Figure 2.7 shows the first four and final four tracks of subjects released in Experiment 2.2, after application of a magnetic disruption treatment.

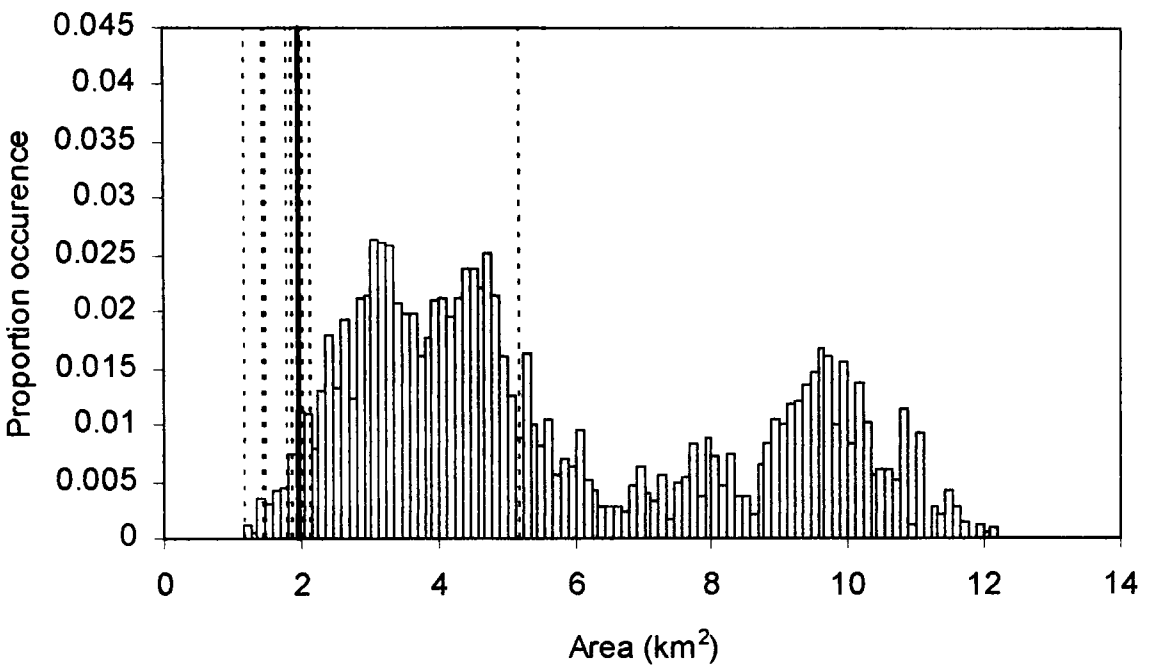
The same analysis as in Experiment 2.1 was repeated. The tracks were divided into blocks of four, and the areas between each possible pair of tracks within these groups was calculated and summed. The cumulative areas for each group of four were then plotted against release block order, and regression lines calculated (Fig. 2.8, Table 2.2). I found that all eight subjects performed increasingly stereotyped routes.

Figure 2.8 The graph shows the cumulative area within blocks of four successive flights plotted against release order. Cumulative area was calculated as the sum of areas enclosed by each possible pair of tracks within a group of four. Each bird is illustrated by a different symbol.



The randomisation procedure described in section 2.2.2 was repeated, comparing the cumulative area between the final three tracks performed by individual birds to the cumulative area of a distribution randomly selected groups of three tracks. I found that in five out of eight subjects the cumulative area between the final three tracks they performed was smaller than would be expected by chance, with a further two birds very close to the lower 0.025 confidence boundary (Fig. 2.9).

Figure 2.9 Results of the randomisation test for individual variation. The cumulative area for the final three tracks flown by each bird are shown by vertical dotted lines, calculated as the sum of the areas enclosed by each possible pair of tracks within a group of three. The histograms show the distribution of cumulative area when the tracks are assigned randomly into groups of three 10,000 times. The solid line shows the lower 0.025 confidence value.



When the distance travelled by each bird in each successive flight was plotted against release number, I found that in every case the birds became increasingly efficient (Fig. 2.10, Table 2.2), whilst not reaching maximal efficiency. The mean track efficiency was 0.81 ± 0.04, which means that on average an extra 1.3 km was travelled, in excess of the 5.3 km bee-line distance home.

Table 2.2 Regression coefficients for the change in track similarity and track length over the course of repeated releases in Experiment 2.2. Similarity was assessed by calculating the sum of areas enclosed by each possible pair of tracks, within a group of four consecutive tracks (see Figure 2.6), and regressed against release block order. The distance travelled on each flight was regressed against flight number.

	Cumulative area			Distance travelled		
Bird	Coefficient	F	P	Coefficient	F	P
c22	-0.000286	4.17	0.134	-0.145038	4.11	0.058
c70	-0.000282	4.56	0.122	-0.258346	4.85	0.041*
k77	-0.000312	17.20	0.025*	-0.232105	9.80	0.006*
l29	-0.001330	3.63	0.153	-0.889474	6.65	0.019*
liv	-0.000241	5.70	0.097	-0.402707	16.62	0.001*
r47	-0.001290	3.24	0.170	-0.296770	5.91	0.026*
s93	-0.000404	5.50	0.101	-0.388346	15.00	0.001*

Figure 2.10 Graph showing the distance flown by individual birds on successive flights. Each bird is illustrated by a different symbol.

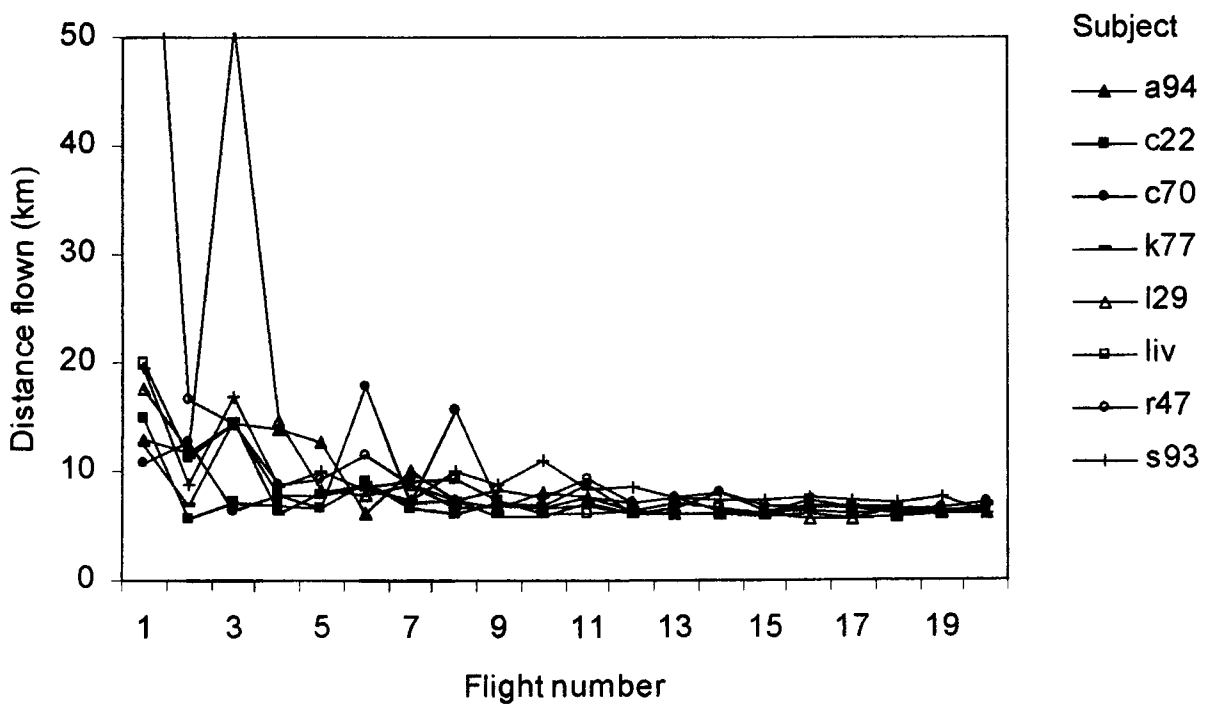
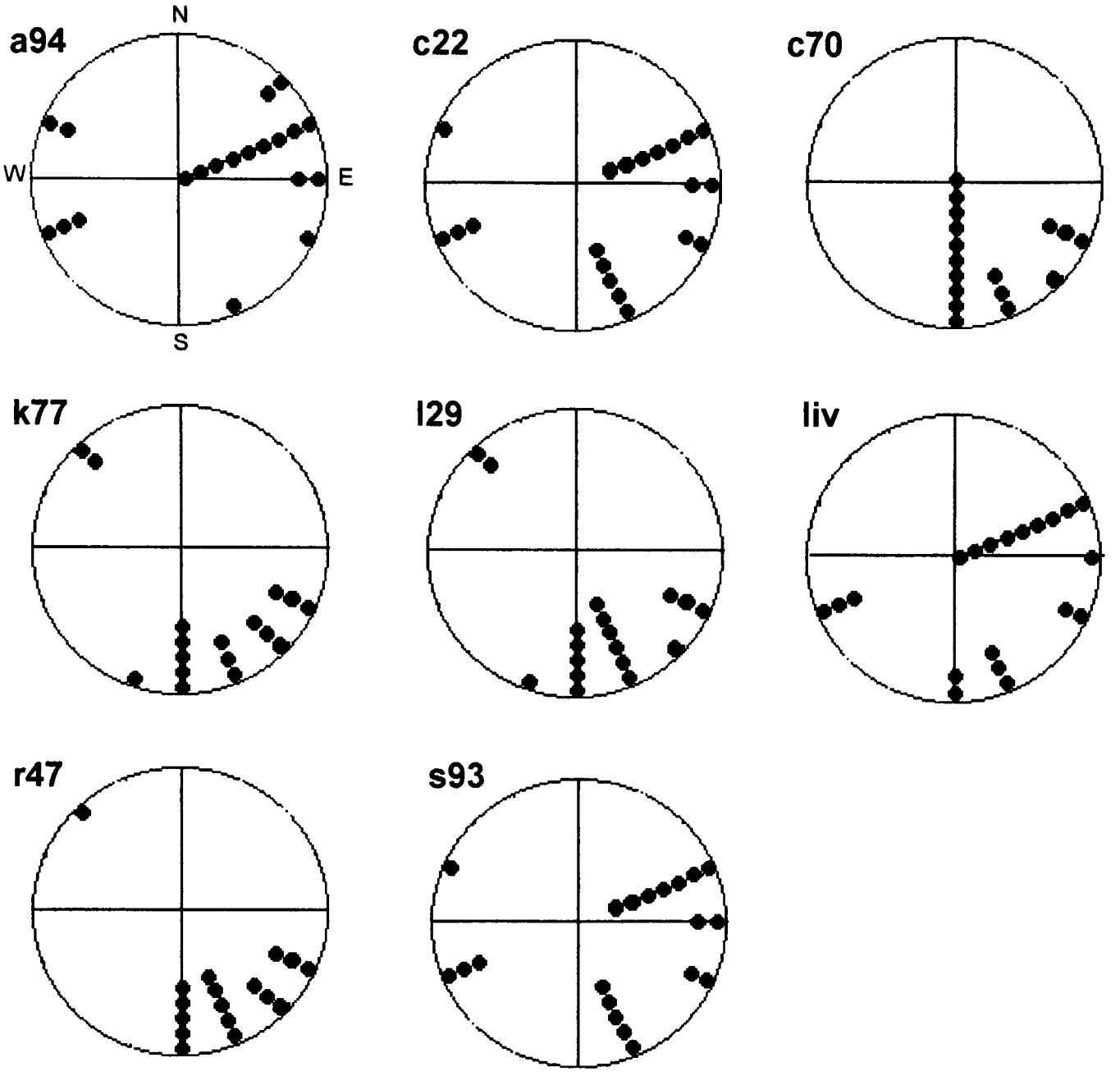


Figure 2.11 Wind direction on day of release. Circles indicate compass rose with a dot placed in the segment the wind was blowing from on the day of release for each bird. Bird identities are indicated by 3 character labels.



These results replicate those found in experiment 2.1. It seems that the magnetic disruption treatment has little or no affect on the birds' ability to accurately recapitulate their chosen routes. The birds in experiment 2.2 cover a much wider area of the landscape in their first few releases than the birds in experiment 2.1, but this is probably due to having received fewer training releases in the vicinity of the release site before testing began, rather than a consequence of the magnetic disruption treatment.

It is interesting to note that in this experiment, as in experiment 2.1, several birds arrive on very similar stereotyped routes (see k77, liv and s93). As, in this second experiment, birds were less familiar with the general area before releases began, and never flew together, it seems likely that various landscape features were similarly attractive or repellent to the birds and influenced their subsequent chosen routes. Again, birds flew under varied wind conditions, with all but two birds flying under winds coming from at least 3 of the 4 cardinal compass quadrants (see figure 2.11). This implies that environmental odours would not have been stable enough across releases to have been used as a cue with which to perform the observed stereotyped routes.

2.4 GENERAL DISCUSSION

I examined route choice by homing pigeons across 20-24 repeated homing flights from the same release site, as recorded by high-resolution GPS loggers. Three core findings emerged after analysis. First, tracks of individual pigeons become stereotyped with increasing experience. Second, individuals vary in their choice of route. Third, although birds' tracks become more efficient with experience, they remain substantially longer than the bee-line distance home.

The finding that pigeons follow highly stereotyped routes even after a large number of releases seems, at first, counterintuitive. During the first few flights from a novel location, birds presumably have only a sparse knowledge of the local area, such that it is then that route-recapitulation would most reduce the risk of navigational error. In fact, as birds become more experienced, their routes become more stereotyped. This, coupled with the finding that routes remain inefficient even once

fully stereotyped, yet vary between individuals (i.e. there is no single best route that can explain the marginal tortuosity at stability), suggests that the main function of route recapitulation is not to reduce navigational risk. A more likely explanation (though not incompatible with a risk reduction strategy) is that route recapitulation reduces cognitive load in a way analogous to the image matching demonstrated in invertebrates (Cartwright & Collet, 1982; 1983; Collett & Rees, 1997; Wehner et al., 1996) and more recently chickens (Dawkins & Woodington, 2000), which is thought to minimise of the number of images that must be remembered. The recognition of 3D visual landmarks requires a high memory load because of the range of angles and distances that landmarks may be viewed from. One way to maintain consistency of viewing angles over many foraging trips is to follow a set route. This fixed route following has been shown in several insects including ants (Rosengren, 1971; Rosengren & Pamilo, 1978; Collett et al., 1992) and bees (Chittka et al., 1995; Dyer, 1991; Dyer et al., 1993). This means that landmarks can only easily be recognised from the set route, but the number of images that must be remembered is greatly reduced.

It seems highly likely that the birds' chosen routes are visually mediated. For a terrestrial animal anchored to the landscape, a range of cues might provide the positional control needed to account for detailed route recapitulation, but for an animal flying well above the landscape, local visual cues seem to constitute the most likely candidate. It is unlikely that environmental odours could specify such a detailed route, particularly since wind conditions varied considerably between successive flights (in all but one case birds experienced wind directions varying across at least 3 of the 4 cardinal compass quadrants; see figures 2.5 and 2.11). Birds in experiment 2.2 had their access to potential magnetic cues disrupted in all releases, but their

routes were still stereotyped. Previous experiments showed that identical magnets disrupt magneto-reception successfully (Haugh et al., 2001a), and because the birds only wore the magnets for the brief release periods themselves, and not constantly in-between, it is most unlikely that they would have been able to adjust to the disruption treatment. It is also suggestive that one of the only birds that did not develop a highly stereotyped route was found to be blind in one eye.

The results thus suggest that visual cues are critical to familiar area orientation not just near release (Braithwaite & Guilford, 1991; Biro et al., 2002) and on final approach to home (Schmidt-Koenig & Schlichte, 1972) but throughout the homeward journey, at least over short distances. This is in contrast to the theory that visual landmarks are used within the familiar area around the home loft in the form of a "mosaic map". This is defined as a "directionally oriented map of familiar landmarks" (Wiltschko & Wiltschko, 1978). Use of visual landmarks in this way (associated with a compass) is thought to be more efficient than the more simple use of landmarks alone (Baker, 1984) as fewer landmarks would have to be remembered in order to recall a homeward route and a straighter course could be taken. Wallraff (1974) likens this system to that used at longer distance, unfamiliar release sites, where site-specific factors (in this case familiar landmarks) are used to determine the homeward direction. Evidence from clock-shifting experiments close to the loft (Graue, 1963; Keeton, 1969) supported this theory and raised the question of whether there was any subsequent input from the visual landscape, once a bird has left a known location.

There are three possible explanations to account for the current results. First, it is possible that the birds use a memorized compass direction from the release site to home and use external landmarks to correct for errors along the route. This seems unlikely, as birds often leave the release site in directions markedly different from that

of home. Second, birds may remember a chain of landmarks with an associated compass bearing between each. An advantage of this model is that it allows for several "waypoints" along each route, so that repetition of the characteristic overall shape of the route could be explained. This is the strategy shown to have been adopted by invertebrates following fixed routes. The set routes are governed by a global vector indicating the total distance and direction required to reach the final goal, but the route is also divided into several sections which are guided by "local vectors" (in ants: Collett et al., 1998; in bees: Collett et al., 2002). These local vectors have been shown to be triggered in sequence by visual landmarks, which act as intermediate goals. One observation consistent with this second hypothesis is that while some of the routes are more widely dispersed, most individuals' flights converge into narrow corridors over various specific locations in the landscape (s93's flight paths provide an example, with arrows illustrating two local constrictions in Figure 2.7). The possible use of waypoints to mediate stereotyped homeward routes in pigeons is discussed further in chapters 4 and 6.

The third possibility is that the route is remembered in fine detail with no primary reference to a compass. This model, which is a form of "pilotage" (Baker, 1984; Papi, 1992), originally known as "Type 1 orientation" (Griffin, 1955), has the advantage that it accounts for very accurate route-recapitulation.

The subsequent chapters will attempt to determine how far the route-recapitulation effect extends away from home and investigate more precisely the nature of the cues used, and exactly how compass-dependent and compass-independent mechanisms of familiar area orientation may be integrated.

CHAPTER 3

Route Recapitulation at longer distances

3.1 INTRODUCTION

3.2 EXPERIMENT 3.1:

3.2.1 Methods

3.2.1.1 Subjects and Procedure

3.2.1.2 Analysis

3.2.2 Results and Discussion

3.3 EXPERIMENT 3.2:

3.3.1 Methods

3.3.1.1 Subjects and Procedure

3.3.2 Results and Discussion

3.4 GENERAL DISCUSSION

N.B. Experiments 3.1 & 3.2 have been reported as: Biro, D., Meade, J., & Guilford, T. (2005). Middle distance pilotage: Route recapitulation and route loyalty in homing pigeons released from 25 km. *The Journal of Navigation.* In press.

3.1 INTRODUCTION

In chapter 2 it was established that when pigeons are released from the same site many times in quick succession they tend to develop highly stereotyped routes, which are individually distinctive, and are not the most efficient homeward routes. It is not known exactly which cues are used to recapitulate routes with such precision, but it is clear that the cues utilised must be present at high resolution to account for the level of detail displayed in recapitulated routes. It seems likely that familiar visual landmarks could be the cues used to mediate route recapitulation, as they are geocentric cues, which can be perceived from a distance, are immobile, and therefore provide consistent information with which birds could potentially perform the observed tracks.

Following the experiments described in chapter 2 (Experiments 2.1 and 2.2, see also Meade et al., 2005), a further experiment releasing birds at sites 10 km from home (Biro et al., 2004) showed that birds were able to accurately recapitulate stereotyped routes from this distance. Furthermore, when released from novel sites perpendicularly displaced along the stereotyped routes, in most cases birds were attracted directly back to their established routes, and recapitulated them from the point of contact. This provided further evidence supporting the use of visual landmarks as the principle cues involved in representing the homeward routes, as birds must have been able to accurately detect the relevant cues from distances of up to 1500 m.

As explored in chapter 2, if visual landmarks were used as cues to mediate the stereotyped routes, then one reason to explain why routes are recapitulated in such fine detail would be that doing so would minimize the number of different views of 3 dimensional landmarks that must be remembered. By remaining faithful to a learned stereotyped route a bird's cognitive load would be reduced, as only the images of

landmarks as viewed from the set route need be remembered. This strategy is used widely by insects (Rosengren, 1978; Collett et al., 1992; Dyer, 1991) and has also recently been demonstrated in chickens (Dawkins & Woodington 2001).

In the first part of this chapter I examine the phenomenon of route recapitulation in greater depth by releasing birds repeatedly from 25 km. This distance was chosen because it is substantially further from home than release sites from which detailed route recapitulation has been previously demonstrated (5 km - Meade at al., 2005; 10 km - Biro et al., 2004), and, at 25 km, lies at the upper limit of the area within which pigeons are thought to navigate via familiar landmarks (see Emlen, 1975; Matthews 1963). I investigate whether detailed route-recapitulation still occurs at this longer distance, where a larger number of images would have to be remembered in order to reconstruct a detailed homeward route.

3.2. EXPERIMENT 3.1:

3.2.1. METHODS

3.2.1.1 *Subjects and Procedure*

Nine homing pigeons were selected as subjects. All were > 2 years old, weighed > 450 g and had participated in previous experiments involving GPS tracking. All birds were fitted with Velcro strips as detailed in chapter 2. The birds were allowed to become accustomed to these strips for 1 day, before 25 g plasticine weights were attached to the Velcro strip. All birds were carefully monitored to check that neither movement on the ground nor in the air was affected. Once it had been observed that all birds were comfortable carrying the weights, subjects were released at distances of 2 km in varying directions around the loft. The release distance was gradually increased to 25 km in the

training phase (see Appendix 2 for more details). Weights were carried at all times for the duration of the experiment except during tracked flights. The subjects were released 20 times from the chosen site (The Ridgeway; distance to home: 25.5 km, direction to home: 359°) and were tracked from their 10th flight onwards using precision GPS loggers.

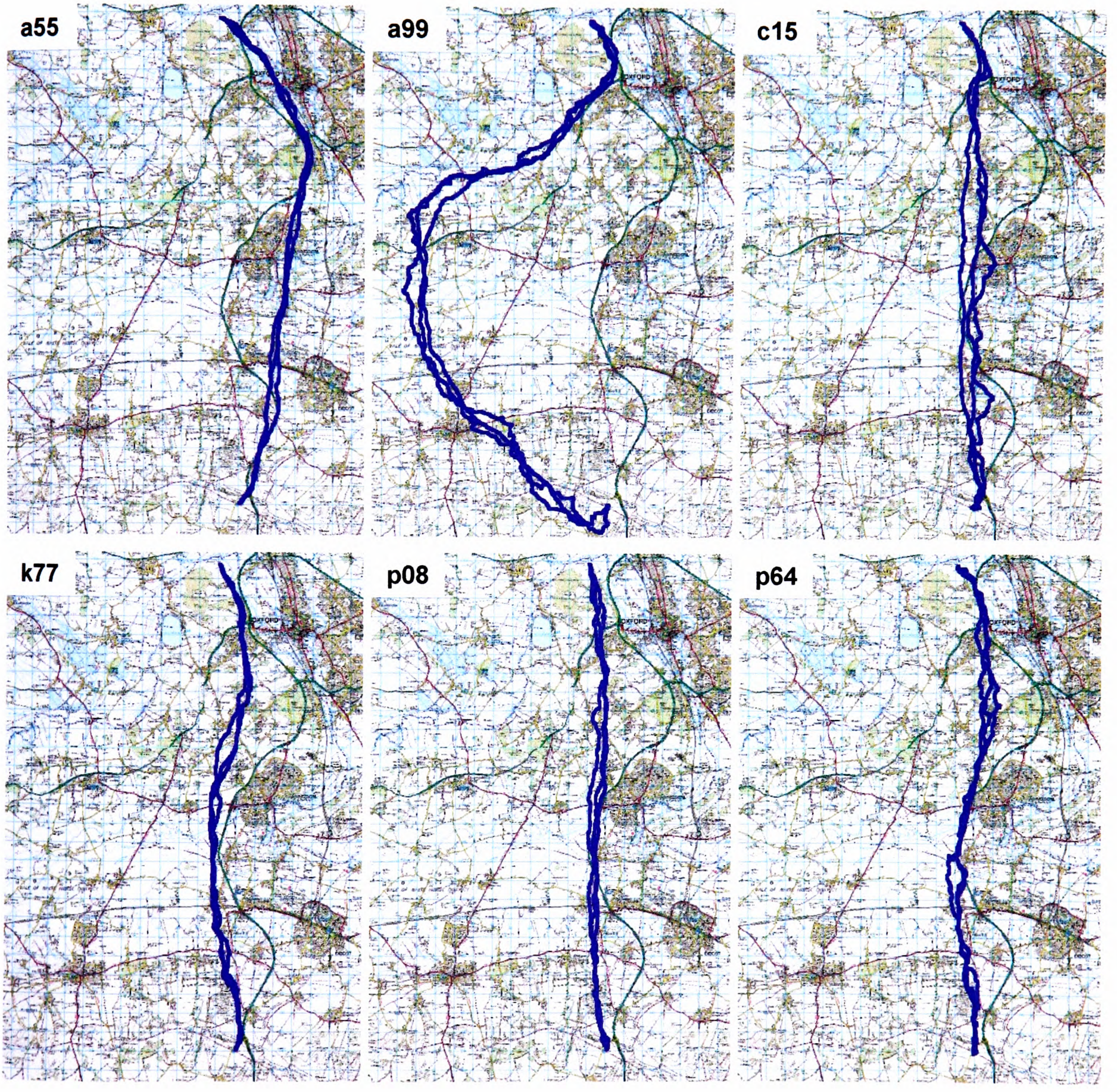
3.2.1.2 *Analysis*

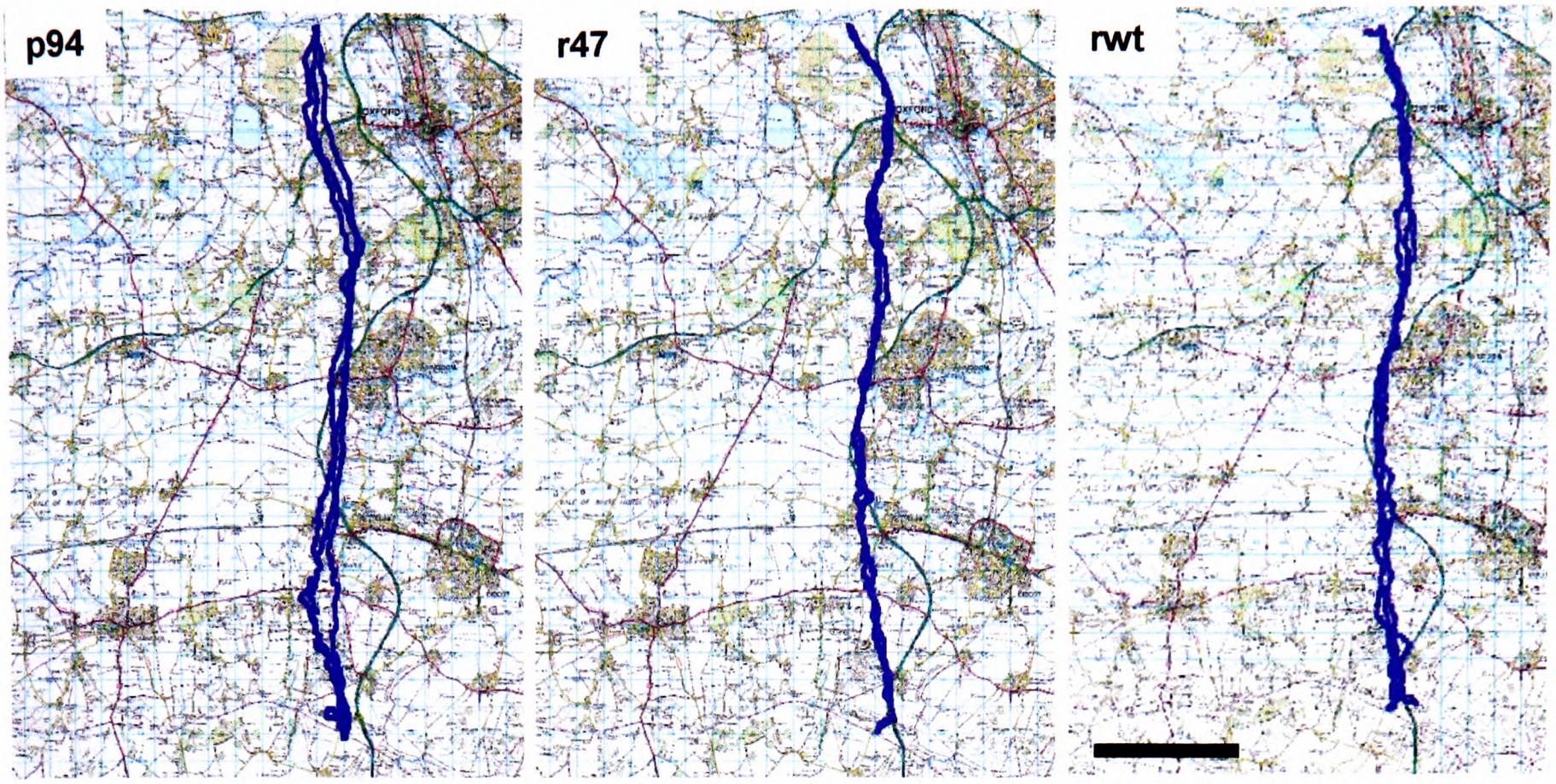
The similarity between a given pair of tracks was measured by recording the area between the two tracks as calculated by a program written in Fortran (see appendix 3). To examine the levels of inter-individual route similarity, the final three tracks performed by each bird (the 18th, 19th and 20th tracks) were compared to each other, and the area between each combination of tracks was summed to give a cumulative area for the final set of three tracks for every bird. This was indicative of track similarity. The final three tracks performed by each bird were then pooled to give a group of 27 tracks. These 27 tracks were then randomly assorted into sets of three, and the cumulative area of the tracks compared to each other within each new group was calculated. This process was repeated 10,000 times to give a sample distribution of the cumulative area between any set of three tracks. The cumulative area between each bird's own final three tracks was then compared to that of the random sample distribution. If the cumulative area of a single bird's tracks fell beneath the 0.025 % boundary, this indicates that the bird's final three tracks were more similar to each other than would be expected by chance.

3.2.2 RESULTS AND DISCUSSION

Figure 3.1 shows the final three tracks performed by each subject (18th, 19th and 20th releases). The tracks appear to be highly stereotyped throughout their length and are

Figure 3.1 Maps showing the final 3 flights performed by each bird. Bird identity is indicated by 3 character labels. The Release site is in the south, with home to the north. A 5 km scale bar is included in the final panel.





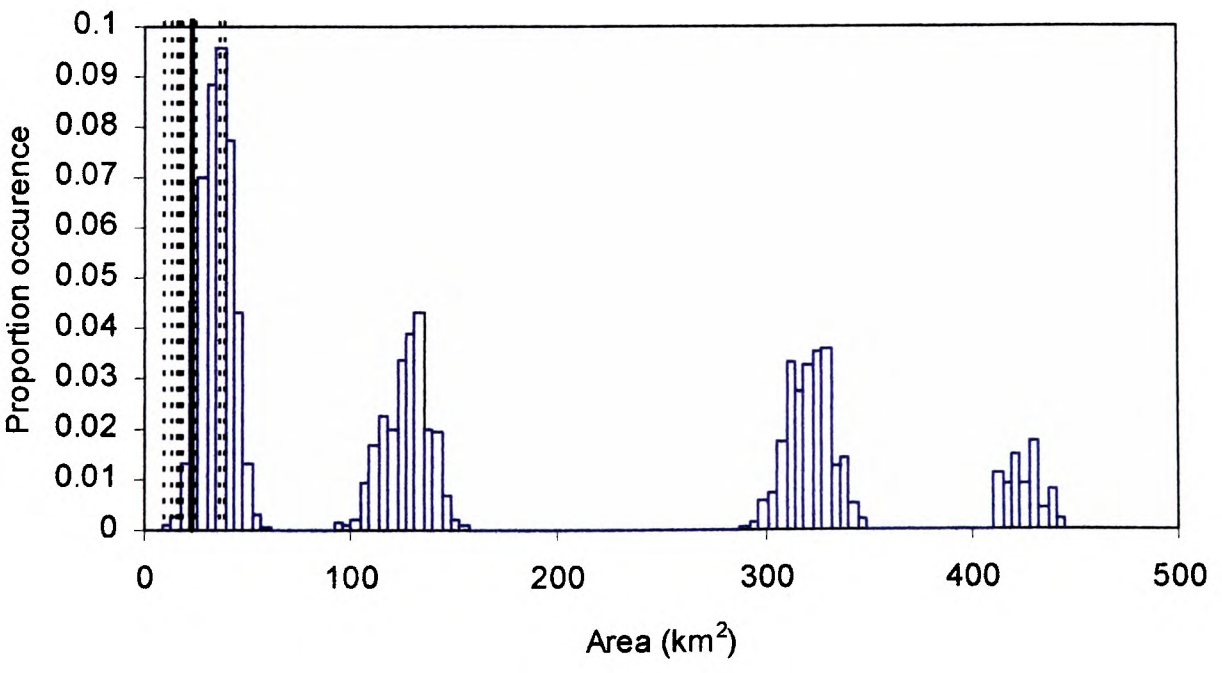
again individually distinctive. To investigate whether the tracks become more stereotyped over time, the areas between subsequent tracks were calculated for each bird, and plotted against release number. Regression lines were also calculated (see table 3.1). In every case but one, the regression lines are negative, and in the one case with a positive coefficient the line is almost flat. This shows that the area between successive tracks becomes smaller with an increasing number of releases. This effect would probably have been more pronounced had the first ten flights also been tracked, thus including the areas between flights when the birds were less experienced.

To investigate the level of individual variation in route choice I performed the randomisation procedure outlined in section 2.2.1.2. The cumulative areas between every combination of the final three tracks performed by each bird were calculated. These values were plotted on a graph showing the distribution of cumulative areas when the final three tracks performed by each bird were pooled and randomly reassigned into groups of three, (see figure 3.2). Six out of the nine subjects fell below the lower 0.025^{th} percentile, and the remaining three were very close to the boundary.

Table 3.1 Table showing the regression coefficient, f and p values when the area between consecutive flights by individual birds are plotted against release number. *s indicate significance.

Bird	Regression Coefficient	F	P
a55	-1.63921	2.82713	0.137
a99	-4.95548	57.4730	0.001*
c15	-0.131480	0.118275	0.741
k77	-0.48061	3.70437	0.096
p08	-0.372627	15.4287	0.006*
p64	-0.533288	1.39136	0.277
p94	+0.0521719	0.000556	0.943
r47	-0.484396	55.1376	0.000*
rwt	-0.684205	4.64985	0.068

Figure 3.2 Results of the randomisation test for individual variation. The cumulative area for the final three tracks flown by each bird are shown by vertical dotted lines, calculated as the sum of the areas enclosed by each possible pair of tracks within a group of three. The histograms show the distribution of cumulative area when the tracks are assigned randomly into groups of three 10,000 times. The solid line shows the lower 0.025 confidence value.



This demonstrates that the cumulative area found when birds' own tracks are compared to each other is smaller than would be expected by chance, indicating that the birds perform highly stereotyped, individually distinctive tracks.

The distance flown in each successive flight was plotted against release number and regression lines calculated, to assess the change in efficiency over repeated flights (see table 3.2). All but one of the regression lines were negative, with the only positive gradient being almost flat. This shows that over repeated flights from the same location, birds perform increasingly efficient routes, though most of the regression lines have very shallow gradients as only the final 10 tracks are included and by this stage most birds are performing stereotyped routes of almost the same length. On average over the final three flights birds remain only 84 % efficient, with on average an extra 4.8 km travelled. Bird a99 remains only 59 % efficient, travelling on average an extra 17.7 km!

Table 3.2 Table showing the regression coefficients and significance values, when distance flown on successive flights is plotted against flight number. *s indicate significance.

Bird	Regression coefficient	F	P
a55	-0.2092	12.81	0.006*
a99	-2.0390	8.58	0.019*
c15	-0.0370	0.02	0.893
k77	-0.4316	20.74	0.002*
p08	-0.2227	7.22	0.031*
p64	-0.2193	0.92	0.362
p94	+0.0096	0.00	0.970
r47	-0.2917	28.11	0.000*
rwt	-1.0710	3.95	0.082

The results replicate those found when birds are released from distances of 5 km (Experiments 2.1 & 2.2, see Meade et al., 2005), as well as those demonstrated at 10 km (Biro et al., 2004). This is very interesting, as the distances covered in this experiment are much greater than in experiments 2.1 and 2.2, but it would seem that the birds are using a

similar strategy in order to home successfully. The memory load required to home along a stereotyped route must necessarily be greater from this longer distance. One of the most interesting observations is the continued presence of characteristic detours in almost every route. Many of these are very short (see the beginning of r47's route and the end of rwt's for examples) and would not present a large energetic disadvantage to the bird, but others such as a55 and a99's obviously very indirect homeward route must require a significantly larger energy input than would be required for a more direct route. This raises important questions as to what the advantages of repeatedly performing an inefficient route are, to outweigh a substantially increased energetic input. a99's route is also important as on average it is 43 km long, and this implies that accurate route recapitulation could still be a favoured strategy for homing at distances greater than 25 km. The possible implications of the presence of such large detours will be discussed in section 3.4.

To further investigate the cues involved in the performance of stereotyped routes at longer distances, I used a technique introduced by Biro et al. (2004), where birds were released 20 times from two sites 10 km from the home loft. After this period of training all subjects performed stereotyped homeward routes. The birds were then released from four sites displaced 1000-1500 m perpendicular to their established homeward routes. In most cases the birds flew towards and joined their stereotyped routes, rather than navigating homeward more directly. This demonstrated that the cues the birds were using were not only available at high resolution, but also that it was possible to perceive these cues at distances of up to 1500 m. This again strongly implies that the cues used to mediate highly stereotyped routes include visual landmarks.

In the following experiment birds were released from two sites perpendicular to their established routes approximately halfway home, and from a further two novel

release points either side of the initial release point, and tracked on each occasion. Yoked control birds that had not been allowed to develop stereotyped route were designated an experienced (route-recapitulating) partner, and were released from the same novel sites.

3.3 EXPERIMENT 3.2:

3.3.1 METHOD

3.3.1.1. *Subjects and Procedure*

The subjects that had completed 20 homeward flights from the Ridgeway (distance to home: 25.5 km, direction to home: 359°) as part of Experiment 3.1 were used (apart from bird p08 who was lost on his 20th training flight). These subjects had all developed highly stereotyped homeward routes. In addition eight new control birds were selected, these birds were all experienced homers and had been used in previous experiments involving GPS tracking. Control birds were fitted with 30 mm x 70 mm Velcro strips, and were trained to carry 25 g weights (see section 3.2.1 for more details). The control birds were given training releases from various directions up to 15 km from home (see appendix 2 for further details).

The final three tracks performed by each bird in experiment 3.1 served as "target" tracks for this experiment, indicating each bird's preferred stereotyped route. Four new "off-route" release sites were selected for each experimental bird. Two sites perpendicular to the target tracks were selected, approximately 2 km either side of each bird's stereotyped route, halfway from the original release site (the Ridgeway) to home. These release sites were specific for each bird, though sometimes the same sites could be used for different birds. A second pair of release points, ~ 2 km either side of the original release site, were also selected, these sites were the same for every bird (each new release

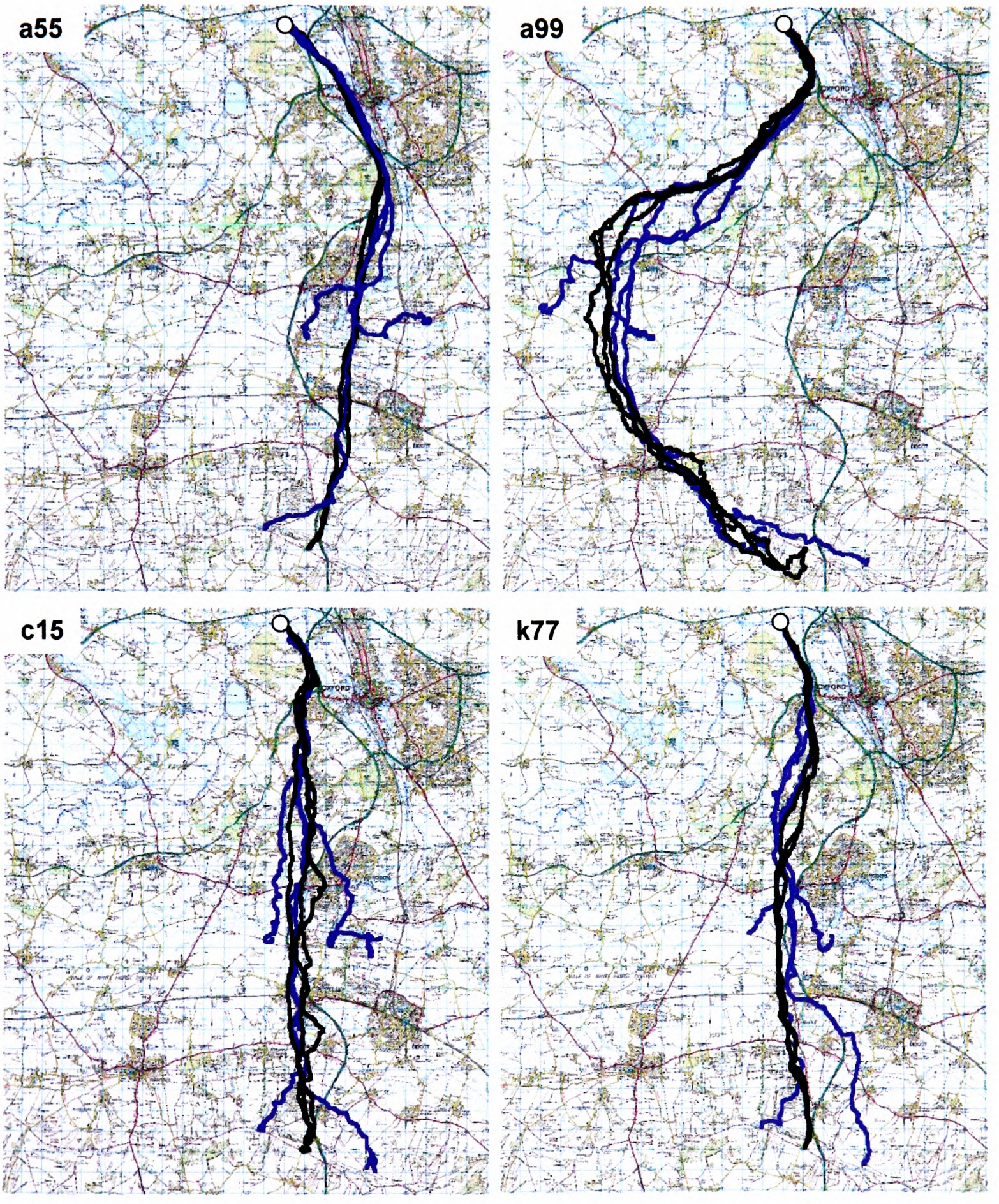
site was between 1 and 3.7 km from the target tracks). Each experimental bird was paired with one control bird, and were released separately (with at least 5 minutes between successive releases) and tracked from the four off-route release sites (for details of release sites see appendix 2).

