PREFACE

INTRODUCTION

For the convenience of the reader, and despite the obvious overlapping of some topics, this manual has been catalogued into five broad divisions of Prof. Keeton's research from 1967 through 1980: Studies of the sun compass, magnetism, map studies, tests of the sensory capabilities of pigeons, and miscellaneous tests. Found in the narration relating to each of these sections are the years and numbers of releases for each type of test; the numbers of release sites used; and the rationale for conducting the investigation together with a brief outline of the methods used. At best, this information is meant to be but a helpful guide to understanding some of the orientation research represented in the Keeton Database. Financial and time constraints have prevented a more thorough treatment of the 14 years of intensive experimentation that went on at the Cornell Homing Pigeon Research Project. Much useful information relating to vanishing behavior and homing performance had to be omitted.

The reader is also provided with bibliographic references as well as the names of the many researchers who contributed to the database. It is strongly recommended that these people be contacted regarding any questions about their experiments. Qualifying statements have been appended to some test series thereby reserving them for further investigation by the primary researchers. Original data sheets and supportive information relative to each experiment are catalogued in 36 loose-leaf volumes and are also available for perusal at Cornell.

The experiments found in the database include both published and unpublished research. A few tests have been omitted because they either lacked sufficient data points or because important information needed for interpretation was obscure or missing.

A few words about general procedures used by the Cornell Horning Pigeon Research Project:

The first few hundred pigeons from several well-known racing pigeon fanciers were brought to Cornell in 1967. Keeton's early stock of birds included the Gordon, VanRiel, and Trenton strains. Over the years donations of Sions, Jansens, Fabreys, and miscellaneous other strains to the Cornell loft, which some years burgeoned to 1500 birds, allowed researchers to choose their test pigeons from a wide range of ages, experience, and special training backgrounds. The experimental birds were generated from several pens of both captive breeders and experimental birds. It was assumed that keeping this mix in the parental generation diminishedthe chances of natural selection by trial. Occasional performance evaluations supported this assumption.

Certain avicultural categories pertain to all birds. Young pigeons were weaned from their parents when they were approximately 4 weeks old and moved to a separate pen. They were then encouraged to fly around the loft area until they evinced a readiness for testing or homing flights. At this stage of development, the birds were either relegated to tests requiring inexperienced, or *first-flight*, birds, or they were taken away for training flights. For the latter, the birds of one pen or one test group were released as a single flock for homing flights from all directions and at increasing distances from the loft. Unless the test protocol called for special training, the basic flock tosses included releases at distances of not more than 15 miles, and were followed by two or three short distance single flights to eliminate any followers that were not able to navigate home independently. Two or three trainings under overcast conditions were included. All birds were trained to immediately trap into their pens. Since return times of flocks and singles were routinely monitored, we had a high level of confidence in the determination of whether or not a bird was new or familiar at a release site.

The *young bird* category refers to birds tested in their natal year, before the advent of sexual maturity. *Yearlings* are birds tested in their second year, after overwintering, and have become reproductively active. *Old birds* refers to pigeons aged 2 or more years. It is generally correct to assume that the experience of the test pigeons increases with their age, and thus very old birds may, indeed, be products of years of selection. Unfortunately, it was not possible to include such information in the database.

The meteorlogical terms used are specifically meant for orientation research. It a release was conducted *under sun,* the sun disk was visible to the human eye throughout the test; this includes times when the haze greatly reduced the amount of blue sky visible. *Overcast* means the sun was neither visible nor localisable; without knowledge of the time, a person could not possibly point to any obvious point in the sky where the sun should be. Ideally, the overcast skies were found both at the release site and at the home loft. We assume that *overcast* birds saw no sun on their homing flights.

Until 1972 the usual transport vehicles were closed vans or carryalls. From that year onwards, pick-up trucks were added to the fleet, and by 1975, having become more aware of outward journey influences, most test birds were carried to release sites in pickup trucks.

It is the hope of the authors that the information compiled in this database may be of help to others who share in the excitement of searching for the elusive answers to the mysteries of the avian navigation system—our hope is that they may continue from where Bill had to stop.

THE SUN COMPASS

In 1967, the year when Willian T. Keeton began his studies of avian orientation at Cornell University, the contemporary hypothesis of pigeon homing assigned an essential navigational role to the sun. Kramer (1952) and his students had shown that birds possess what has come to be called a sun compass; later Kramer (1953) and Hoffman (1954) working with caged birds, demonstratad that birds couple circadian rhythm (the internal clock) with their observations of the sun's azimuth in determining compass directions. About the same time, although he was later proven to be wrong, G.V.T. Matthews (1953) suggested that pigeons get far more information than cornoass bearings from the sun; instead, Matthews postulated a bicoordinate navigation system based on information extrapolated from the sun's arc and altitude. The process of sorting out these hypotheses generated a flurry of research, and produced evidence in general support of the Kramer model of a map and compass system. While the avian map remains a mystery, much has been learned about the compass, and Bill Keeton's contributions were important in elucidating the role of the sun.

The origins of the current multi-cue concept of pigeon orientation are found in some of Keeton's earliest examinations of the importance of the sun. A series of clock-shift tests conducted under both sun and overcast skies resulted in demonstrating that the sun, although preferentially used by experienced birds, was not essential to orientation, and that, in the absence of the sun, other cues were available (Keeton, 1969).

Recognizing that phase-shifting the internal clocks of pigeons was a valuable tool not only in the study of the sun compass itself, but also in examining the concept of multiple and hierarchal cues, Keeton his his colleagues embarked on a 12 year mission in exploring the nature and the development of the sun compass and its re1ationship to other available cues. Is the sun compass innate or is it learned? At what age is it learned? Once learned, can it be re-calibrated? Are there contraints on its use? Can orienting pigeons be made to alter their interpretation of the sun compass by manipulating cues during the clock-shifting period? Bill Keeton's responses to these challenging auestions were reflected in the diversity of his experiments.

One experimental apnroach to separating alternative compasses involved flying birds that could not or would not use solar cues. An early design disrupted the time-compensation component of the sun compass by keeping test birds under conditions of constant dim or bright light until their circadian rhythms were no ionger normal. Later, in collaboration with R. and W. Wiltschko, pigeons were reaised without ever seeing the sun. There were also tests of birds that had previously been found to give greatly reduced deflections when they were clock-shifted, presumably because they had down-graded the importance of the sun compass.