3.3.2 RESULTS AND DISCUSSION

Figure 3.3 shows the final 3 tracks (in black) performed by each bird in experiment 3.1. These tracks serve as target tracks, illustrating each experimental bird's preferred route. The four off-route tracks performed by each experimental bird are also included in blue. Figure 3.4 includes the experimental birds' target tracks, this time with the tracks performed by the yoked control birds (that had not been allowed to develop stereotyped routes) displayed in red.

It is clear from figure 3.3 that the experimental birds are strongly attracted back to their established stereotyped routes. In every case the experimental birds reach and join their established route considerably before reaching the vicinity of the home loft. In most cases this occurs much sooner than would be expected if the bird was simply trying to navigate homeward from the novel release sites, indeed there is little evidence that any experimental bird was not influenced by their established tracks, and attempted to navigate homeward directly. The control birds' tracks (Figure 3.4) cover a larger proportion of the landscape, and whilst they often cross and coincide with the experimental birds' target tracks there is much more deviation from the target tracks than shown by the experimental birds.

Figure 3.3 The maps show the final 3 tracks performed by each bird in the training period (in black) and the 4 off-route releases in blue. Bird identity is indicated by 3 character labels. A white circle indicates the home loft. A 5 km scale bar is included in the final panel.



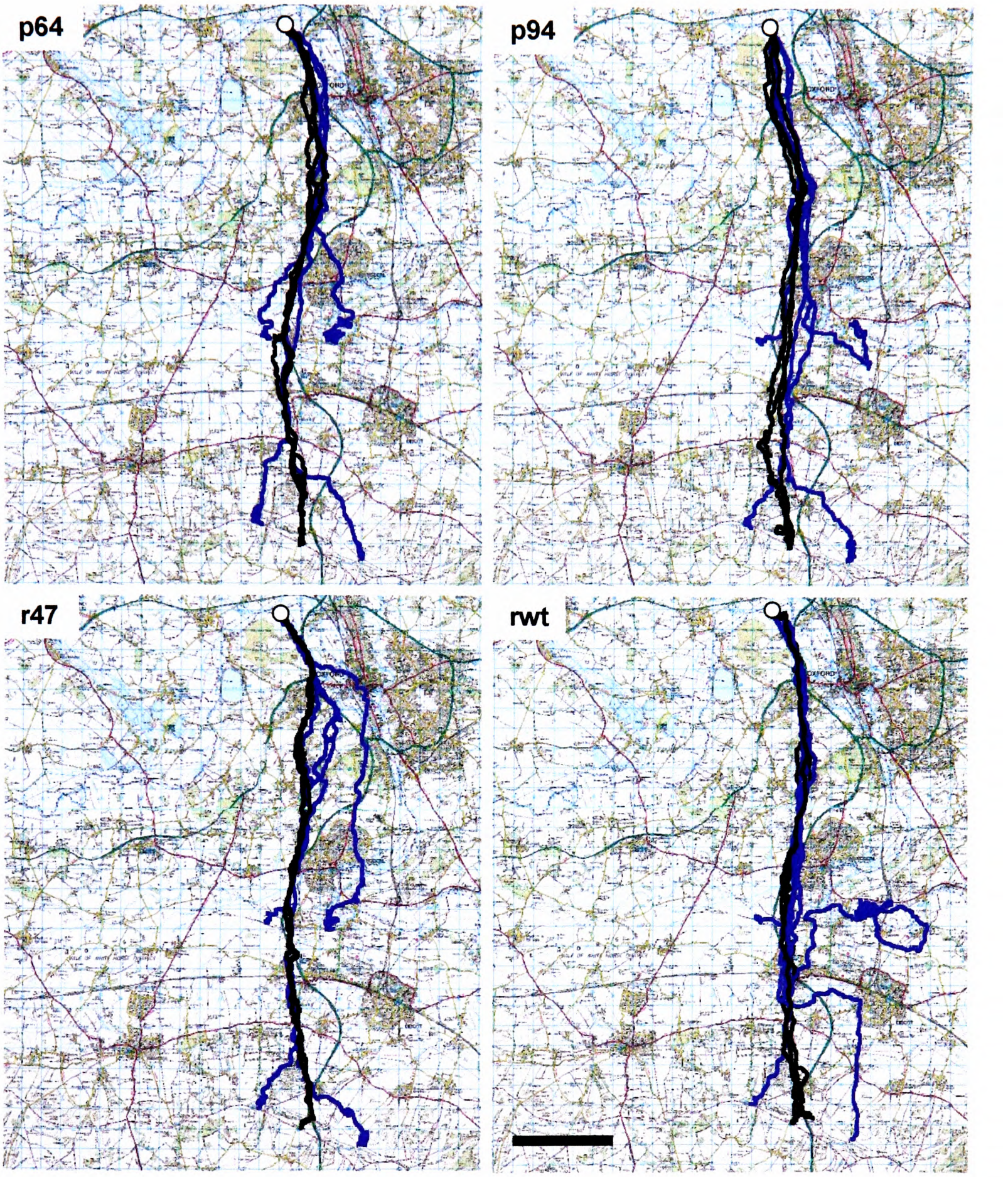
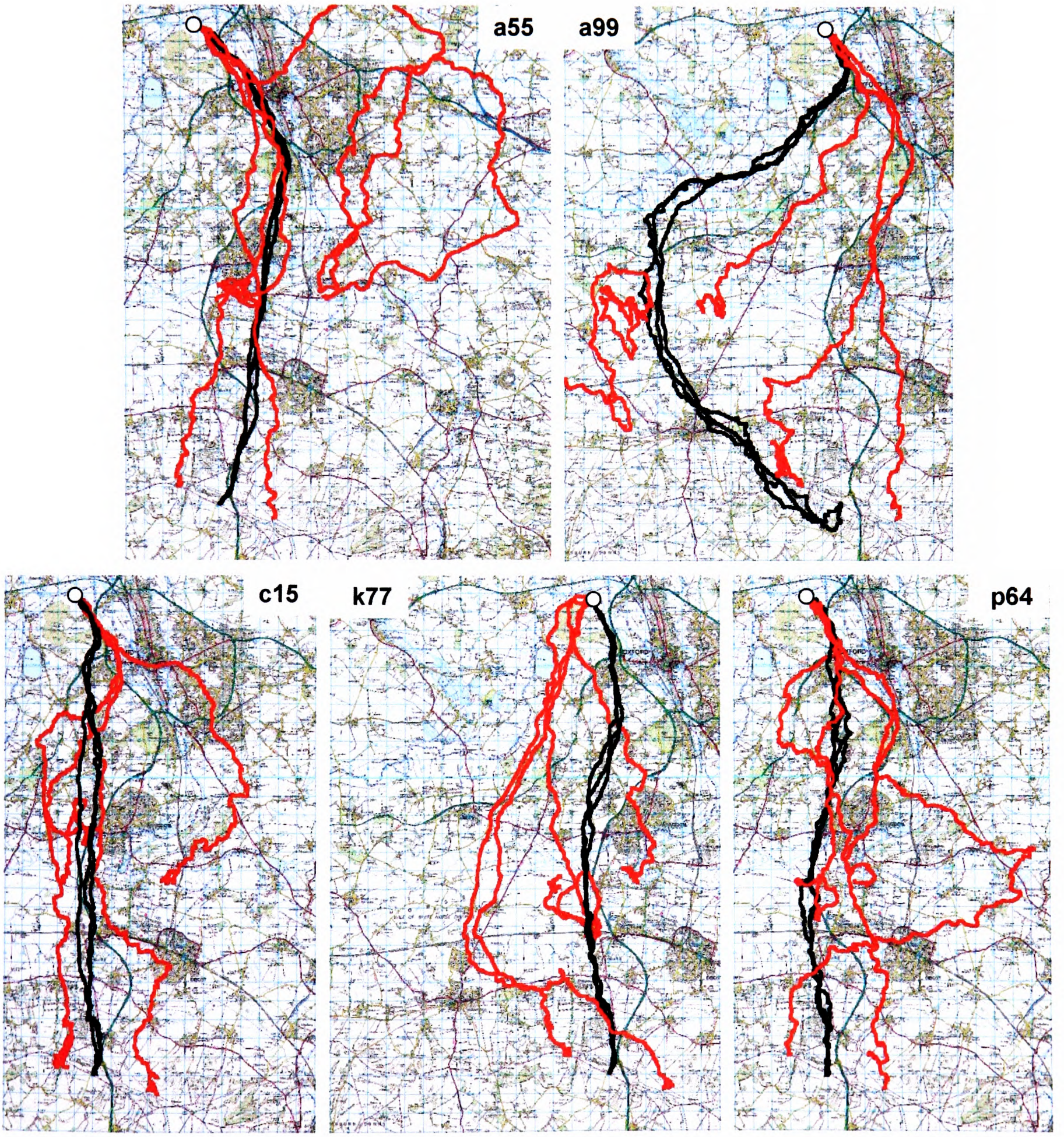
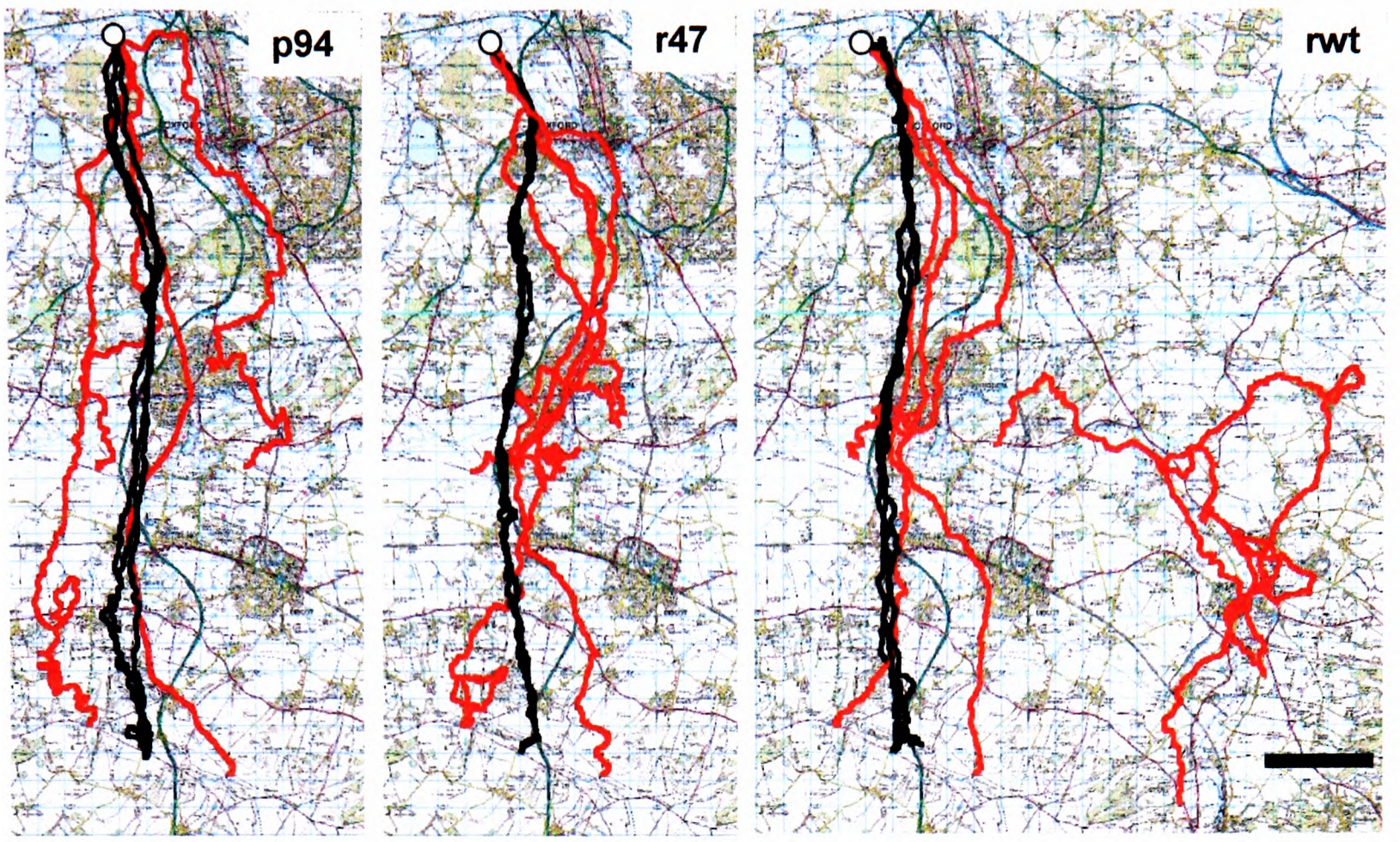

p64
p94
r47
rwt

Figure 3.4 Maps showing the final 3 tracks flown by the experimental birds (in black) with the yoked control birds' off-route tracks shown in red. The 3 character labels indicate the identity of the experimental birds. Home is indicated by a white circle. A 5 km scale bar is included in the final panel.





To examine these tracks more formally I first recorded the point at which each off-route track first crossed one of the three target tracks (each control bird was paired with an experimental bird, and the point where their off-route track first crossed one of their partner's target tracks was recorded). Not every off-route track crossed one of the target tracks (31/31 experimental tracks did, 28/32 control tracks did). In the case where the track does not "join up" (Fig 3.4 rwt) the battery on the GPS unit ran out before the bird reached home. Then, to test if any change in heading occurred as the birds crossed the target tracks, I calculated the direction of each bird's heading in the 500 m before first crossing one of the target tracks, and then calculated the bird's heading over the 500 m after crossing the track. From this, the angular change in heading was calculated.

The direction the bird was travelling in before first crossing the target track was standardised to 0° and any change in heading was recorded in degrees. If a bird was approaching its target track from the left hand side and was indeed influenced by crossing the target tracks, changing its heading in order to more closely match the heading direction of the target track, then you would expect a negative angular change. If the bird

were approaching its target track from the right you would expect a positive angular change. If the target tracks had no influence over the bird's heading direction you would expect no change in heading direction. To avoid the angular changes being cancelled out as birds approached target tracks from novel sites on both sides, the resulting heading direction changes were divided into two groups; one group of tracks performed from release sites displaced to the left of the target tracks, and one group of tracks performed from release sites displaced perpendicularly to the right of the target tracks. I used standard circular statistics to analyse the data (Batchelet, 1981).

Figure 3.5 a) shows the angular change in direction when a target track is crossed by experimental birds, and figure 3.5 b) shows the angular change when a target track is crossed by control birds. In all cases the birds are significantly orientated (see table 3.3 for details). 95 % confidence intervals were calculated for the angular change in heading of birds approaching target tracks from the left and from the right, for both experimental and control birds. In each case the 95 % confidence interval did not include 0° for the experimental birds, and always included 0° for the control birds (see table 3.3). This means that overall, experimental birds exhibited a significant change in heading when passing over the target tracks, whereas the control birds did not show a significant heading change when crossing one of the three target tracks performed by their experimental partner.

Secondly, I compared each bird's heading from the point of first crossing one of the target tracks for a distance of 500 m, to the heading of the target track from the point of crossing, for the same distance. In this case a value of 0° indicates that there is no difference in heading between the off-route track and the target track it crosses. I again used circular statistics to evaluate the difference in heading between off-route and target

Figure 3.5 Circular diagrams a & b show the angular change in heading between the 500 m before and 500 m after first crossing a target track. Diagrams c & d show the difference in heading between off-route and target tracks for the 500 m after first point of contact. White triangles indicate birds released on the right of the target tracks, black triangles indicate birds released on the left of the target tracks. Data is shown for both experimental birds (with a stereotyped route), and control birds (without a stereotyped route).

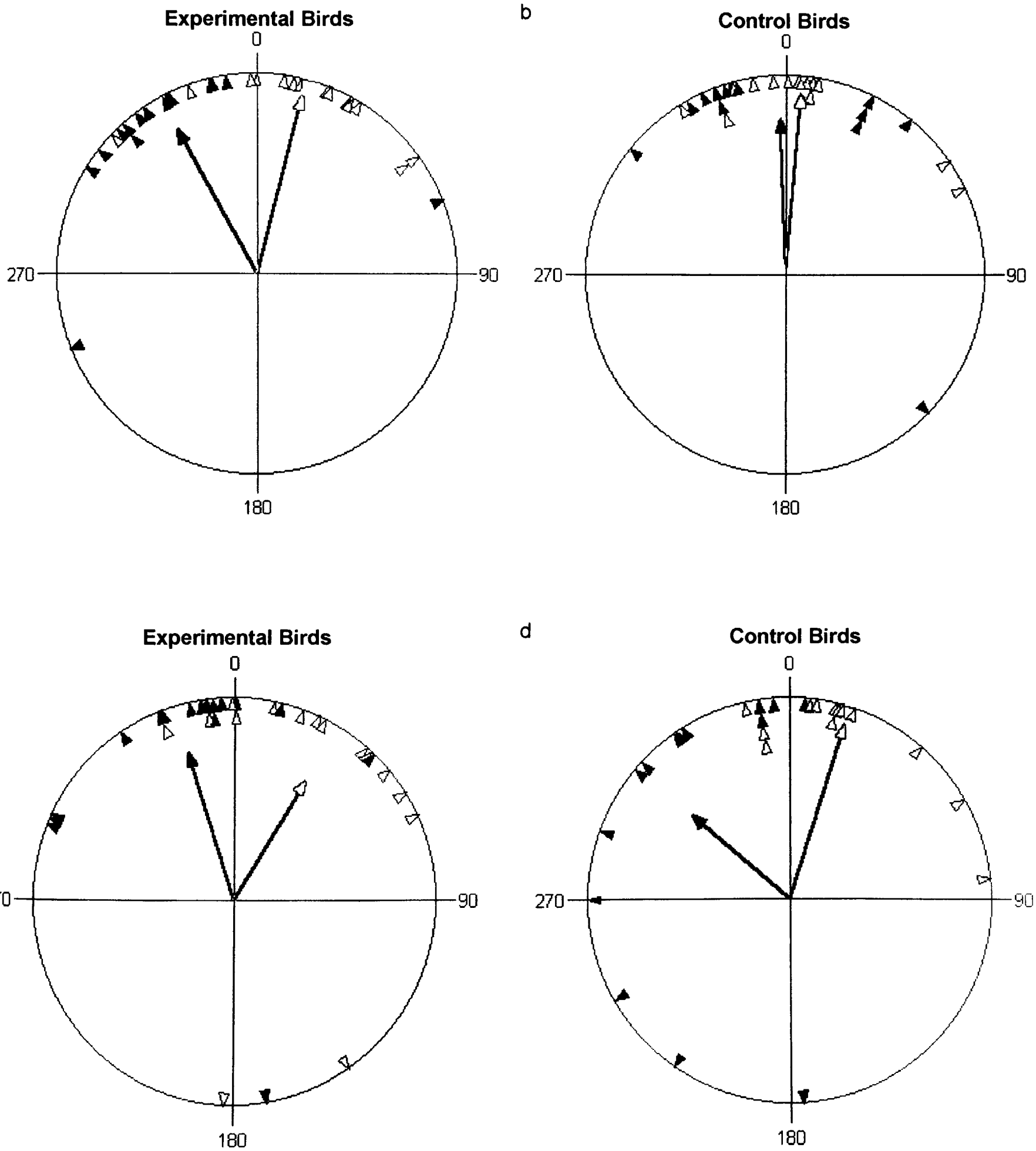


Table 3.3 Table showing the direction and length of the mean vector, the 95 % confidence intervals (values in bold indicate that the direction of heading includes 0°) and Rayleigh test statistics for each circular diagram - where a significant value indicates groups of birds being significantly orientated. Each is divided into two subgroups, one including off-route tracks approaching target tracks from the left, and the second including tracks approaching the target tracks from the right. Significant values are indicated by *s.

	Angular change in heading (approach left)	**Angular change in heading (approach right)**	**Angular difference between off-route and target track (approach left)**	**Angular difference between off-route and target track (approach right)**
Experimental birds				
Mean vector	331.5°	14.6°	342.7°	31.2°
Length of mean vector	0.819	0.912	0.759	0.0691
95 % confidence interval	313.9°-349.1°	0.8°-28.4°	**322.1°-3.4°**	5.7°-56.6°
Rayleigh test statistic P value	0.000*	0.000*	0.000*	0.000*
Control birds				
Mean vector	357.8°	5.2°	311.2°	18.3°
Length of mean vector	0.779	0.909	0.638	0.905
95% confidence interval	**334.3°-21.3°**	**350.5°-19.9°**	281.4°-341.0	3.3°-33.2°
Rayleigh test statistic P value	0.000*	0.000*	0.002*	0.000*

tracks for experimental and control birds (see figure 3.5 c & d). In each case the groups were significantly orientated (see table 3.3). 95 % confidence intervals were calculated to test whether the differences in heading between the target tracks and off-route tracks included 0°.

In both cases the 95 % confidence interval of the control birds did not include 0°. The 95 % confidence interval of the experimental birds approaching the target tracks from the left included 0, but the confidence interval of the tracks approaching the target from the right did not include 0. This suggests that, after the point of contact with target tracks, off-route tracks performed by experimental birds were marginally more similar in heading direction to target tracks than off-route tracks performed by control birds. This result may

have been affected by a slight tendency of experimental birds to "overshoot" their established routes after the first point of contact.

Finally, the straight-line distance from the off-route release site to the point where each bird's flight first crossed one of the target tracks, was measured for both the experimental and control birds. GLMs (General linear models) were performed on the data using the variables "Bird" to account for individual variation, and "Group" which separated the birds into experimental (with a stereotyped route) and control (without a stereotyped route) groups. The variable "Bird" did not have a significant effect on the data ($F=0.39$, $p=0.971$), but the variable "Group" was found to have a significant effect ($F=10.64$, $p=0.002$*). The experimental birds flew a significantly shorter distance before reaching a target track than the control birds.

3.4 GENERAL DISCUSSION:

Experiment 3.1 showed that birds perform highly stereotyped, individually distinctive, yet often inefficient routes from a distance of 25 km from the home loft. This suggests that birds use a very similar strategy when performing a homing task from 25 km as used at distances of 5 – 10 km from the home loft. This is very interesting as, at 25 km, the current release site is towards the upper limit of the area within which it has previously been suggested that pigeons navigate using familiar visual landmarks (see Emlen, 1975; Matthews 1963). Furthermore, when released from novel sites perpendicularly displaced along their established routes, experimental birds are attracted back to their own stereotyped routes, rather than navigating homeward directly. Experimental birds were shown to change trajectory markedly when passing over their established routes. Control birds were not shown to change trajectory

significantly when crossing their experimental partner's routes, nor did the post-contact heading match the established routes as closely as the experimental birds' tracks. Experimental birds were also shown to fly a significantly shorter distance than control birds before reaching their established routes.

These results add further weight to the findings of experiments involving route recapitulation at shorter distances (Experiments 2.1 & 2.2, Meade et al., 2005), and previous off-route releases (Biro et al., 2004). In chapter 2 I put forward three possible explanations to account for the detailed route-recapitulation found at short distance releases (5.0, 5.2 km). These were first; that a memorized compass direction from the release site is recalled, with landmarks used as external reference points to correct for error. Second; that birds remember a chain of landmarks with an associated compass bearing between each, so that the overall shape of the homeward path is controlled by several "waypoints". The third possibility was that routes are remembered in very fine detail with no primary reference to a compass (a form of pilotage (Baker, 1984; Papi, 1992)). Biro et al.'s (2004) experiment, with birds performing stereotyped routes from distances of 10 km and including four novel off-route sites, refined these hypotheses proposing that highly experienced birds build up a representation of the homeward route in the form of a "Route Map" which consists of a series of memorised visual landmarks or "waypoints". A route map might work in one of two ways, the first is very similar to the second possibility above; for each waypoint, an associated compass bearing (or even vector) would be recalled, that would direct the bird to the next waypoint, thus making up the home route. Alternatively, as it is now clear that "waypoints" can be detected at distances of 1-3.7 km, sequential waypoints may be within visual range of each other, allowing birds to progress homeward through a form of pilotage known as steeple-chasing (Baker, 1984), with no external reference to a compass.

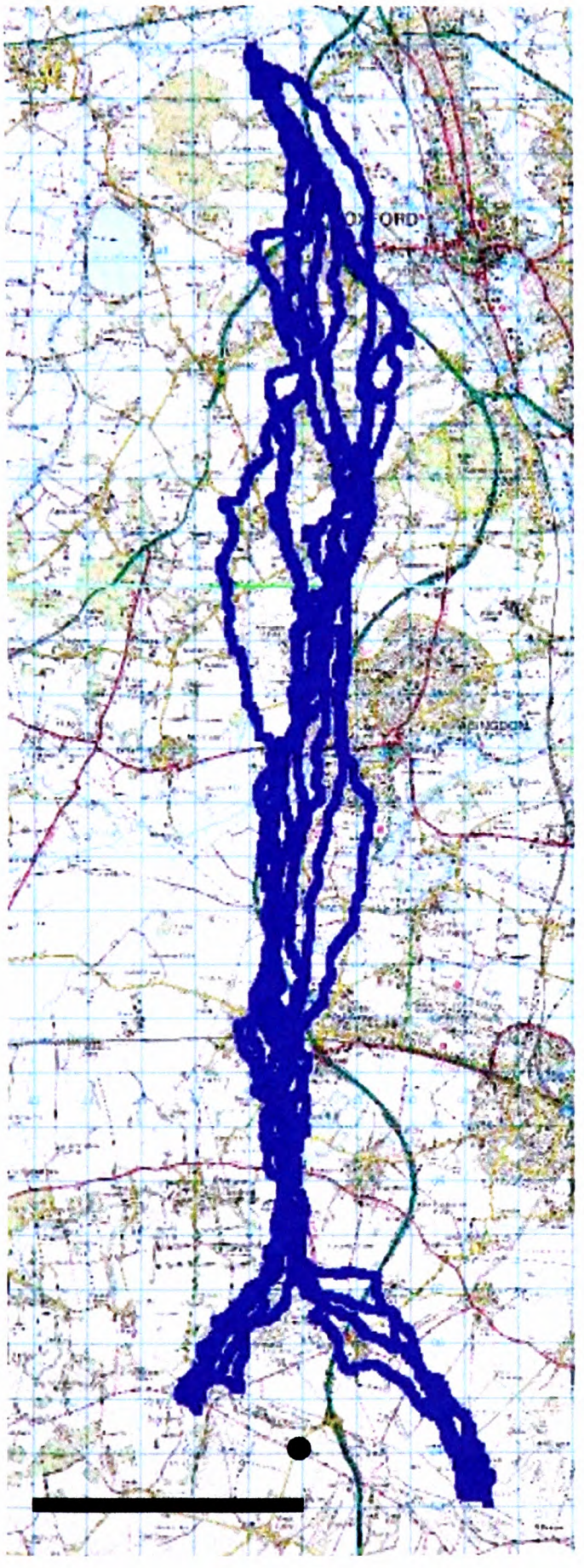
The performance of extremely inefficient routes (such as a99's) suggests that it is unlikely that successive waypoints are linked by vectors, as this would make it possible for birds to recognise that they were taking large detours and allow birds to refine their routes. If compass directions between successive waypoints were remembered, birds would be aware of a heading change, but would not necessarily be able to compute a more direct route purely on this basis. If the homeward route was made up of waypoints linked simply by visual attraction, birds may not be aware that a more direct route might be available. These different possibilities are examined experimentally in chapter 5.

The exact nature of these waypoints in a bird's representation of space remains unclear. It is interesting to note however, that the birds whose stereotyped routes lead homeward in a fairly straight line and are therefore similar, (c15, k77, p64, p94, r47, rwt) tend to rejoin their stereotyped routes, when released either side of the original release site, at approximately the same point (see Figure 3.6a). This occurs in nine out of the12 off-route releases. In the remaining three off-route releases, the stereotyped routes are joined again at approximately the same point across birds, slightly further along the route (Figure 3.6b). When the birds are released off-route closer to home, there doesn't seem to be a point common to several birds where stereotyped routes are re-joined, most birds however, join their own route at almost the same point on the two releases. It is possible that places along the route where re-joining of target tracks occur constitute waypoints.

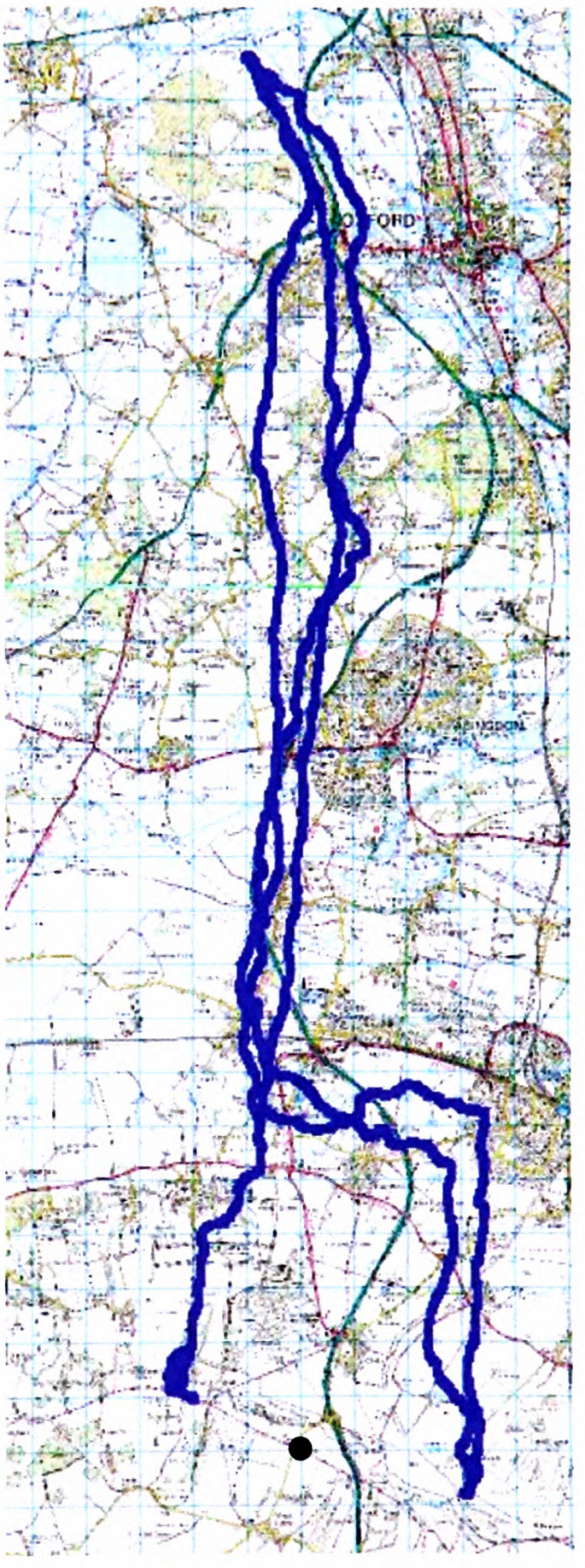
The second set of off-route release points were chosen to be either side of the initial release site, as, since this site is always the beginning of the homeward journey, it is likely that the release site should act as a waypoint. None of the experimental birds went directly to the original release site however, or took the shortest path to

Figure 3.6 Maps showing off-route releases. In (a) 9 tracks are shown, 3 tracks are shown in (b). A black circle marks the Ridgeway release site. A 5 km scale bar is shown in the left hand panel.

a



b



rejoin their track when released further along the route. All birds took "local shortcuts". Rather than making directly for their established routes at sharp right-angles, they joined their routes more obliquely at a point closer to home, a phenomenon noted in Biro et al. (2004).

There are several possible reasons why birds might join their routes at a point closer to home than the point on the route closest to the off-route release site. If the route-map is made up of several discrete waypoints, linked by visual attraction, it is possible that birds could see more than one waypoint from each off-route release site, and have a representation of the order in which they occur along the homeward journey. Birds therefore choose the waypoint they know to be closer to home, and create a more efficient route. This could also occur if the waypoints were associated with a general compass direction, so that when recognized, they are lined up in the homeward order with reference to the bird's internal compass, with birds again choosing to fly directly to the waypoint they know to be closer to home. Finally, birds could be attracted to waypoints closer to home, because they would be viewed from angles more closely resembling those usually encountered as they flew along their stereotyped routes. It is possible that birds may not recognise waypoints that they had not previously viewed from the novel angles of the off-route release sites.

It is not known whether birds performing stereotyped routes from longer distances would include a greater number of waypoints into their route map, or whether at longer distances waypoints would simply be further apart. It may be possible to investigate in greater detail how many waypoints are encoded into a route by performing a greater number of off-route releases along birds' stereotyped routes, but it will never be easy to extract exactly what birds are attending to, and encoding in their representations of space, over such a large scale. The way that the space between

waypoints is encoded into a bird's representation of a stereotyped route is investigated further in Chapter 5.

CHAPTER 4

Can aerial familiarity trigger ground-level visual recognition of release sites by the homing pigeon?

4.1 INTRODUCTION

4.2 EXPERIMENT 4.1:

4.2.1 Methods

4.2.1.1 Subjects, Apparatus and Training

4.2.1.2 Test Releases

4.2.1.3 Analysis

4.2.2 Results and Discussion

4.3 EXPERIMENT 4.2:

4.3.1 Methods

4.3.1.1 Subjects and Procedure

4.3.1.2 Analysis

4.3.2 Results and Discussion

4.3 GENERAL DISCUSSION

N.B. Experiment 4.2 has been accepted for publication as: Meade, J., Biro, D., & Guilford, T. An investigation of route recognition in homing pigeons, in *Animal Behaviour.*

4.1 INTRODUCTION

In this chapter I investigate further the role of familiar visual landmarks along the length of a pigeon's homeward journey, as introduced in Chapter 3. Unlike the accepted use of familiar visual landmarks at the release site (Braithwaite & Guilford, 1991; Braithwaite, 1993; Braithwaite & Newman, 1994; Burt et al., 1997; Biro et al., 2002; Biro et al., 2003), and in the final stages of homing (Schmidt-Koenig & Schlichte, 1972), it is only recently that there has been strong evidence that familiar visual landmarks are used throughout the length of the homeward journey (Biro at al., 2004; Meade et al., 2005; see also chapters 2 and 3).

Experiments demonstrating the use of visual landmarks at familiar release sites manipulated the view available to the pigeon before release (Braithwaite & Guilford, 1991; Burt et al., 1997; Biro et al., 2002; Biro et al., 2003), and demonstrated that a 5 min preview of a familiar release site before takeoff allowed pigeons to home up to 18 % faster than pigeons denied a preview. This effect is lost when pigeons are given a 5 min preview of an unfamiliar release site (Braithwaite & Newman, 1994). This means that an increase in homing speed following a 5 min preview can be used as a measure of whether or not a release site is recognized as familiar by a pigeon. Braithwaite (1993) used this approach to investigate the use of visual landmarks along the homing route more directly. Pigeons were repeatedly released from several sites, and points along the straight-line route home, over which they were assumed to have flown, were chosen for test releases. The subjects were released with either a 5 min view or no view of the landscape, under the assumption that if the landscape were recognised as familiar then the preview would increase their homing speed. No homing speed increase was found. There are three alternative explanations for this result. It could be that birds do not attend to visual features along

the homeward route, resulting in a lack of subsequent recognition of any point along the route, though results of the previous chapters indicate this is very unlikely. Alternatively, birds may well attend to visual features throughout the homeward route as seen from the air, but may not subsequently be able to recognise these landmark arrays from the novel viewpoint of ground-level, possibly due to a sort of template matching visual system, where remembered landmark arrays must be closely approximated to allow recognition (Cartwright & Collett, 1982, 1983; Dawkins & Woodington, 2000). Finally, the birds may not have flown home along a straight line, and therefore may not have over flown the sites that they were assumed to have done.

In these experiments I used precision GPS technology (Steiner et al., 2000; von Hünerbein et al., 2000) to track two groups of birds, one that was known to have flown over particular sites, and a second group that had not over-flown the sites. Both groups were released from the chosen sites under preview and non-preview conditions. In this way, the uncertainty as to whether birds had over-flown their chosen test release sites was eliminated, and the issues raised in Chapter 2 of possible limitations to pigeons' visual recognition were examined, as well as allowing the homing performance of the two groups of birds (one aerially familiar with the sites and one naïve) to be compared.

4.2 EXPERIMENT 4.1

In the first of this pair of experiments, pigeons were tracked after a single training flight so that points that they were known to have flown over at least once could be selected. Each aerially familiar bird was then paired with a naïve partner, and both

birds were released under preview and no-preview conditions from the chosen sites, and the homing performances compared.

4.2.1 METHODS

4.2.1.1 *Subjects, Apparatus and Training*

Sixteen homing pigeons *Columba livia* L, were selected as subjects. All were successful homers and had been used in previous experiments involving GPS tracking. All birds were at least two years old and > 450 g in weight. All birds were fitted with a Velcro strip 30 x 70 mm, attached to their back with flexible leather glue applied to trimmed feathers (see Chapter 2 for more details). All birds lived with a dummy weight of ~ 25 g for two weeks before the experiment during which time they were trained from a variety of release sites up to 7 km from the loft (see appendix 2 for more details) to ensure that they had experience carrying the weights.

The birds were trained for release from a specially made Perspex release box mounted on a stepladder of 1.5 m height. Based on the original design of Braithwaite and Guilford (1991), the box had clear Perspex sides, but could be made opaque by the addition of four opaque Perspex sheets, which could be slid into position. The aim of the box was to allow the experimenter to manipulate access to the visual panorama of landmarks at a chosen release site for a 5 min period prior to release. Under both conditions a view of the sun and sky was available. The base consisted of a wire mesh – allowing access to local odour cues. The box lid was spring-mounted and could be operated remotely by an experimenter pulling on a string. The birds were given successive releases from the box close to the loft until they showed no agitation within the boxes, and no hesitation to fly out when the string was pulled.

During the test releases the birds carried GPS logging devices (Steiner et al., 2000, see appendix 1 for more details). The devices were attached to the Velcro strip on the bird's back. The loggers were 70 mm in length 30 mm wide ~ 3 mm in depth and weighed 28-32 g. Time stamped positional fixes (longitude, latitude and altitude) accurate to ± 4 m (Weimerskirch, 2002) were logged every second and could be downloaded on recovery of the device using μ-blox software. The positional data was superimposed onto ordnance survey maps using Fugawi™ mapping software (Copyright 2000-2002 Northport Systems Inc.), see appendix 1 for more details.

4.2.1.2 *Test Releases*

The 16 birds were randomly assigned into pairs. One member of each pair was given a training release from the initial release site (Victoria Arms: Distance to home, 5.2 km; direction to home, 277.8°) and a second test flight from the same site, during which the bird was tracked using a GPS logging device, on the morning of each test day. The second member of the pair had had extensive experience of releases around the loft, but had never been previously released from the site, and had received no training flights from that direction (see appendix 2 for more details).

Following the first test flight, the bird and logger were recovered at the home loft and the data downloaded and plotted onto a map. A point that the bird had flown over and that was easy to access with the necessary apparatus was chosen. The bird that had flown over the chosen point (flyover: F+) was then taken to the site, along with its partner (non-flyover: F-). Subjects were transported in an aluminium box covered by a black sheet allowing no view of the landscape. At each chosen point both birds were released under preview (VIS+) conditions, which consisted of 5 min in a clear-sided box with access to visual cues, and no-preview (VIS-) conditions

which involved 5 min in an opaque sided box with no access to the visual landmarks at the release site. Each pair received the releases in the same order, but across pairs the order was pseudo-randomly assigned so that four pairs were released in the order VIS+, VIS- and the other four pairs were released in the opposite order. As each bird was removed from the carrying box, I cupped my hand over the bird's head to prevent any access to the visual landscape before release. Each bird was then fitted with a GPS logger, before being placed in the release box. All birds spent 5 min in the release box before the lid was sprung open. Pairs of birds were released separately, with at least 5 minutes elapsing between successive releases. After the first box release, the birds and trackers were recovered from the home loft and brought back to the same release site for the final release of the day. The releases were never more than two hours apart, and all releases for a given pair of birds took place on the same day.

4.2.1.3. *Analysis*

Two measures were recorded from each flight; first, efficiency was calculated by dividing the straight-line distance from the release point to home, by the total distance that the bird travelled (a derived measure calculated within Fugawi mapping software by summing the distance between each consecutive pair of points). The ends of the tracks within a 100 m radius of home were cropped so that non-navigational circling around the loft was not included in homing distance. This conversion from homing distance to efficiency was carried out to correct for the fact that the chosen release points were at necessarily differing distances to home. Secondly, the distance travelled by each bird before flying out of a 1 km radius around the release site was recorded.

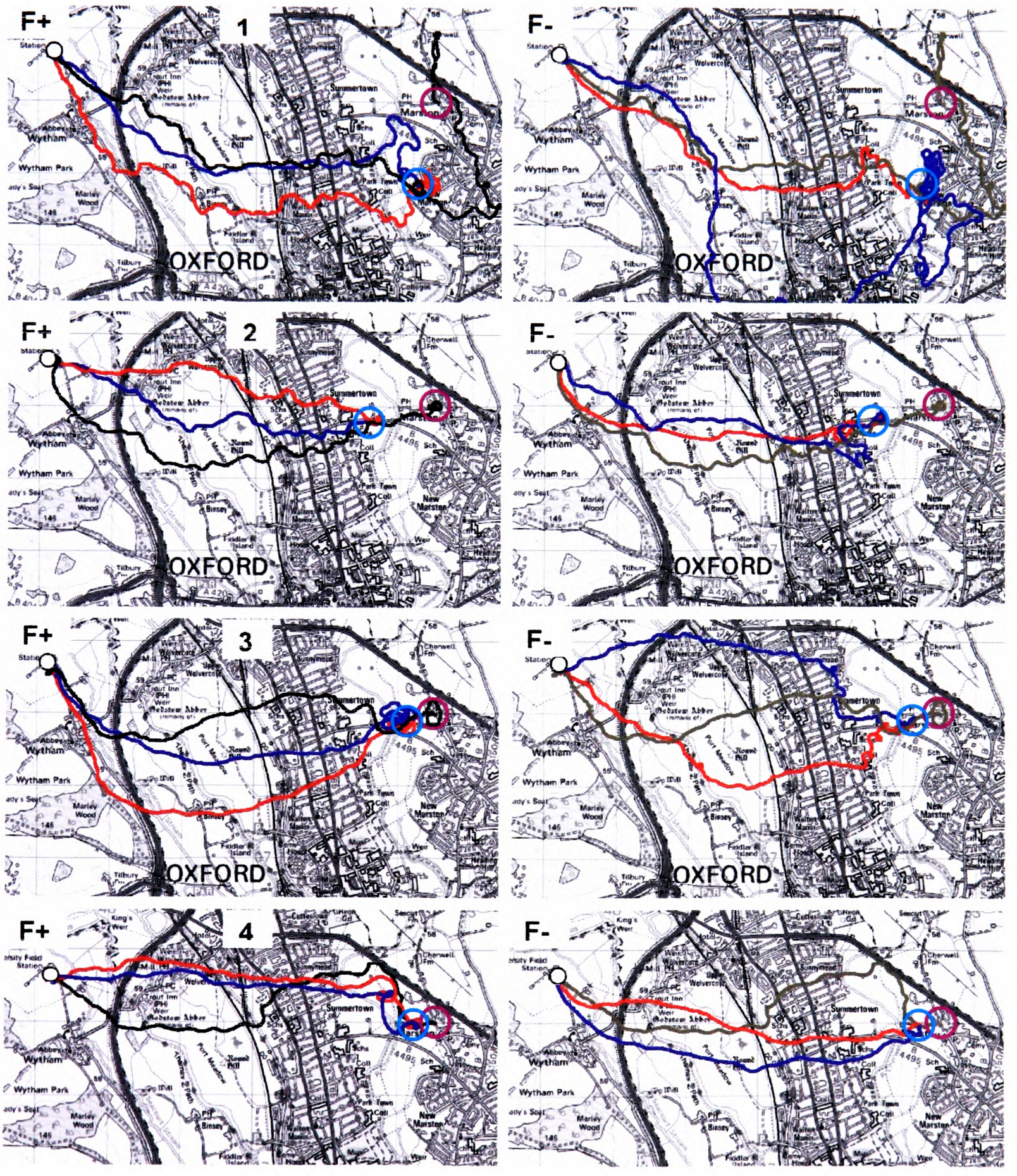
General Linear Models (GLMs) (Grafen & Hails, 2002) were performed on the data. The variables included were: Bird - to investigate if there were individual differences between birds; Group indicating whether the bird had, F+, or had not, F-, previously flown over the chosen point, and Treatment, indicating whether the bird had had a preview of the site before release, VIS+, or no such preview, VIS-. The interaction between Group and Treatment was included as this would indicate whether a preview before release had a greater effect on one of the groups of birds (F+ or F-). Release Number (whether it was the bird's 1st or 2nd test release of the day) was also included. For results see Table 4.1.

4.2.3 RESULTS AND DISCUSSION

Figure 4.1 shows, for each pair of birds, the tracks recorded under preview (VIS+) and no-preview (VIS-) conditions. The first member of each pair had over-flown the site and the second member of the pair had not. Neither bird had been released from the chosen point before. It is interesting to note that many of the aerially familiar (F+) birds, when released part way along their route tend to recapitulate parts of their training release, or perform two similar tracks from the release box (e.g. F+ birds; panel 1, 4, 7, 8).

Figure 4.2 shows graphs of the data for both entire flight efficiency and distance flown within a 1 km radius of the release site. Squares indicate aerially familiar (F+) birds and diamonds indicate unfamiliar (F-) birds. Open symbols indicate releases where a 5 min preview is given, and closed symbols indicate releases from an opaque box.

Figure 4.1 Tracks of aerially familiar (F+) and naïve (F-) pigeons. The left hand panels show the initial flight performed by the F+ birds in black, with the subsequent flights performed from part way along the routes shown in red where a 5 min preview was given, and in blue where no preview was given. The right hand panels show the corresponding tracks performed by the F+ birds' naïve partners from the same release sites (the F+ birds' tracks are shown in grey). Purple circles indicate initial release site, light blue indicate en-route release sites. Home is indicated by a white circle. A 1 km scale bar is included in the final panel.



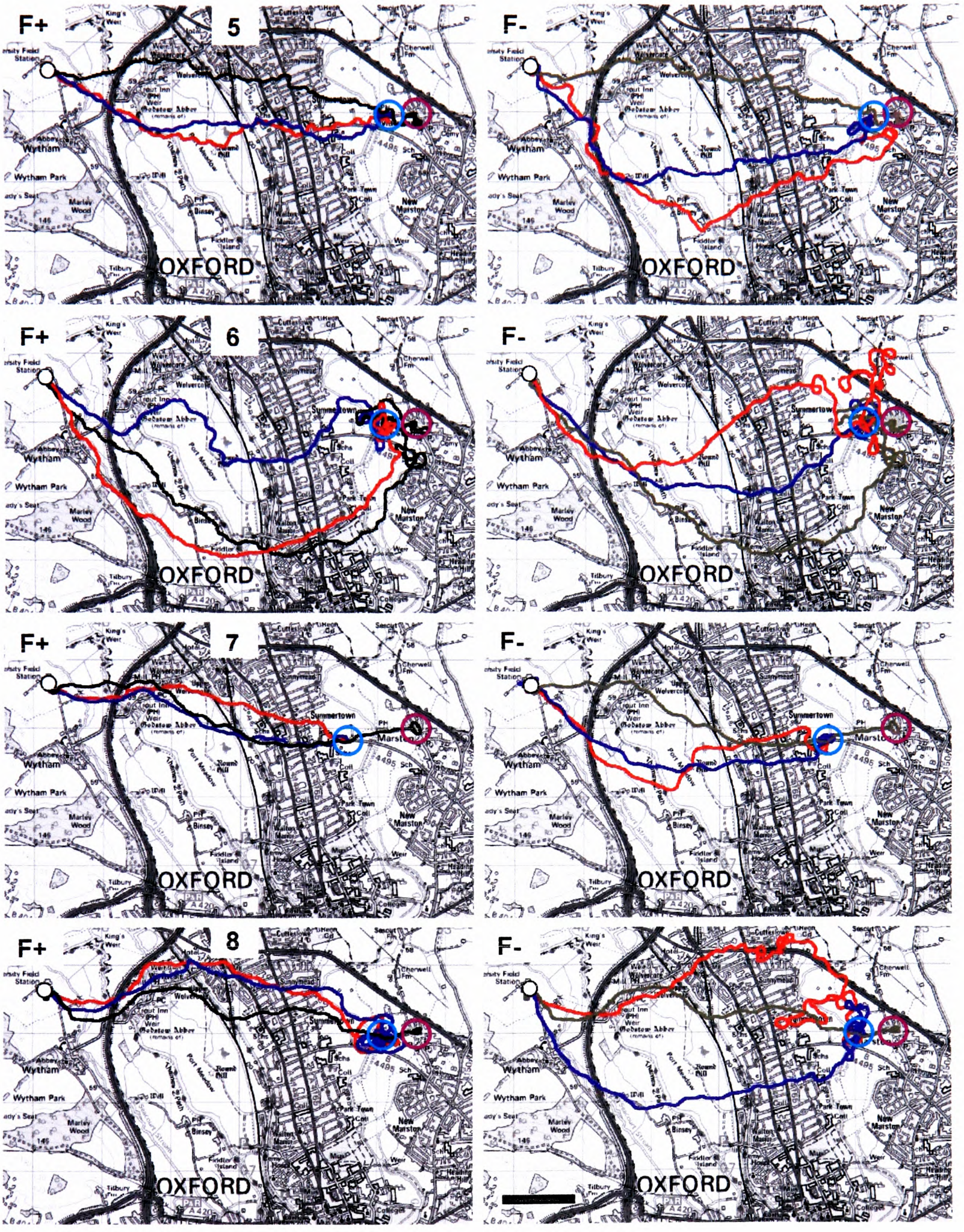
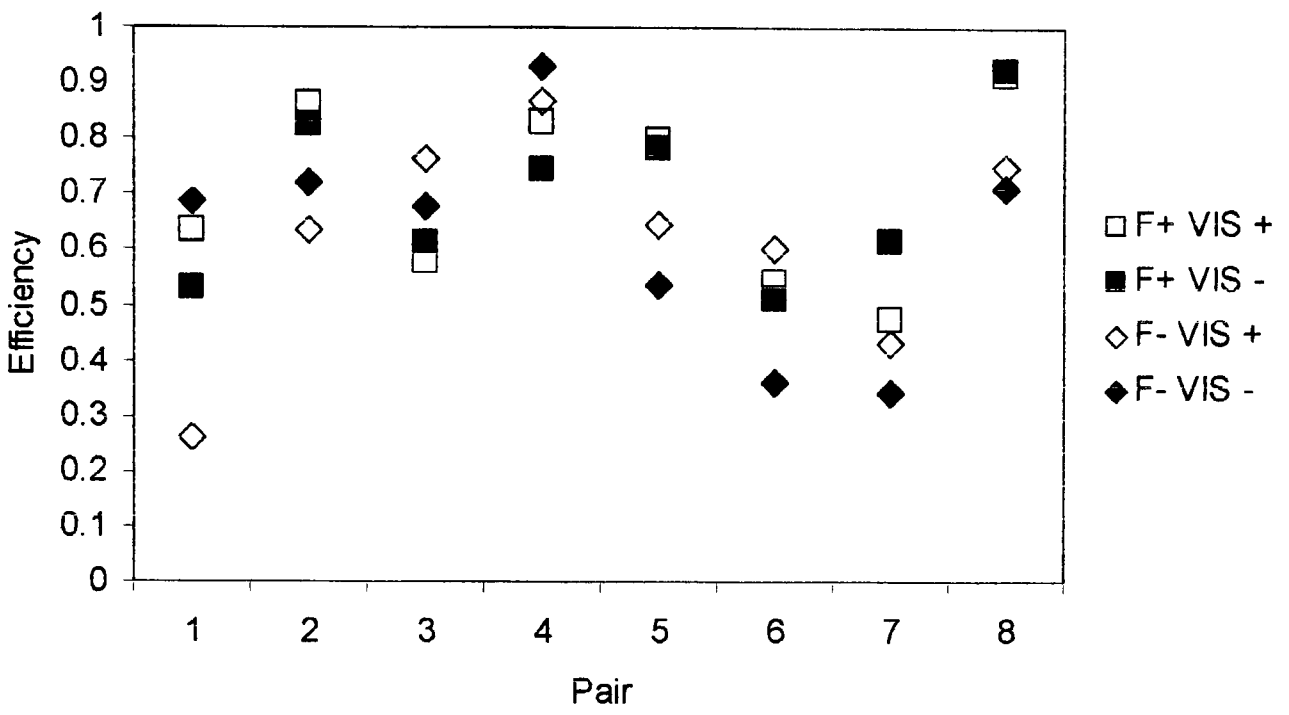

F+
5
F-
F+
6
F-
F+
7
F-
F+
8
F-
OXFORD
Wytham
Wytham Park
Marley Wood
Summertown
New Marston
Sunnymead
Cherwell Fm
Binsey
Park Town
Trout Inn (PH)
Rebatow Abbey
Port Meadow
Rowel Hill
Tilbury Fm
Fiddler Island
Walton Manor
Headington Hill
A420
A4495

Figure 4.2 Graphs showing (a) the homing efficiency and (b) distance flown within a 1 km radius of the release site in experiment 4.1. Squares indicate aerially familiar (F+) birds and diamonds indicate unfamiliar (F-) birds. Open symbols indicate preview (VIS+) conditions and closed symbols indicate no-preview (VIS-) conditions. Pairs of birds were released from the same location.

(a)



(b)

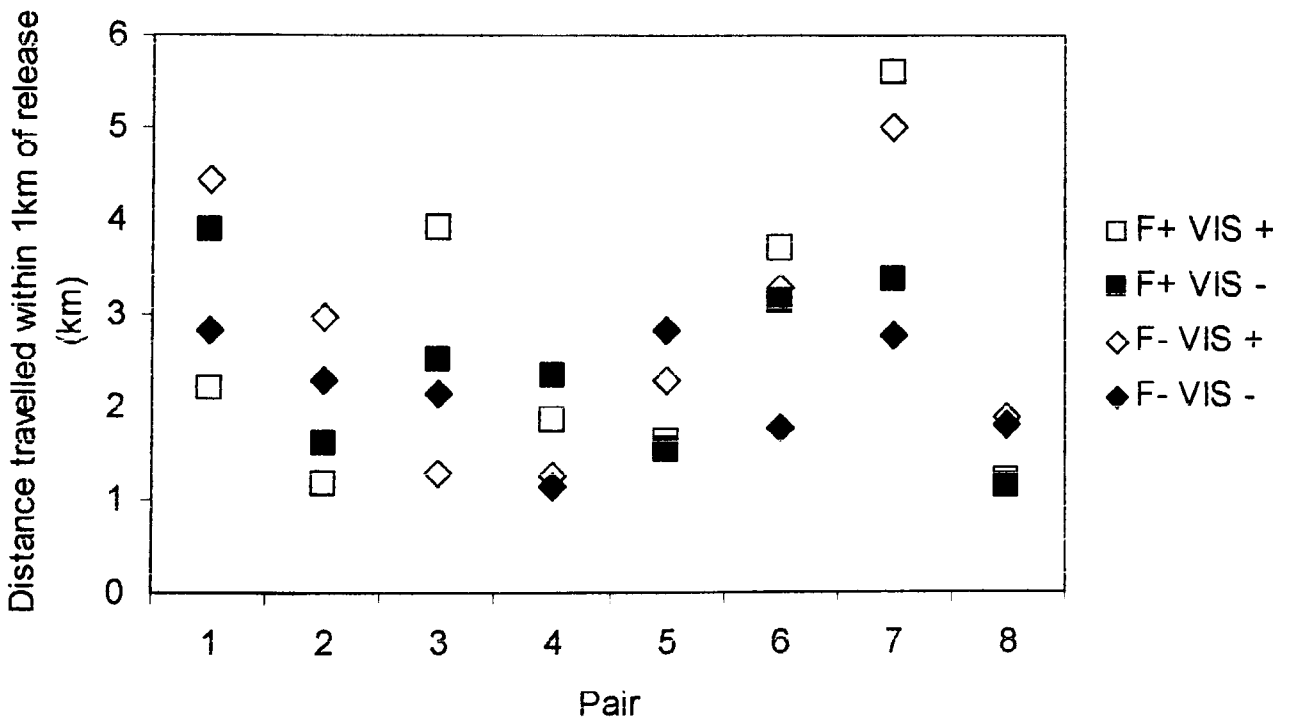


Table 4.1 Results of General Linear Models carried out on both efficiency data and distance flown within 1 km of the release site. *s indicate significant values.

Variable	DF	F	P
Efficiency of entire flight			
Bird	14	13.90	0.000*
Group	1	4.54	0.054
Treatment	1	2.23	0.161
Group*Treatment	1	0.78	0.395
Release Number	1	1.55	0.237
Distance flown within 1km of release			
Bird	14	4.70	0.004*
Group	1	0.01	0.944
Treatment	1	0.82	0.381
Group*Treatment	1	0.58	0.461
Release Number	1	0.00	0.965

The results show that individual differences between birds (variable "Bird") accounted for much of the variation for both measures. When the efficiency of the entire flight is taken into account the results suggest that the birds that had previously flown over the release sites homed more quickly than the birds that had not, with results very close to significance (variable "Group", $p = 0.054$). A 5 min preview of the release site before take-off had no significant effect on the homing performance of either group of bird (variable "Treatment"). Release number (whether it was the 1^{st} or 2^{nd} test release of the day) had no significant effect on the results.

This experiment therefore suggests that birds aerially familiar with a release site are able to home more efficiently than naïve birds, when released from the site, but do not gain a homing advantage from a view of the release site before take-off. Two alternative explanations account for the lack of effect of the preview treatment on birds aerially familiar with a release site. The first is that birds do not attend to visual landmarks whilst flying along the homing route, at least not throughout the

entire homing flight, thus resulting in a lack of recognition. This possibility seems unlikely. The results of the previous chapters suggest that visual landmarks are attended to throughout the homeward journey, and is reinforced by the observed tendency of the many of the aerially familiar birds to recapitulate parts of their training route or perform two similar routes in the test releases.

The second possibility is that birds may not recognise from the ground, an array of visual landmarks that they have only previously seen from the air, possibly because a single fly-over is not sufficient to allow recognition from a novel viewpoint, or because recognition of a site from a novel viewpoint is not possible. The finding that the aerially familiar (F1) birds homed more quickly than naïve birds from a release site part-way along their homeward route is more consistent with this second hypothesis. It is possible that the aerially familiar birds recognised the area around the release site as familiar, and were able to utilise this recognition to home more efficiently than birds that had not previously over-flown the release sites, but it seems that this recognition occurred only once the aerially familiar birds had a chance to view the landmark array from the air. It is also possible that other, non-visual factors, may also contribute to this increase in efficiency, such as a general familiarity with the odours in the region of release.

Previous experiments using this technique have shown that birds are able to use a 5 min preview of the landscape to home more quickly after only one training release from the same viewpoint (Biro et al., 2001, 2003), but this increase in homing efficiency was not found if birds were given a novel viewpoint of the same site. After four training releases birds were able utilise a novel viewpoint of a familiar release site to increase homing speeds. It is possible that if the birds in the present experiment

had over-flown the release site a greater number of times they would then be able to utilise the novel preview to increase their homing efficiency.

To investigate this question further, I conducted a second experiment where birds were released many times from the same site, and a point which had been consistently over-flown was chosen for each bird. Again birds were tested with a naïve partner, to investigate if flying over an area repeatedly allowed the birds to integrate novel viewpoints and utilise them to increase their homing efficiency.

4.3 EXPERIMENT 4.2:

In this second experiment I utilised the route-recapitulation phenomenon (demonstrated in chapters 2 and 3) to enable me to choose points in the landscape that had been consistently flown over in successive homeward journeys. Birds that had been released 20 times from the same site as part of experiment 4.2 were used as experienced subjects, and for each bird a point that had been repeatedly flown over was selected as the site from which the birds would be subsequently released under preview and no-preview conditions.

4.3.1 METHODS

4.3.1.1 *Subjects and Procedure*

The same 16 birds as in experiment 4.1 served as subjects. The same apparatus was used. A new release site was chosen (Church Hanborough; Distance to home: 5.3 km Direction to home: 129°). Each "familiar" (F+) bird was released 20 times from the site, during which time they began to follow a stereotyped route (Meade et al., 2005).

An area which had been repeatedly flown over was chosen for each bird and used as a site for test releases. Each chosen site had been flown over by the experienced member of the pair at least six times. From these chosen points both the aerially familiar (F+) birds and the naïve (F-) birds were released under preview (VIS+) and no-preview (VIS–) conditions, and the homing efficiencies and distance flown within a 1 km radius of release compared.

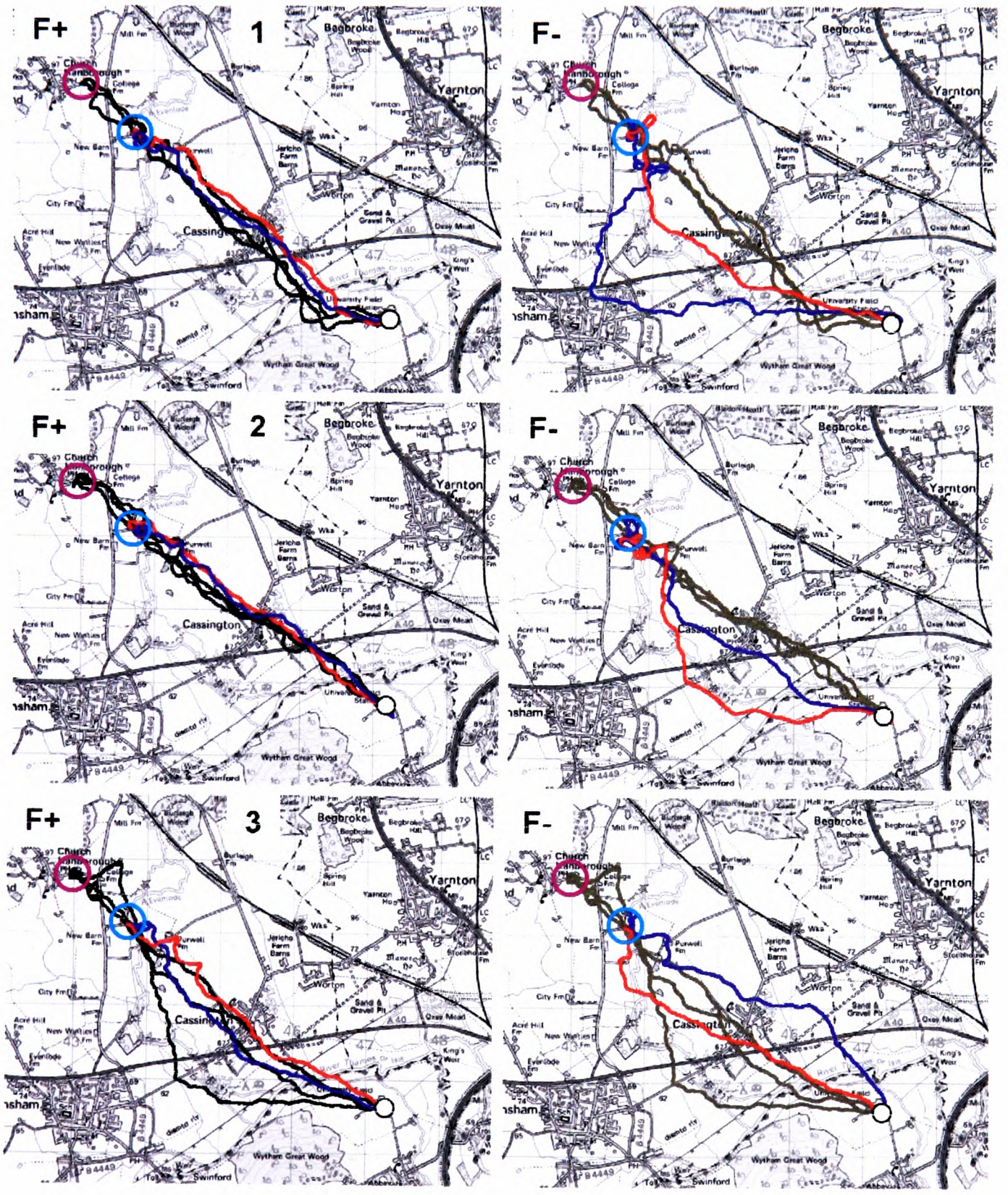
4.3.1.2 *Analysis*

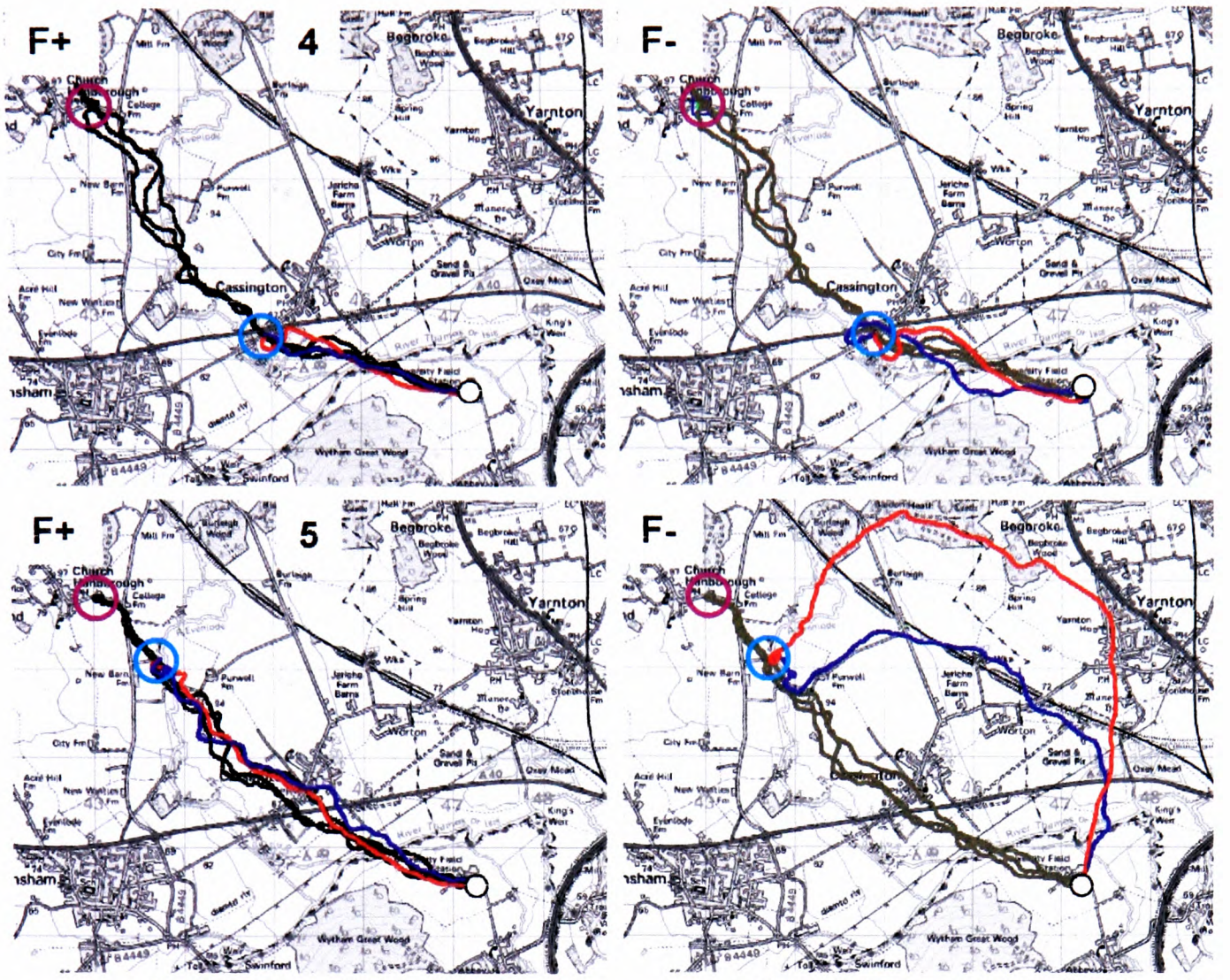
A second set of General linear models (GLMs) were carried out on both the efficiency data for the entire flight, and the distance flown within a 1 km radius of the release site, using the same variables as detailed in section 4.2.1.3. For results see Table 4.2.

4.3.2 RESULTS AND DISCUSSION

Figure 4.3 shows the tracks performed by each pair of birds under preview (VIS+) and no-preview (VIS-) conditions. The first member of each pair had over-flown the chosen point at least six times, the second member of the pair was not known to have over-flown the site. In this second experiment the tendency for aerially familiar birds to recapitulate their training routes in both test releases is even more pronounced, occurring in almost every case. The tracks of the less experienced birds are more varied between releases.

Figure 4.3 Maps showing three tracks illustrating the habitual route (in black) taken by the first bird (F+) in each pair of panels. In the second panel, for the birds that have not flown over the sites (F-), the same route is shown in grey. The flights subsequently performed by each bird from a point along the route are shown in red where a 5 min preview was given, and in blue where no preview was given. Purple circles indicate the initial release site, light blue circles indicate the en-route release sites. Home is indicated by a white circle. A 1 km scale bar is included on the final panel.




F+
4
F-
F+
5
F-
F+
6
F-
F+
7
F-
Begbroke
Yarnton
Cassington
Worton
Wytham Great Wood
Swinford

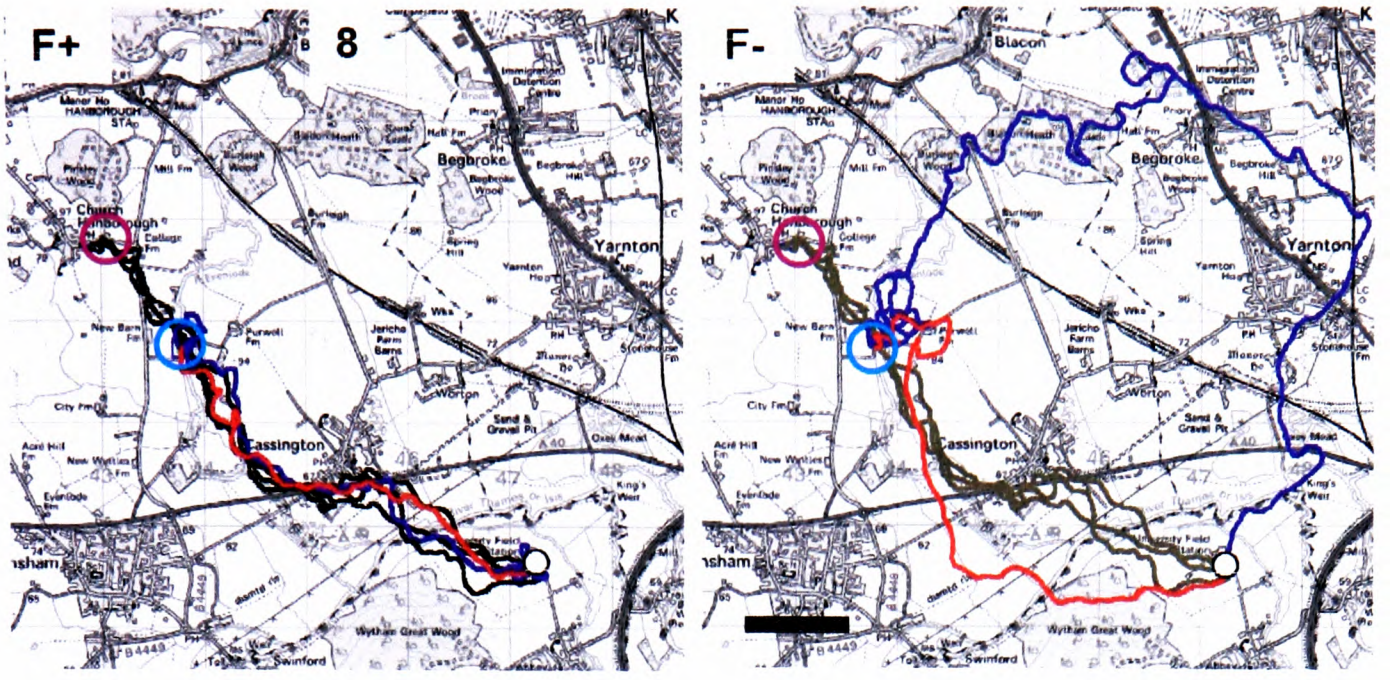


Figure 4.4 shows the data for both efficiency of the entire flight, and distance flown within a 1 km radius of the release site, plotted as 2 graphs. Squares indicate aerially familiar (F+) birds and diamonds indicate unfamiliar (F-) birds. Open symbols indicate releases where a 5 min preview is given, and closed symbols indicate releases from an opaque box.

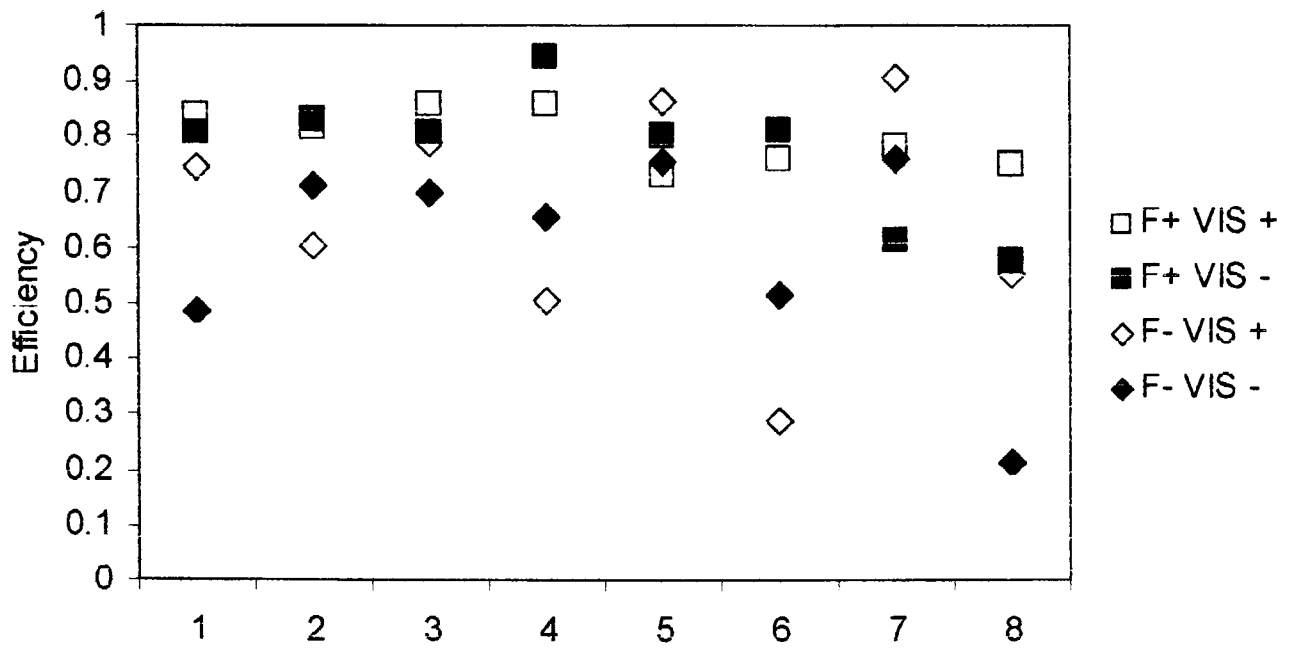
Again I found that the variable "Bird" was significant both for the efficiency data and for the distance flown within 1 km of the release site. This indicates that individual birds performed consistently differently, which accounted for much of the variation found.

I found that birds that had previously flown over the sites (F+) homed significantly more efficiently (an increase of 28 %), and left the release site more quickly, than those that had not (F-). The interaction between group and treatment was not significant for either measure. This shows that birds that had flown over the release site many times did not gain a greater advantage from being given a preview of their surroundings than the inexperienced birds.

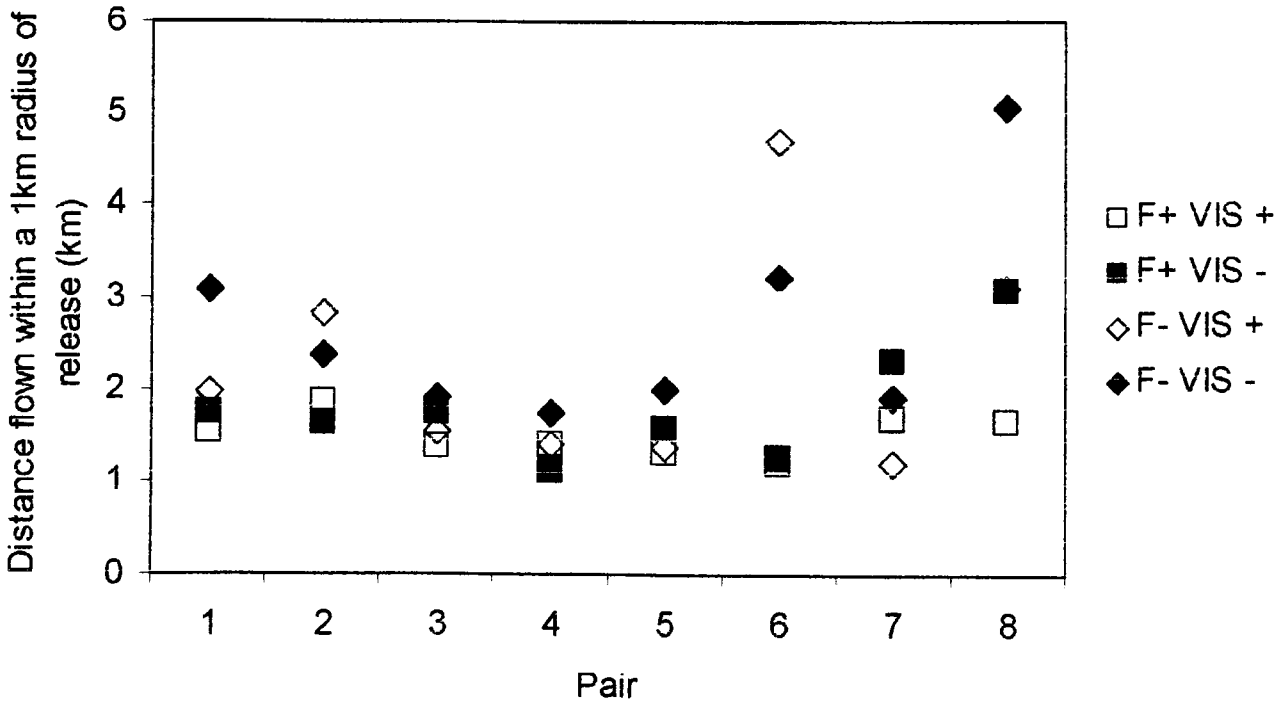
The variable "release number" was found to be significant in this experiment, both for the efficiency data for the entire flight, and for the distance flown within a

Figure 4.4 Graphs showing (a) the homing efficiency and (b) distance flown within a 1 km radius of the release site, in experiment 4.2. Squares indicate aerially familiar (F+) birds and diamonds indicate unfamiliar (F-) birds. Open symbols indicate preview (VIS+) conditions and closed symbols indicate no-preview (VIS-) conditions. Pairs of birds were released from the same location.

(a)



(b)



1 km radius of release. Birds on their second release of the day homed significantly more quickly and left the release site more quickly than on their first release of the day.

The variable "treatment" (whether or not birds received a 5 min preview before release) had a significant effect when the distance flown within 1 km of release was examined. This means that the treatment before release had a similar effect on both birds that had over-flown the release site and birds that had not. Birds that had had a 5 min preview of the site left the vicinity of the release site significantly more quickly than those that had not. Treatment was no longer found to be significant when data for the whole flight was examined (see Table 4.2 for results of GLMs).

Table 4.2 Results of General Linear Models performed on both efficiency data and distance flown within 1 km of the release site. *s indicate significant results.