Because he had found that the behavior of very young birds was relatively plastic, Keeton frequently used young, inexperienced pigeons in his experiments. For example, there was a series of 57 tests using hundreds of untrained pigeons that were clock-shifted at different ages and at different times of the year in order to track the age and circumstances of sun compass utilization. An extension of this study examined the effects of inactive overwintering on the maintenance of the sun compass mechanism. Another series, conducted collaboratively with the Wiltschkos and also involving young birds, looked at the coupling of time, direction, and sun azimuth in pigeons that had been reared under a permanent clock-shift. The Wiltschkos continued researching the question of coupling in yet another way by rearing very young pigeons within an altered magnetic field so that information from the sun could only be perceived against a geomagnetic field that was rotated clockwise from the natural one.

There were also several series of tests that studied the time-sun coupling by exposing pigeons of different ages to the sun during each of the five or more days of their clock-shifting period. Modifications of this basic design were incorporated first in collaborative research with J. Alexander and later with work done by W. Edrich. While in some of these sun-exposure designs, pigeons sat in aviaries passively observing the sun during the period of being clock-shifted to a new time; in other designs they were actively flown, either freely around the loft or in long exercise cages aligned in specific compass directions.

In an attempt to find a pattern that would explain the variability of deflections in vanishing bearings resulting from standard 6-hour clock-shifts, clock—shifted birds were flown from over 40 nearby and distant 1ocations in all directions. Because there were also tests designed to study the interaction of solar and magnetic cues, bar magnets were attached to birds while they were being clock-shifted or, in other tests, just before release. Three tests of clock-shifted birds wearing bar magnets were conducted at the Jersey Hill Fire Tower, a site known for its disorienting effect on Cornell pigeons, but from where birds wearing bar magnets can orient very well when they can see no sun. By releasing clock-shifted pigeons within visual range of their home lofts, pitting familiar landmarks against the sun information, the relative importance of solar and visual cues was compared. And in still other studies spanning three years, the process of returning clock-shifted internal rhythms to normal times was investigated by releasing pigeons in different stages of normalization from two release sites.

Like so many studies purporting a main focus, the breadth of the scientific endeavors described under the sun compass rubric leads to an inevitable interweaving with the other subjects of avian navigation research, not a totally unexpected out-come in the liqht of the discoveries of redundant orientation strategies. But even if they are considered separately, the array of sun compass investigations conducted at Cornell remain a stimulating testimonial to 14 years of cooperative and collaborative research encouraged and enhanced by Bill Keeton.

AC Alexander Clock-shift. Several series of clock-shift tests conducted by J. Alexander in fullfillment of the requirements for a doctoral degree.

AR Aviary Resets. Test birds were allowed a view of the sun from their aviaries while they were being clock-shifted.

CS Clock-shift. The circadian rhythm of pigeons were shifted by six hours.

CSN Clock-shift Normalization. After 5 days of clock-shifting, birds resumed living on normal time and were then tested on each day of this normalization period.

CSW Clock-shift: Weiler. Bar magnets were continually worn during clock-shifting and release.

EC Edrich Cage. In collaborative tests with W. Edrich, pigeons were given daily flights in exercise cages while they were being clock-shifted.

EQ Equinox Tests. Before being tested, birds were prevented from observing the sun during the vernal and autumnal equinoxes.

+FF Clock-Shifts Of First-Flights. Inexperienced pigeons of varying ages were clock-shifted before their first homing flight.

+K Clock-Shifts Of K Birds. Pigeons that had been repeatedly flown from a single site in the K series were released as clock-shifted birds from the same site.

+MB Magnet-Brass. Brass or magnet bars were attached to clock-shifted pigeons either during or just prior to release.

+NRBY Nearby Clock-Shifts. Clock-shifted pigeons were released from locations in close to their home loft.

+NGR Non-Ranging. Inexperienced young pigeons that had never flown away from the loft area while being exercised were clock-shifted before their first homing flight.

NRR Normalized Returned Resets. Pigeons that cave unsual deflections when flown clock-shifted were re-tested as normalized birds.s

NSK No-Sun Birds: Keeton. A continuation of the NSW study of young birds that were raised without seeing the sun.

NSW No-Sun: Wiltschko. Collaborative tests with R. and W. Wilkschko using pigeons that were raised without seeing the sun.

PPSE Pseudo-Permanent Clock-Shift: Edrich. Collaborative tests with W. Edrich in which experienced birds were given homing flights while they were being permanently clock-shifted.

PPSW Psuedo-Permanent Clock-Shift: Wilkschko. Collaborative tests with R. and W. Wiltsohko in which experienced birds were given homing flight from all directions while being permanently clock-shifted.

PSE Permanent Clock-Shlft With Exercise. Young, inexperienced birds were raised and trained while living on a permanently clock-shifted schedule.

PSK Permanent Shift: Keeton. Young birds that were raised and trained while living on a permanently clock-shifted schedule, were normalized and then flown with attached bar magnets.

PSN Normalized Permanently Shifted. Birds that were raised permanenently clock-shifted were tested after a year of Iiving a normal day.

PSW Permanent Shift: Wiltschko. Collaborative tests with R. and W. Wiltschko using young pigeons that were raised on a permanently clock-shifted day.

RA Random Activity. Pigeons lived under constant light until their circadian rhythm was no longer normal.

REP-CS Repeated Clock-Shifts. After normalizing their circadian rhythms, the sarae group of birds was clock-shifted again.

RG Ranging First-Flights. Inexperienced young birds that had flown away from their home loft while being exercised were clock-shifted before their first homing flight,

RR Returned Reset. Clock-shifted pigeons that had homed from tests before the end of the clock-shift day were returned to the clock-shifting rooms and re-tested the following day

SCO Sun Compass Ontogeny. To study the ontogeny of the sun compass, pigeons of different apes were clock-shifted.

SE Shift And Exercise. Pigeons of different ages were given flying exercise while they were being clock-shifted, and in some tests they were flown with bar magnets.

ALEXANDER CLOCK SHIFT

In 1970–72 there were over 70 releases from I2 sites of clock-shifted pigeons including some that had daily exposures to the sun during their clock-shifting period. First-flight birds were used in 12 tests. Six of the releases were conducted within 1 mile of the loft. See Alexander (1975).