Variable	DF	F	P
Efficiency of entire flight			
Bird	14	4.95	0.003*
Group	1	28.64	0.000*
Treatment	1	1.91	0.190
Group*Treatment	1	0.3	0.594
Release Number	1	12.06	0.004*
Distance flown within 1 km of release			
Bird	14	8.26	0.000*
Group	1	38.23	0.000*
Treatment	1	12.81	0.003*
Group*Treatment	1	0.69	0.422
Release Number	1	11.94	0.004*

4.4 GENERAL DISCUSSION

I performed two experiments designed to investigate the role of visual landmarks along a pigeon's homeward route. In the first experiment birds were released with and without a 5 min preview from sites that they were known to have flown over at least once, and in the second experiment birds were released from sites they were known to have flown over at least six times and which formed part of a habitual homeward route (Meade et al., 2005; also see Chapter 2). In both experiments less experienced birds were used as controls.

In experiment 4.1 I found that birds that had previously over-flown the chosen release sites at least once, homed more efficiently than their naïve partners, though the result was not quite significant ($p = 0.054$). This, coupled with the observation that aerially familiar birds once released from the box tended to perform routes either similar to their training release or similar across box releases, strongly hints that birds aerially familiar with a release point were able to utilise information gathered in their previous flight in order to home more efficiently, though perhaps they could only gain this information once airborne. Experiment 4.2 further confirmed this result; birds that had over-flown the release sites at least six times homed significantly more efficiently, and left the release site significantly more quickly, than birds that had not previously over-flown the sites. This first finding suggests that recognition of the previously flown route must have occurred at least somewhere between the experimental release site and approach to home, and the second finding establishes that recognition occurred as early as within 1 km of the site. This is again supported by the observation that in almost every case aerially familiar birds' flights from the release box were very similar both to each other, and to their established routes. It is

possible therefore that F+ birds did in fact recognise the release site, but only after they had left the release box and acquired an aerial view of the location.

It has been shown in previous studies (Braithwaite & Guilford, 1991; Braithwaite, 1993; Burt et al., 1997; Biro et al., 2002; Biro et al., 2003) that a 5 min view of an array of familiar landmarks before release resulted in a significant homing advantage, when compared to homing performance of birds denied such a preview. It has also been shown that birds do not gain the same homing speed advantage when given a preview of an unfamiliar site (Braithwaite & Newman, 1994). An increase in homing speed following a view of the landscape before release can therefore be interpreted as an indication that a bird is "familiar" with the landscape of the release site. In neither experiment reported in this chapter was an interaction found between Group (indicating whether a bird was aerially familiar (F+) or naïve (F-)) and Treatment (whether or not the birds received a 5 min preview of the landscape before release). This indicates that the aerially familiar birds did not recognise areas which they had previously flown over, from ground level. The possible causes of this recognition failure are discussed later in this section.

In experiment 4.2 it was found that a 5 min preview of the site before release caused both aerially familiar and unfamiliar of birds to leave the 1 km radius of the release site more quickly than birds that had not had a 5 min preview. No significant result was found when efficiency for the entire flight was examined. It is unlikely that non-specific motivational effects (i.e. increased motivation to home when given a view of the landscape regardless of whether it is familiar) are the cause, as the effect was not found in experiment 5.1 for either group (a view supported by Braithwaite & Newman's original experiments (1994)). Another possibility is that there may have been some more distant feature visible to birds in the second set of releases that

attracted them away from the site immediately on release which, although not necessarily a familiar landmark, was seen as attractive to both F+ and F- birds in the preview period. It is quite common, for example, for birds to be attracted to villages or smaller settlements soon after release (Kiepenheuer, 1993). The true cause of this effect however, cannot be determined from the current results.

The main finding of the two experiments is that having flown over a release site allows birds to home more efficiently than birds that were not known to have over flown the sites. This implies that birds become "familiar" with a large number of points along a homeward route, so much so, that it endows a substantial homing advantage when subsequently released from one of these points. From experiment 4.2 I cannot be certain which cues the birds are using in order to recognise that they have previously over-flown the sites. If, however, vision is involved as a cue for site recognition (as it is known to be when birds are released from the ground) it seems likely that a homing advantage does not occur when a preview of the landscape is provided because the birds are unable to recognise sites that they have seen from the air from the substantially different view-point of ground level. Previous experiments on homing pigeons have also suggested that recognition failure can occur when birds are presented with substantially different views of the same release site (Biro et al., 2003). Insects (Rosengren, 1971; Collett et al., 1992; Dyer, 1991) and more recently chickens (Dawkins & Woodington, 2000) are thought to follow stereotyped routes in order to encounter landmarks from familiar orientations, and this is also a possible explanation for why pigeons develop the highly stereotyped individual homing routes recently found in related studies (Biro et al., 2004; Meade et al., 2005; see chapters 2 and 3). It is possible that the lack of recognition of landmarks from novel viewpoints reflects a limitation of the avian visual processing system, which may have profound

implications for visually guided navigation strategies in birds, as it does in insects. These possible implications are discussed further in section 6.2.

CHAPTER 5

Tracking clock-shifted birds

5.1 INTRODUCTION

5.2 EXPERIMENT 5.1:

5.2.1 Introduction

5.2.2 Methods

5.2.2.1 Subjects and Procedure

5.2.2.2 Analysis

5.2.3 Results

5.2.4 Discussion

5.3 EXPERIMENT 5.2:

5.3.1 Introduction

5.3.2 Methods

5.3.3 Results

5.3.4 Discussion

5.1. INTRODUCTION

The mechanism of pigeon homing is traditionally described as a two-stage process. In the first stage, the "map step", a bird determines its position with respect to home, and in the second stage, the "compass step", the bird determines the direction it must fly in to reach home. As discussed in section 1.2.2, the time compensated sun compass is the dominant compass system used by pigeons. The use of the sun compass has been demonstrated by the procedure of clock-shifting; where birds kept in light-tight conditions have their light-dark cycle artificially shifted by several hours. This causes birds to misread their compass upon release, resulting in a predictable deflection of initial orientation compared to control birds, traditionally characterised by recording vanishing bearings.

When birds are released from unfamiliar distant locations, an olfactory map is likely to be used to determine position with respect to home (Papi, 1992, also see section 1.2.1), after which a compass is used to assume the homeward direction. If a bird is released under clock-shift conditions from such a site, conflict between the homeward direction as indicated by the shifted sun compass and the true homeward direction may not be immediately apparent. An olfactory map is necessarily a "point map", and thus freely rotatable, as birds can only perceive the smells available where they are, not which smells are available in the distance, so such a map provides no inherent directional information (Wallraff, 1991). In a familiar area however, birds have a further set of cues available to them; familiar visual landmarks.

Pigeons have been shown to be able to home more quickly from familiar release sites, when given a view of the landscape before release (Braithwaite & Guilford, 1991; Burt et al., 1997; Gagliardo et al., 2001; Biro et al., 2002), though it is not known

exactly how these familiar visual landmarks are used to aid homing. There are currently two hypotheses as to how they might be used. The first involves memorising site-specific visual information, which is then used to recall the homeward bearing from the release site. This was first referred to as a "mosaic map" by Wallraff (1974) and also as a "point map" (Wallraff, 1991). In this model the possible directional information provided within an array of landmarks is not used; the landmarks are used purely for site recognition. Secondly, the landmarks themselves could be used to specify the homeward direction and birds could orient homeward using the remembered relationships between visual landmarks, without reference to a compass system. This is referred to as piloting (Papi, 1992). There is some evidence (Gagliardo, 1999; 2002) that pigeons are able to utilise familiar landmarks in both of these ways (see section 1.3.1).

In theory, performing clock-shift experiments from familiar release sites should clarify which hypothesis more accurately describes the mechanisms used by pigeons when homing from previously visited sites. Many experiments however, have provided contradictory evidence. Experiments releasing birds extremely familiar with a release site under clock-shift conditions have sometimes resulted in birds' headings being deflected by the full expected degree (Füller et al.1983; Luschi & Dall'Antonia, 1993), which has been taken as evidence that familiar visual landmarks at a release site are used only to recall the homeward bearing. Other experiments involving clock-shift from familiar release sites have indicated that pigeons are unaffected by the treatment, and have been interpreted as evidence of visual landmarks being used without the aid of a compass (Bonadonna et al., 2000; Holland et al., 2000), though often when their olfactory map had been made unavailable via anosmia (Bingman & Ioalè, 1989; Gagliardo et al., 1999, 2005) and also when released in direct sight of the home loft (Graue, 1963). Clock shift experiments performed at familiar release sites often result in

increased scatter and reduced deflection, and this could also be attributed to a conflict between the homeward direction as indicated by the sun compass and the homeward direction as indicated by familiar landmarks (see Chappell, 1997 for a review).

The experiments reported above involved recording the vanishing bearings of clock-shifted homing pigeons and comparing them to those of un-shifted control birds. This methodology would not necessarily allow experimenters to distinguish whether different birds were using different strategies in order to home (i.e. some using memorised homeward bearings, and some piloting via landmarks), whether birds were taking intermediate headings (averaging the direction indicated by familiar landmarks with that indicated by the shifted sun-compass), or whether birds initially move off in a shifted direction but recognise conflict with ground features and begin to correct their heading before vanishing, resulting in a reduced shift. In this chapter I report two experiments where birds are tracked under clock-shift conditions from familiar sites, using GPS loggers. In the first experiment birds were released from sites which they had previously visited at least twice under a one hour phase shift. In the second experiment of the chapter, birds that had established highly stereotyped homeward routes from various sites, were released under a four hour phase shift, and their performance compared to that of less experienced control birds.

5.2. EXPERIMENT 5.1:

5.2.1 INTRODUCTION

The experiment in the first part of this chapter details the first reported time that clock-shifted birds have been tracked using GPS technology. Two groups of pigeons were

released from familiar sites; one un-shifted control group, and one group that had experienced a one-hour phase shift relative to the natural light-dark cycle. The rationale for this experiment was to determine whether this small degree of phase shift would lead to a detectable difference between the performance of the clock-shifted birds and un-shifted control birds.

This experiment was designed to complement experiment 5.2 where birds that had developed highly stereotyped routes are released under a 4 hour phase shift (leading to an expected deflection of ~ 90°), in an attempt to determine how familiar visual landmarks are encoded into a bird's homeward route. If birds were able to accurately recapitulate their stereotyped routes under the clock-shift treatment, this would imply that birds were progressing between successive waypoints via visual attraction (as suggested in section 3.4) without reference to a compass system. If, however, birds fail to accurately recapitulate their established routes, this could be explained in two ways. First, the links between waypoints could be encoded as bearings or vectors (see section 5.3.1 for more details), thus requiring birds to use their sun-compass to progress between waypoints. Second, birds might not accurately recapitulate their established routes because of a lack of release site recognition due to the dramatic change in the expected position of the sun relative to the other visual landmarks caused by the 4-hour phase shift. For example, a bird has become extremely familiar with travelling homeward from a site where at 9.00 am the sun is e.g. shielded by tall trees. If the bird is subsequently released from the same site under a 4-hour phase shift, at 9.00 am in the bird's subjective daytime the sun's azimuth will be shifted by 90° and will e.g. no longer be shielded by the trees. This large discrepancy between the actual and expected position of the sun relative to other familiar landmarks used for site recognition, may cause birds not to recognise the site as familiar.

This second explanation could potentially be eliminated by releasing stably route-recapitulating birds under a 1 hour phase shift, thereby reducing the discrepancy between the shifted position of the sun relative to other familiar landmarks, making site recognition more likely to occur. If birds with established stereotyped routes continued to be deflected under a 1-hour phase shift, this would strongly suggest that the sun-compass was essential for recapitulating stereotyped routes, without the possible confounding factor of a lack of release site recognition. The current experiment was therefore performed to determine whether this small degree of shift would result in a detectable difference, when the performance of non-route-recapitulating birds phase shifted by one hour was compared to that of un-shifted controls.

5.2.2 METHODS

5.2.2.1 *Subjects and Procedure*

Sixteen homing pigeons were selected as subjects. All were at least 2 years old, > 450 g in weight, and had been used in previous experiments involving GPS tracking. All birds were fitted with a Velcro strip as detailed in chapter 2. Birds were left for 1 day after application of the Velcro strip, and observed to ensure their movement was not restricted in any way, either in the air or on the ground. The following day birds were fitted with 25 g plasticine weights, attached to the Velcro strip, and again monitored to ensure their movement was unrestricted. Following these two days, birds were taken to a variety of release sites, initially at distances of < 2 km, increasing to 7 km from home (see appendix 2 for details). The birds were then given two releases from the first test site, Friar's Farm (Distance to home: 7.1 km, Direction to home: 63.7°). Having completed two test flights from Friar's Farm the birds were placed in the Clock-Shift loft at

Wytham Field Station. The loft consisted of two light-tight chambers with ventilation via fans. Birds were provided with food, water and grit ad libitum. The 16 birds were randomly split into two groups, eight control birds were put into one chamber and the lights were turned on and off at the same time as natural sunrise and sunset. The second set of eight birds were placed in the second chamber, and the lights were turned on one hour later than natural sunrise, and turned off one hour later than natural sunset. This phase shift should have resulted in an approximately 15° clockwise shift in the birds' heading upon release (see table 5.1 for more details). The birds remained in the clock-shift facility for three days.

On the morning of the fourth day, the birds were transported in aluminium carrying boxes to the release site. The box was covered by a black sheet so that the birds could not see the position of the sun on the outward journey. At the release site birds were fitted with GPS trackers, and released singly. Birds were followed using binoculars (10 x 40 magnification) after release, and the next bird wasn't released until 5 minutes after the preceding bird had been lost from sight. This was carried out to reduce the possibility of birds pairing up in flight.

The next day birds were given two training releases from the second test release site; Sescut Farm (Distance to home: 5.9 km, Direction to home: 261°). Following two successful training releases the birds were returned to the clock-shift loft. The two groups of birds were switched, such that the birds that had not been phase shifted in the previous release received a phase shift treatment for the second release. Again the light-dark cycle was shifted by one hour; the lights were turned on one hour after natural sunrise, and off one hour after natural sunset. The birds that had been phase shifted in the previous release were placed in the second chamber, and the lights were turned on and off at the same time as natural sunrise and sunset. This meant that each bird only

underwent the clock-shift treatment once during the experiment. Again the birds remained in the clock-shift loft for three days. On the fourth day, birds were transported to the test release site (Sescut Farm), and the same procedure as performed at Friar's Farm was repeated.

Table 5.1 Table showing the times birds were released from different sites under different conditions, for both experiments 5.1 and 5.2, and the expected degree of shift.

Release Site	Date	Sunrise	Sunset	Phase Shift	Release times	Range of expected shift	Average expected shift
Friar's Farm	19/4/04	6.00	20.10	1 hour late	10.14 - 13.13	14.3° - 22.3°	18.3°
Sescut Farm	24/4/04	5.50	20.18	1 hour late	10.00 - 12.30	14.1° - 21.5°	17.8°
Bladon Heath	8/6/04	4.48	19.21	4 hours early	9.08 - 12.04	95.8° - 82.5°	89.15°
Hinksey Heights	5/8/04	5.35	20.47	4 hours early	9.46 - 14.45	96.0° - 51.5°	73.75°
High Cogges	19/7/04	5.10	21.13	4 hours early	9.10 - 12.56	91.6° - 68.1°	79.85°
Weston Wood	25/6/04	4.48	21.28	4 hours early	8.55 - 11.35	94.1° - 83.8°	88.95°

5.2.2.2 *Analysis*

To analyse the tracks "virtual vanishing bearings" (Biro et al., 2002) were recorded; these were the bearings from the release site to each track at increasing straight-line distances from the release site. The bearings were recorded the first time a bird crossed boundaries from the release site of 500 m, 1000 m, 1500 m etc, until the distance between release site and the home loft was reached.

At each distance the mean bearing and mean vector for both groups were calculated. The data were normalised so that home direction for both release sites was set to 0°. The mean bearing indicates the average direction of each group from the release site, and the length of the mean vector indicates the degree of scatter, with a short vector length indicating high levels of scatter. Rayleigh tests were performed to

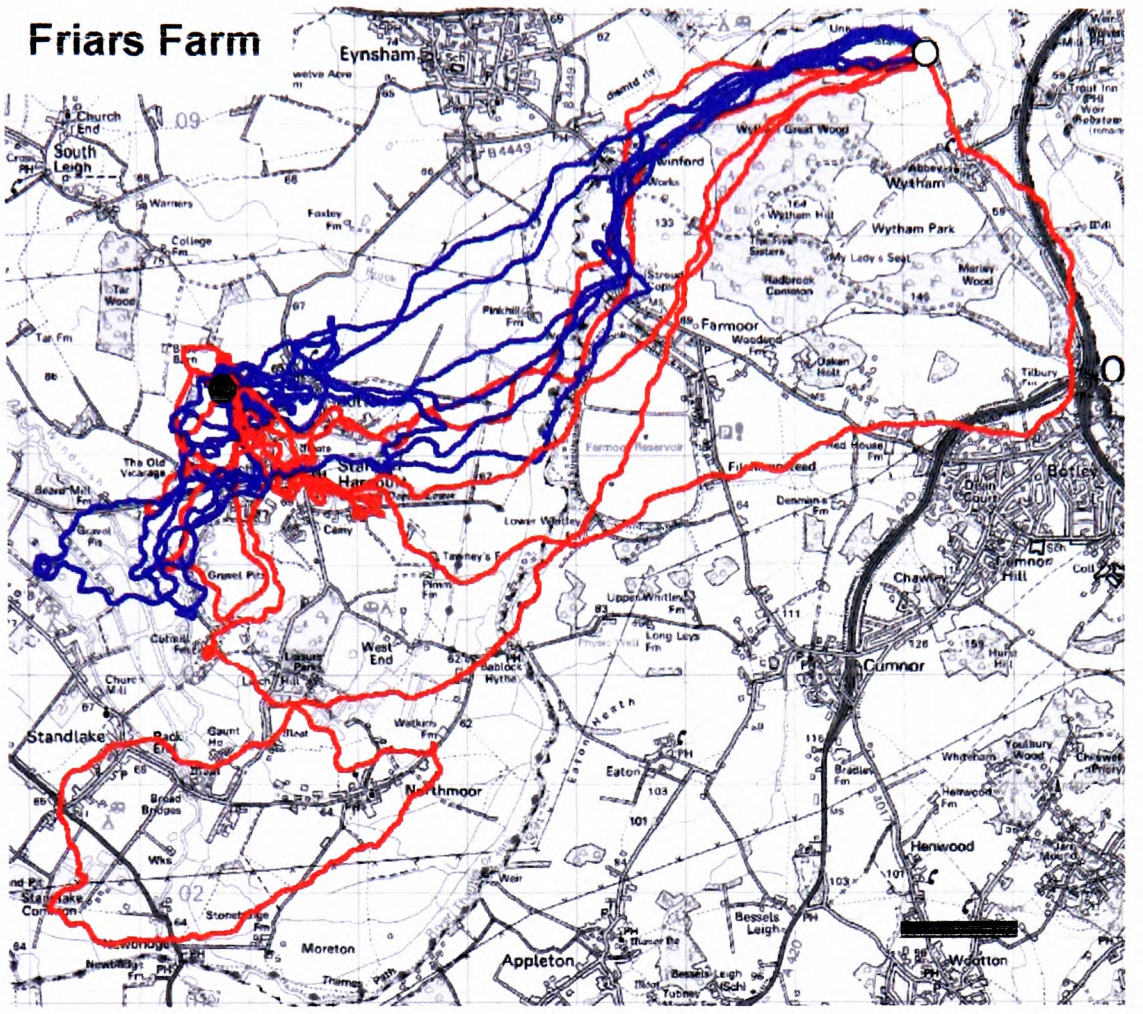
test whether the groups were significantly orientated. 95 % confidence intervals for each data set were also calculated to test whether the groups of birds were homeward oriented (if the interval includes 0° this indicates that the group is significantly homeward oriented). Mardia-Watson-Wheeler tests were used to investigate whether there was a significant difference between the virtual vanishing bearings of the control and experimental groups at each straight-line distance from the release site.

5.2.3 RESULTS

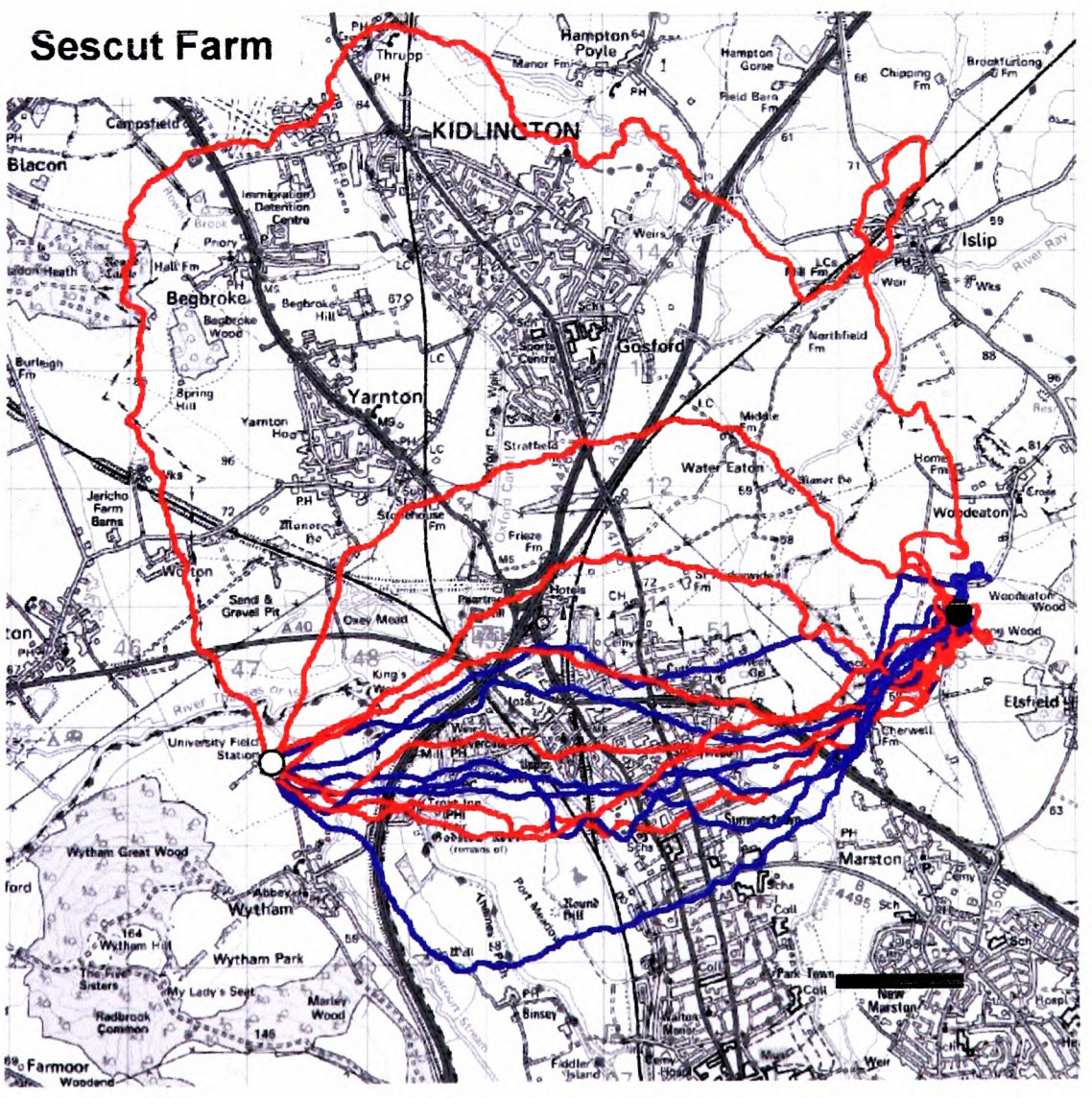
Figure 5.1 (a) shows the tracks performed by control birds (in blue) and birds released under clock-shift conditions (in red) from Friar's Farm. Two trackers in both the control and experimental (clock-shifted) group stopped working as the birds were released, and one of the birds in the clock-shift group's tracker ran out of power before the bird reached home. Therefore there are six complete tracks for the control group and five complete tracks for the experimental group. The birds that experienced a 1 hour slow phase shift (which is expected to lead to a clockwise shift of ~15° see table 5.1 for further details) took routes distributed to the clockwise side of the routes taken by the control birds, though there is some overlap between the two groups. Figure 5.1 (b) shows the release from Sescut Farm; control birds' tracks are shown in blue, and the experimental birds' tracks (released under a 1 hour clockwise shift) are shown in red. Seven tracks of clock-shifted birds were successfully recorded, and six tracks for control birds were recorded. Again the phase shift was expected to lead to an ~15° clockwise shift. In this release the experimental (clock-shifted) birds' tracks are more widely

Figure 5.1 Maps showing releases from (a) Friars Farm and (b) Sescut Farm. Blue tracks indicate flights by control birds, red tracks indicate flights by experimental birds phase shifted by 1 hour in the clockwise direction. Black dots represent release sites, white dots indicate the home loft. 1 km scale bars are included on each panel.

a



b



dispersed, with three birds taking routes shifted further in the clockwise direction than any of the control birds, but with the remaining four experimental birds' routes interspersed amongst those performed by control birds.

Table 5.2 shows the results of circular statistics performed on the data (control groups' results at the top of each cell, clock-shifted group below in bold) for each group at each distance. The table includes the mean bearing and vector, the results of the Rayleigh test for directedness, the 95% confidence intervals (where birds are homeward directed the interval includes 0°) and the results of Mardia-Watson-Wheeler tests for a significant difference in heading direction between the two groups. The results for both release sites are standardised so that a bearing of 0° indicates the home direction.

From Friar's Farm the clock-shift group is significantly orientated throughout, but not significantly homeward oriented until 3500 m from the release site. Before this distance the experimental group is deflected in the clockwise direction, as predicted by the clock-shift treatment. The control group becomes significantly oriented at 2500 m from the release site, and the 95% confidence interval for the control group is within 1° of the homeward direction at every distance measured. From 4500 m onwards the control group become extremely tightly clustered making the calculation of the 95% confidence intervals unreliable. This clustering probably occurs because all the birds fly around the edge of Wytham hill (see Figure 5.1), nevertheless the mean bearing over this period ranges from 355-359° indicating a high level of homeward directedness. The results of Mardia-Watson-Wheeler tests show that at various points along the homeward journey (500, 1500, 4000, 5500, 6000, 6500 m) there is a significant difference in heading between the control and clock-shifted groups. The clock-shift group is consistently shifted to the clockwise side of the control group throughout the homeward

Table 6.2 The table shows the directedness and distribution of both the control group (top) and the clock-shifted group (bottom in bold) at increasing distances from both release sites. The Rayleigh P statistic indicates whether the groups of birds are significantly orientated. All values are normalised so that the home direction is 0°. An H indicates that the 95% confidence interval includes the home direction. Results of Mardia-Watson-Wheeler tests for a bearing difference between control and experimental groups are included. Significant values are indicated by *s.

	Distance from release site (m)	Mean Vector (μ)	Mean Vector length (r)	95% confidence interval		Rayleigh P Value	M-W-W P Value
Friar's Farm	500	52.2°	0.606	0.8° - 103.5°		0.108	0.050*
		84.5°	**0.814**	**45.7° - 123.4°**		**0.012***	
	1000	39.2°	0.487	326.3° - 112.1°	H	0.250	0.820
		81.9°	**0.843**	**46.3° - 117.4°**		**0.008***	
	1500	50.1°	0.500	340.7° - 119.5°	H	0.228	0.011*
		70.8°	**0.827**	**33.5° - 108.2°**		**0.010***	
	2000	47.7°	0.521	342.2° - 113.2°	H	0.202	0.820
		66.2°	**0.824**	**28.5° - 104.0°**		**0.010***	
	2500	17.0°	0.963	0.3° - 33.8°		0.000*	0.368
		53.4°	**0.853**	**13.2° - 93.6°**		**0.017***	
	3000	13.2°	0.979	0.8° - 25.7°		0.000*	0.368
		44.7°	**0.866**	**6.5° - 82.9°**		**0.014***	
	3500	6.3°	0.989	357.3° - 15.4°	H	0.000*	0.368
		36.2°	**0.836**	**353.6° - 78.8°**	**H**	**0.021***	
	4000	358.1°	0.999	355.3° - 0.9°	H	0.000*	0.018*
		28.4°	**0.848**	**347.5° - 69.3°**	**H**	**0.018***	
	4500	355.6°	0.999			0.000*	0.223
		23.2°	**0.759**	**330.6° - 75.8°**	**H**	**0.047***	
	5000	355.4°	0.999			0.000*	0.820
		20.3°	**0.698**	**335.5° - 65.8°**	**H**	**0.082**	
	5500	355.2°	0.999			0.000*	0.018*
		3.8°	**0.973**	**346.9° - 20.7°**	**H**	**0.002***	
	6000	355.8°	0.999			0.000*	0.018*
		3.9°	**0.977**	**348.6° - 19.2°**	**H**	**0.002***	
	6500	357.0°	0.999			0.000*	0.018*
		4.9°	**0.980**	**350.5° - 19.4°**	**H**	**0.002***	
	7000	358.6°	0.999			0.000*	0.368
		5.7°	**0.980**	**351.3° - 20.0°**	**H**	**0.002***	
Sescut Farm	500	343.4°	0.833	306.6° - 20.1°	H	0.009*	0.135
		343.0°	**0.663**	**302.2° - 23.7°**	**H**	**0.040***	
	1000	329.6°	0.992	321.9° - 337.2°		0.000*	0.135
		352.8°	**0.699**	**315.6° - 30.1°**	**H**	**0.026***	
	1500	329.1°	0.965	312.8° - 345.4°		0.000*	0.607
		2.3°	**0.724**	**319.2° - 45.4°**	**H**	**0.019***	
	2000	331.4°	0.969	316.2° - 346.7°		0.000*	-
		6.6°	**0.779**	**328.9° - 44.4°**	**H**	**0.009***	
	2500	337.3°	0.972	322.9° - 351.7°		0.000*	-
		10.3°	**0.795**	**334.1° - 46.5°**	**H**	**0.007***	
	3000	342.6°	0.974	328.5° - 356.6°		0.000*	0.607
		10.3°	**0.812**	**335.8° - 44.9°**	**H**	**0.005***	
	3500	346.2°	0.973	332.0° - 0.5°	H	0.000*	0.607
		1.2°	**0.835**	**329.0° - 33.4°**	**H**	**0.003***	
	4000	349.8°	0.980	337.6° - 2.0°	H	0.000*	0.607
		9.9°	**0.833**	**337.5° - 42.3°**	**H**	**0.004***	
	4500	350.4°	0.986	340.0° - 0.8°	H	0.000*	0.223
		7.9°	**0.900**	**343.1° - 32.7°**	**H**	**0.000***	
	5000	351.3°	0.989	342.3° - 0.2°	H	0.000*	0.223
		7.2°	**0.910**	**343.8° - 30.7°**	**H**	**0.000***	
	5500	354.2°	0.999			0.000*	

journey, with the amount of shift gradually decreasing as the birds get closer to the home loft.

From Sescut Farm both groups are significantly orientated throughout. Interestingly the control birds are not significantly orientated in the homeward direction until 3500 m from the release site. Most of the control birds set off in a direction ~ 30° anticlockwise of the home direction, and all pass over the farm buildings which lie in this direction. This means that the clock-shifted birds, though deflected in the clockwise direction with respect to the control birds, are significantly homeward orientated from the start. No significant difference was found between the two groups at any point along the homeward flight.

5.2.4 DISCUSSION

This study utilised GPS trackers to investigate the effect of a 1 hour phase shift on the flight paths of birds released from two different sites, from which they had received two training releases. Thus far there has been no published data on the flight paths of clock-shifted birds recorded using GPS trackers. In this experiment the flight paths of birds that had been slow-shifted by 1 hour (resulting in an expected deflection of ~15° in the clockwise direction, see table 5.1 for more details) were compared to those of control birds, which had experienced a light-dark cycle corresponding to natural sunrise and sunset.

Despite the small degree of expected shift, the average heading of clock-shifted birds from both sites (virtual vanishing bearings, see table 5.2) was shifted consistently to the clockwise side of the control birds, and from one of the two release sites (Friar's Farm) significant differences between the two groups were found.

The reasons for performing an experiment involving such a small degree of phase shift were twofold. As this was the first time that I had performed an experiment involving clock shift, and this was the first time that the new clock-shift facility at Wytham Field Station had been used, I wanted to gain experience with the procedure of clock-shifting, whilst keeping the possibility of losing birds to a minimum. Secondly I wanted to demonstrate that a one-hour phase shift could result in a detectable deflection of experimental birds compared to un-shifted controls. As explained in section 5.2.1, this experiment was designed as a pilot study for a potential follow-up to experiment 5.2 (the following experiment), in which birds that had developed highly stereotyped routes were released under a four-hour clock-shift treatment (leading to an expected shift of ~90°). If the birds in experiment 5.2 were deflected by the clock-shift treatment, this could indicate that birds were relying on the sun-compass in order to progress down their stereotyped routes, but a possible confounding factor might be that birds are unable to recognise the release sites as familiar, due to the large change in the expected position of the sun relative to other familiar visual landmarks. Such a lack of recognition would cause birds to navigate homeward as if from an unfamiliar site (in the deflected direction). When birds are subjected to only a one-hour phase shift, the change in the sun's position relative to other familiar visual landmarks would be small, thus reducing the possibility that the release site would not be recognised.

In the following experiment, stably route-recapitulating birds are subjected to a four-hour phase shift, in order to determine what effect this 90° expected deflection will have on their ability to recapitulate their established routes. It can then be determined whether it would be necessary to release stably route-recapitulating birds under a smaller degree of phase shift.

5.3 EXPERIMENT 5.2:

5.3.1 INTRODUCTION

In chapter 2 the phenomenon of route-recapitulation (Meade et al., 2005) at short distances (~5 km) was introduced, and it was hypothesised that the accurate route-recapitulation found was likely to depend on the use of familiar visual landmarks. This was further confirmed by experiments involving releases at 10 km (Biro et al., 2004) and 25 km (see Chapter 3). Birds were shown to accurately recapitulate individually distinctive routes from these distances. Furthermore, when released at novel sites perpendicularly displaced (1-3.7 km) from their established routes, birds were able to fly to and rejoin these routes. This showed that birds were able to perceive, accurately assess, and use route cues from these distances, lending weight to the theory that the relevant cues dictating the routes were familiar visual landmarks. The question as to how these familiar visual landmarks are used by the birds to perform the observed stereotyped routes remains open to discussion.

Following the experiments mentioned above involving displacements to novel sites "off-route", the hypothesis was put forward that familiar visual landmarks along the homeward route act as "waypoints"; a certain number of discrete points that a bird flies to in order, making up a homeward route with a characteristic shape. Insects performing set routes have been shown to divide routes into shorter segments controlled by "local vectors" (in ants: Collett et al., 1998; in bees: Collett et al., 2002). These local vectors were shown to be triggered in sequence, by a view of familiar landmarks acting as intermediate goals. It is possible that pigeons encode the space between waypoints in a similar way to insects; as vectors (including distance and direction), alternatively birds

could travel between waypoints referring to remembered bearings (direction only), or finally, birds could proceed down an established route from waypoint to waypoint using visual attraction without reference to a compass (the off-route releases in Chapter 3 demonstrated that the birds are able to perceive the cues that make up their stereotyped routes from distances of 1-3.7 km).

In the second experiment of this chapter I investigate the possibility of compass-independent homing by releasing stably route-recapitulating homing pigeons under clock-shift conditions, and I attempt to relate the findings to previous experiments involving clock-shift detailed in sections 1.3.1 and 5.1.

5.3.2 METHODS:

A total of 35 birds were chosen as subjects. All were > 2 years old and > 450 g in weight. All had previously taken part in GPS tracking experiments. All birds were fitted with Velcro strips as detailed in the methods section of chapter 2. Once birds had become accustomed to the Velcro strip (unrestricted movement in the air and on the ground), a 25g plasticine weight was attached via the Velcro. Birds were allowed 1 day to get used to carrying the weights in and around the lofts. Following this time period, birds were released from sites less than 2 km from the home loft in varying directions. The distances were gradually increased in the training phase (see appendix 2 for more details). Birds wore the weights at all times during the remainder of the experiment unless wearing a tracking device.

Four release sites were chosen; two shorter distance sites: Bladon Heath (Distance to home: 5.1 km, Direction to home: 151°) and Hinksey Heights (Distance to home: 5.2 km, Direction to home: 331°), and two longer distance sites: High Cogges

(Distance to home: 9.4 km, Direction to home: 89°) and Weston Wood (Distance to home: 10.7 km, Direction to home: 221°). The two sites in each pair were situated in approximately opposite directions. Training and test releases were carried out at each of the release sites in turn.

First, eight subjects, selected as experienced route-recapitulating birds, were given 20 training releases in quick succession, the final five of which were tracked in order to ensure they had developed stereotyped routes. Eight further birds received four training releases, the last of which was tracked (The experiments reported in Chapter 2 suggest that four training releases is not sufficient for birds to develop stereotyped routes). After this training procedure, the 16 birds (eight route-recapitulating birds, eight non-route-recapitulating birds) were placed in the clock-shift loft. Both groups received the same treatment. The light-dark cycle was shifted so that the lights came on an hour earlier each day, this was increased until the lights came on four hours before natural sunrise, and went off four hours before natural sunset. This phase shift led to a predicted deflection upon release of approximately 90° in the anticlockwise direction (see table 5.1 for more details). The birds remained in the clock-shift lofts for five days.

On the morning of day following the confinement in the clock-shift loft, both the route-recapitulating and control birds were transported to the selected release site in an aluminium carrying case covered with a black sheet, so that birds were unable to see the position of the sun before release. Birds were fitted with GPS trackers and released in random order. Each bird was followed using binoculars (10 x 40 magnification) until vanishing and the next bird was not released until 5 minutes after the previous one disappeared from view.

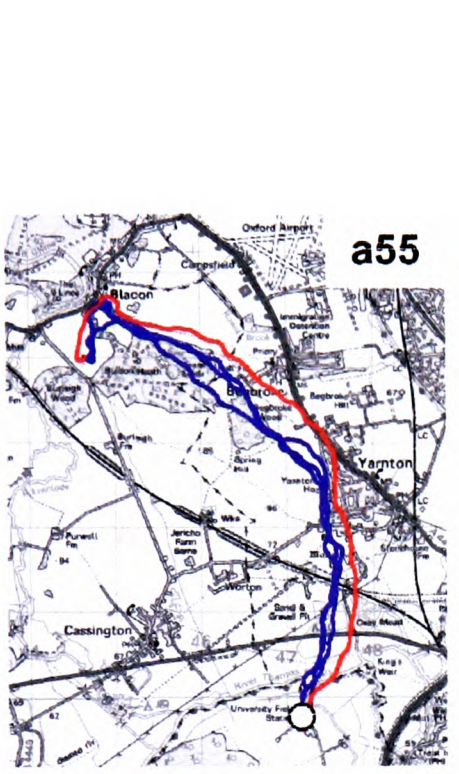
This procedure was repeated for each of the four selected sites. Eight birds acted as experienced route-recapitulating birds from both Bladon Heath and Hinksey Heights

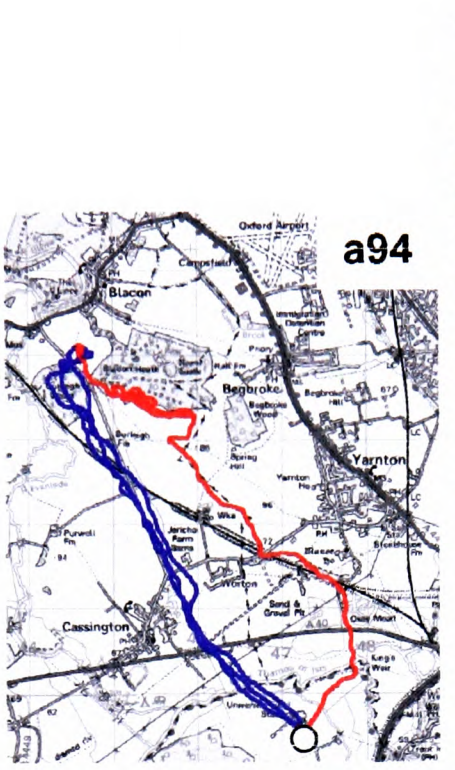
(the two shorter distance sites), and eight different birds acted as experienced route-recapitulating birds from High Cogges and Weston Wood (the two longer distance sites). The remaining 19 birds were randomly selected to act as less experienced control birds from the four sites. Birds were not released from a new site until the releases from the previous site had been completed. Individual birds were subjected to the clock-shift treatment no more than twice, and at least 12 days elapsed in-between time spent in the clock-shift lofts.