Matthews (1953,1955a) proposed a bicordinate navigational system based on information extrapolated from the sun's position. However, Schmidt-Koenig's (1958, 1960, 1961) phase-shifting experiments dernonstrated that birds use the sun as a compass rather than as a more complex navigational aid. Because many questions about the mechanism of a sun compass remained unanswered, J.R. Alexander conducted seven series of investigations of clock-shift responses in horning pigeons as her doctoral research.

Alexander's investigations included the following topics: the process of normalisation after phase-shifting (CSN Series); the role of familiar landmarks on phase-shifted birds (the NRBY

Series); the effects of age and experience on the clock-shift responses of pigeons (the CS FF series); the effects of the availability of solar information or the lack of it on pigeons that were either kept in aviaries or excercised during the clock-shifting period (the AR and SE series). The results of the AR tests (Aviary-exposed Resets) in which pigeons that were undergoing clock-shifting were allowed to observe the sun while in an aviary are reported in Alexander and Keeton (1974).

AVIARY-RESET

In 1970,1973, and 1978–80 there were 31 tests at 7 sites of pigeons that, while they were being clock-shifted, were exposed to the sun within the confines of an aviary (Alexander and Keeton, 1972a).

Matthews' (1953) sun-arc hypothesis proposed an avian navigation system based on information extrapolated from the sun's position; however, the clock-shift experiments reported by Schmidt-Koenig (1958, 1960, 1961) gave evidence that birds used the sun merely as a compass. Matthews (1968) argued that since the incarceration associated with the clock-shifting process deprives experimental birds of important sun information for 5 or more days, a clock-shift itself could be interpreted by such a bird as a longitudinal displacement from home.

In the first attempt to evaluate this argument at Cornell, pigeons that were undergoing a clock-shift were allowed to sit in an outdoor aviary (attached to the shifting rooms at the main loft) during the overlap period between their shifted day and the true day. Thus, they had an opportunity to obtain information concerning the daily changes in the sun's arc and its altitude while they were at the home loft. After the normal incarceration period of approximately 5 days, the test pigeons were released for a homing flight to determine whether access to this solar information during the shifting process might result in initial bearings different from those characteristic of ordinaryclock-shift tests. Seeing the sun while being shifted could prevent the shifted L:D cycle from entraining the birds' circadiar. clocks, or the daily conflict between changing solar cues and circadian rhythms could be sufficiently confusing to produce random vanishing bearings.

The clock-shifted birds in the 1970 and 1973 AR tests behaved no differently than what would be expected of normally clock-shifted birds given no opportunity to observe the sun during the shifting process. The results of seven of the AR tests in this series are reported in Alexander and Keeton (1974).

However, the possibility could not be disregarded that the aviary exposures may have had some smaller effect on the shifted birds because the earlier tests did not include a comparative treatment of normally shifted birds (i.e., birds with no opportunity to view the sun during the clock-shifting period). From the accumulating results of regular clock-shift tests at Cornell, it was also becoming apparent that the variability in the magnitude of clock-shift deflections was not a function of any manipulation during the clock-shifting period but rather a function of the test day or the test site.

Therefore, some of the 1973 and all of the 1978-1980 AR tests included at least two treatments of normally shifted group of birds that had no sun exposure, and a group of shifted birds that spent their overlap period sitting in an aviary attached to the shifting rooms.

Sometimes, pigeons used in clock-shift tests were shifted in rooms at the Liddell facilities, which are about 2 miles north of the main loft. (This information generally appears in the test comments.) In still other clock-shift tests, when birds were kept in the regular shift rooms at the main loft, their home pens were sometimes in separate buildings a short distance away from the main loft. The procedure of moving birds from their normal home location for a period of manipulation raised questions regarding the effect of this displacement, particularly in the cases of pigeons that were given sun exposure during the shifting period: Was there a stronger motivation to home from a new location with consequent increased attentiveness to cues? Did the integration of cues change when the birds were away from the familiarity of their home loft?

To investigate some these questions, there were 7 releases in 1978 that included treatments of shifted birds which were exposed to the sun in free-standing aviaries located in the field south of the main loft, and in one test, in the aviaries attached to the test birds' home pen.

In all the above tests both the regularly shifted birds and the aviary exposed shifted birds were kept in the same clock-shifting room during the period of manipulation. Because the question of the social facilitation was raised by this procedure, the two groups of shifted birds were put into separate shifting rooms for the eleven AR tests in 1979 and 1980. In 1979 all treatments were manipulated at the main loft; in 1980, the regularly shifted birds were kept in the shift room at the Liddell facilities while the controls and aviary exposed birds stayed at the main loft.

In 1979 there were two pairs of tests conducted synchronously at two release sites. The 1980 AR tests compared the orientation of young manipulated birds to that of old manipulated birds.

CLOCK-SHIFT TESTS

From 1967 through 1980 there were 328 releases 49 sites of pigeons that had their internal clocks shifted hours in advance or behind the natural day.

Kramer (1953) and Hoffman (1954) clearly demonstrated that birds couple their internal clock with their observation of the sun's azimuth in determining compass directions. Later Schmidt-Koenig (1960) showed that pigeons whose internal clocks had been experimentally shifted six hours out of phase with the true sun time chose initial bearings roughly 90 degrees from those of control pigeons when released under sunny conditions. Their clocks had been shifted a quarter of a day, and as a consequence, they misread the sun compass and chose bearings a quarter of a compass circle different from those of the controls. In these and subsequent tests, the clockshift technique has been used as a powerful tool to study not only the avian sun compass but also the integration of cues and the ontogenetic development of orientation capabilities.

Early findings at Cornell suggested that the age and experience of test birds are important in prediciting orientation behavior. Included in the CS series, therefore, are clock-shift tests of young, yearling, and old birds; first f1iqht and experienced birds; releases at nearby and distant sites; and birds that are new or familiar to the release sites. The latter included clock-shifts of the extreme case of familiarity to the site of the K birds that had been repeatedIy released from Weedsoort for severaI months prIor to being clock-shifted.

The data from many years of clock-shift tests at Cornell showed that at some release sites 6 hour shifts regularly produce the expected 90 degree deflection, but that at other sites such shifts result in deflections of considerably less or more than predicted. These results suggested that the magnitude of the deflection resulting from a clock-shift may be release-site dependent. To control for possible temporal effects that may be a factor in this variability of clock-shift deflections, there ware 15 tests conducted in 1972-73 and 1977-80, in which samples of the same clock-shifted birds were released synchronously at two sites. Other clock-shift tests were conducted at locations known for their unusual orientation, such as the Castor Hill and Jersey Hill Fire Towers. To test for the possibility of interacting solar and magnetic cues, bar magnets were attached to the clock-shifted birds flown at Jersey Hill. Bar magnets were also attached to clock-shifted birds in 13 other tests (see CS MB).