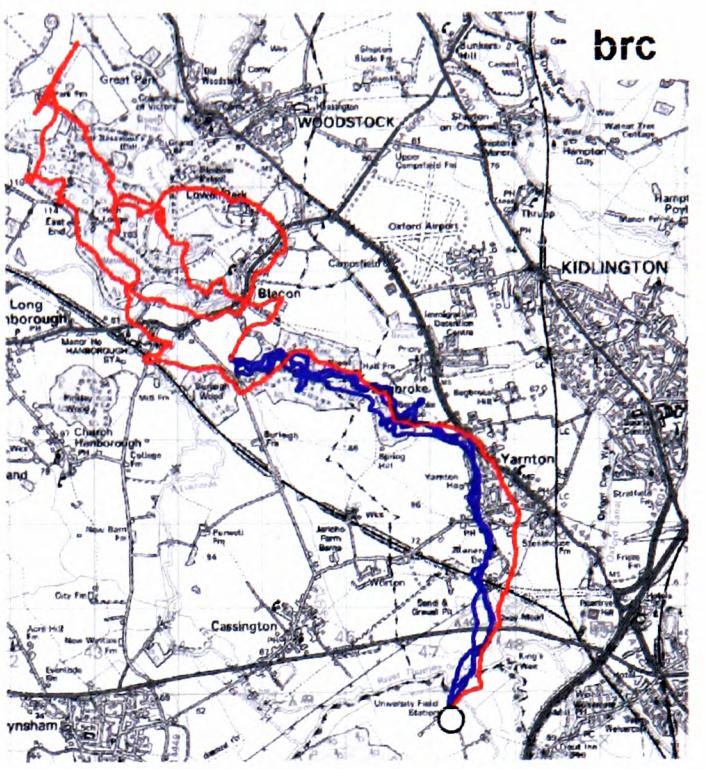
5.3.3 RESULTS

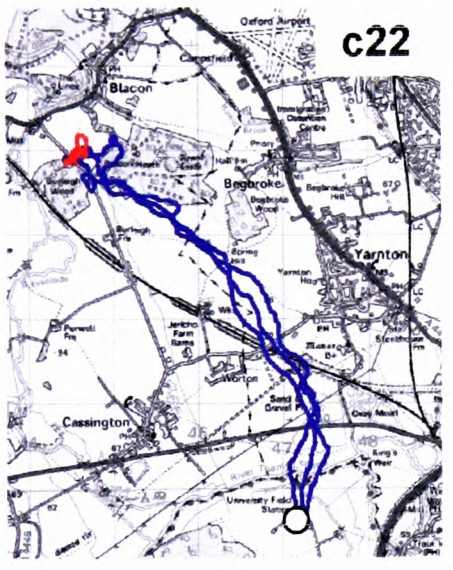
Figure 5.2 shows the tracks performed by route-recapitulating birds released at Bladon Heath (5.1 km from home). The final three tracks performed are shown in blue to illustrate the birds' established routes, and the flight performed under clock-shift is shown in red. Of the seven birds from which a clock-shifted track is available (c22 sat down shortly after release and the tracker ran out of power), all birds are deflected to the anti-clockwise side of their established routes, though none to the expected degree. Of all the birds a55 follows closest to the established route, and reproduces the shape, though slightly shifted in the anti-clockwise direction throughout the route. r47 also remains close to the established route, particularly in the latter half of the journey. It is interesting to note that brc, though initially disorientated, returns almost to the release site and from there recapitulates the established route fairly closely.

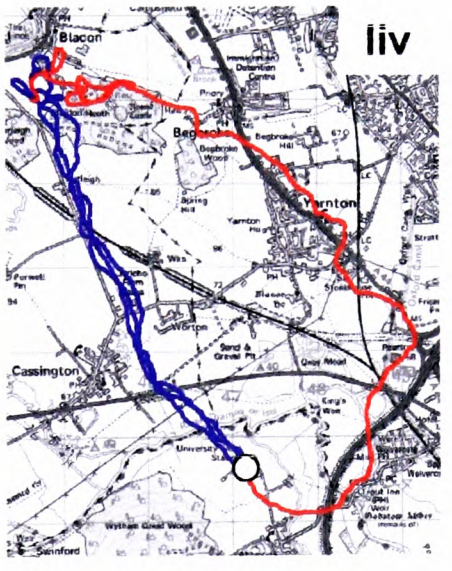
Figure 5.2 Maps showing tracks of birds with stereotyped routes released from Bladon Heath. Blue tracks indicate their final 3 training flights, red tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1km scale bar is included on the final panel.

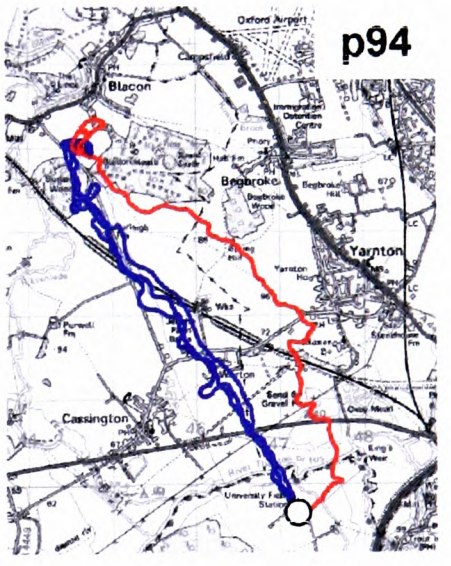


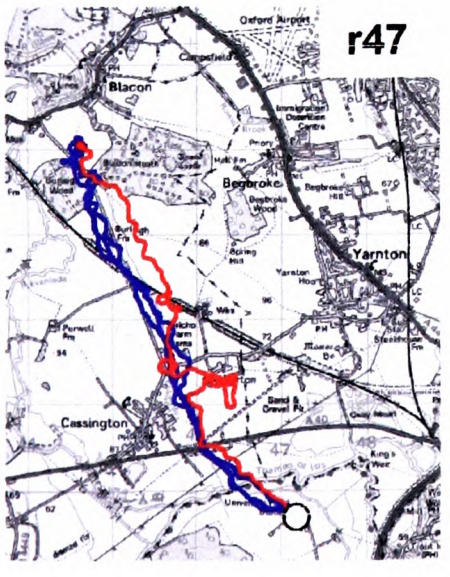












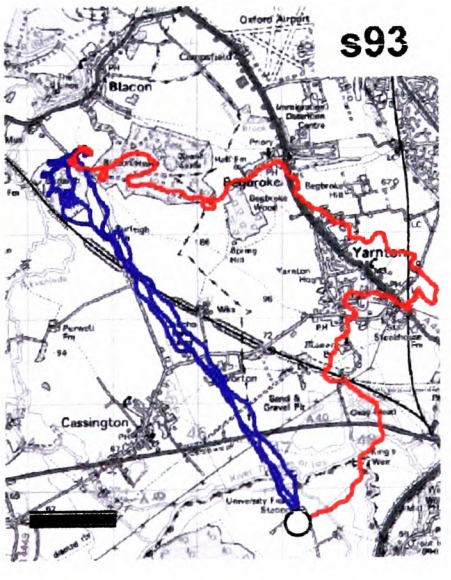


Figure 5.3 Maps showing tracks of birds without stereotyped routes released from Bladon Heath. Dark blue tracks indicate their last training flight, brown tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1km scale bar is included on the final panel.

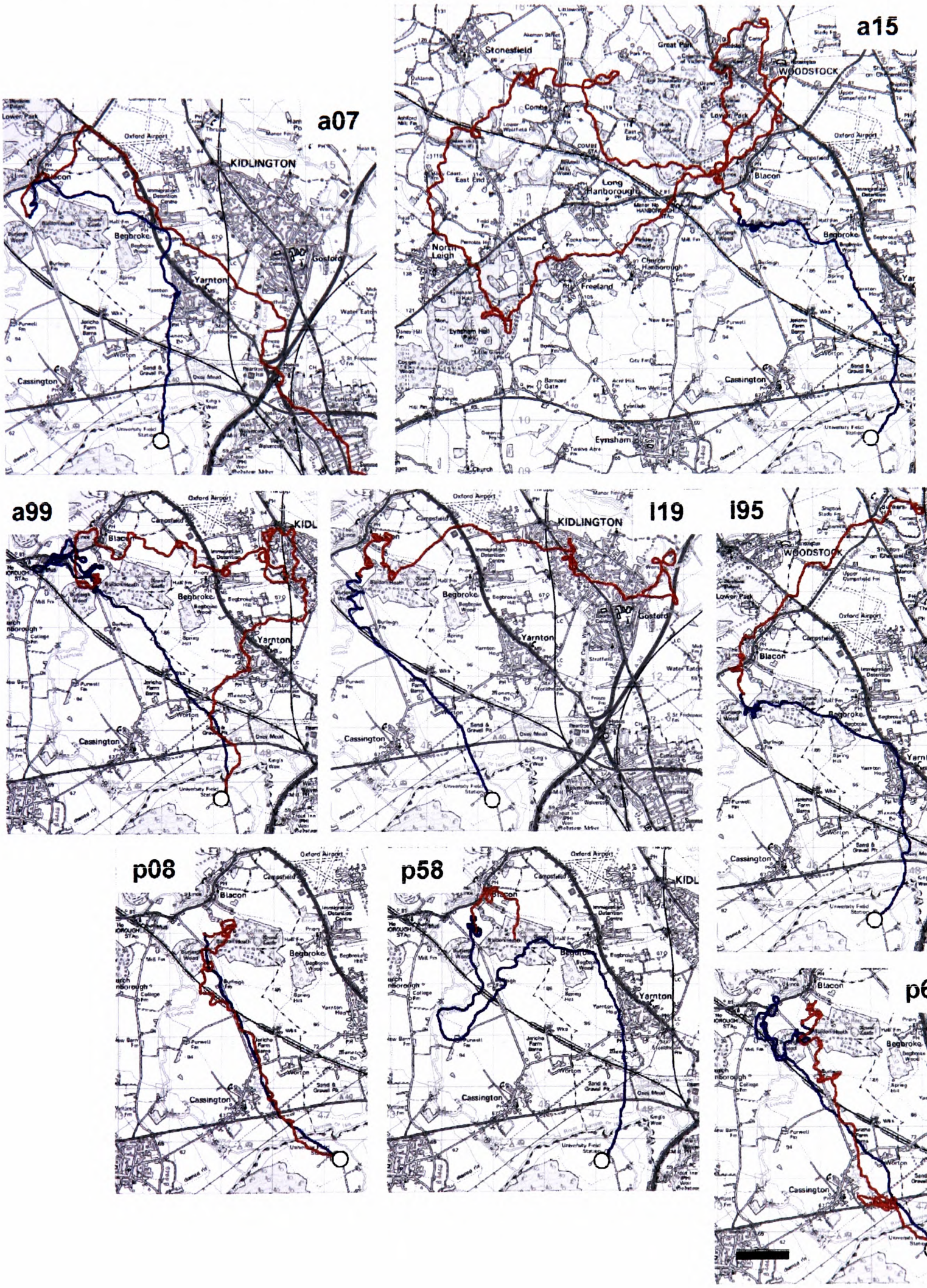


Figure 5.4 Maps showing tracks of birds with stereotyped routes released from Hinksey Heights. Blue tracks indicate their final 3 training flights, red tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

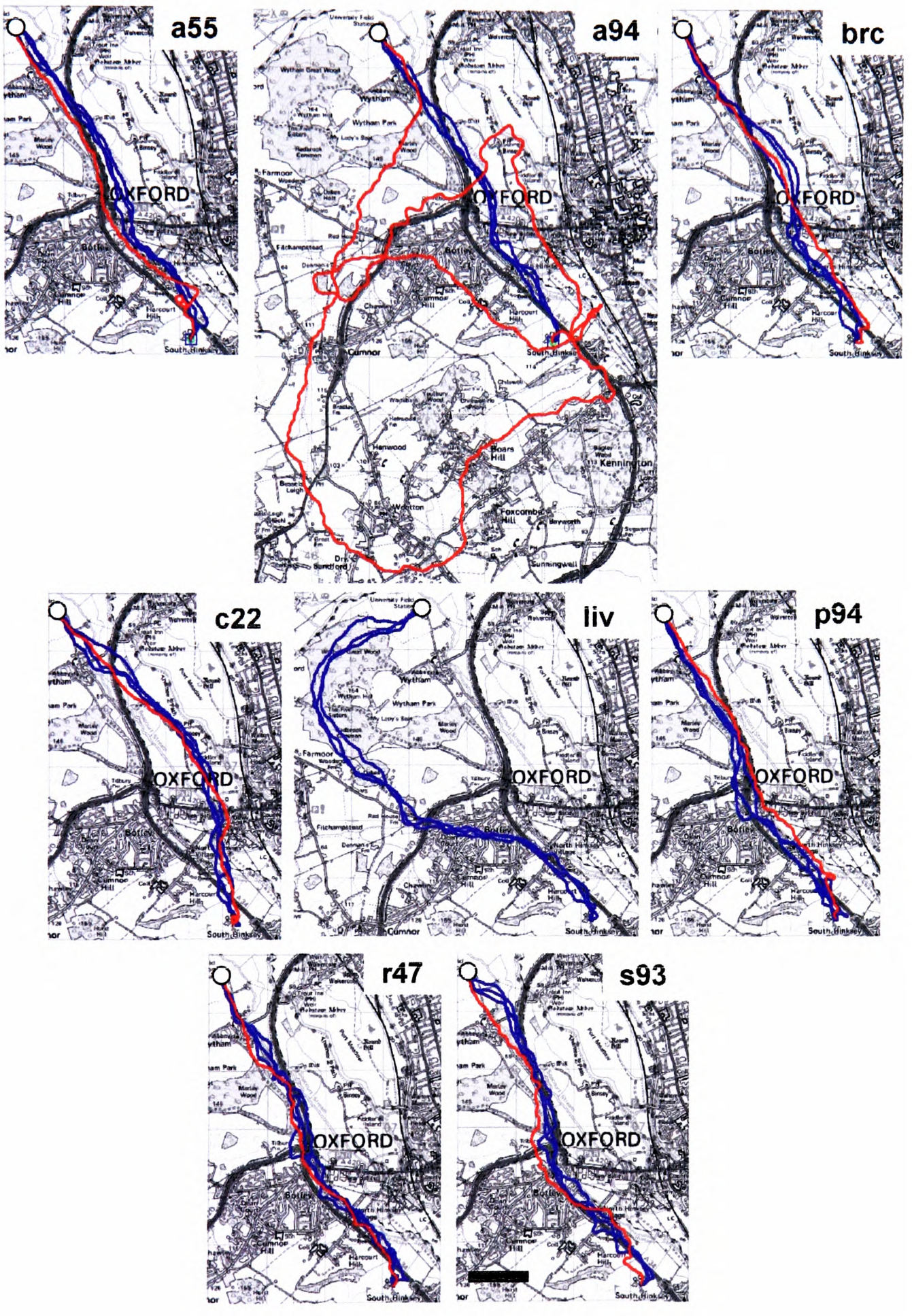


Figure 5.5 Maps showing tracks of birds without stereotyped routes released from Hinksey Heights. Dark blue tracks indicate their last training flight, brown tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

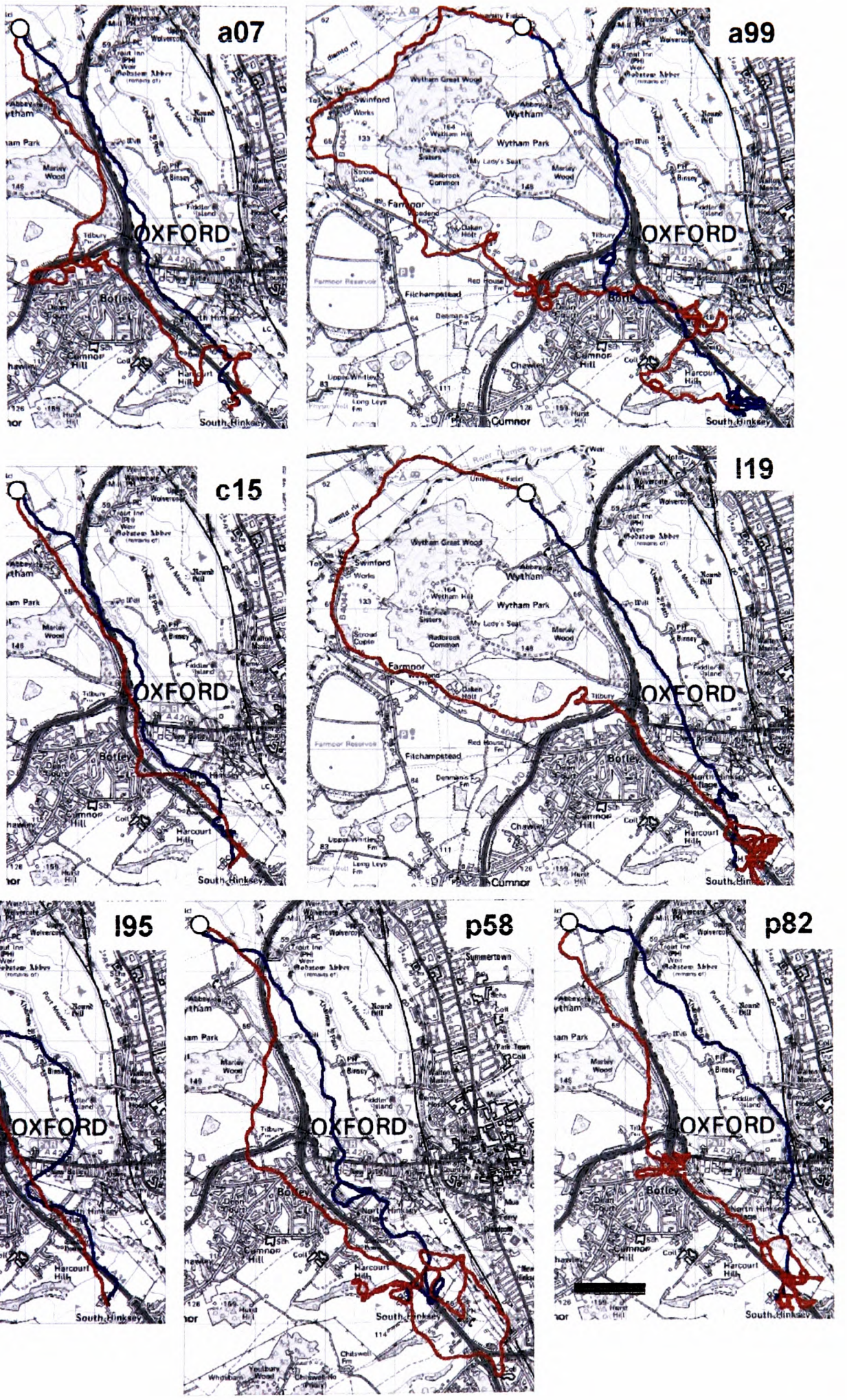


Figure 5.6 Maps showing tracks of birds with stereotyped routes released from Weston Wood. Blue tracks indicate their final 3 training flights, red tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

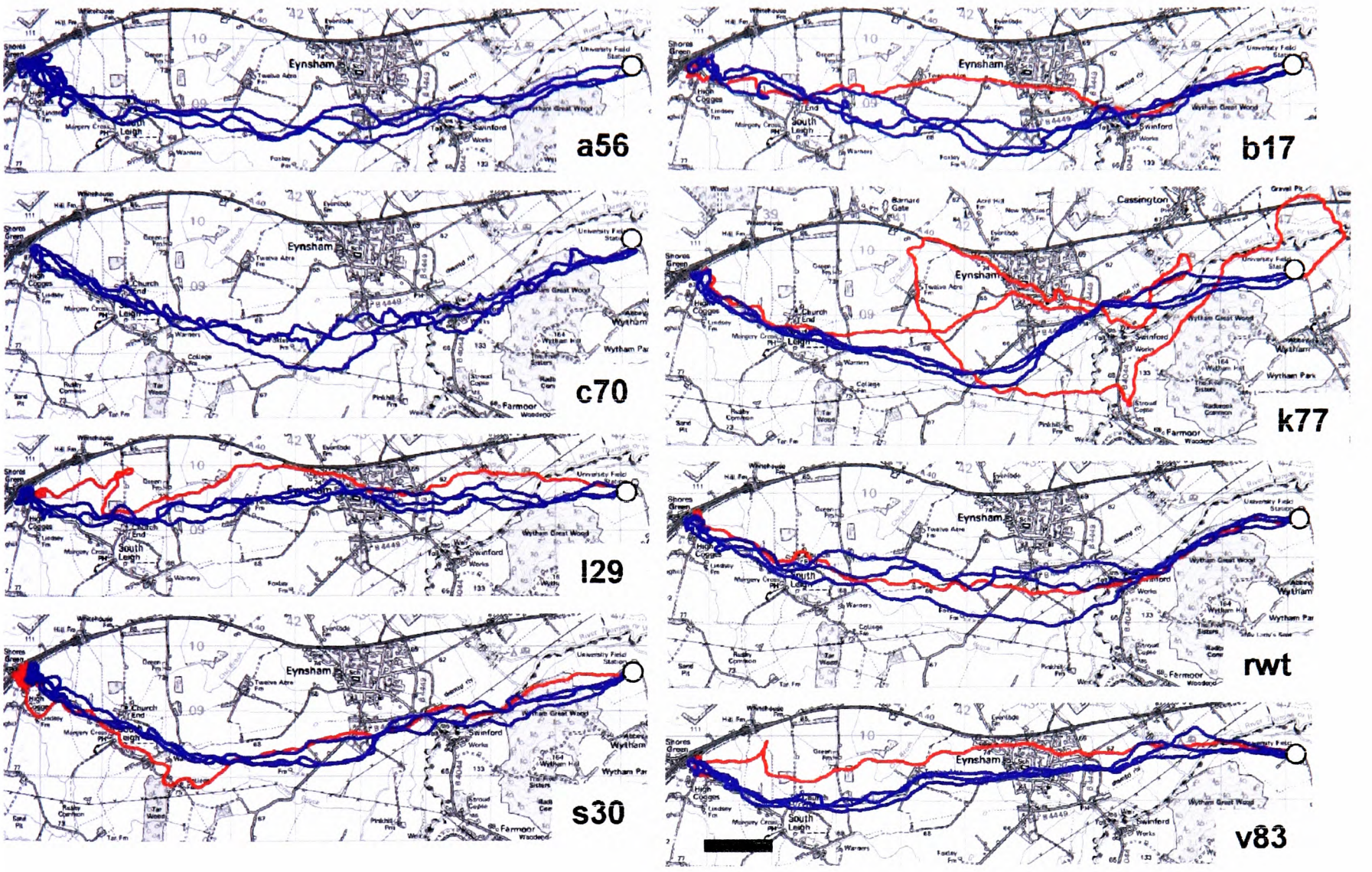


Figure 5.7 Maps showing tracks of birds without stereotyped routes released from High Cogges. Dark blue tracks indicate their last training flight, brown tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

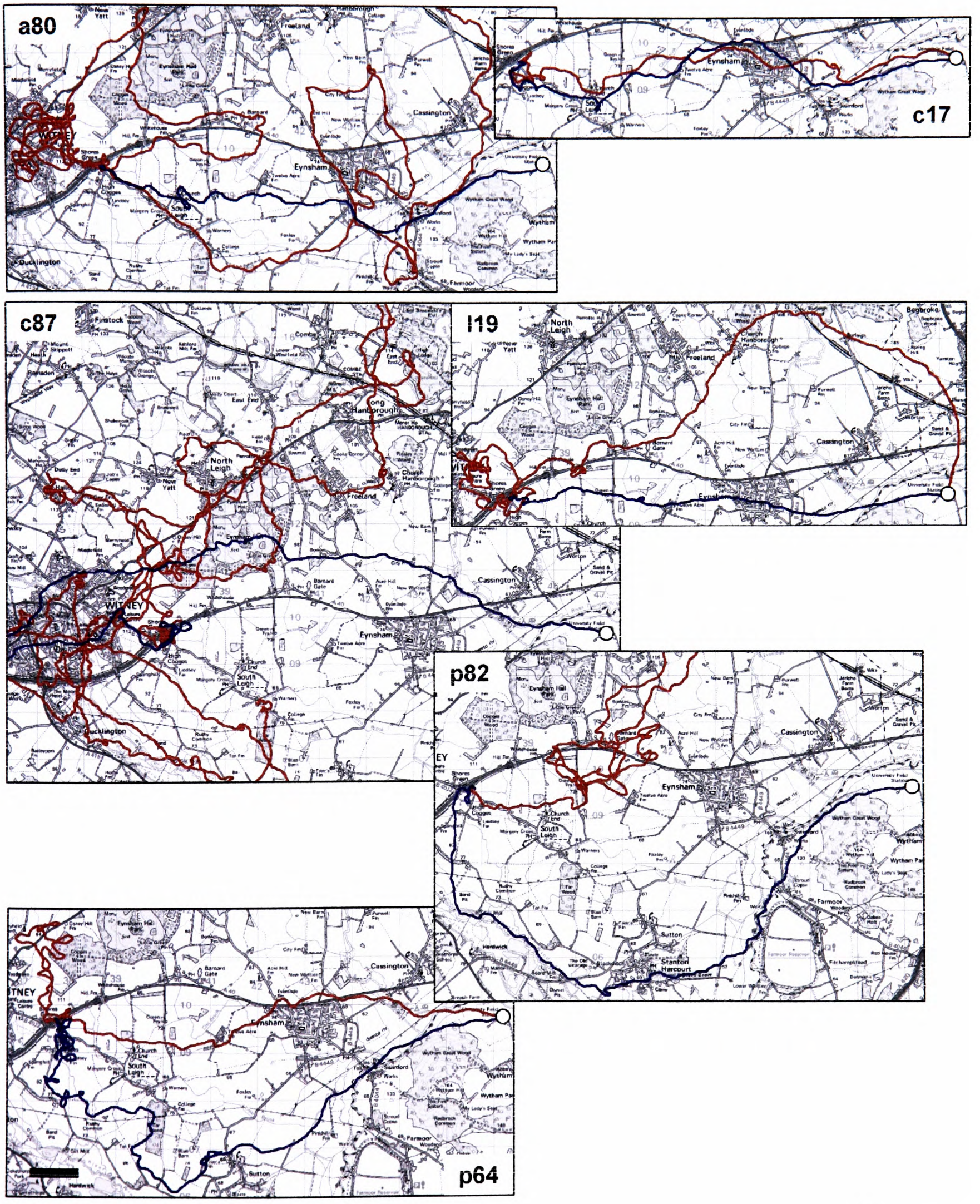


Figure 5.8 Maps showing tracks of birds with stereotyped routes released from Weston Wood. Blue tracks indicate their final 3 training flights, red tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

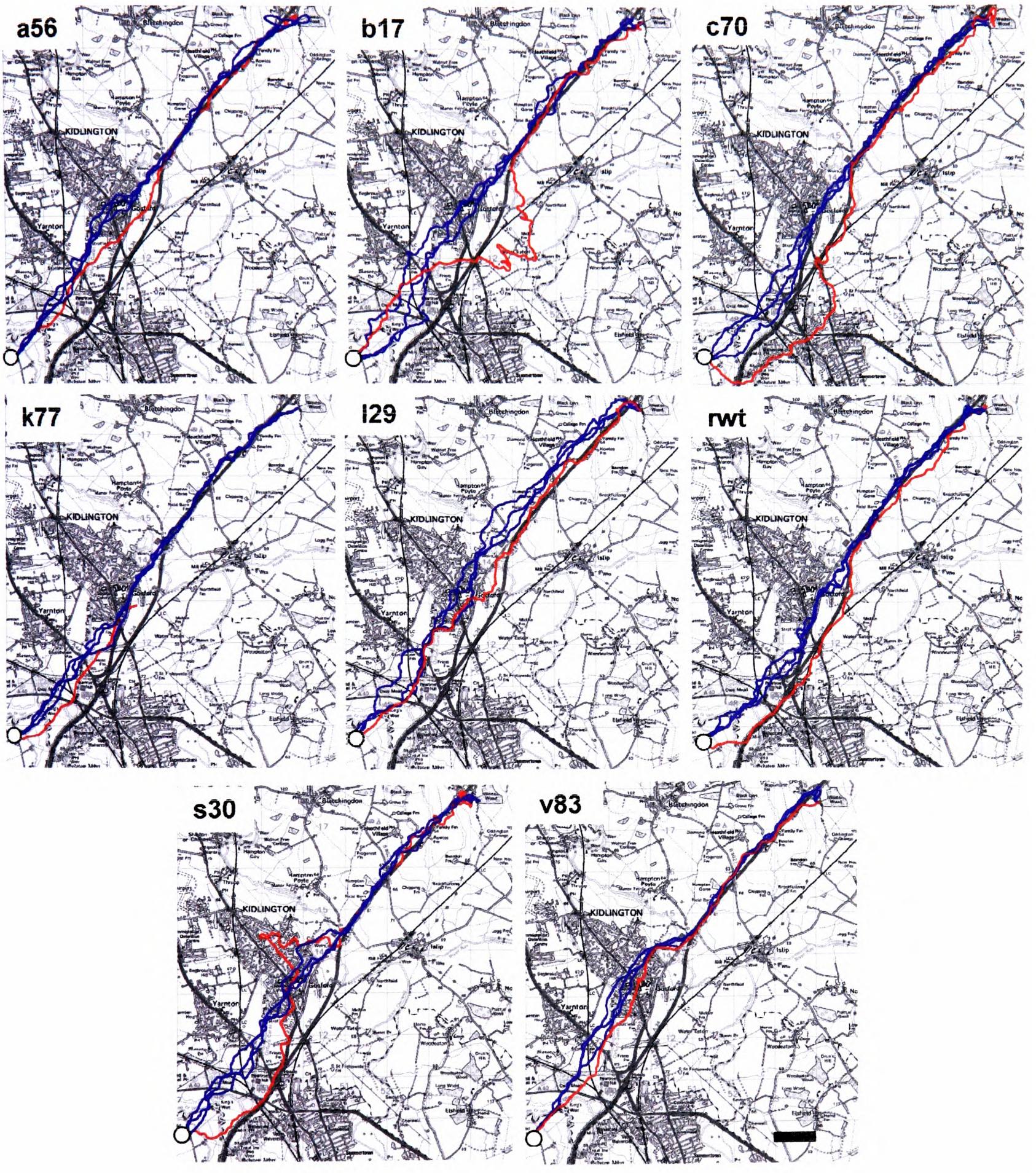


Figure 5.9 Maps showing tracks of birds without stereotyped routes released from Weston Wood. Dark blue tracks indicate their last training flight, brown tracks indicates flights performed under clock-shift conditions. 3 character labels indicate bird identities. White dots indicate the home loft. A 1 km scale bar is included on the final panel.

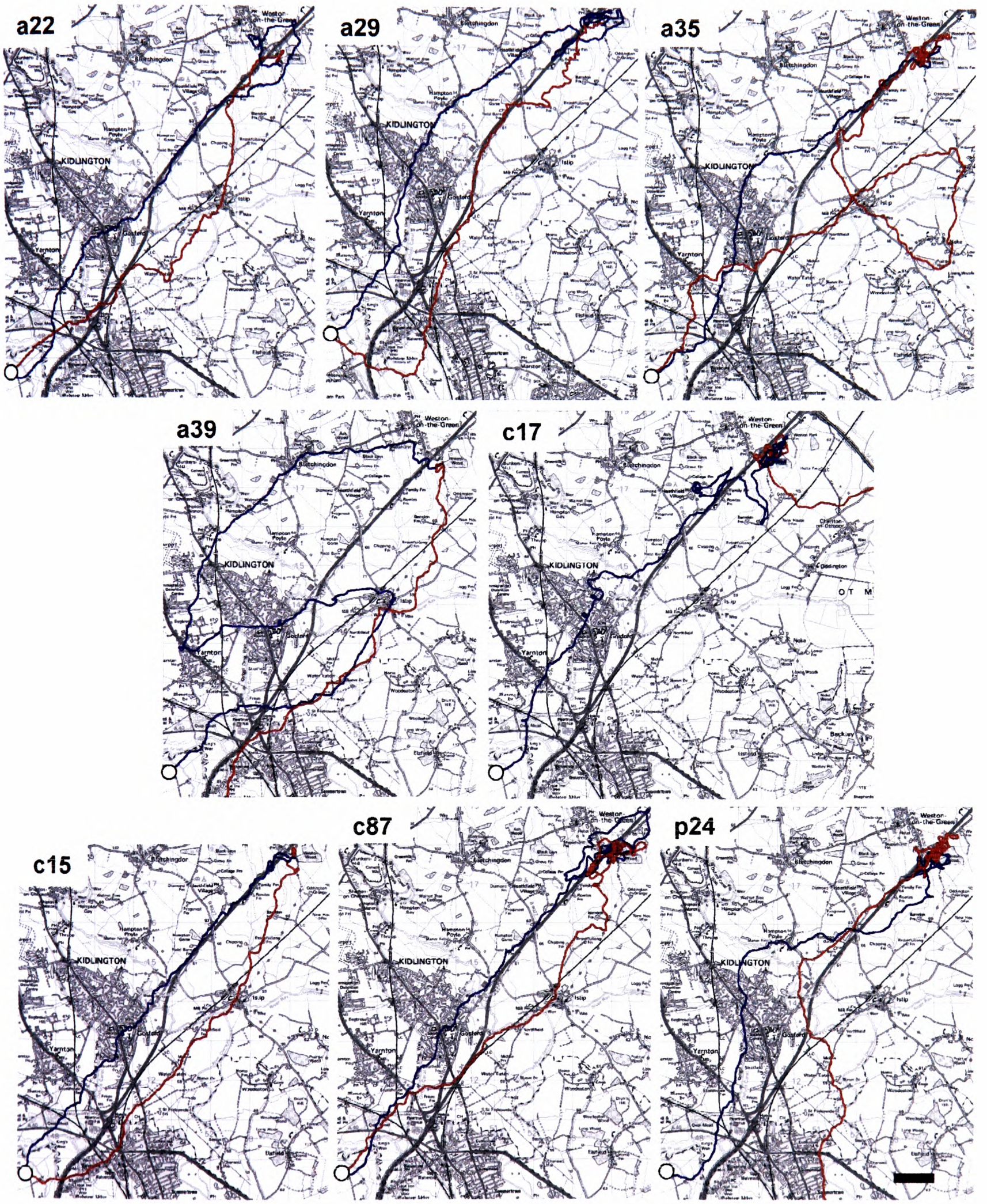


Figure 5.3, shows the non-route-recapitulating birds' tracks (non-route-recapitulating birds received only four training releases). The final training flight for each bird is in dark blue and the clock-shifted track in brown. When compared to the tracks of the route-recapitulating birds it is clear that in most cases the clock-shift treatment had a more drastic effect on the birds without established routes. a15, a99, l19 and l95 exhibited an anticlockwise shift close to the expected 90°, and bird a07 was also deflected in the anticlockwise direction. The remaining two birds for which a full clock-shift track is available (p58's tracker broke shortly after release) seem largely unaffected by the clock-shift treatment.

Figure 5.4 shows the individual tracks of route-recapitulating birds from the other short distance site; Hinksey Heights (6.2 km from home). Three tracks illustrating the established routes are shown in blue, and the tracks performed under clock-shift conditions are shown in red. From this site, where clock-shifted tracks are available (liv returned without a tracker), six out of the seven birds perform tracks similar to their established routes. a94 seems to have been disrupted by the treatment, only joining the established route very close to home. Figure 5.5 shows the corresponding release performed by the non-route-recapitulating birds. Dark blue tracks show each bird's final training flight, and tracks in brown are performed under clock-shift conditions. Again the treatment seems to have a greater effect on the non-route-recapitulating birds than on the birds that had been allowed to develop stereotyped routes. Although many of the tracks are homeward directed, they are all shifted to the anti-clockwise side of the training flights. Only c15 appears unaffected by the treatment, and a99 and l19's routes take them around the far side of Wytham Hill. The remaining birds are deflected in the expected direction, but not to the expected extent (the 8th bird returned home without a tracking device).

Figure 5.6 shows the tracks of route-recapitulating birds from one of the longer distance sites; High Cogges (9.4 km from home). Six clock-shifted tracks were recorded (a56 and c70's test flights were not recorded). Of the available tracks, five remain largely faithful to their established routes, but k77, though following the route closely for the first 2 km, appears disorientated from that point onwards. When compared to the paths of birds without established routes in figure 5.7 (again two tracks missing); three birds (a80, c87 and p82) seem very disoriented, l19 and p64 seem to be deflected in the correct (anti-clockwise) direction, and c17 seems unaffected by the treatment.

Figure 5.8 shows the tracks of route-recapitulating birds released from Weston Wood (10.7 km from home); blue tracks illustrate the birds' established routes; red tracks are performed under clock-shift conditions. The most striking thing when looking at this figure is that all the birds (k77 first part of track is missing) travel straight down the road directly towards home, both in their test flights under clock-shift conditions, and as part of their established routes. It is only when the road begins to curve away from the home direction that any birds deviate from their established routes (v83 and l29 continue to follow their established routes). After this point most of the birds continue to their left of their established routes (as would be expected under anti-clockwise shift), but none deviate far from their routes. Figure 5.9 shows the tracks from the same release site, performed by non-route-recapitulating birds (training tracks in dark blue, clock-shifted tracks in brown). These tracks deviate more widely from the training flights and any effect of the road upon the tracks is not so apparent, only in one case (a35) is the road initially followed on both training and clock-shifted tracks. In most cases the deviation is to the expected side of the training track but not to the expected degree (excepting c17's track which appears fully deflected).

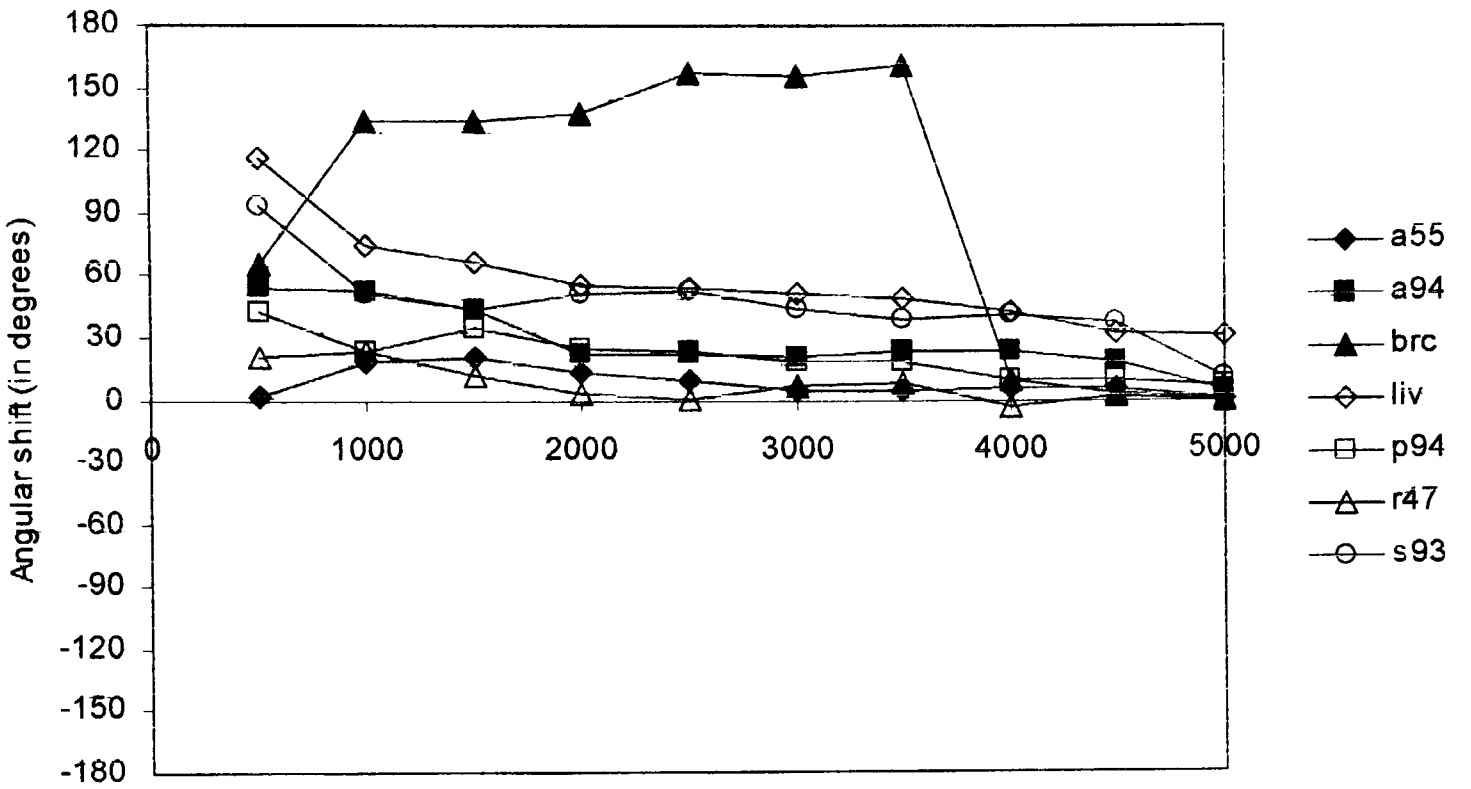
To examine the difference between tracks performed under training and clock-shift conditions more formally, I recorded the bearing from the release site to each bird's track at increasing distances from the release site ("virtual vanishing bearings", see Biro et al., 2002). A measurement was taken every 500 m until the distance from the release site to home was reached. At each distance the virtual vanishing bearing for the first time that a bird crossed a boundary distance was recorded. The virtual vanishing bearings for each boundary distance along the clock-shifted flight were subtracted from the corresponding values along the final training track, such that an anti-clockwise shift gave a positive difference, and a clock-wise shift resulted in a negative difference. The difference in bearings between the two flights were plotted on two graphs for each release site, one showing the individual deflection of birds with established routes and one showing the individual deflection of non-route-recapitulating birds. These graphs are shown in Figure 5.10 for Bladon Heath, Figure 5.11 for Hinksey Heights, Figure 5.12 for High Cogges and Figure 5.13 for Weston Wood.