In other investigations of cue integration, the clock-shifting technique was used in tests of walking pigeons (see W CS), pigeons whose visual acuity was greatly reduced by frosted lenses (LENS tests), of pigeons that had special directional training (TB tests), of feral pigeons (COM tests), and of pigeons that had I exhibited unusual orientation strategies (NB tests).

METHODS:

In 1967 and 1968, pigeons were clock-shifted in rooms at the Langmuir Laboratory. Subsequently the four clock-shift rooms at the main loft were used for most of tests, and the test comments usually note if other shifting rooms were used. The loft shifting rooms (actually remodeled pens) werelocated at the far end of the loft building where noise and daily activity levels are minimized. Each room was equipped with enough perches to accommodate 5060 birds, and exterior mounted exhaust fans ventilated, each of the rooms. Both the control and experimental shift rooms were light-tight with artificiaI Iighting regulated by either automatic timers or by astronomic clocks. In 1973, fluorescent lights were added to the incadescent bulbs and an Esterline evert recorder, activated by shift room light sensors, continuously monitored and recorded the light phases in all four rooms.

On the day of incarceration, the test birds were always given either exercise around the loft (in the case of inexperienced birds) or some flock training before being put into the shift rooms where they remained undisturbed (except for routine feeding and watering) for a minimum of 5 mornings of clock-shifted time but for never more than 10 days.

For a fast shift, the day for the experimental birds was advanced, e.g. the artificial sunrise and sunset times were 6 hours earlier than the natural times of these events; for a slow shift, the artificial sunrise and sunset times were 6 hours later than the- natural events. Fast shifts were generally used because the morning releases maximized homing success.

The control birds lived on a light schedule in synchrony with the natural day. To test for possible effects of incarceration, some releases included a sample of control birds that had continued living in normal pens.

If weather conditions prevented the completion of a clock-shift test on the first release, the unflown shifted and control birds were returned to the shift rooms before the end of the artificial day and the test was resumed on the next sunny day.

CLOCK-SHIFT NORMALIZATION TESTS

To investigate the process of resetting the internal clocks of pigeons from a phase-shifted to a normal L:D condition, clock-shifted pigeons, in varying stages of normalization, were flown on successive days in 30 releases from 3 sites in 1970, 1975, and 1978.

Hoffmann's (1953) studies of the internal clocks of starlings demonstrated that phase-shifting was a gradual process, taking to 3 days to complete the transition from the normal to a new rhythm. Schmidt-Koenig (1958), working with caged pigeons, found that 3 or 4 days were required to complete a 6 hour phase shift, and that the rhythms of phase-shifted pigeons' could be returned to normal time in 2 to 3 days under artificial light but in less time under the natural conditions of an aviary.

After undergoing a phase-shifting manipulation in clock-shifting rooms for 4 or 5 days, Cornell pigeons exhibit the predicted deflected orientation when they are flown, and they seldom return home on the first day. However, because some do return on the second or third day, it appears that less time is required for the pigeon internal clock to return to a natural circadian rhythm than it does initially to phase-shift it.

To investigate the mechanism of normalizing clock-shifted pigeons, several series of shift normalisation tests were conducted. The initial 1970 series of 3 tests (13 releases) were conducted at Marathon II and are reported in Alexander (1975).

Alexander found that when the L:D cycle in pigeons has been phase shifted by 6 hours and the birds were flown from Marathon II, they exhibited the predicted 90 degree deflection in vanishing bearings. However, after the clock-shifted birds had lived on the natural cycle for two days and then tested, there were no significant orientational or homing differences between the experimentals and controls.

The accumulating results from Cornell clock-shift tests indicated that, although a 90 degree deflection in the orientation of clock-shifted pigeons may be expected at Marathon II, much larger clock-shift deflections appear to be the norm at some other release sites. These data raised the question of the relationship of magnitude of deflections resulting from clock-shift tests to the normalization process. Using other release sites, another series of normalization tests was conducted.

In 1975 a single series (2 releases) of normalization tests was conducted at Auburn, and in 1978 there were 3 series (15 releases) of normalization tests at Catatonk II. Both sites have been known to produce exaggerated deflections in clock-shifted birds.

METHODS:

The L:D cycle in the 1975 and 1978 CSN test series was advanced by 6 hours for all the experimental birds while the control birds lived on the normal L:D cycle for that time of year. For each series of normalization tests, a group of 50 pigeons of similar age and experience was incarcerated in each of the experimental and control clock-shift rooms at the main loft* for a minimum of 5 days. As soon as the first test group of approximately 20 birds was taken to a release site, the clock-operated lights in the experimental shift room were reset to the L:D cycle corresponding to the natural day, and the remaining experimental and control birds were permitted unlimited access to the aviaries attached to the shifting rooms. In some cases, because the shifting rooms were needed for other tests, the samples of birds designated for normalization were returned to their regular pens where they commenced living on the normal time and had free access to attached aviaries. On each successive sunny day after the initial test of fully clock-shifted birds, a sample of about 20 of the normalizing birds was flown at the same release site that had been used for the initial test.

* The single exception were the birds used in the CSN test series commencing on July 3, 1979; because of the unavailability of space at the main loft, this group of birds underwent their clock-shifting in rooms at the Liddell facilities. After the first group was taken out to be tested, the remaining birds were normalized in the aviaries of their home pens at the main loft.

CLOCK-SHIFT: WEILER

In 1976 there were 7 releases from 2 sites of clock-shifted birds that in 6 of the tests were flown with attached bar magnets whicn they had worn during the clock-shifting process.

The time-compensated sun compass first proposed by Kramer (1953) has been demonstrated in many tests using clock-shifted pigeons. When such pigeons are flown under sunny conditions, they choose vanishing bearings that are predictably deflected from those of their controls, and even when such tests are conducted within full view of the home loft, the orienting clock-shifted birds still choose deflected vanishing bearings perferentially using information from the sun rather than from familiar landmarks (Keeton, 1974a).

However, even in the presence of the sun, very small changes in the geomagnetic field were found to have a measureable effect on experienced old birds (Keeton et al.1974; Larkin and Keeton,1976), suggesting that sun and magnetic cues may not be entirely independent of each other in the avian navigation system.