The average difference in direction (between the final training flight and the clock-shift flight) of route-recapitulating and non-route-recapitulating birds at each distance was also plotted, separately for each release site (see Figure 5.14). In every case the degree of shift of non-route-recapitulating birds is more variable than in the birds that had developed stereotyped routes, and in every case the average deflection of non-route-recapitulating birds is further anticlockwise than that of the birds with stereotyped routes.

At each boundary distance, from each release site, circular statistics were performed on the data for both the group of birds that had been allowed to develop stereotyped routes, and the group of birds that had not.

Figure 5.10 Graphs showing the angular difference between training flights and clock-shifted flights at increasing distances from the release site (Bladon Heath) for (a) birds with stereotyped routes, (b) without stereotyped routes. Positive values indicate anti-clockwise shift, negative values indicate clockwise shift. Individual birds are identified by different symbols.

a



b

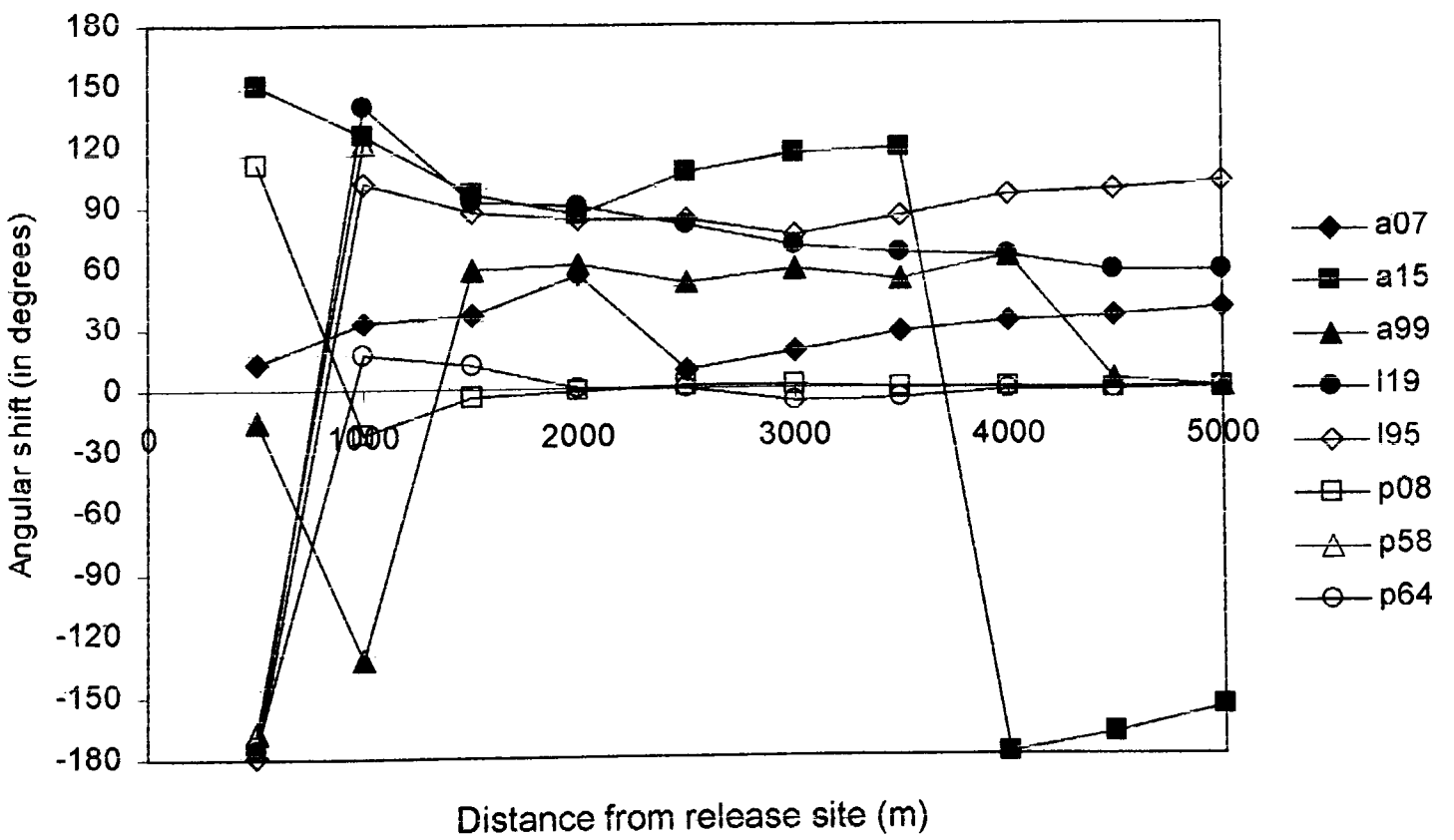
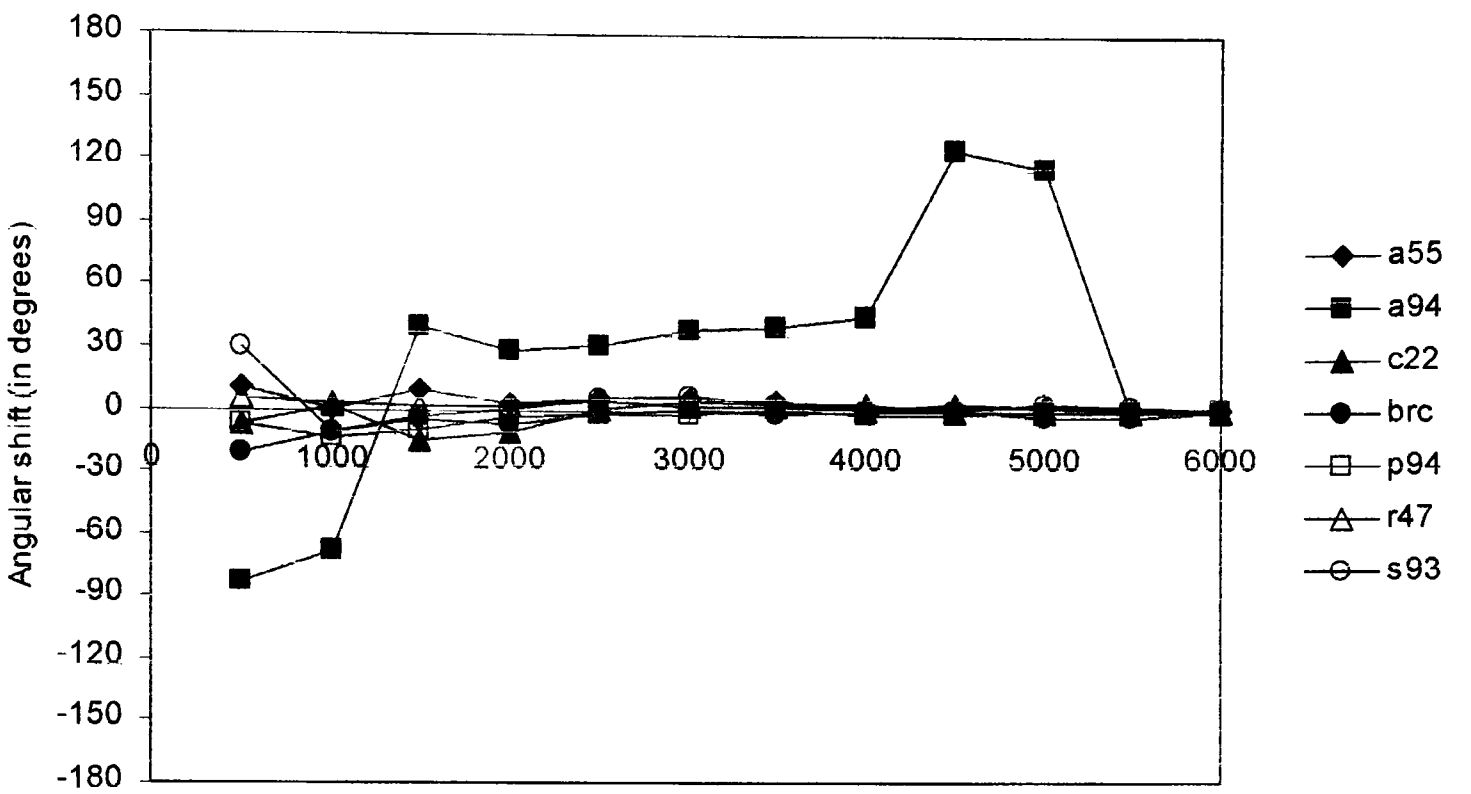


Figure 5.11 Graphs showing the angular difference between training flights and clock-shifted flights at increasing distances from the release site (Hinksey Heights) for (a) birds with stereotyped routes, (b) without stereotyped routes. Positive values indicate anti-clockwise shift, negative values indicate clockwise shift. Individual birds are identified by different symbols.

a



b

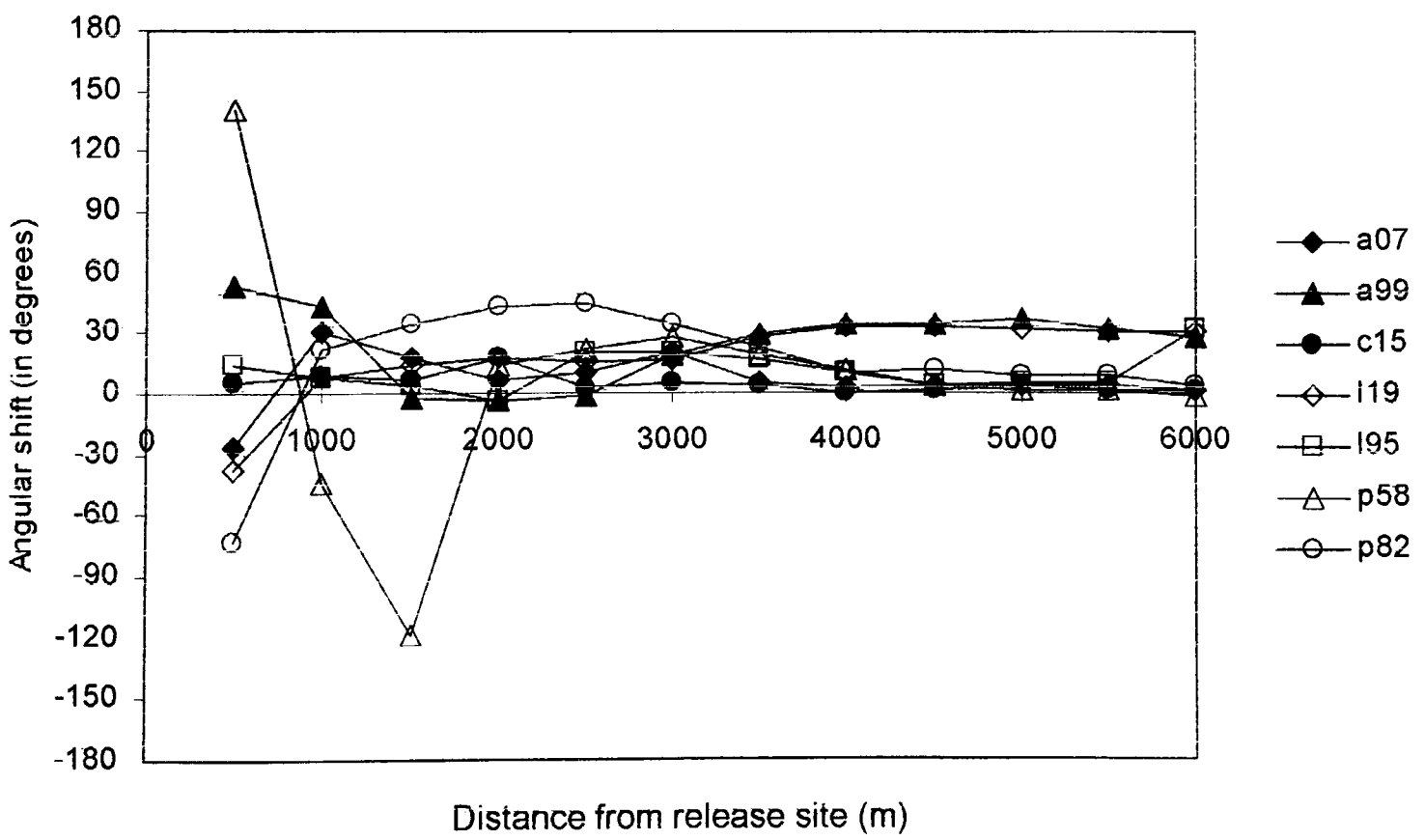
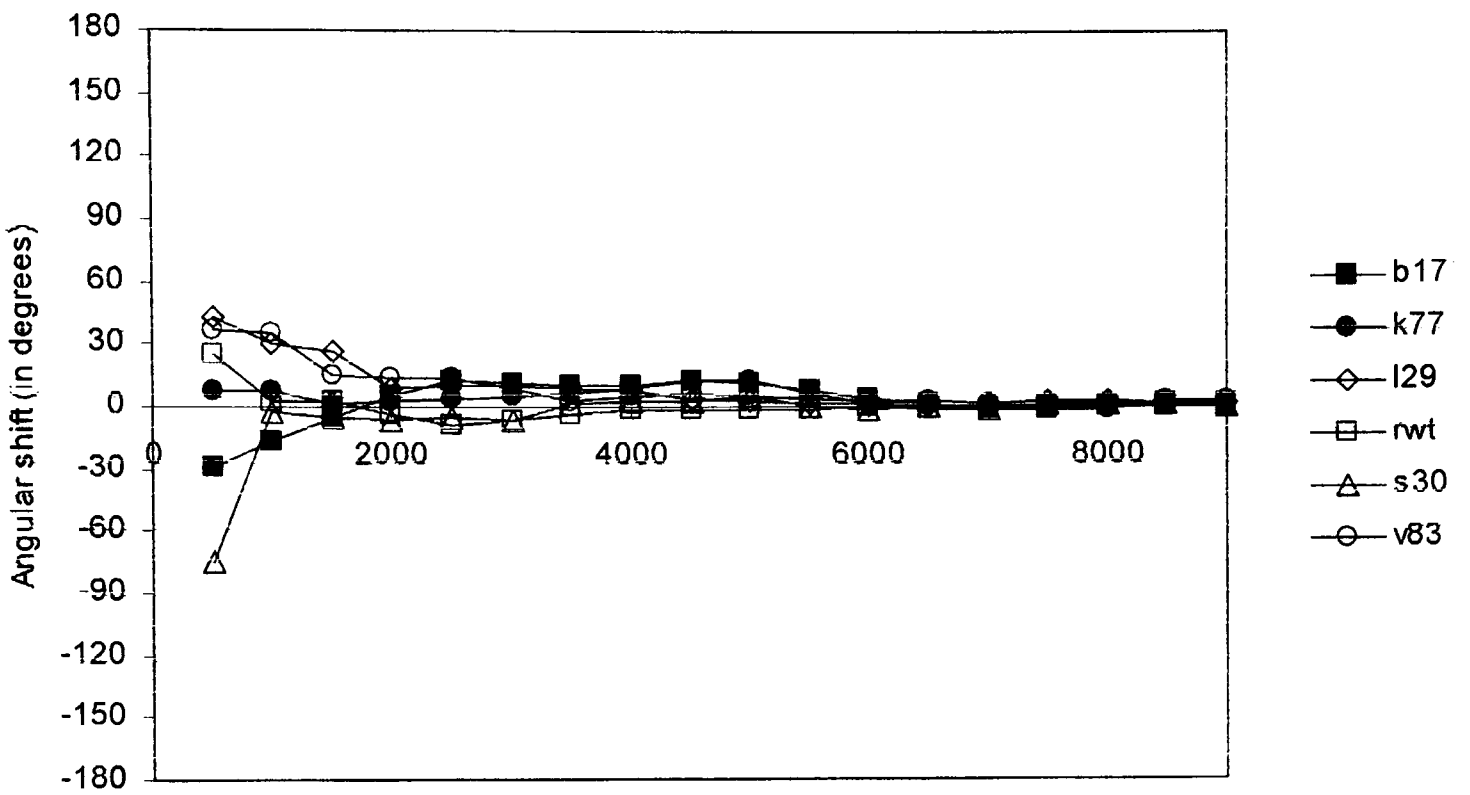


Figure 5.12 Graphs showing the angular difference between training flights and clock-shifted flights at increasing distances from the release site (High Cogges) for (a) birds with stereotyped routes, (b) without stereotyped routes. Positive values indicate anti-clockwise shift, negative values indicate clockwise shift. Individual birds are identified by different symbols.

a



b

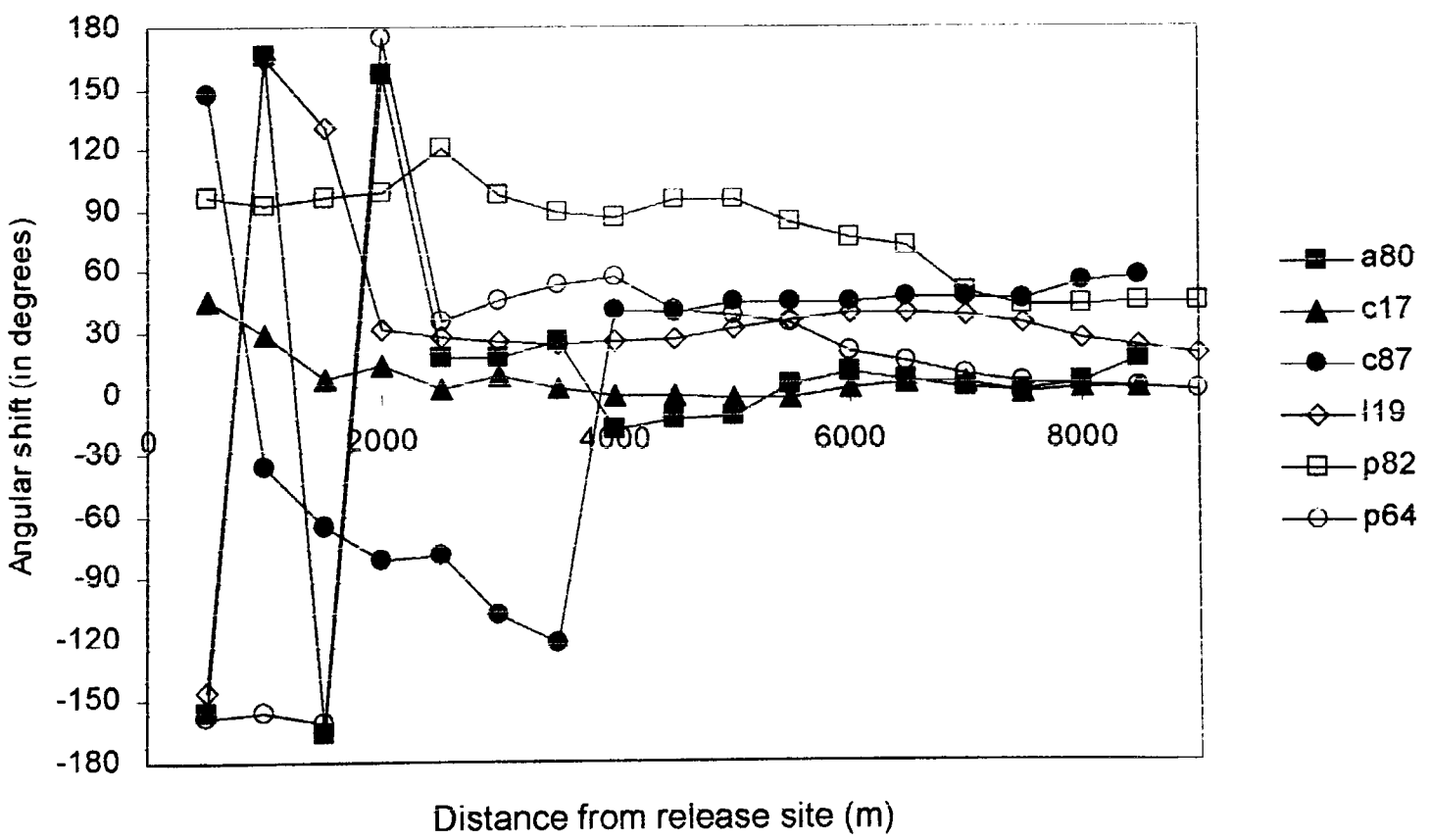
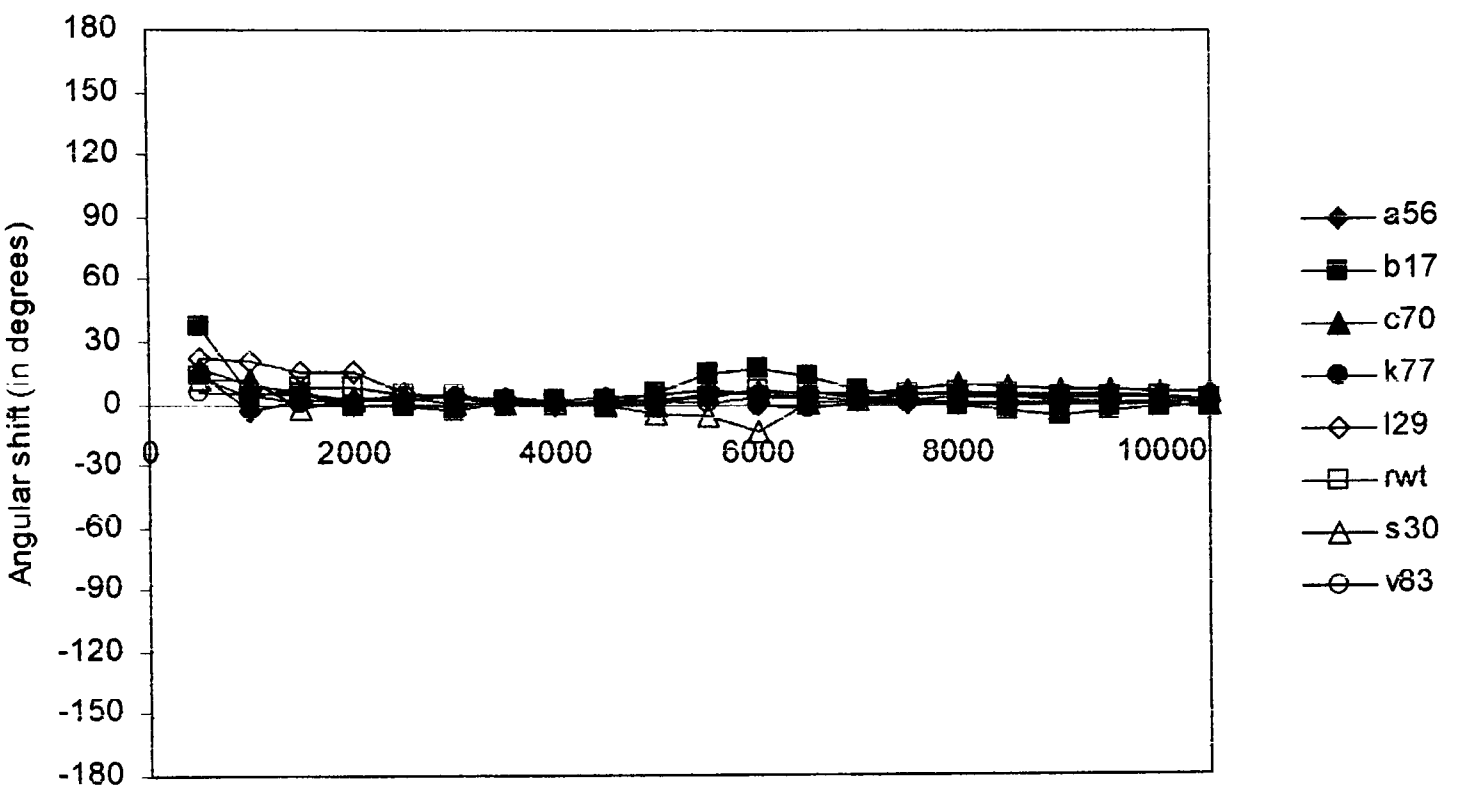


Figure 5.13 Graphs showing the angular difference between training flights and clock-shifted flights at increasing distances from the release site (Weston Wood) for (a) birds with stereotyped routes, (b) without stereotyped routes. Positive values indicate anti-clockwise shift, negative values indicate clockwise shift. Individual birds are identified by different symbols.

a



b

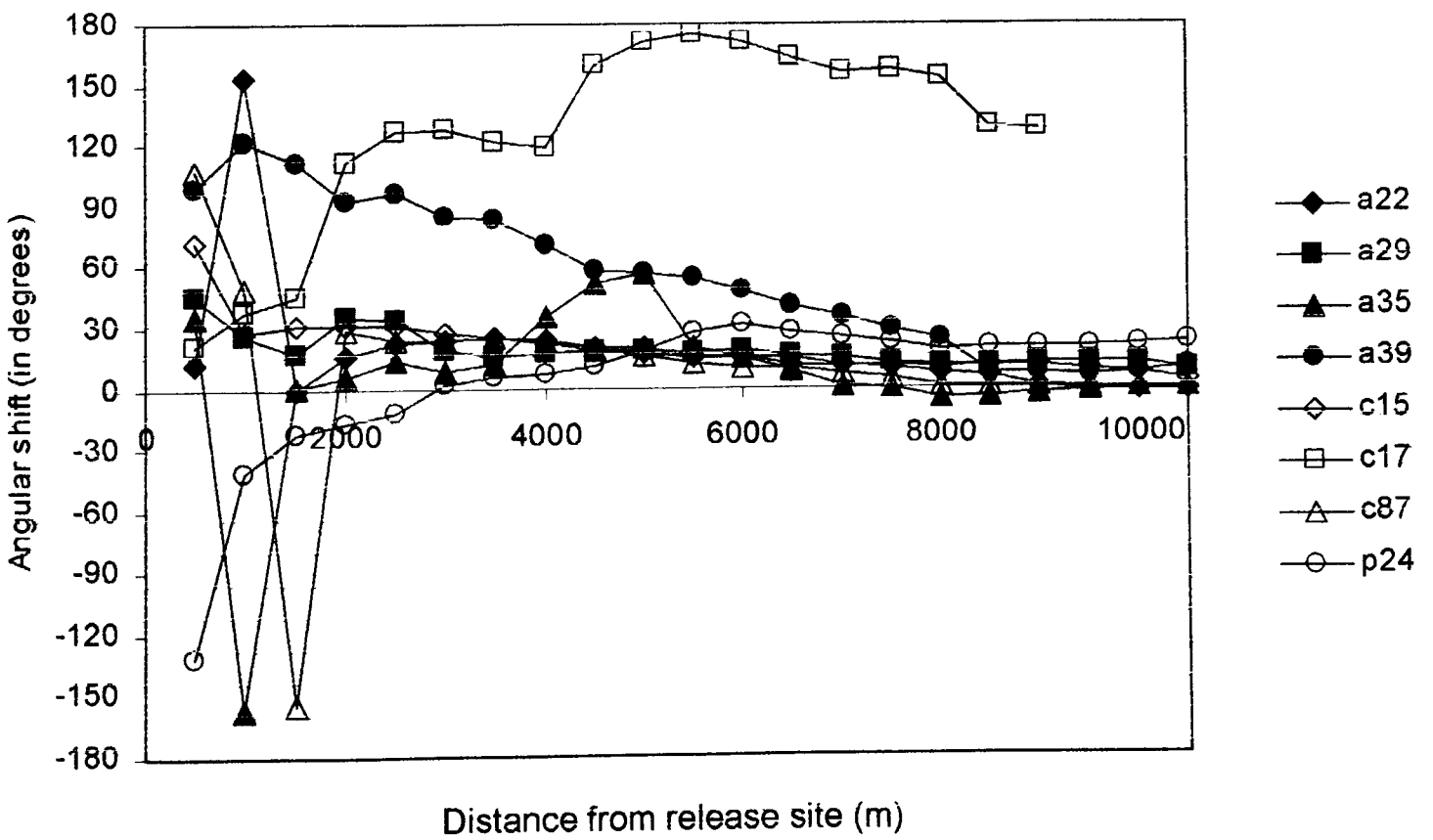
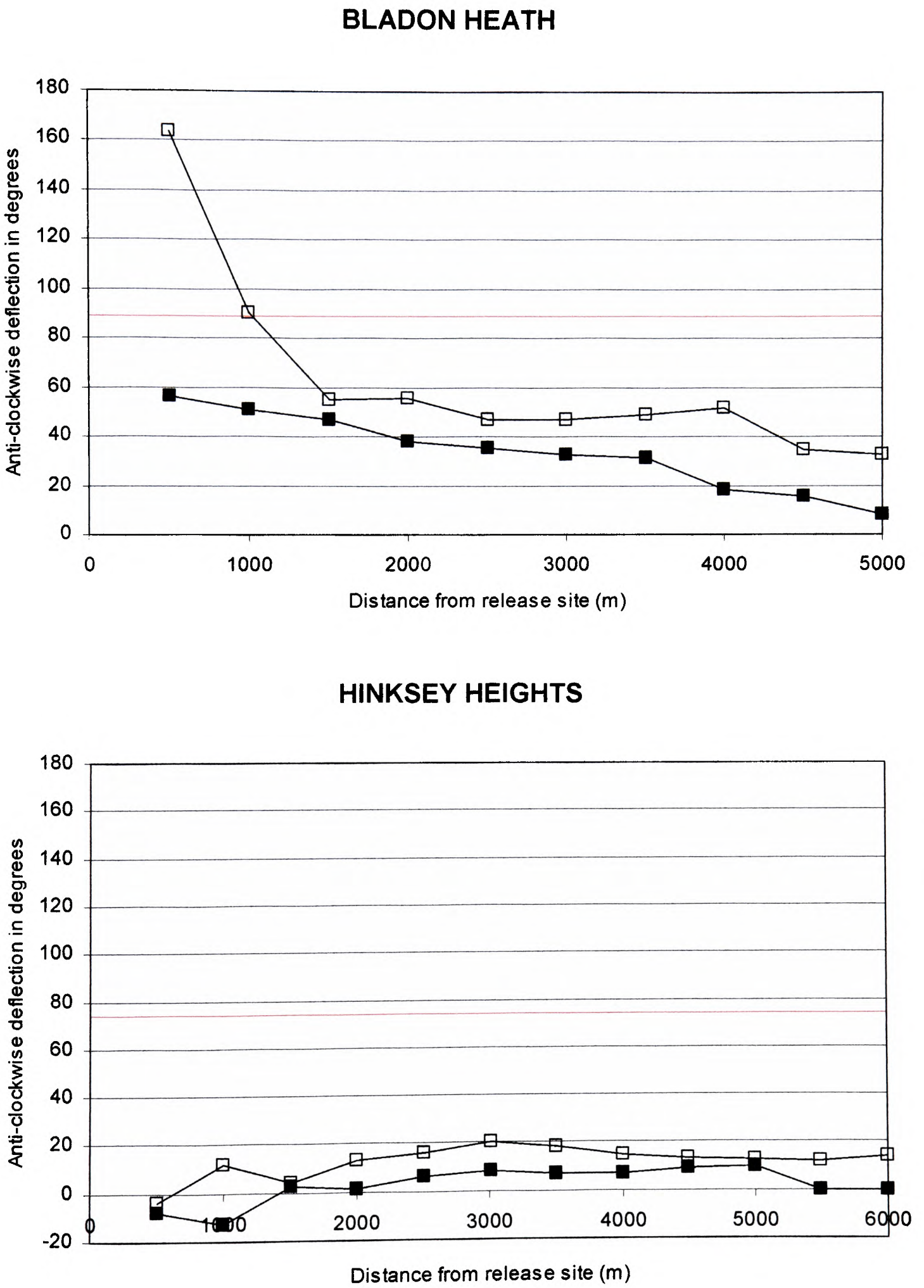
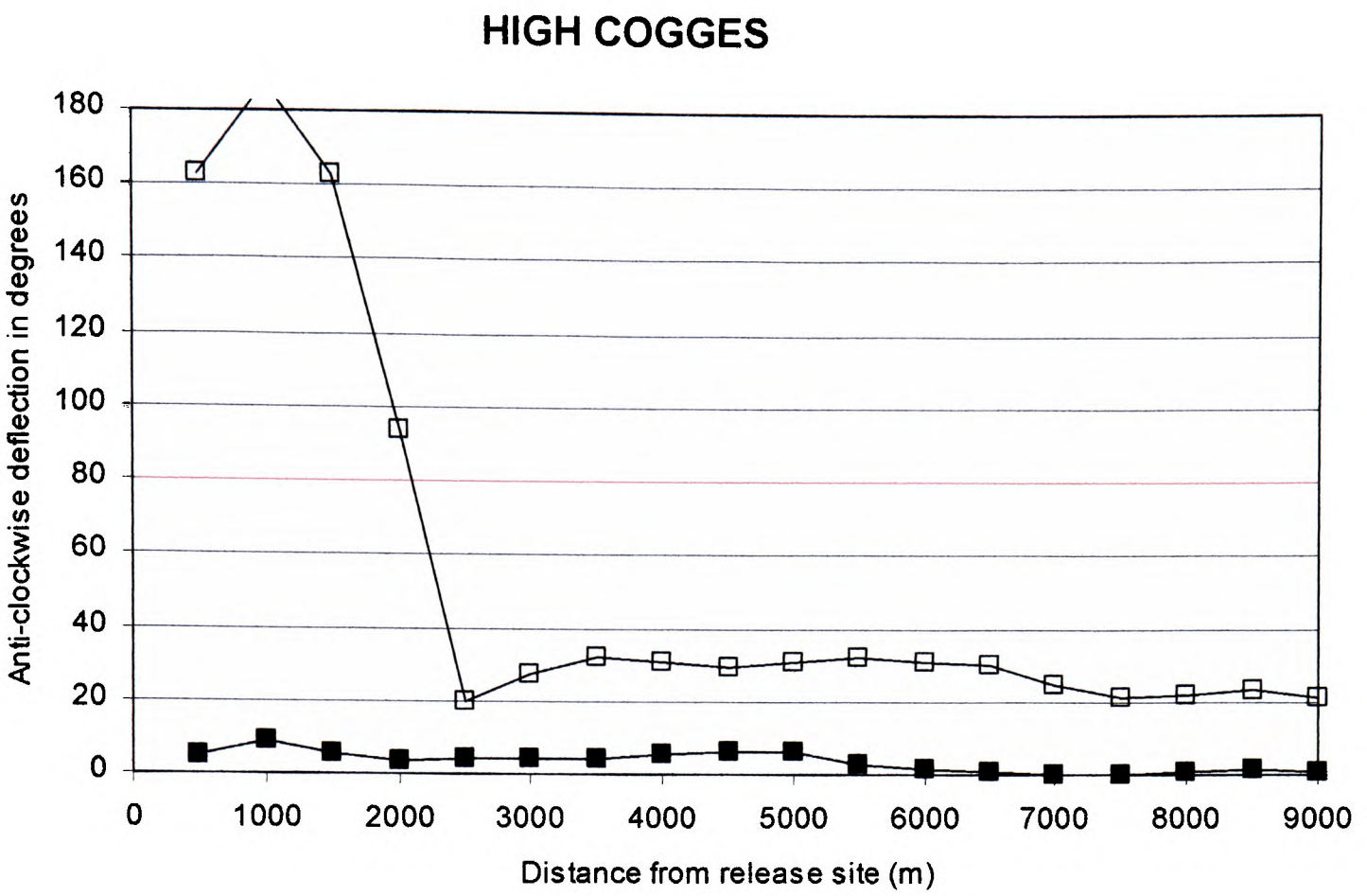
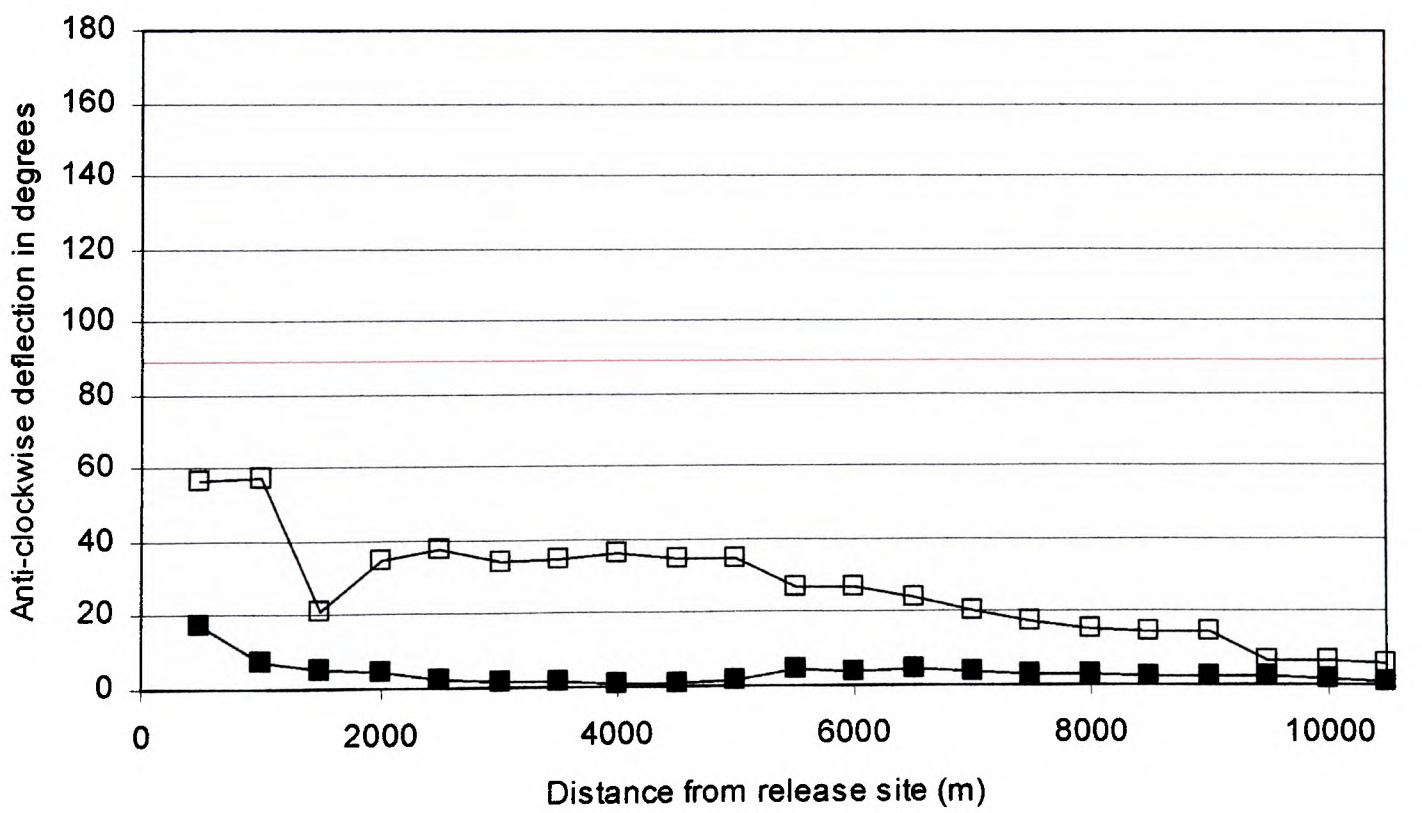


Figure 5.14 Graphs showing the average angular difference in deflection between the birds that had established stereotyped routes (black squares) and those that had not (white squares) at increasing distances from each release site. Red lines illustrate the average predicted shift.




HIGH COGGES
Anti-clockwise deflection in degrees
180
160
140
120
100
80
60
40
20
0
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
Distance from release site (m)


WESTON WOOD
Anti-clockwise deflection in degrees
180
160
140
120
100
80
60
40
20
0
0
2000
4000
6000
8000
10000
Distance from release site (m)

First, the average bearing from the release site to each boundary distance was calculated for both groups of birds (shown as mean vector direction in table 5.3). Secondly, the vector length for both groups of birds was calculated, indicating the degree of scatter in the bearings from each group (shown as mean vector length in table 5.3). The Rayleigh test for directedness was performed for both groups of birds at each boundary distance where p values of <0.05 indicate significant directedness. 95% confidence intervals were calculated, indicating that birds are significantly homeward directed when 0° is included. Finally, Watson-Williams F tests were performed to compare the mean heading directions of the two groups of birds (those that had been allowed to develop stereotyped routes, and those that had not) at all boundary distances from all sites. Table 5.3 shows the results of these calculations, which were carried out using Oriana™ software.

Table 5.3 The table shows, at increasing straightline distances from each release site, the direction and length of the mean vector, the p value for the Rayleigh test for directedness, and the interval within which 95% of the bearings fell, both for birds with established stereotyped routes and those without. Numbers in bold indicate that the group is significantly orientated (Rayleigh test significant) and that the 95% confidence interval includes 0° - the homeward direction. The P values for the Watson-William's F test for difference between the two groups is also included. *s indicate tests are significant.