This possibility was explored by M. Weiler who conducted the CSW series as an Indpendent Undergraduate Research Project. To examine if there was a coupling of magnetic information with circadian rhythms, bar magnets were worn by the experimental birds throughout the test series, including during the clock-shifting process.

In an attempt to make the birds less familiar or less dependent on naturally occurring magnetic cues, bar magnets were attached to very young pigeons upon weaning on May 311 and continued to be worn thoughout all training tosses. (For additional procedural details see the CS and the PBW series.) Different groups of permanent magnet birds were used in each of the first two clock-shift tests comparing the orientation of magnet-laden birds that were clock-shifted for the first time to magnet-laden birds that were living on the natural time. Treatments of clock-shifted and control birds, both wearing brass bars, were also included.

A second series of 4 tests used another group of birds that also wore bar magnets during the clock-shifting periods and the test flights. The successful homers of each treatment were returned to their respective clock-shifting rooms and retested three days later. Before the final test in this series, the birds were normalized for several days, the treatments were reversed, and after five days in the shifting rooms, the birds were retested at the same site.

EDRICH CAGE

In 1974-75 and 1978-79 there were 4 releases at 7 sites of clock-shifted birds that had been exercised in cages during the clock-shifting period.

Alexander (1975) demonstrated that it was possible to alter the predicted orientational response in clock-shifted pigeons by giving the birds exercise flights around the loft area during the overlap time while they were being phase-shifted. The Edrich cage tests were designed to quantify the exercise needed to affect orientation of clock-shifted pigeons. The results of the 1974-75 tests can be found in Edrich and Keeton (1978).

Edrich and Keeton reported that the restricted flight in cages was sufficient to alter orientation of clock-shifted birds, and that the geographical alignment and the location of the flight cages relative to the loft appeared to affect the magnitude of the orientational change. Another methodological point relevant the the cage tests was also raised by the results of Alexander and Keeton (1974), who reported that an aviary exposure during clock-shifting had no affect on the orientation of clock-shifted birds. Were the changes in orientation seen in the clock-shifted birds of the Edrich cage tests a result of their exercise in aviary-type cages, or a result of the cages being detached from, but in sight of the main loft, a factor that may have affected the motivation involved in the process of integrating navigational cues. Because the exercise during clock-shift technique has the potential for determining how pigeons integrate cues, and to resolve some of the questions raised by this technique, additional cage tests were conducted in 1978-79.

The pigeons used in the 1978 EC test were residents of the main loft, but they were clock-shifted and exercised at Liddell Lab, about 2 miles north of the main loft. Designated samples of controls and experimentals spent 4 to 5 hours of each day's overlap period (between the natural and phase-shifted day) in cages located in a field south of Liddell. During this sun-exposure sequence, half of the control and shifted birds groups designated as aviary exposure birds were flagged every 45 minutes for a minimum of 10-15 minutes, forcing them to fly back and forth in the 5 foot long, east-west oriented exercise cage. The other half of the aviary-exposure birds remained inactive and were allowed to sit on perches within the confines of a 4 foot aviary-type cage. A third sample of each treatment stayed in the clock-shifting rooms until the test day.

This preliminary test was designed to compare the orientation of normally shifted birds to that of shifted birds that had sun exposure in an aviary during the overlap period (see the AR series) and to that of shifted birds that were exercised in aviary-type cages during the overlap period.

The EC series was continued with 3 releases in 1979 using a self-contained, mobile shift room unit with activity monitoring equipment that enabled Cornell birds to be shifted and exercised in locations other than their own loft area. The general procedures described in the 1978 series were used, and the locations of the mobile shift room and exercise cages are found in the test commentaries.

EQUINOX TESTS

Matthews' sun arc hypothesis was tested in 1969-70 and 1972, when there were 7 releases from 4 sites of pigeons that were prevented from seeing the sun at the times of the vernal and autumnal equinoxes.

Although the sun has been considered as an important source of navigational information for birds, its exact function in this role was originally given different interpretations. Matthews (1951, 1953) proposed that when pigeons are taken to a new location, they use information extrapolated from the sun's path as they remembered it at their home loft. The difference between the noon altitudes of the sun at the two locations (home and the release site) could provide the test birds with information about their latitudinal displacement; the difference in local sun time at the two sites could give the birds their longitudinal placement. Although other investigators could not replicate Matthews' tests, Matthews used the results from his sun occlusion experiments to support his sun-arc hypothesis. Using this test design, Matthews argued that if birds are prevented from seeing the sun for several days during the times of the equinoxes (when the rate of the apparent changes of the sun's position is maximally accelerated), the navigational error resulting from making the hypothetical extrapolation would cause reverse orientation.

Keeton's first series of sun occlusion experiments was with experienced birds that were tested in the autumn from a southerly site. See Keeton (1970b). Subsequent occlusion experiments, using both experienced and inexperienced pigeons, were from north sites and were conducted in the spring. See Keeton (1974a)

CLOCK-SHIFTS WITH FIRST-FLIGHT PIGEONS.

To study the ontotioney of the sun compass, first-flight pigeons of different ages.were flown from 11 sites in more than 60 clock-shift tests in 1968, 1970-73, and 1975-1980.

First-flight pigeons (i.e.birds with no training prior to their first homing flight) frequently exhibit orientational behavior that differs from that of trained pigeons. For example, young first-flight birds are disoriented when flown under overcast conditions whereas experienced birds are not; and also unlike experienced birds, first-flight birds are disoriented by bar magnets in the presence of the sun. It appears that inexperienced birds may require more navigational information in order to orient properly, or perhaps alternatively, the naive birds are faced with orientational information that is conflicting because they have not yet adopted a heirarchial weighting system, a flexible, integrative process that is enhanced by homing experience. See Keeton and Gobert, 1970; Keeton, 1971.

At some release sites, first-flight birds choose non-random bearings that differ significantly from those of experienced birds; in most cases however, second-flight birds choose bearings similar to those of old, experienced birds even if their single previous flight was from a different release site. Hence it appears that very important learning takes place on the first homing flight (Windsor, 1972; Keeton 1974a). Because these findings suggest that homing experience can affect the basic navigational strategies of pigeons, first-flight birds hypothetically provide a unique opportunity to study some of the fundamental cues used by pigeons.

The ability to manipulate the setting of pigeons' internal clocks is a powerful tool for investigating questions concerning the interaction between tne sun compass and other orientational cues. For instance, Keeton (1969) found that clock-shifted experienced pigeons orienting under complete overcast rely entirely on cues that require no time compensation. By clock-shifting first-flight birds, presumably birds with only fundamental or innate navigational abilities, the ontogeny of the sun compass mechanism can be studied.

In reporting the results of 11 clock-shift tests of young and over-wintered first-flight birds conducted at 7 sites from 1970-72, Alexander (1975) found that the experimental groups usually gave random vanishing bearings. Alexander interpreted the random departures to be a result of a conflict caused by the shifting procedure which appeared to confuse untrained birds; perhaps the successful coupling of the internal clock and sun azimuth or the ability to weight cues is a function of experience, and homing flights are a prerequisite for the utilisation of the pigeon sun compass.

Using clock-shifited first-flight pigeons released at 6 sites, Keeton continued the ontogenetic studies of the sun compass in 1973 and from 1975 through 1980; in 3 tests, clock-shifted first-flight birds wore bar magnets. Preliminary tests demonstrated that the orientational behavior of first-flights could be affected by the ranging flights away from the loft in which young birds occasionally engage; the orientational results of some experiments suggest the possibility that these ranging birds may have trained themselves. Consequently, the categories of NRG (non-ranging) and RG (ranging) were established to identify the daily exercise behavior of first-flight birds around the loft; birds that remained out of sight for 20 minutes or more are classified as RG. Because age may also be an important factor in the development of the sun compass, the ages of first-flights, as well as their ranging history, are given in the test commentaries whenever this information is available.

To investigate the effects of experience and age on the clock-shift response of first-flight pigeons, J. Jones (Undergraduate Research) conducted 21 clock-shift tests in 1978 at South Danby V using young, ranging and non-ranging first-flight pigeons aged from 6 to 19.5 weeks.

Because the clock-shift response of young first-flight birds in many tests was found to differ from that of yearling first-flights, the Keeton-Brown series of 19 releases from South Danby V using birds of different ages was conducted from 1978-80. Included in this series were groups of first-flight pigeons that were clock-shifted in their natal year; the remaining first-flights from each group were then over-wintered and clock-shifted as yearlings the following spring. The first-flights in this series were from 6 to 5 weeks old. These tests were continued through 1983, and the results are reported in a manuscript in preparation (1985).

To further investigate the effect of experience on the clock-shift response, groups of specially trained birds (derived from the Keeton-Brown first-flights) were included in 6 releases of the Keeton-Brown series from 1978 to 1980. One sample of the exercised first-flight birds in each year's series was given an additional 1 or 2 very, short-distance homing flights prior to being clock-shifted and tested in the fall. Another, untested, sample of these specially trained birds was over-wintered along with the remaining, untested first-flights; both were then tested as clock-shifted yearlings in the following spring. Additional information about the special- trained birds is found in the test commentaries.

CLOCK-SHIFTS OF K BIRDS

In 1973-75 there were 6 tests of clock-shifted K birds from Weedsport, a site from which the birds had been repeatedly released prior to clock-shifting.

Keeton et al. (1974) reported that the day-to-day fluctuations in the bearings selected by a single group of pigeons at a given release site are correlated with natural fluctuations in the earth's magnetic field, as measured by the K values assigned by the U.S. Geomagnetic Observatory. The correlation probably reflects a direct cause-and-affeet relationship between the magnetic events and the orlentational behavior (Larkin and Keeton, 1976).

The reported tests had been conducted under sunny skies, when pigeons were presumably using the sun compass (Keeton, 1971, 1972), yet magnetic disturbances produced a measurable effect on the birds' orientation. Although pigeons rely primarily on the sun for the compass portion of their navigation, perhaps they also refer to their magnetic compass as well; or perhaps information from the magnetic field contributes to the map portion of the navigational system.

To study the interaction of the sun compass and the fluctuations of the geomagnetic field as well as the effects of repeated flights from the same site on the utilization of the sun compass mechanism, a series of clock-shift tests was initiated in the late fall of 1973 after the 47 K tests of that year had been completed. Because the K birds were divided into two alternately flown samples, each bird had been flown from the Weedsport release site a minimum of 23 times before being shifted, and its orientational behavior was well established.

Subsequent clock-shift tests, using the same birds, were conducted in June of 1974 and 1975 and in November and December of 1974. The two groups of K birds were alternated between the control and clock-shift treatments. Information about the groups and their experience prior to testing is found in the test comments.

MAGNET-BRASS TESTS OF CLOCK-SHIFTED BIRDS

In 1974 and 1976-1980 there were 21 releases from 5 sites of clock-shifted pigeons that wore bar magnets; 3 of the tests were from the Jersey Hill Fire Tower.

Birds, repeatedly released from the same site, show small day-to-day changes in their choices of departure directions; these orientational changes have been correlated with the fluctuations of the earth's magnetic field. Keeton et al.1974; Larkin and Keeton, 1976. Because this effect is found oh sunny days when the birds are presumably using their sun compass, an interrelationship between solar and magnetic cues is suggested.

To explore this possibility, bar magnets and brass bars were attached to clock-shifted pigeons prior to their release at a test site; in 7 releases there were similar treatments of control birds.

Experienced pigeons, familiar to site, flown under sunny conditions at the Jersey Hill Fire Tower are almost always disoriented; bar magnets do not affect this orientational pattern. However, when similar birds wearing bar magnets are flown there under overcast, they are able to orient significantly suggesting a relationship between sun and magnetic cues at this particular release site. To investigate this possibility, a series of 3 clock-shift tests was conducted at the Jersey Hill Fire Tower in 1978 and 1979. Control and clock-shifted birds wore either bar magnets or brass bars.

For other tests including bar magnets on clock-shifted birds, see the PSK, PSN, RR, and the SE series.

In another study of the sun compass, bar magnets were used in overcast tests of a special group of first-flight pigeons which had been deprived of sun information. See the NS series.

NEARBY CLOCK-SHIFTS

From 1970 to 1975 there were 46 releases of clock-shifted pigeons from 11 sites varying in distance from 0.5 to 3.6 miles. Three of the tests were under overcast conditions.

Pigeons may use different orientational components arranged in some hierarchical fashion, and the weighting of one cue over another might vary not only due to differences in the age and experience of birds, but also due to environmental conditions. (Keeton, 1969, 1971; Keeton and Gobert, 1970). One approach to determining the relative navigational importance of familiar landmarks and solar cues is to release clock-shifted birds at sites within view of the home loft, thus pitting two orientational cues against each other.