Distance from release site	Mean vector direction (°)		Mean vector length		P value for Rayleigh test		95% confidence interval (°)		P value for Watson - William F test
Bladon Heath	RR	NRR	RR	NRR	RR	NRR	RR	NRR	
500	56.0	163.7	0.805	0.423	0.006*	0.246	20.9 - 91.2	238.6 - 88.8	0.009*
1000	50.7	90.1	0.807	0.376	0.006*	0.334	15.7 - 85.7	358.8 - 181.4	0.292
1500	47.2	55.1	0.814	0.799	0.005*	0.006*	12.8 - 81.5	19.3 - 91.0	0.715
2000	38.1	55.6	0.772	0.81	0.010*	0.005*	**359.6 - 76.6**	20.9 - 90.4	0.446
2500	35.6	47.2	0.722	0.757	0.020*	0.012*	**352.2 - 78.9**	7.3 - 87.1	0.654
3000	32.6	47.0	0.730	0.755	0.018*	0.013*	**350.0 - 75.2**	6.9 - 87.1	0.577
3500	31.5	48.7	0.727	0.753	0.018*	0.013*	**348.7 - 74.4**	8.5 - 89.0	0.509
4000	18.3	51.7	0.959	0.599	0.000*	0.077*	2.7 - 34.0	3.8 - 99.5	0.185
4500	15.3	34.9	0.973	0.562	0.000*	0.107	2.7 - 27.9	342.2 - 87.8	0.439
5000	7.9	32.9	0.984	0.544	0.000*	0.125	**358.2 -17.6**	337.6 - 88.3	0.335

Hinksey Heights	RR	NRR	RR	NRR	RR	NRR	RR	NRR	
500	352.2	356.4	0.847	0.539	0.003*	0.130	**321.1 - 23.1**	300.2 - 52.5	0.887
1000	347.4	11.8	0.925	0.904	0.000*	0.001*	**326.1 - 8.7**	**347.6 - 36.1**	0.102
1500	2.5	4.0	0.958	0.753	0.000*	0.013*	**346.7 - 18.2**	**323.6 - 44.3**	0.936
2000	1.6	13.0	0.980	0.967	0.000*	0.000*	**350.6 - 12.5**	**359.0 - 27.0**	0.162
2500	6.1	16.2	0.983	0.970	0.000*	0.000*	**356.0 - 16.2**	2.9 - 29.5	0.187
3000	8.0	20.6	0.975	0.989	0.000*	0.000*	**355.9 – 20.0**	12.7 - 28.5	0.065
3500	7.0	17.9	0.973	0.986	0.000*	0.000*	**354.3 - 19.8**	8.8 - 27.0	0.134
4000	6.9	14.5	0.963	0.976	0.000*	0.000*	**352.2 - 21.7**	2.6 - 26.4	0.370
4500	9.1	13.0	0.785	0.974	0.008*	0.000*	**331.9 - 46.4**	0.5 - 25.4	0.822
5000	9.5	12.8	0.805	0.972	0.006*	0.000*	**334.3 - 44.8**	**359.9 - 25.7**	0.840
5500	359.7	11.8	1.000	0.977	0.000*	0.000*	**358.3 - 1.1**	0.2 - 23.4	0.034*
6000	0.0	13.6	1.000	0.969	0.000*	0.000*	-	0.1 - 27.2	-
High Cogges	RR	NRR	RR	NRR	RR	NRR	RR	NRR	
500	4.9	162.9	0.762	0.507	0.023*	0.221	**320.3 - 49.5**	94.6 231.2	0.003*
1000	9.0	187.5	0.872	0.158	0.005*	0.871	**337.0 - 40.9**	-	0.062
1500	5.8	163.0	0.980	0.222	0.000*	0.761	**353.5 - 18.1**	-	0.027*
2000	3.2	94.1	0.992	0.207	0.000*	0.788	**355.6 - 10.8**	-	0.115
2500	4.4	20.0	0.988	0.592	0.000*	0.121	**355.1 - 13.8**	326.7 - 73.2	0.550
3000	4.0	27.7	0.991	0.583	0.000*	0.130	**355.9 -12.2**	333.1 - 82.2	0.375
3500	4.1	31.9	0.997	0.570	0.000*	0.143	**359.1 - 9.1**	335.3 - 88.4	0.308
4000	5.2	31.0	0.998	0.825	0.000*	0.010*	1.1 - 9.4	**353.4 - 68.6**	0.127
4500	6.0	29.6	0.996	0.829	0.000*	0.009*	0.5 - 11.5	**352.4 - 66.8**	0.156
5000	5.9	30.7	0.996	0.828	0.000*	0.010*	0.5 - 11.2	**353.4 – 68.0**	0.138
5500	2.9	32.1	0.998	0.884	0.000*	0.004*	3.2 - 359.5	28.4 - 1.8	0.042*
6000	1.2	31.1	1.000	0.912	0.000*	0.002*	**359.3 - 3.1**	4.9 - 57.3	0.020*
6500	1.0	29.8	1.000	0.911	0.000*	0.002*	**359.8 - 2.1**	3.4 - 56.2	0.025*
7000	0.3	24.6	1.000	0.938	0.000*	0.001*	**359.2 - 1.4**	2.8 - 46.4	0.023*
7500	0.2	20.9	1.000	0.940	0.000*	0.001*	**359.2 - 1.3**	**359.3 - 42.4**	0.044*
8000	0.4	21.8	1.000	0.935	0.000*	0.001*	**359.0 - 1.8**	**359.4 - 44.2**	0.044*
8500	1.2	23.4	1.000	0.936	0.000*	0.001*	0.3 - 2.1	1.3 - 45.6	0.036*
9000	0.9	21.2	1.000	0.954	0.000*	0.051	**359.7 - 2.1**	342.6 - 59.8	0.042*
Weston Wood	RR	NRR	RR	NRR	RR	NRR	RR	NRR	
500	17.5	56.4	0.987	0.598	0.000*	0.052	8.9 - 26.2	12.0 - 100.8	0.108
1000	7.5	57 1	0.993	0.355	0.000*	0.376	0.9 - 14.1	315.7 - 158.5	0.157
1500	5.3	21.4	0.996	0.561	0.000*	0.077	0.3 - 10.4	332.4 - 70.3	0.508
2000	4.1	35.2	0.995	0.775	0.000*	0.004*	**359.0 - 9.3**	0.7 - 69.7	0.075
2500	2.5	37.4	0.999	0.754	0.000*	0.006*	0.4 4.6	1.0 - 73.8	0.057
3000	1.6	34.4	0.999	0.780	0.000*	0.004*	**358.9 - 4.2**	0.3 - 68.5	0.057
3500	1.5	34.9	1.000	0.804	0.000*	0.003*	0.5 - 2.4	2.9 - 66.9	0.041*
4000	1.0	36.3	1.000	0.834	0.000*	0.001*	0.1 - 2.0	7.1 - 65.5	0.022*
4500	1.1	34.5	1.000	0.758	0.000*	0.006*	0.1 - 2.0	**358.5 - 70.6**	0.064
5000	1.7	34.6	0.999	0.740	0.000*	0.008*	**359.0 - 4.3**	**357.0 - 72.2**	0.078
5500	4.1	27.1	0.995	0.743	0.000*	0.008*	**358.7 - 9.5**	**349.8 - 64.5**	0.203
6000	3.8	26.7	0.990	0.752	0.000*	0.007*	**357.0 - 10.6**	**350.1 - 63.3**	0.177
6500	4.1	23.6	0.997	0.760	0.000*	0.006*	0.5 - 7.6	**347.8 - 59.5**	0.231
7000	3.4	20.6	0.999	0.766	0.000*	0.005*	1.5 - 5.3	**345.3 - 55.9**	0.282
7500	3.1	17.8	0.999	0.765	0.000*	0.005*	1.1 - 5.1	**342.3 - 53.2**	0.357
8000	3.0	14.9	0.998	0.766	0.000*	0.005*	0.1 - 5.8	**339.5 - 50.3**	0.450
8500	2.0	14.5	0.998	0.807	0.000*	0.002*	**358.9 - 5.1**	**342.9 - 46.1**	0.382
9000	2.0	14.3	0.998	0.811	0.000*	0.002*	**359.0 - 4.9**	**342.9 - 45.7**	0.383
9500	2.0	6.2	0.999	0.991	0.000*	0.000*	**359.5 - 4.5**	**359.0 - 13.4**	0.201
10000	1.4	6.3	0.999	0.991	0.000*	0.000*	**359.3 - 3.6**	**359.0 - 13.7**	0.143
10500	0.7	5.9	0.999	0.990	0.000*	0.000*	**358.8 - 2.6**	**358.3 - 13.5**	0.129

In every case, the birds with an established route were significantly orientated from 500 m onwards, and in most cases the 95% confidence interval included the homeward direction, or was < 2° from doing so. The control birds, without stereotyped routes, took slightly longer to become significantly orientated, and the 95% confidence interval was less likely to include the homeward bearing. The 95% confidence interval for the route-recapitulating birds never included the bearing expected according to the clock-shift treatment. From Bladon Heath, and in the early stages of the release from High Cogges (up to 3500 m from the release site), the average bearings expected according to the clock-shift treatment were included in the 95% confidence interval for the non-route-recapitulating birds (see table 5.1 for expected degree of deflection). The mean vectors were consistently longer for birds with established routes, indicating a lower level of scatter. The Watson-Williams F tests, used to investigate whether there was a significant difference between the mean bearings of the two samples, was significant only at the very beginning of the release from Bladon Heath, and at the very end of the release from Hinksey Heights. At Weston Wood significant results were found at distances of 3500 and 4000 m from the release site. At High Cogges (9.5 km from home) a significant difference was found between the two groups at 500 m from the release site, and then again from 5500 m onwards.

5.3.4 DISCUSSION:

This experiment demonstrates that the level of experience with a homing task has a substantial effect on birds' responses to clock-shift treatment. Clock-shifting consistently had a greater effect on less experienced birds than on birds that had developed stereotyped homeward routes. In many cases the very experienced birds

accurately recapitulated their own established routes, thus demonstrating that homing pigeons are capable of completing their entire homeward route without reference to a sun compass.

In section 5.3.1 I proposed three possible explanations for how birds that have developed stereotyped routes might progress between remembered waypoints (see Chapter 3), producing the characteristic stereotyped routes observed. The space between waypoints could be remembered as: 1; vectors (including distance and direction, this is the strategy adopted by insects performing stereotyped routes; Collett et al., 1998; 2002), 2; bearings (direction only), or 3; by visual attraction, without reference to a compass system. This experiment demonstrates that some birds with extensive experience from a release site are able to accurately recapitulate their established routes under clock-shift conditions, implying that these birds are relying upon visual attraction between waypoints in order to complete their homeward routes, without reference to a compass. There are various hints however, to suggest that under normal conditions the sun compass does have a role to play in detailed recapitulation of routes, though there seems to be individual differences in encoding various elements of a homeward route; some birds cope well with the clock-shift treatment whereas others seem severely disrupted. It is possible that some birds encode at least some of the links between successive waypoints in their homeward route as compass bearings, whereas other birds may rely more strongly on visual attraction between waypoints.

The birds that accurately reproduce their established routes under clock-shift conditions seemed to have a tendency to fly slightly to the anticlockwise side of their routes (e.g. a55 & r37 from Bladon Heath, v83 & l29 from High Cogges, a55 from Hinksey Heights, a56 & rwt from Weston Wood). This tendency suggests that even the birds recapitulating their routes most faithfully may still be affected by the clock-shift

treatment (though a reduction precision route recapitulation could also be attributed to birds having been in clock-shift loft for five days before release).

The different release sites seemed to have a significant effect on the behaviour of the birds. For example, the clock-shift seemed to have a greater effect on birds released at Bladon Heath, than at Hinksey Heights. At Hinksey Heights and Weston Wood the A34 dual carriageway points approximately in the homeward direction (315° compared to 330° for HH, 223° compared to 230° for WW), and from both of these sites the route-recapitulating birds followed their established routes fairly closely. It may be that the presence of prominent linear features pointing in approximately the homeward direction close to a release site might make the conflict between sun compass and landmark information more apparent to birds, than when non-linear landmarks are available as site markers. This quicker recognition of a conflict between familiar visual landmarks and the sun compass may cause birds to abandon their sun-compass in favour of visual landmark use (though see later in the discussion for alternative explanation of tracks recorded at Weston Wood). The presence of Wytham Hill (164 m in height) to the anti-clockwise side of the release site at Hinksey Heights, may also have had an effect on the tracks from this site, possibly reducing the anti-clockwise shift, as birds seem reluctant to fly directly over a large hill. At Bladon Heath and High Cogges the available linear features are not as prominent as at Hinksey Heights and Weston Wood, nor do they match the homeward direction as closely. The experienced birds from High Cogges all recapitulate their established routes fairly accurately, and it is only from Bladon Heath that several of the birds with stereotyped routes deviate consistently from their established routes.

Examples of experienced birds deviating widely from their established routes were observed at three of the four sites. At Bladon Heath, brc initially left the release

site in almost the direction expected due to the clock-shift treatment (~90° anticlockwise) before changing direction, landing for some time, and finally returning almost to the release site, from which the established route was recapitulated fairly accurately (see Figure 5.2). From Hinksey Heights a94 seemed similarly disorientated leaving the release site in a clockwise direction, performing a long loop, returning again almost to the release site, but turning the wrong way up the road and eventually joining the established route shortly before home (see Figure 5.4). This apparent confusion at the release site is interesting, and implies a lack of recognition of the release site. This could be caused by the change in the expected position of the sun relative to the position of the other visual landmarks, causing the release site to appear unfamiliar (as discussed in sections 5.2.1 & 5.2.4). In this way the sun could act not only as a compass, but also as a visual landmark (though birds must compensate for its movement through the sky during the day). It is possible therefore that the sun plays a part in familiar site recognition, as well as being used as a time compensated compass. Because this apparent lack of recognition seemed relatively rare, it did not seem necessary to repeat the experiment using the smaller degree of shift carried out in experiment 5.1.

Other birds that deviated from their established routes did so later in the journey. For example, from High Cogges k77 initially followed the established homeward route very accurately with almost no initial circling (in comparison to b17 and s30 who circled the release site for some time), but ~ 2 km into the flight began to deviate to the anticlockwise side of the established route, rejoined the route again further on, but then made a sharp 180° turn before approaching the loft from the opposite side (see Figure 5.6). This sort of delayed response to the clock-shift treatment is extremely interesting, particularly in light of the tracks collected at Weston Wood. From this site the A34 dual carriageway initially points almost directly homeward (223°, compared to 230° for

home), and made up the first 4 km of every bird's established route, until the point where road curves towards the east, away from home. Here the birds' established routes diverged with most choosing no longer to follow the road. When these birds were released under clock shift conditions, as mentioned in the results section, all birds still headed directly down the road in the homeward direction for the first 4 km of the flight. It was only when the birds reached the point were they would usually leave the road that any deviation from their established stereotyped routes occurred (see a56, b17, c70, rwt and s30's tracks in Figure 5.8) with, for example, b17 being deflected sharply in the anti-clockwise direction, before being drawn back to the established route. It is possible that the birds accustomed to homing repeatedly from Weston Wood had learnt that the road points almost directly towards home, and only when the road curves away from that homeward direction do they use a compass system to direct them to the next waypoint. This would explain this delayed clock-shift effect observed here.

Alternatively it could be that the first straight 4 km stretch of the A34 acts as a single waypoint for the birds, in the same way as a single large building might. Birds might therefore only become affected by the treatment once they had passed over the waypoint, and attempted to progress to the next one in the sequence.

One of the few studies where birds were released a large number of times from the same site was performed by Füller et al. (1983). In this experiment birds were trained > 60 times from the same site but, when released under clock-shift conditions, were fully deflected in comparison to control birds. As these birds were released "regularly" from each site it is puzzling that at least some of the birds did not develop stereotyped homeward routes - resulting in a reduction in the degree of observed shift. It is possible though that the birds used in this experiment had received only directional training, and therefore knew to fly in a particular compass direction, without encoding a

route in a map-like way. A second possibility is that because the release sites used in Fuller et al.'s experiment were 40.6 km and 56.4 km from the home loft, it might have become uneconomical for birds to develop stereotyped routes of these lengths, causing them to rely instead on a homeward compass bearing. In Chapter 3 though, one of the subjects (a99) developed a stereotyped route which was 43 km long, suggesting that development of stereotyped routes of these sorts of lengths may be feasible. A third possible explanation for the full degree of shift displayed in Füller et al.'s experiment is that at longer distances, fewer waypoints along the homeward route may be remembered in order to reduce memory load, and therefore the distance between remembered points must increase as release sites become further from the home loft. At some point the distance between remembered waypoints must become too great for visual attraction alone to allow a bird to move between successive points, and therefore a compass bearing between waypoints must be remembered instead. This possible increase in distance between waypoints may account for the results observed in Füller et al.'s experiment.

In several cases, birds which had not experienced a large number of releases seemed unaffected by the clock-shift treatment (see c17 from High Cogges or p08 from Bladon Heath for examples), similarly some birds which had developed stereotyped routes still seemed extremely disorientated by the treatment (see a94 from Hinksey Heights or k77 from High Cogges for examples). It is likely that these extreme examples significantly affected the results when the average deflection of each group was calculated for each site because of the relatively small sample sizes, and this probably contributed to the lack of significant differences between control and experimental groups. It has been shown in previous experiments (Foà & Albonetti, 1980; Bingman & Ioalè, 1989) that familiarity with a release site reduces the degree of deflection under

clock-shift conditions. It is possible that if control birds had had less experience from the release site a greater deflection might have been seen, though this is not always the case (see Chappell, 1997; Wiltschko et al., 1994 for reviews), and it is likely that with fewer training releases more birds (and trackers) would have been permanently lost. Releasing birds without any training releases would also have made it impossible to compare the control birds' clock-shifted tracks to previous un-shifted tracks.

In summary, this experiment has shown that birds allowed to develop a stereotyped homeward route from a release site are able to recapitulate their established routes without primary reference to the sun compass. The results are not entirely clear-cut though, and there is some suggestion that there are individual differences in the strategies birds use to remember their own distinctive stereotyped homeward routes, and that the strategy chosen may vary at different release sites. The study has provided a fascinating insight into the mechanisms controlling detailed route recapitulation, but further work must be carried out in order to determine exactly how birds encode their established routes.

CHAPTER 6

Conclusions and Future Directions

6.1 SUMMARY AND CONCLUSIONS OF CHAPTERS 2-5

6.2 ROUTE RECAPITULATION AND THE ROLE OF WAYPOINTS IN FAMILIAR AREA NAVIGATION

6.3 FUTURE DIRECTIONS

6.3.1 Experiments involving Route Recapitulation

6.3.2 Further experiments using GPS tracking

6.4 CONCLUDING REMARKS

The previous chapters report a variety of experiments utilising GPS technology to track homing pigeons as they navigate within a familiar area around the home loft. In this chapter I summarise the experimental results, give an overview of the phenomenon of route recapitulation, and outline possible future experiments which would expand on the findings of the current thesis.

6.1 SUMMARY AND CONCLUSIONS OF CHAPTERS 2-5

The experiments in Chapter 2 were designed to investigate the use of familiar visual landmarks along a pigeon's homeward route. These experiments were inspired by the line of research investigated by Biro (2002). Pilot studies utilising GPS trackers showed that on successive releases from the same sites, some birds would take very similar often indirect homeward routes and would often pass over the same points in the landscape even when released from sites in different directions. This, coupled with the result that pigeons more readily recognise landmarks from viewpoints they have been trained to rather than from novel viewpoints (Biro, 2003), suggested that birds may use the strategy of recapitulating already flown routes in order to approach landmarks from familiar angles. This is likely to improve the ease of recognition of familiar landmarks using "image matching" in a similar way to insects (Cartwright & Collett, 1982; 1983) and more recently chickens (Dawkins & Woodington, 2000).

To investigate this possibility further I released birds from the same sites (~5 km from home) 20-24 times in quick succession. I found three key results. First, tracks of individual pigeons become stereotyped with increasing experience. Second, individuals vary in their choice of route. Third, although birds' tracks become more efficient with experience, they remain substantially longer than the beeline distance

home. Several factors suggest that these stereotyped routes are visually mediated. Birds' routes remain consistent across varying wind directions, indicating that use of environmental odours is unlikely. Routes are not disrupted by a magnet treatment and, suggestively, the only bird never to develop a highly stereotyped route was found to be blind in one eye.

Three hypotheses were put forward to explain the patterns of stereotyped routes found. Firstly, birds could remember the homeward compass bearing from the release site and use familiar landmarks along the homeward route in order to correct for error along the way. This seemed an unlikely explanation as birds often left the release sites in directions inconsistent with that of home. Secondly, birds could remember a chain of landmarks including the homeward bearing between each. Thus a set of "waypoints" and associated bearings would make up the characteristic shape of the homeward route. This hypothesis was supported by track data because many of the stereotyped routes found included local constrictions, between which birds' flights were more varied. The third hypothesis was that birds remember their homeward routes in fine detail and proceed via "pilotage" (see Papi, 1992) without reference to an external compass system.

In Chapter 3 the phenomenon of detailed route recapitulation was investigated in greater depth. First, birds were released repeatedly from a distance of ~ 25 km from the home loft (route recapitulation had previously been demonstrated at ~ 5 km; Meade et al., 2005, and ~ 10 km; Biro et al., 2005), and again it was demonstrated that birds performed increasingly stereotyped, individually distinctive routes which often remained substantially inefficient. These birds were subsequently released singly from novel "off-route" sites perpendicular to their stereotyped routes (first carried out by Biro et al., 2005) with naïve partners that had not been allowed to develop a

stereotyped route acting as yoked controls (also released singly). Experienced birds with stereotyped routes were shown to fly to their established routes from distances of 1-3.7 km and in most cases accurately recapitulated their routes from the point of contact. Prominent changes in direction occurred when experienced birds crossed their own routes, but these direction changes were not seen in birds without their own established routes. This adds extra weight to the theory that the birds' routes are visually mediated as the cues used must have been detected and accurately assessed from distances of > 1 km.

In the light of the results of experiment 3.2 and those found previously (Biro et al., 2005) using off-route releases displaced along stereotyped routes, the hypotheses proposed in Chapter 2 were refined in favour of an extension of the second possibility; that homeward routes are broken down into shorter segments controlled by visual landmarks acting as waypoints. The space between waypoints could then be encoded as vectors (including distance and direction; the strategy adopted by some insects performing stereotyped routes; Collett et al., 1998; 2002), as bearings (direction only) or, as it has been shown that birds are able to access route information from distances of 1-3.7 km, it is possible that birds proceed down an established route relying on the visual attraction between successive waypoints (the different possibilities are examined experimentally in Chapter 5).

In Chapter 4 the role of visual landmarks along a pigeon's homeward route was investigated further. In an extension of Braithwaite's (1993) experiment, I tracked birds homing from particular sites in order to pinpoint areas they had flown over, and subsequently released them from these sites with and without a preview before take-off. Birds were released with naïve partners that were not known to have over flown the chosen flights, and therefore I was able to test (1) whether "aerial familiarity" with

a release site allowed birds to home more efficiently, and (2) whether a preview of a site allowed aerially familiar birds to recognise the site before release, and translate this recognition into a homing speed advantage. I performed two experiments, the first where the aerially familiar birds were known to have over-flown the release points at least once, and the second where the chosen release points were part of aerially familiar birds' habitual homeward routes.

I found that aerially familiar birds homed significantly more quickly than their naïve partners, and that this increase in homing efficiency was more apparent when the chosen release sites made up part of a bird's habitual homeward route. There was no evidence that aerially familiar birds recognised sites they had flown over from ground level. It seems that experienced birds could only utilise their knowledge of the sites they had flown over once they became airborne. It is possible that this lack of recognition was due to the substantially different view of a landmark array at ground level, compared to that viewed from the air, lending weight to the idea that pigeons are able to more readily recognise objects when they are viewed from similar distances and directions.

In Chapter 5 the technique of clock-shifting was introduced. In the first experiment of the chapter pigeons were tracked from two sites (from which they had received four training releases), under a one-hour phase shift. This is the first reported instance of birds under phase shift being tracked using GPS loggers. The experiment demonstrated that a small degree of shift still deflects birds in the expected direction, and that this small degree of shift can be detected statistically from certain release sites.

In the second part of this chapter, the technique of clock-shifting was used to experimentally address the theories put forward in Chapters 2 and 3. Stably route

recapitulating birds and less experienced partners were released from four sites 5 – 10 km from home under clock-shift conditions (leading to an expected anticlockwise deflection of ~ 90°). The clock-shift was shown to have a greater effect on the less experienced birds, and many of the birds with established homeward routes accurately recapitulated their stereotyped routes. This indicates that stably route-recapitulating birds are able to perform their established homeward routes without reference to the sun compass. Some birds did however deviate widely from their stereotyped routes, which suggests that there may be a certain amount of individual preference as to how detailed stereotyped routes are remembered, and some suggestion that the sun compass does play a role when birds are released under un-manipulated conditions.

6.2 ROUTE RECAPITULATION AND THE ROLE OF WAYPOINTS IN FAMILIAR AREA NAVIGATION

Over the course of the present thesis all the experiments have investigated the use of familiar visual landmarks along a pigeon's homeward journey. The most striking result found was that when released repeatedly from the same site, pigeons develop individually distinctive, highly stereotyped routes. Following this initial discovery, the finding has been shown to be a very robust result such that every bird repeatedly released from a site has eventually developed a highly stereotyped route (excepting the bird found to be blind in one eye). Several factors have reinforced the idea that these routes are mediated by familiar visual landmarks; the established routes are recapitulated accurately over varying wind conditions; the routes are shown to be unaffected by a magnetic disruption treatment; route cues can be detected from

distances of up to 3.7 km. Visual landmarks remain the only environmental cue to successfully fulfil all these criteria.

The highly stereotyped routes performed by pigeons are reminiscent of those found in experiments involving insects (Rosengren, 1978; Collett et al., 1992; Dyer, 1991) and more recently chickens (Dawkins & Woodington, 2000). These animals are thought to navigate using a strategy known as "image matching". This was first demonstrated in experiments where honeybees were shown to remember retinal "snapshots" of landmarks associated with a goal (Cartwright & Collett, 1982). When returning to a target they moved so as to reduce the discrepancy between their retinal image and the remembered snapshot. Because of the large range of distances and directions that 3D landmarks can be viewed from, remembering them all would incur a high cost in terms of memory load. "Image matching" serves to reduce the number of images that must be remembered. In order to make the recognition of complex landmarks easier many animals follow set routes, maintaining consistency of viewing angles over many journeys, and thus making object recognition easier. As pigeons have also been shown to recognise landmarks more readily when viewing them from familiar distances and directions (Biro et al., 2003), it is possible that pigeons use a similar form of image matching to recognise familiar landmarks, and perform highly stereotyped routes in order make recognition of a smaller number of views of landmarks easier.

Consistent with this hypothesis is the finding that when birds are released from novel sites perpendicularly displaced alongside their established routes, most birds take "local shortcuts". Rather than joining their route at the closest point (at a right-angle) most birds joined their routes at points slightly further along the route, closer to home. One reason why birds might be attracted to visual landmarks further along the

homeward route is because from this more oblique angle the view of the landmark would more closely match the view of the landmark array usually encountered on the homeward journey, more readily facilitating recognition.

One of the most important features of this model of route recapitulation is the use of visual landmarks as "waypoints" along the homeward route. The possible use of waypoints was first suggested by Biro (2002) who showed that birds tended to pass over particular points in the landscape that were not only similar across releases (both from the same and different release sites) but also across birds. The idea that a homeward route might consist of a sequence of waypoints was hinted at by the results of the experiments 2.1 & 2.2, where birds flew indirect routes which could not be explained by a single homeward direction, and within which there were many examples of particular landscape features being associated with local constrictions in routes. This idea was further confirmed by the finding that some birds released from novel off-route sites tend to return to their routes at the same point, and again these points were often consistent across birds. Interestingly it has been shown that stereotyped routes performed by insects, though governed by a global vector indicating the total distance and direction required to reach their final goal, are subdivided into shorter sections guided by "local vectors" (in ants: Collett et al., 1998; in bees: Collett et al., 2002). It was experimentally demonstrated that these local vectors (including distance and direction) were triggered in sequence by visual landmarks acting as intermediate goals. It seems that these visual landmarks encoded into an insect's map of space might act in a similar manner to "waypoints" within a pigeon's homeward route.

In Chapter 5 it was established that accurate route recapitulation could still occur without reference to the sun compass. Some results however, such as the

"delayed clock-shift" seen in the releases from Weston Wood, imply that the sun compass does play a part in route-recapitulation under normal circumstances. Whether this depends largely on individual preferences remains to be resolved.

Though this series of experiments has provided much information about the strategies of birds homing repeatedly from the same site, there are still some intriguing questions left open. How far can the strategy of route recapitulation extend away from the loft? Releases from the Ridgeway showed that birds can accurately recapitulate routes from sites 25 km from home, and one bird (a99) performed a route of average length 43 km which implies that route recapitulation could still remain a viable strategy from release sites up to this distance from home. It is likely, though, that the strategy of remembering views of visual landmarks would become inefficient if the distance from release site to home continued to be increased.

Another interesting question is whether, when homing from increasingly distant release sites, the distance between waypoints remains the same as in shorter distance releases, or whether the distance between successive waypoints is increased as a mechanism of reducing the number of images that must be remembered when homing from further away. If this were the case it is likely that the distance between waypoints would become too large for birds to proceed from one waypoint to the next by direct visual attraction, and that at longer distances bearings or vectors between waypoints would have to be included into the homeward route. Methods of experimentally addressing these questions are included in the following section.

6.3 FUTURE DIRECTIONS

6.3.1 EXPERIMENTS INVOLVING ROUTE RECAPITULATION

As mentioned in the above section, it would be very interesting to determine just how far from the loft route-recapitulation remains a viable strategy. Theoretically this would be a simple experiment to perform, though repeatedly releasing birds at distances of > 25 km would be a time consuming and expensive process. Perhaps more can be learned about the distribution of waypoints along a homeward journey at the distances at which route recapitulation has already been demonstrated. If a greater number of off-route releases were carried out, distributed evenly along a bird's established route, the points where birds join their stereotyped routes may shed light on the positioning of waypoints making up the shape of the route. For example, if at longer distances waypoints are very spaced out, it is possible that the same waypoint may be the appropriate place to join the route from several off-route sites. This may provide some information about the distribution of waypoints along stereotyped routes at differing distances from home. The technique of clock-shifting stably route recapitulating birds at a range of distances from home may also indicate whether, at increasing distance from the home loft, there is a greater tendency to rely on a compass-based mechanism of proceeding from one waypoint to the next. If so, this would indirectly indicate that waypoints making up longer stereotyped routes were more spaced out, so much so that it would not be possible to proceed from one to the next via visual attraction alone.

It would also be interesting to investigate the endurance of birds' route-based memory. This could be examined simply by letting a certain amount of time elapse

after a bird is stably recapitulating an established route before releasing it again from the same site, and comparing the route performed to the bird's previously established route. The degree of disruption that birds are able to endure could also be examined by releasing birds from other sites in between releases from the site from which they perform their established routes. In the current thesis birds were not released from any other sites during their training releases (apart from the off-route release sites in Chapter 3) so it is not known whether disruption of this sort would interfere with the development of highly stereotyped routes.

The phenomenon of detailed route recapitulation also lends itself to investigations which would not be possible without prior knowledge of the route a bird was likely to take. For example, investigations into the flight patterns of pigeons travelling in groups led to hypotheses that a group's orientation may depend on the navigational tendencies of a bird acting as "leader" or on some averaging of tendencies within the group (Wallraff, 1978). Though GPS technology has revolutionised the ability of researchers to determine which bird is ahead of the others (and can therefore be interpreted as the "leader"), if birds are flying close together this may be difficult due to the resolution of the GPS technology (± 4 m) and could give misleading results. It is also possible that a bird marginally in front of another may in fact be attending to the movements of birds behind that remain in vision. With prior knowledge of the routes birds are likely to take from particular sites it would be much easier to determine whether the route followed is one bird's established route, indicating that this bird is the "leader", or whether some compromise route is taken.

Similarly, experiments investigating the effect of differing wind directions on a bird's flight speed could be performed more easily if the route a bird is likely to take is known prior to release. For example it has been shown that long distance migrants

maximise the distance they travel on a given amount of energy (see Alerstam & Hedenström, 1998 for a review), by reducing their airspeed in a tailwind, and increasing their airspeed in a headwind. Whether pigeons also attempt to maximise the distance flown on a given amount of energy, over short distances, can be examined more easily if (a) birds fly in an almost straight line and (b) that expected routes are known in advance so that releases can be performed when wind direction is suitable (i.e. it is known that birds will be flying approximately into a headwind or tailwind). Straight paths for at least part of the journey could be obtained by releasing birds close to a prominent linear feature pointing in approximately the home direction (e.g. the A34 from Weston Wood) or by selecting birds that tend to develop very straight homeward routes (e.g. c15, p08 from the Ridgeway).

6.3.2 FURTHER EXPERIMENTS USING GPS TRACKING

An important question in pigeon homing which remains unsolved is whether pigeons remember the homeward course from a previously visited release site as a compass bearing towards home, or as a homeward vector. Vanishing bearings obtained from clock-shift experiments demonstrate that at least a homeward bearing is recalled, but provides no information as to whether distance as well as direction is included. Using GPS loggers to track the entire homeward journey of clock-shifted birds would provide much more detailed results and would potentially shed light on whether the homeward course is remembered as a bearing or as a vector. Several releases under clock-shift conditions hint that the expected distance from the release site to home may be remembered; Holland (1998) reconstructed a track from a route-recorder carried by a pigeon released under clock-shift conditions less than 2 km from the

home loft. The track showed the bird spiralling in towards home, making marked "corrections" in its trajectory close to previously visited release sites. These corrections occurred when the bird had flown the approximate distance necessary to reach the home loft from the release site or previous correction point, thus suggesting that the bird may have been utilising remembered vectors from familiar points, rather than bearings alone. In the current thesis there are two examples of clock-shifted birds flying the approximate distance required to reach home and then landing for an extended period of time (Figure 5.3; 119 and 195), possibly to reassess their position because the home loft had not come into view at the expected distance from the release site.

To address this issue more formally, birds could be released from previously visited sites (though not sites from which they had developed stereotyped routes) at varying distances from home, and the distance of "correction points" from the release site compared to the distance between the release site and home. If there were a strong correlation between the two, this would suggest that birds remember not only the direction but also the distance to home from previously visited sites. This may also provide insight into whether birds are able to encode the space between waypoints along a stereotyped route in the form of vectors.

Another interesting question is whether pigeons might perform "orientation flights" in a similar manner to some flying insects. When insects such as wasps leave a goal that they intend to return to they fly in arcs centred on their target (Zeil, 1993; Collett, 1995). As they turn at the edge of these arcs they inspect the goal from one or two favoured directions and on their subsequent return move along one or both of these favoured bearings, thus viewing their target from a familiar angle. Pigeons perform many seemingly random circuitous flights around their home lofts (or roosts)

daily, but it is possible that these flights may serve some information gathering purpose, perhaps in a way analogous to orientation flights. It would be interesting to track spontaneous flights of pigeons around the loft, to attempt to ascertain whether there are similarities between flights, e.g. preferred angles of viewing the loft, and if so whether these similarities are associated with preferred directions in which the loft is approached when birds are subsequently released.

Finally, as technology improves further, GPS devices are likely to become increasingly light weight (the trackers utilized in this thesis were reduced in weight by 13 g, see appendix 1), thus increasing the number of bird species which can potentially be investigated using this technology. The reduction in weight also opens up the possibility of incorporating additional devices such as altimeters (see Weimerskirch et al., 2005) to address the second main limitation of GPS technology; the relatively poorer vertical than horizontal resolution. This potential increase in accuracy in the vertical plane would provide very interesting data. Do birds fly higher when less familiar with a homing task, in order to gain visual access to a wider area? Do birds recapitulate their routes in three dimensions?

6.4 CONCLUDING REMARKS

In the present thesis I hope to have shown that GPS technology is a powerful method of reconstructing pigeons' homeward paths, recording birds' movements in extremely high resolution both in space and in time, resulting in tracks of unprecedented detail which lend themselves well to detailed data analysis.

The studies reported constitute an important advance in the knowledge of how pigeons navigate within a familiar area, particularly when they become very

experienced with a homing task. These studies also suggest that certain limitations apply to pigeons' visual recognition abilities, which may have profound effects on the way that familiar visual landmarks can be used when navigating within a familiar area. GPS technology remains a valuable tool with which unresolved areas of pigeon navigation, the investigation of which was previously constrained by methodological difficulties, can be now be investigated.

APPENDIX 1

A1.1 TECHNICAL DESCRIPTION OF GPS TRACKERS

The main component of all devices was the SAM (Smart antenna module, see Figure A1.1a) available from u-blox (Copyright © 2003, u-blox AG). The SAM is a GPS (Global positioning system) receiver and data logger allowing storage of up to 100,000 logs of GPS data. An integrated ceramic patch antenna (25 x 25 mm) is included. The SAM device is useful for bio-telemetry, due to its small size (w = 31.5 mm, l = 47.0 mm, h = 9.5 mm, weight = 23 g), accurate GPS performance, and low power consumption.

The SAM device includes power management functions, which allow power consumption to be minimized, allowing smaller, lighter batteries to be used to power the devices. All the devices used were powered by Lithium Polymer batteries. These batteries are designed for use with portable equipment and have a very high power to weight ratio.

The GPS trackers used in chapter 2 were supplied by H. P. Lipp and G. Dell'Omo, of Zurich and Rome Universities. These trackers consisted of the integrated SAM device, attached via a voltage regulator to a 640 mAh lithium polymer battery weighing 14 g. They were operated using a 3 pin switch, and had a serial port additional to the one available as part of the SAM module. The first generation tracker was encased in a plastic box, taking the total weight of the tracker to 35 g. For further details see Steiner et al. (2000). The devices were attached to the birds by means of Velcro strips measuring 30 mm x 70 mm. A strip of "male" Velcro was attached to the birds' back (see Chapter 2 for more details) and a strip of "female" Velcro was attached to the plastic box containing the GPS device. Five second generation trackers, without the plastic casing, weighing 32 g, and five third

generation trackers, with a smaller (13 x 13 mm) antenna, weighing 28 g were later supplied (and used for experiments in chapters 2 and 4).

A smaller, lighter tracker was developed by K. K. Lau, based on the design available on the u-blox website. This tracker again consisted of the SAM device, with a 3.7 v, 120 mAh lithium polymer battery attached via a 3.9 Ω resistor to the SAM device. The resistor itself was used as a switch, plugged into a metal clip attached to the wire attached to the positive terminal of the battery. The logging device ran on continuous mode for ~ 40 min, taking fixes at 1 s intervals.

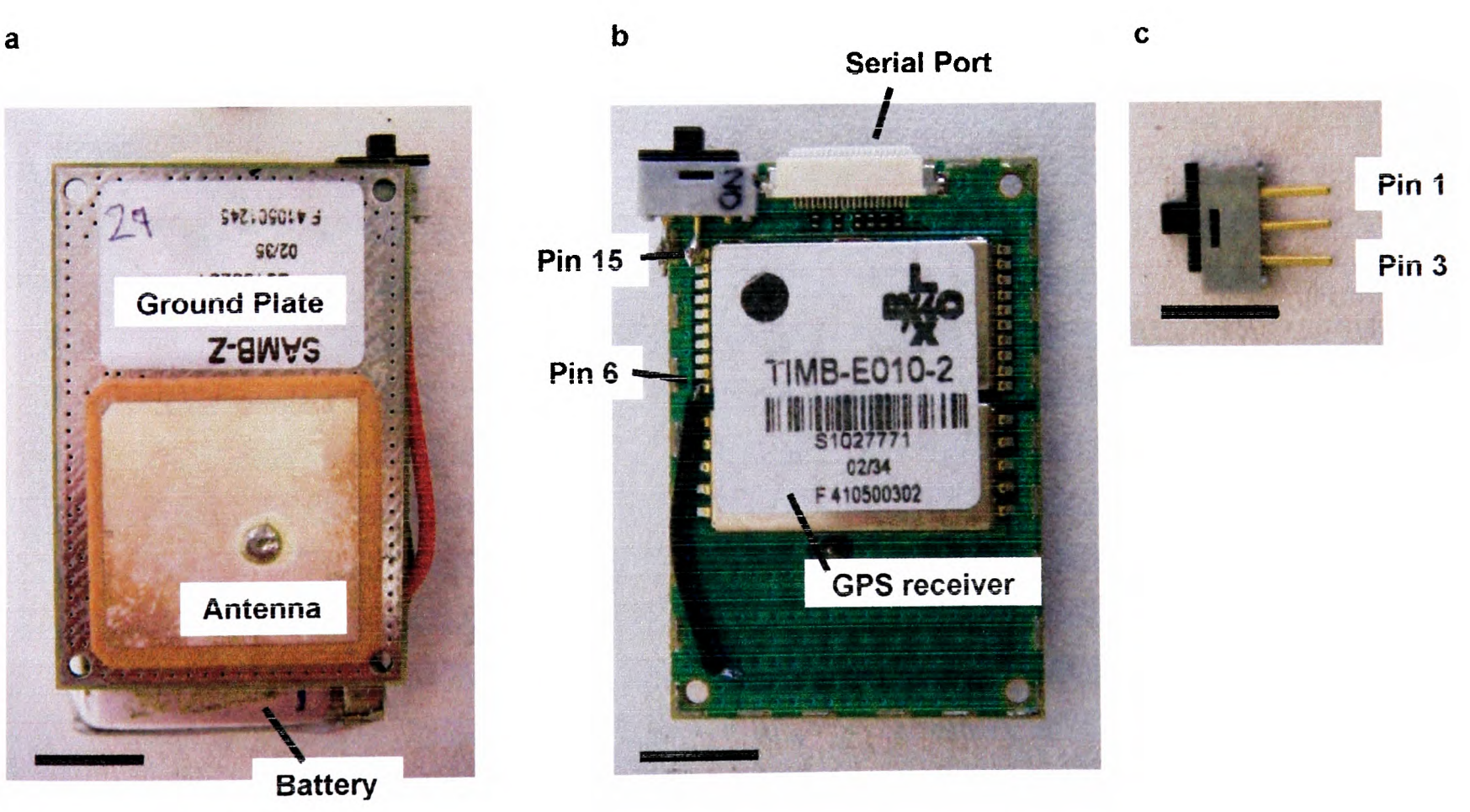
This design was further modified, as the resistor was found to be unnecessary. The maximum voltage input of the GPS receiver was 3.6 v, and though the nominal voltage of the batteries was 3.7 v, the actual output of 120 or 150 mAh batteries did not exceed 3.6 v. The batteries could therefore be attached directly to the SAM device without use of a resistor. This increased running time, as power was no longer wasted through the resistor. A 3 pin switch was also included (see Figure A1.1c), super-glued to the back of the ground plate, to increase ease of use and robustness of the devices. This design was used for the majority of the experiments detailed in the current thesis (experiments in chapters 3, 4 & 5) and weighed 23 g. The weight could be further reduced to 16 g, by replacing the 25 x 25 mm ceramic patch antenna with a 13 x 13 mm antenna, but as these trackers were slightly less reliable the 23 g trackers were preferentially used.

Several power functions are available for the SAM device and can be downloaded onto each device via the serial port, using software designed by u-blox and available from their website. The first; continuous mode, allows fixes to be taken every second as long as a view of the sky is available. The second; TricklePower™ mode is one of the low power settings. This mode also allows fixes to be taken every second if required, but the device goes into sleep mode for ~ 700 ms in between each

fix. This allows the devices to run for approximately three times as long as in continuous mode, with only a small reduction in performance (~ 1 fix missed every 20 seconds). The third setting; Push-to-Fix™ mode allows the user to define periods within which the device takes fixes, between which the device will enter sleep mode for periods of up to 2 hours. Trickle-power mode was used for the experiments in chapters 3 and 5, and allowed a tracker life of up to 2 hours using a 150 mAh battery.

A1.2 MAKING A GPS TRACKER

Figure A1.1 The figure shows (a) a GPS tracker viewed from above, (b) a tracker viewed from beneath, and (c) a 3 pin switch. Various components referred to in the text are labelled. 1 cm scale bars are included in each picture.



First the metal plating must be removed from the back of the SAM device. The exposed wire cage is then twisted off using wire clippers. The brown plastic clip is removed from the serial port.

Before attaching the switch, the third pin must be removed (see Figure A1.1c), and the second pin trimmed to ½ length. Place a blob of solder on pin 15 of the GPS receiver and superglue the switch to the back of the ground plate (see figure A1.1b), so that pin 2 of the switch rests on the solder blob on pin 15 of the GPS receiver. Solder the two pins together when the glue is dry.

Blu-tack a wired, 3.7 v, 150 mAh lithium polymer battery to the back of the ground plate with solder pads downward. Trim the black wire and solder it to pin 6 on the GPS receiver. Trim the red wire and solder it to the first pin on the switch. Add sticky backing to the back of the GPS receiver to bring it to the same thickness as the battery. Superglue a 27 mm x 40 mm strip of "female" Velcro across the battery and sticky backing.

Figure A1.2 GPS tracker made to the above specifications attached to the back of a pigeon.



A1.3 DATA HANDLING

In order to retrieve data from the GPS tracking device described in the previous section, a data cable was made following the specifications on the u – blox website (http://www.u-blox.com/products/). This was inserted into the serial port (see Figure A1.1a) and allowed data to be downloaded using the u-blox software; u-logger2, also available from the u-blox website.

The data is then saved as a tab delimited text file, giving positional information in the form of a spreadsheet. The recorded data includes GPS coordinates of latitude and longitude, the date and time each data point was recorded, altitude (m), speed (m/s), and details of how many satellites the logger received data from. The positional fixes are in the GPS WGS84 coordinate system, which uses the centre of the mass of the earth as the origin. Latitude and Longitude data are in the format d.ddddd° and provide a series of x and y coordinates plotted sequentially, making up the track data. Altitude provides the Z coordinate, but, for reasons discussed in section 1.4.5, it remains less accurate than the horizontal position determination, and has therefore been disregarded in the studies reported in the current thesis.

Once the data had been saved in the appropriate format, the positional data could be superimposed onto digitised Ordnance Survey maps using the commercially available Fugawi™ Moving Map software (Northport Systems Inc. Toronto, Canada). The maps used were calibrated using three or more known coordinates, including the home lofts. The Fugawi software allows tracks to be displayed in a variety of formats (different colours, different point sizes and line thickness) and also enables track data to be exported back into text format. This allows conversion from GPS to OSGB36 National Grid eastings and northings, which are measured in metres, and are therefore

useful for measures such as track similarity (used in Chapters 2 & 3; see appendix 3), and straightline distance from the release site (used in Chapter 5).

APPENDIX 2

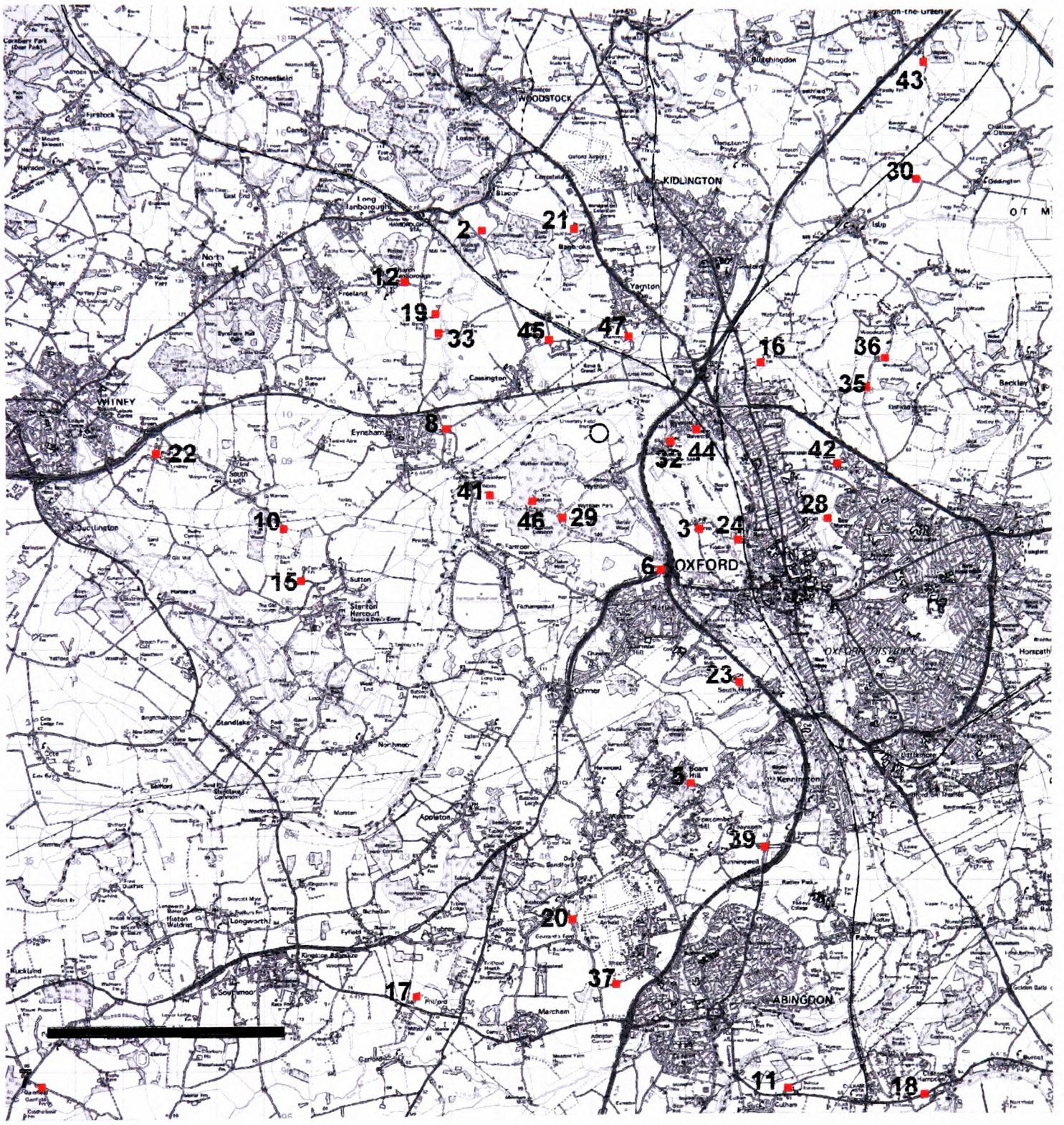
A2.1 DETAILS OF RELEASE SITES

The table lists the name of each release site and its distance and direction to the home loft, as well as GPS co-ordinates. The final column gives details of which sites were used for each experiment, both for training and test releases.

	Name	Distance from home (m)	Direction to home (°)	Longitude	Latitude	Used as part of the following experiments (T = training, E = experimental releases)
1	LOFT	0		1° 19' 03.43"	51° 46' 58.15"	
2	Bladon Heath	5.1	151.0	1° 21' 10.40"	51° 49' 20.53"	E = 2.1
3	Binsey	2.9	314.2	1° 17' 12.23"	51° 45' 51.02"	T = 2.1, 2.2, 3.1, 4.1, 5.1, 5.2
4	Blewbury	25.8	345.8	1° 13' 41.64"	51° 34' 02.05"	T = 3.2
5	Boars Hill	7.8	346.4	1° 17' 23.60"	51° 42' 52.13"	T = 3.1, 3.2
6	Botley Roundabout	3.0	333.0	1° 17' 51.88"	51° 43' 31.30"	T = 2.1, 2.2, 3.1, 4.1, 5.1, 5.2
7	Carfield Farm	18.5	41.1	1° 29' 34.79"	51° 39' 31.69"	E = 3.2
8	Cassington	3.0	92.1	1° 21' 54.51"	51° 47' 02.34"	T = 2.1, 2.2, 3.1, 4.1, 5.1, 5.2
9	Churn Farm	24.7	1.6	1° 20' 24.51"	51° 33' 43.64"	E = 3.2
10	College Farm	7.0	73.3	1° 24' 59.08"	51° 45' 53.02"	T = 2.1, 2.2, 3.1, 4.1, 5.1, 5.2
11	Culham	16.0	344.1	1° 15' 13.69"	51° 38' 44.89"	E = 3.2
12	Church Hanborough	5.3	128.4	1° 22' 39.57"	51° 48' 44.72"	E = 2.2 T = 2.1, 3.1, 3.2, 4.1, 4.2
13	Drayton	15.4	3.9	1° 19' 57.53"	51° 38' 42.85"	E = 3.2
14	East Hanney	17.3	18.0	1° 23' 40.32"	51° 38' 04.76"	T = 3.2
15	Friar's Farm	7.1	63.7	1° 24' 38.87"	51° 45' 16.49"	E = 5.1 T = 2.1, 2.2, 3.1, 3.2
16	St Frideswides Farm	3.9	245.9	1° 16' 01.83"	51° 47' 49.58"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
17	Frilford	12.9	18.8	1° 22' 39.57"	51° 40' 26.02"	T = 3.2
18	Fullamoor	15.8	335.5	1° 13' 06.82"	51° 39' 13.97"	E = 3.2
19	Goose Eye Farm	4.3	126.5	1° 22' 04.43"	51° 48' 21.81"	E = 4.2
20	Gozzards Ford	10.5	3.8	1° 19' 37.55"	51° 41' 15.10"	T = 3.1, 3.2
21	Hall Farm	4.3	171.0	1° 19' 37.84"	51° 49' 16.29"	T = 2.1
22	High Cogges	9.4	89.3	1° 27' 06.59"	51° 46' 55.65"	E = 5.2
23	Hinksey Heights	6.2	331.1	1° 16' 28.63"	51° 44' 03.72"	E = 5.2 T = 2.2, 3.1, 4.1, 5.1, 5.2
24	Jericho	3.8	307.7	1° 16' 26.30"	51° 45' 44.67"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
25	Knob Down	26.6	352.4	1° 15' 59.56"	51° 32' 44.10"	E = 3.2
26	Landmead Farm	15.2	7.7	1° 20' 49.47"	51° 38' 53.14"	E = 3.2
27	Lyford Grange	16.6	24.7	1° 25' 08.77"	51° 38' 52.87"	E = 3.2
28	Marston Cricket Pitch	5.2	290.7	1° 14' 46.70"	51° 45' 59.71"	E = 4.1
29	My lady's Seat	2.0	21.3	1° 19' 44.92"	51° 45' 58.40"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
30	Oddington	8.8	232.6	1° 12' 58.78"	51° 49' 53.60"	T = 3.1, 3.2
31	Osney	15.5	352.2	1° 17' 09.09"	51° 38' 42.76"	E = 3.2
32	Port Meadow Carpark	1.6	276.6	1° 17' 41.91"	51° 46' 51.34"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
33	Purwell Farm	4.0	122.7	1° 22' 01.03"	51° 48' 08.77"	E = 4.2
34	Ridgeway	25.6	358.8	1° 18' 39.10"	51° 33' 14.84"	E = 3.1, 3.2 T = 3.1, 3.2
35	Sescut Farm	5.9	261.4	1° 14' 01.33"	51° 47' 28.96"	E = 5.1 T = 2.2, 3.1, 3.2, 5.1, 5.2
36	nr Sescut Farm	6.4	255.8	1° 13' 40.52"	51° 47' 49.07"	T = 2.2
37	Shippon	11.9	358.4	1° 18' 50.64"	51° 40' 33.66"	T = 3.1, 3.2
38	Steventon	17.3	3.6	1° 19' 57.73"	51° 37' 40.34"	T = 3.2
39	Sunningwell	9.9	340.0	1° 16' 03.56"	51° 42' 01.50"	T = 3.1, 3.2
40	Sutton Wick	14.8	357.5	1° 18' 29.97"	51° 39' 06.05"	T = 3.2
41	Swinford	2.7	59.2	1° 21' 03.62"	51° 46' 15.61"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
42	Victoria Arms	5.2	277.8	1° 14' 31.68"	51° 46' 36.99"	E = 4.1 T= 2.1, 2.2, 3.1, 4.1, 5.1, 5.2
43	Weston Wood	10.7	221.2	1° 14' 31.68"	51° 46' 59.13"	E = 5.2 T = 5.2
44	Wolvercote	2.0	267.5	1° 17' 15.54"	51° 47' 01.34"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
45	Worton	2.3	152.9	1° 19' 57.07"	51° 48' 04.10"	T = 2.1, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
46	Wytham Hill	2.1	45.8	1° 20' 19.71"	51° 46' 12.52"	T = 2.1, 2.2, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2
47	Yarnton Manor	2.2	197.4	1° 18' 28.05"	51° 48' 06.38"	T = 2.1, 3.1, 3.2, 4.1, 4.2, 5.1, 5.2

A2.2 MAP OF RELEASE SITES

Each release site is marked by a red square and labelled with a number relating to the table in section A2.1. Release sites > 15 km from home are not included. Home is marked by a white circle. The scale bar indicates 5 km.



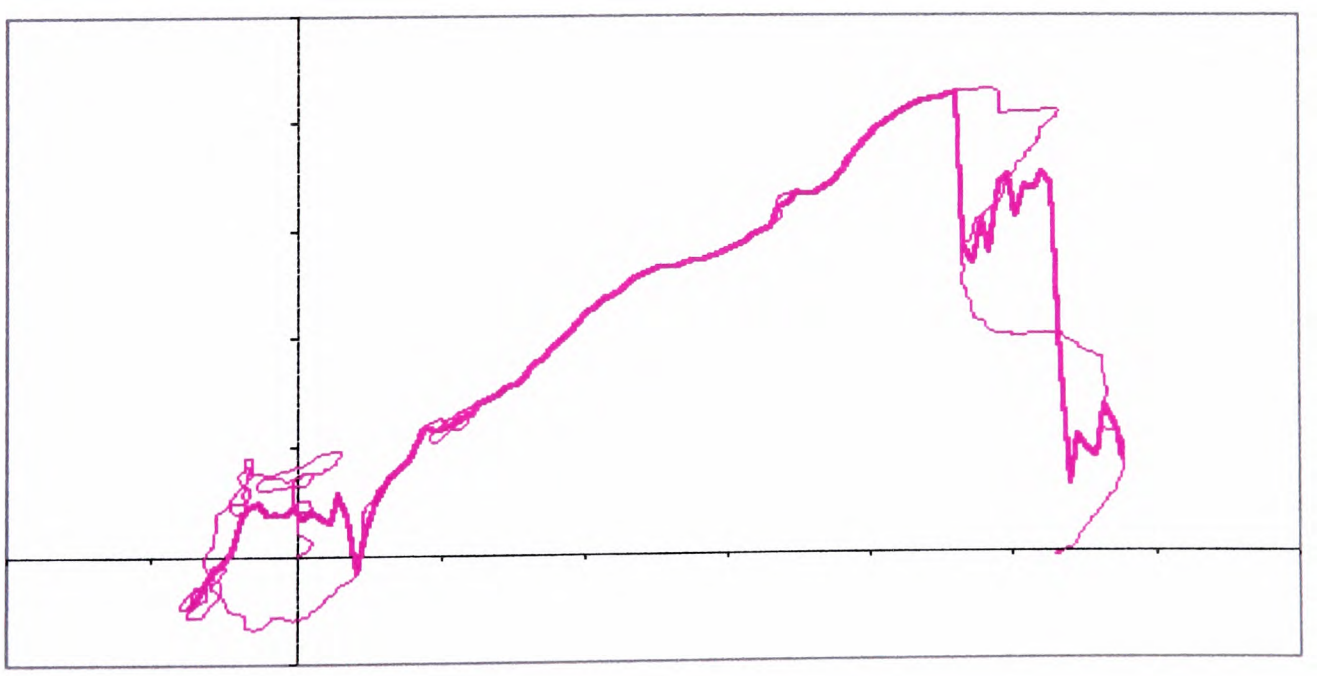
APPENDIX 3

A3.1 DESCRIPTION OF TRACK SIMILARITY PROGRAM

This program was developed to allow a single measure for track similarity to be calculated for any given pair of tracks. The program measures the area between two tracks that both start and end at the same points, where a small area indicates high levels of track similarity, and a large area indicates highly dissimilar tracks.

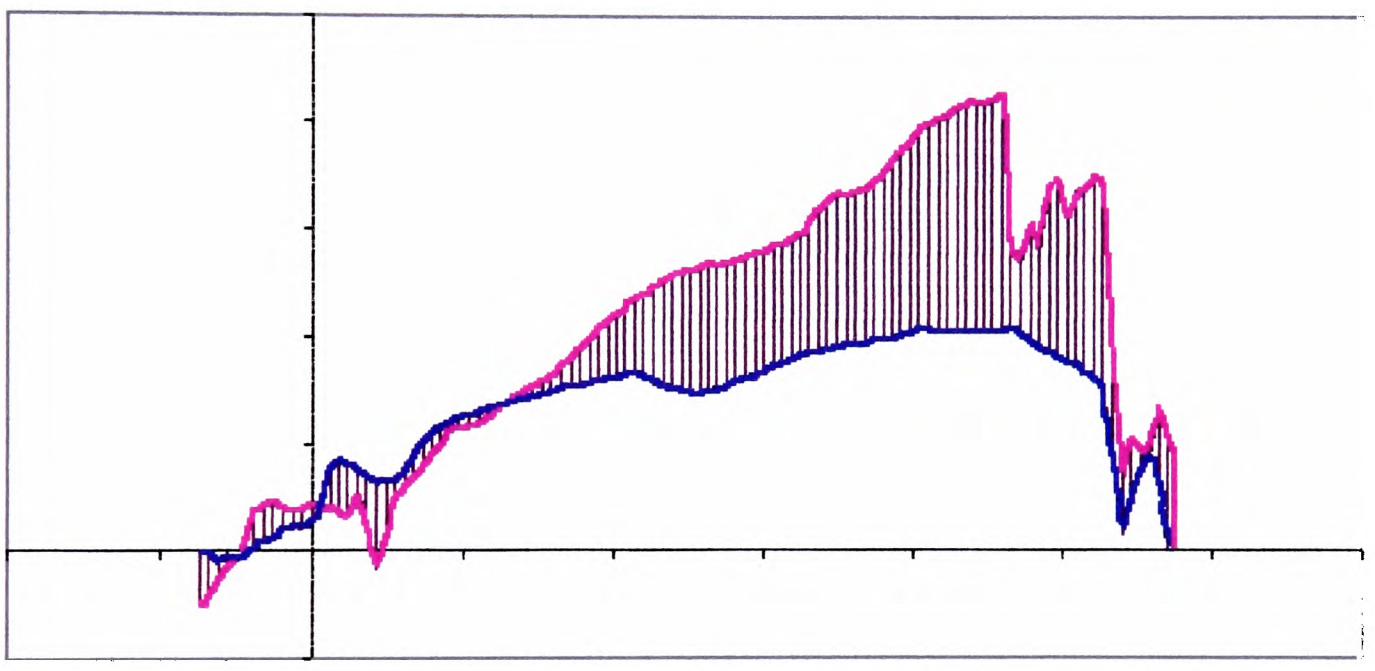
The measurement of area is complicated by the tendency pigeons have both to perform loops and also to double back on themselves. In order to simplify the measurement of area, a straight line was drawn between the start and end point of a bird's journey. This straight line was then divided into segments, controlled by the number of points in the tracks. Any multiple lines occurring in one of these segments (see figure A2.1) are then averaged. The thin pink line in figure A2.1 shows a bird's original track, and the thick pink

Figure A3.1 The graph shows a pigeon track (thin pink line) which is divided into small segments and any multiple lines occurring in a segment are averaged. The resulting track is shown by the thicker pink line. The axes represent positional x y coordinates.



line demonstrates what the track looks like when multiple lines occurring within any segment are averaged. Figure A2.2 shows a pair of averaged tracks with vertical lines indicating segment width. The area between a pair of averaged tracks is then measured, resulting in a measure of track similarity, where a small area represents a pair of highly similar tracks and a large area represents a pair of very dissimilar tracks.

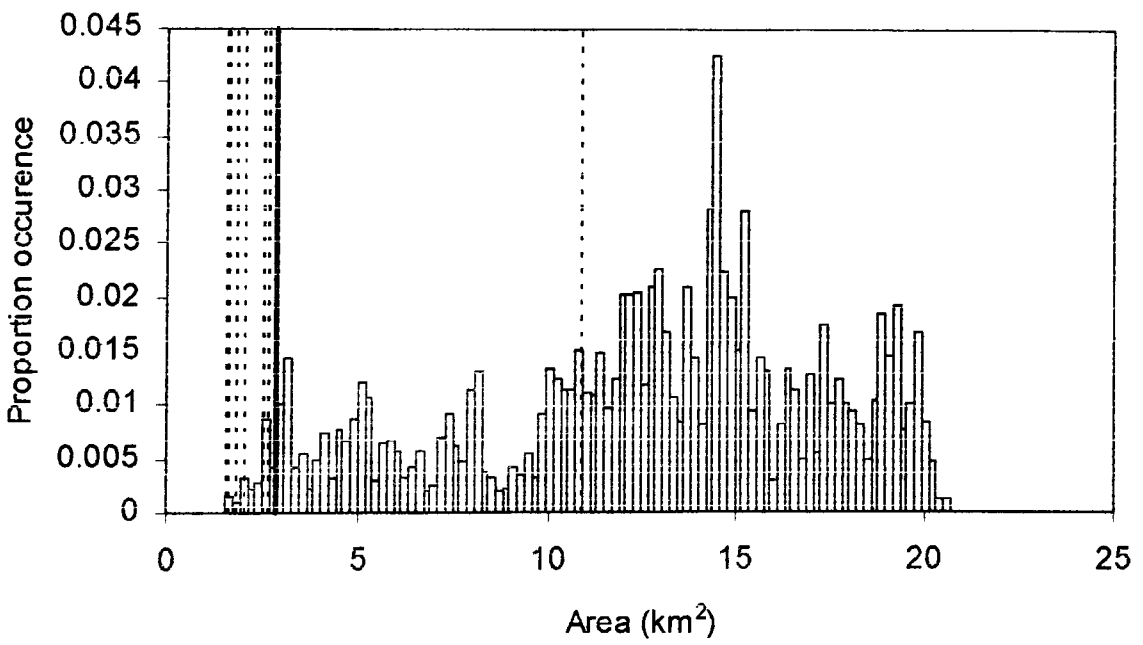
Figure A3.2 The figure shows a pair of averaged tracks including vertical lines indicating segment width. The area within each segments are summed to give an overall measurement of track similarity. The axes represent positional x y coordinates.



The program allows up to 50 tracks of up to 30,000 points in length to be entered at a time. Once a certain number of tracks are entered into the program they are all compared to each other, resulting in a symmetric matrix of areas between tracks. Once the tracks have been entered the user can choose whether to use the randomisation function. This function was used in chapters 2 and 3 (see sections 2.2.2, 2.3.2 & 3.2.2) to assess whether the final three tracks (birds received a total of 20-24 releases) performed by individual birds were more similar to each other, than to tracks performed by other birds. This function randomly

selects groups of three tracks (though this number can be altered) from all the tracks that have been fed into the program. Each combination of the three tracks are compared to each other, and the results summed, providing a cumulative area which reflects the similarity of the three tracks. This randomisation procedure is reiterated 10,000 times to provide a test distribution of track similarity. The cumulative areas between the final three tracks performed by individual birds can then be compared to this distribution. Figure A3.2 is taken from chapter 2 and demonstrates a test distribution of cumulative areas, with the cumulative areas found when birds' own tracks are compared to each other shown by dotted lines.

Figure A3.2 The figure (taken from chapter 2) shows the test distribution of cumulative areas found when sets of tracks are selected at random and the areas enclosed by each possible pair of tracks within a group of three are plotted. The randomisation procedure is reiterated 10,000 times. The cumulative area found when the final three tracks actually flown by individual birds are shown by vertical dotted lines. The solid line shows the lower 0.025 confidence value.



A3.2 TRACK SIMILARITY PROGRAM

The program was written in Fortran, and is listed below.

```
c-------------------------------------------------------------------------+
c                                                                         |
c-------------------------------------------------------------------------+
      program pigeon
 use msimsl
 parameter (max_ser=50,max_obs=30000)
      implicit double precision (a-h,o-z)
 double precision x(max_ser,max_obs),y(max_ser,max_obs)
 double precision distance(max_ser,max_ser)
 integer n_points(max_ser)
 character*20 filename(max_ser),listfile,adum
 logical file_exist
 open(12,file='summary_table.txt',status='unknown')
 open(13,file='details_table.txt',status='unknown')
 write(*,*) ' +-----------------------------------------------+'
 write(*,*) ' |        Track Difference Metric Program        |'
 write(*,*) ' +-----------------------------------------------+'
 write(*,*)
 write(12,*) '********* Track Difference Metric Program *********'
 write(12,*)
  1   write(*,*) 'Write either:'
 write(*,*) '              the name of the list file'
 write(*,*) '      or'
 write(*,*) '              Q for individual data file entry'
 read(*,*) listfile
 rewind(2)
 close(2)
  if(listfile.ne.'Q'.and.listfile.ne.'q') then
c  Read file names from list
      inquire(file=listfile,exist=file_exist)
    if(file_exist) then
      open(2,file=listfile,status='old')
          do i=1,max_ser
        rewind(1)
        close(1)
        read(2,'(a)',end=3) filename(i)
            inquire(file=filename(i),exist=file_exist)
        if(file_exist) then
          open(1,file=filename(i),status='old')
              do j=1,max_obs
            read(1,*,end=5) x(i,j),y(i,j)
            n_points(i)=j
          enddo
        else
          write(*,*) 'File missing or name misspelt'
          stop
        endif
    5          n_files=i
      enddo
    else
      write(*,*) 'List file missing or name misspelt'
      goto 4
    endif
    3    continue
     else
c  Read file names individually
    i=0
```

```
1     i=i+1
2     write(*,*) 'Enter filename or Q to finish'
      read(*,*) filename(i)
      rewind(1)
      close(1)
      if(filename(i).ne.'Q'.and.filename(i).ne.'q') then
            inquire(file=filename(i),exist=file exist)
        if(file_exist) then
          open(1,file=filename(i),status='old')
               do j=1,max_obs
            read(1,*,end=1) x(i,j),y(i,j)
            n_points(i)=j
          enddo
        else
          write(*,*) 'File missing or name misspelt'
          goto 2
        endif
      else
        n_files=i-1
      endif
    endif
c
    write(*,'(2x,i4,a)') n_files,' Tracks read in'
    write(12,'(2x,i4,a)') n_files,' Tracks_read_in'
    write(*,*) 'Track                    Number of points'
    write(12,*) 'Track                    Number_of_points'
    do i=1,n_files
      write(*,*) filename(i),n_points(i)
      write(12,*) filename(i),n_points(i)
    enddo
c
        write(12,*)
        write(*,'(a)') 'The difference between routes can be measured by:'
        write(*,'(a)') '    a)   Using area'
        write(*,'(a)') '    b)   Using average distance between routes'
        write(*,'(a)') '          (area/average number of points)'
        write(*,'(a)') ' Input a or b'
    read(*,*) adum
    if(adum.eq.'B'.or.adum.eq.'b') then
      i_div=1
           write(12,'(a)')
    1            'Distance metric: (area/average number of points)'
    else
      i_div=0
           write(12,'(a)')
    1            'Distance metric: area'
    endif
        write(12,*)
c
    call matrix_prep(n_files,x,y,n_points,distance,i_div)
c
        write(*,'(a)') 'Distance matrix is in Summary_table.txt'
        write(*,'(a)') 'Details are in Details_table.txt'
        write(12,'(20x,50a)') (filename(j),j=1,n_files-1)
        do i=2,n_files
          do j=1,i-1
            write(13,*)
            write(13,*) filename(i),'(i) vs ',filename(j),'(j)'
            write(13,*) 'Step_no',' Step_value',' Deviation_i',
    1     ' Deviation_j'
      enddo
           write(12,'(a,50f20.8)') filename(i),(distance(i,j),j=1,i-1)
```

```
 enddo
c
      write(*,*) 'Input Q to quit or R to randomise'
 read(*,*) adum
 if(adum.eq.'Q'.or.adum.eq.'q') stop
c
      write(*,*) 'The total of N differences will sampled'
      write(*,*) 'Input N (N > 1)'
 read(*,*) n_diff
 n_diff=min0(n_files,max0(n_diff,2))
      write(12,'(a,i3,a)') 'The total of ',n_diff,
 1                                          ' differences will sampled'
 call randomise(n_diff,n_files,distance)
c
      stop
 end
c-----------------------------------------------------------------------+
c                                                                       |
c-----------------------------------------------------------------------+
      subroutine matrix_prep(n_files,x,y,n_points,distance,i_div)
 parameter (max_ser=50,max_obs=30000)
      implicit double precision (a-h,o-z)
 double precision x(max_ser,max_obs),y(max_ser,max_obs)
 double precision distance(max_ser,max_ser)
 integer n_points(max_ser)
      x_s=0
 y_s=0
 x_f=0
 y_f=0
 do i=1,n_files
   x_s=x_s+x(i,1)
   y_s=y_s+y(i,1)
   x_f=x_f+x(i,n_points(i))
   y_f=y_f+y(i,n_points(i))
 enddo
c  Average start and finish points
 x_s=x_s/dfloat(n_files)
 y_s=y_s/dfloat(n_files)
 x_f=x_f/dfloat(n_files)
 y_f=y_f/dfloat(n_files)
c  Rotate Axes
      phi=datan((y_f-y_s)/(x_f-x_s))
 cos_phi=dcos(phi)
 sin_phi=dsin(phi)
 do i=1,n_files
   do it=1,n points(i)
     xx=x(i,it)-x_s
     yy=y(i,it)-y_s
     y(i,it)= xx*cos_phi+yy*sin_phi
     x(i,it)=-xx*sin_phi+yy*cos_phi
        enddo
 enddo
c  Compute Distance matrix
      do i=1,n_files
        do j=1,n_files
     distance(i,j)=0.0
   enddo
 enddo
c
      do i=2,n_files
        do j=1,i-1
     call area_metric(x,y,i,j,n_points,area)
```

```
            divisor=1.0d0
          if(i_div.eq.1) then
            divisor=0.5d0*(n_points(i)+n_points(j))
          endif
          distance(i,j)=area/divisor
          distance(j,i)=area/divisor
        enddo
      enddo
c
      return
      end
c-----------------------------------------------------------------------+
c                                                                       |
c-----------------------------------------------------------------------+
          subroutine area_metric(x,y,ii,jj,n_points,area)
      parameter (max_ser=50,max_obs=30000)
          implicit double precision (a-h,o-z)
      double precision x(max_ser,max_obs),y(max_ser,max_obs)
      double precision yy(2*max_obs),x1(2*max_obs),x2(2*max_obs)
      double precision max_x1,min_x1,max_x2,min_x2
      integer n_points(max_ser)
c  Move requested tracks to dummy vectors
          do it=1,n_points(ii)
        yy(it)=y(ii,it)
        x1(it)-x(ii,it)
        x2(it)=-999.
      enddo
          do itt=1,n_points(jj)
            it=itt+n_points(ii)
        yy(it)=y(jj,itt)
        x1(it)=-999
        x2(it)=x(jj,itt)
      enddo
      n_total=n_points(ii)+n_points(jj)
c  Sort observations along Y axis
          call sortdata(yy,x1,x2,n_total)
          write(13,*)
cdo it=1,n_total
c  write(13,'(i5,3f20.8)') it,yy(it),x1(it),x2(it)
cenddo
c  Divide up range into segments
          n_coarse=4
c          n_coarse=5
          n_segment=min0(n_points(ii),n_points(jj))/n_coarse
      step=(yy(n_total)-yy(1))/dfloat(n_segment)
      iy_start=1
      area=0.0d0
      y_limit=yy(1)+step
      do istep=1,n_segment
        ave_x1= 0.0d0
             n_x1=0
        max_x1=-1.0d16
        min_x1=+1.0d16
        ave_x2= 0.0d0
             n_x2=0
        max_x2=-1.0d16
        min_x2=+1.0d16
        it=iy_start
        do while (yy(it).le.y_limit.and.it.le.n_total)
          if(x1(it).ne.-999) then
c                 if(istep.ge.171.and.istep.le.174) write(14,*)
c1          istep,'x1',x1(it)
```

```
              ave_x1=ave_x1+x1(it)
            n_x1=n_x1+1
            max_x1=dmax1(max_x1,x1(it))
            min_x1=dmin1(min_x1,x1(it))
          endif
          if(x2(it).ne.-999) then
c                 if(istep.ge.171.and.istep.le.174) write(14,*)
c1          istep,'x2',x2(it)
              ave_x2=ave_x2+x2(it)
            n_x2=n_x2+1
            max_x2=dmax1(max_x2,x2(it))
            min_x2=dmin1(min_x2,x2(it))
          endif
          it=it+1
        enddo
            if(n_x1.gt.0) then
              ave_x1=ave_x1/dfloat(n_x1)
        endif
            if(n_x2.gt.0) then
              ave_x2=ave_x2/dfloat(n_x2)
        endif
        write(13,'(i4,10f25.8)') istep,y_limit,ave_x1,ave_x2
c
c       if(2*(istep/2).eq.istep) then
c         write(14,'(2i4,10f25.8)') istep,n_x1,y_limit,ave_x1
c         write(14,'(2i4,10f25.8)') istep,n_x2,y_limit,ave_x2
c       else
c         write(14,'(2i4,10f25.8)') istep,n_x2,y_limit,ave_x2
c         write(14,'(2i4,10f25.8)') istep,n_x1,y_limit,ave_x1
c       endif
c
            iy_start=it
       y_limit=y_limit+step
       area=area+step*dabs(ave_x1-ave_x2)
     enddo
     return
     end
c-----------------------------------------------------------------------
c  Sorts vectors arr,x,y in ascending order of arr
c-----------------------------------------------------------------------
          subroutine sortdata(arr,x,y,n)
c  --  Parameters controlling maximum problem size
     parameter (max_obs=30000)
          double precision arr(max_obs),x(max_obs),y(max_obs)
          double precision dummx(max_obs),dummy(max_obs),dumma(max_obs)
          integer index(max obs)
c         use IMSL routine
          do i=1,n
       index(i)=i
     enddo
          call dsvrgp(n,arr,dumma,index)
c  **  re-order x and y according to order given by index
          do i=1,n
            dummx(i)=x(i)
            dummy(i)=y(i)
            dumma(i)=arr(i)
          enddo
          do i=1,n
            if(index(i).le.0.or.index(i).gt.n) then
         write(*,*) 'i,index(i) =',i,index(i)
         stop
       endif
```

```
          karg=index(i)
          x(i)=dummx(karg)
          y(i)=dummy(karg)
          arr(i)=dumma(karg)
        enddo
        return
  end
c-----------------------------------------------------------------------+
c                                                                       |
c-----------------------------------------------------------------------+
        subroutine randomise(n_diff,n_files,distance)
  parameter (max_ser=50,max_obs=30000,n_sample=10000)
        implicit double precision (a-h,o-z)
  double precision distance(max_ser,max_ser)
  double precision tot_d(n_sample)
  integer index(max_ser)
C Initialize seed of random number
  ISEED = 324571
  CALL RNSET (ISEED)
        do i_sample=1,n_sample
    call rnsri(n_diff,n_files,index)
          tot_d(i_sample)=0.0d0
          do i=1,n_diff-1
       do j=i+1,n_diff
              ii-index(i)
         jj=index(j)
           tot_d(i_sample)=tot_d(i_sample)+distance(ii,jj)
         enddo
          enddo
        enddo
c
        call histogram(n_sample,tot_d)
c
  return
  end
c-----------------------------------------------------------------------+
c                                                                       |
c-----------------------------------------------------------------------+
        subroutine histogram(nobs,data)
  parameter (nqprop=10,m_axis=500)
        implicit double precision (a-h,o-z)
  double precision data(nobs),qprop(nqprop)
  double precision xemp(nqprop),XLO(nqprop),XHI(nqprop)
  double precision histo(m_axis),xaxis(m_axis+1)
  data qprop/0.01,0.02,0.03,0.04,0.05,0.10,0.25,0.50,0.75,0.9/
c  find mean
        sum=0
        do it=1,nobs
          sum=sum+data(it)
        enddo
        z_mean=sum/float(nobs)
c  find higher moments
        sum2=0
        sum3=0
        sum4=0
        z_max=-10000.
        z_min= 10000.
        do it=1,nobs
          z_max=dmax1(z_max,data(it))
          z_min=dmin1(z_min,data(it))
          dev=data(it) - z_mean
          sum2=sum2 + dev*dev
```

```
          sum3=sum3 + dev*dev*dev
          sum4=sum4 + dev*dev*dev*dev
        enddo
C
 xn=nobs+1
        z_sd    = dsqrt(sum2/float(nobs-1))
        z_skew = (xn/((xn-1)*(xn-2)))*sum3/(z_sd**3)
        z_kurt =((xn*(xn+1))/((xn-1.)*(xn-2.)*(xn-3.)))*sum4/(z_sd**4)
 1 -(3.0*(xn-1)*(xn-1.))/((xn-2.)*(xn-3.))

        write(12,104) nobs,z_max,z_min,z_mean,z_sd,z_skew,z_kurt
 104    format(/10x,'Number of observed values      ',i7/
       210x,'Maximum value                  ',f15.9/
       310x,'Minimum value                  ',f15.9/
       410x,'Mean value                     ',f15.9/
       510x,'Standard deviation of values   ',f15.9/
       610x,'Skewness of values             ',f15.9/
       710x,'Excess Kurtosis of values      ',f15.9/)
C
 CALL dEQTIL (NOBS, data, NQPROP, QPROP, xemp, XLO, XHI, NMISS)
        write(12,'(a)') '          %tile          Value'
 do iq=1,nqprop
   write(12,'(10x,2f15.9)') qprop(iq),xemp(iq)
 enddo
C
        n_histo=nobs/100
        n_histo=max0(n_histo,5)
        n_histo=min0(n_histo,m_axis)
 z_range=z_max*1.0001d0-z_min
 do ih=1,n_histo+1
   xaxis(ih)=z_min+dfloat(ih-1)*z_range/dfloat(n_histo)
 enddo
 do ih=1,m_axis
   histo(ih)=0.0d0
 enddo
 do ir=1,nobs
   do ih=1,n_histo
     if(data(ir).ge.xaxis(ih).and.data(ir).lt.xaxis(ih+1)) then
       histo(ih)=histo(ih)+1.0d0/dfloat(nobs)
       go to 4
     endif
        enddo
   4    continue
       enddo
       write(12,*)
 write(12,*) 'Histogram - use XY plot in Excel'
        zero=0.0d0
 do ih=1,n_histo
   write(12,'(3f15.9)') xaxis(ih),zero
   write(12,'(3f15.9)') xaxis(ih),histo(ih)
   write(12,'(3f15.9)') xaxis(ih+1),histo(ih)
 enddo
 write(12,'(3f15.9)') xaxis(n_histo+1),zero
C
 return
 end
```

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