Graue (1963) reported that clock-shifted pigeons, released within 1 mile of their loft, oriented in an appropriate deflected direction except when they had a direct view of their loft; in this case, their orientation was comparable to that of control birds. However, Schmidt-Koenig (1972), in tests at similar distances, found the expected clock-shifted orientation when the loft was visible.

To resolve the discrepancy in these reported results, Alexander (1975) conducted 16 clock-shift tests from sites within 4 miles of the Cornell loft. Alexander found that at distances of less than 1 mile, the direct view of the loft can sometimes override the effect of a clock-shift, and that at distances of more than 3 miles, the birds depart in a shifted direction even if the loft is visible to the observer. These results suggest that the birds are using their navigation systems, rather than piloting by landmarks, even in an area familiar to them from their daily training flights.

Because there was no obvious reason for the differing results in the Alexander tests from Dodge Road, and because Blough (1971) reported that the visual acuity of homing pigeons is less than that of human beings (thus changing earlier interpretations of tests conducted at 3 or more miles; see Keeton, 1974a), the NRBY series was continued with 14 additional releases in 1972-73. Samples of the clock-shifted birds used in the first NRBY tests in 1973 were synchronously released from a site 45 miles north. See the CS series.

In 1974 clock-shifted birds were flown from nearby release sites in conjunction with the Edrich Cage series. In 1975 there were nearby clock-shift tests which served as preparatory experience for the Returned Reset series. (see RR)

CS OF NON-RANGING INEXPERIENCED BIRDS

In 1975 and 1977-78 there were 16 tests at 2 sites of clocshifted, non-ranging inexperienced birds.

Some early tests using inexperienced clock-shifted pigeons (see the FF series) suggested that the orientation of inexperienced pigeons night be affected by the pre-test ranging, a behavior frequently seen in young birds during their routine exercise flights around the loft. Pigeons that flew out of sight of the observer for 20 minutes or more were designated Ranging, and those that continued to fly nearby were designated Non-Rangers.

A single test In 1975 compared the clock-shift responses of inexperienced birds that had ranged to those that had not.

To study the effects of age and ranging experience on the acquisition of the sun compass in young inexperienced pigeons, J. Jones (Independent Undergraduate Research Project) conducted 1 releases in 1978 of clock-shifted birds at South Danby V; non-ranging birds were included in 9 tests.

NORMALIZED RETURNED RESETS

In 1973 there were 3 tests from 3 sites of normalised pigeons that had previously exhibited unusual deflections as clock-shifted birds.

When pigeons that are clock-shifted by 6 hours are flown, their vanishing bearings are usually deflected by approximately 90 degrees from the bearings of controls. However, in many tests the magnitude of the deflection is either considerably more or less than the predicted 90 degrees; in such cases, the bearings of the clock-shifted birds show an increased scatter or bimodality. The NRR series investigated the possibility that this variation in clock-shifted orientation reflects individual differences in some basic navigational mechanisms of a group of test birds rather than difference in responses to the changing of circadian rhythms.

Pigeons that homed from clock-shift releases were returned to their regular pens where they resumed living on the natural day; before they were retested as normalized birds, they were given several flock-tosses. The three treatment categories in the NRR tests were determined on the basis of the clock-shift deflections shown by the individual birds in previous tests.

KEETON TESTS WITH NO-SUN BIRDS

In 1977 there were 7 releases from South Danby V of clock-shifted yearlings that had been raised without view of the sun. Prior to the clock-shift tests, samples of inexperienced no-sun birds were flown in tests under overcast.

Keeton and Gobert (1970) found that orientation by untrained pigeons requires the sun. However, Wiltschko et al. (in press) reported that young untrained birds could orient under overcast if, unlike normal birds, they had been raised and trained without seeing sun; moreover, only a brief sun exposure enabled these inexperienced birds to learn and use the sun compass. See NSW series.

The pilot NSK series was designed to investigate the possibility of a critical period for learning to use the sun compass. If there is a critical period, (e.g. if pigeons prevented from seeing the sun until they are sexually mature, cannot later learn the sun compass as already has been found to be the case for learning the star compass; see Emlen, 1963,1972) it would be of great value in designing experiments with birds in whose navigational behavior the normally subordinate cues would be dominant and hence more exposed to manipulation.

By testing birds with no knowledge of the sun, the ontogenic questions related to the sun compass could also be addressed. The importance of homing flights in the acquisition of the sun compass; and the amount, as well as the time, of sun exposure required before pigeons can use solar information.

Following the 1974-75 Wiltschko procedures for raising no-sun birds, 60 pigeons were weaned into each of 2 nearby pens in August of 1976. While one group had free access to an open aviary and was exercised in a normal manner around the loft, the second group was incarcerated in an artificially illuminated pen and was permitted aviary and exercise experience only during periods of total overcast. Any inadvertent exposures to the sun were recorded. Although the control group was usually flown under sunny skies, they were also exercised along with the experimentals on some of the overcast days. The two groups had approximately equivalent flying times around the loft.

A few, unusually long sun-exposures of some birds as well as two inexplicable fly-aways, reduced the original number of both experimentals and controls to approximately 70 testable birds. During the 15 months of pre-test exercise flights, the individual experimental birds had accrued from 0.2 to 12 hours inactive sun-exposure from sitting in or on top of the aviary; the totals of sun-exposures occurring while the birds were flying ranged from .16 to 1.0 hour.

Samples of inexperienced no-sun yearlings were released in preliminary overcast tests, first to demonstrate that the birds were able to orient in the absence of solar cues, and secondly, to compare their orientation to that of very young inexperienced pigeons.

Prior to being clock-shifted, the controls and experimentals were divided into untrained or trained treatments. One subset of trained birds had 7 flock-tosses under sunny skies while a second subset had 8 flock tosses under overcast skies. Both overcast and sun trainings were from identical sites located in the four cardinal directions within miles of the loft. Directly after the completion of the training program, all the no-sun birds and their normally raised controls, including the group that remained untrained, were put into clock-shifting rooms where one group was shifted by 6 hours earlier than the natural day and the other remained on a natural day schedule.

WILTSCHKO NO-SUN BIRDS

In 1974-75 there were 24 collaborative releases from 11 sites of pigeons that had been raised without view of the sun. Included in this series are 12 releases of first-flight birds under overcast, 3 clock-shifts, and 9 orientation checks of normalized no-sun birds. Bar magnets were used in 12 releases.

Keeton and Gobert (1970) and Keeton (1971) found that orientation by untrained pigeons requires the sun, and that untrained pigeons wearing bar magnets were disoriented under sunny skies. From these experiments Keeton (1974) concluded that inexperienced birds require both sun and magnetic cues, and that one effect of training flights is to make birds more adept at horning so that they can orient with less information,

Experiments with migratory birds, however, indicate that magnetic orientation can develop independently of celestial cues (Wiltschko and Gwinner 1974, Gwinner and Wiltschko 1976, Beck and Wiltschko 198). To examine the role of the sun during the ontogeny of the homing pigeon orientation system, young pigeons were raised without view of the sun, and because they presumably had no knowledge of it, were forced to use another compass mechanism. Wiltschko et al. (in press).

Tests conducted under overcast conditions compared the orientation of young, untrained no-sun birds to that of the normally raised untrained controls in continuing overcast tests, bar magnets and brass bars were attached to the test birds.

After short-distance flock tosses (under overcast for the no-sun birds and under sun for their controls), three clock-shift tests were conducted.

To investigate the long-term effects of the initial deprivation of solar cues, 9 releases were conducted to study the orientation of former no-sun birds that had been living in a normal manner for 6 months or more. Bar magnets were used in 4 of these tests.

EDRICH PSEUDO-PERMANENT SHIFT & EXERCISE

In 1975 and 1979-80 there were 16 collaborative tests from 9 sites of normally raised pigeons that were directionally trained while being permanently clockshifted.

The results of many clockshift tests show that a compass system based on sun information is preferentially used by homing pigeons. Investigations using young birds that were permanently clock-shifted (see the PSW series) demonstrate that the sun compass is not innate, but that rather it is learned and can be re-calibrated (Wiltschko, et al.1978).

The clock-shift response of normal birds is affected by giving flight exercise to the birds while they are undergoing a clock-shift (see SE series). Furthermore, the directional alignment of exercise cages used in some SE test designs had a specific orientational effect on clock-shifted pigeons (Edrich and Keeton, 1975; also see the EC series).

In collaboration with W. Edrich, the PPSE tests continued investigating the the basis of the clock-shift response by using normally reared and trained birds that were subseouentiy permanently clock-shifted, and that were given directional training during the entire clock-shifting period.

The results of the first series of PPSE tests conducted itt 1975 are found in Edrich and Keeton (1978).

In 1979 and 1960, normally raised and trained birds were assigned to either the control or permanently-shifted treatment. While the controls lived in a clock-shift room on normal time, the experimentals were kept on a schedule that was 6 hour in advance of normal time. Starting on the morning after the first clock-shifted night, two equally sized groups, consisting of both experimentals and controls, were synchronously given daily homing flights either on a north or an east training line during the overlap period between the normal and the shifted days. After a minimum of 15 training flights, simultaneous tests were conducted from a north and an east release site, comparing (at each site) the orientation of permanently shifted birds that were trained only on the north line to those that had been trained exclusively on the east line. A treatment of standard clock-shifted birds were included in the 1980 tests.

WILTSCHKO PSEUDO-PERMANENT SHIFT

In 1975 there were 7 collaborative tests from 5 sites of normally raised young birds that were given training flights while they were being permanently cIock-shifted. The results of many clock-shift tests with pigeons support the Kramer model of a time-compensated sun compass system. The Wiltschko tests of young pigeons that had been raised as permanently shifted birds (the PSW series) demonstrated that the sun compass is not innate, but rather that it is learned and can also be recalibrated. Wiltschko, at aI., 1976.

The collaborative Wiltschko pseudo-permanent shift tests investigated the process of sun compass recalibration in permanently shifted birds that had been raised under normal conditions and that had previous homing flights before they were put into the permanently shifted state.

After homing from tests as normally raised first-flights, young pigeons were given 4 flock tosses, and on July 29th they began living on a 6 hour slow schedule. The controls were also held in a clock-shift room but were kept on the natural schedule.

After their first test as regular clock-shifted birds on August 2, 1975 at Richford, the experimentals continued living on the 6 hour slow schedule, and together with the controls, they began their daily training consisting of afternoon homing flights, mostly under sun conditions, during the overlap period between the normal and clock-shifted day. Before being tested, the groups had 18 flights from all directions at distances 10 miles or less; by their second test they had completed homing flights from all directions at distances up to 15 miles.

This sequence of trainings and tests continued until after the Venice Center release. Preceding the next test from Auburn, the training flights were exclusively from the north and up to 30 miles in distance; by this time the permanent1y shifted birds and their controls had experienced a total of 36 homing flights. On October 1st, after one additional north training flight, the experimental group began living on normal time in preparation for their final test as normalized birds on October 6th.

PERMANENT CLOCK-SHIFT AND EXERCISE

In 1977 there were 3 tests from two sites of permanently-shifted birds that were given homing flights while they were alternately normalized and re-shifted.

Wiltschko et al. (1976) demonstrated that the pigeon sun-compass is learned, and that it can be recalibrated. These results suggest that the orientation system may adjust from one time phase to another by, perhaps, combining some of the recalibration of their sun compass with an alteration of their cue-weighting scheme (e.g., possibly elevating the importance of magnetic cues). The subsequent PSN (Permanent Shift Normalization) PSK (Keeton Permanent-Shift) series investigated the possible role of magnetic cues in this readjustment process. Another approach to studying cue-weighting was used in the PSE tests.

By subjecting pigeons to homing flights while they were being alternated between different circadian rhythm schedules , the pilot PSE tests conducted by D. McCorkle and M. Weiler attempted to sufficiently confuse test pigeons, forcing them to forego using the sun compass and to substitute some other, possibly magnetic, cue as a source of compass information.

The experimental birds in this series were raised and trained while living on a permanently clock-shifted day that was 6 hours later than the natural day. After 29 flock tosses from distances up to 10-15 miles in all directions under both sun and overcast, all the birds were given 2 solo, short-distance homing flights before their preliminary test as permanently shifted birds on July 3rd. All birds returned to the loft on the day of the test and were immediately put back into closed shift rooms, but on a natural day schedule for 3 days. A preliminary orientation test was conducted on July 7th.

A sample of the same group of pigeons, living on the naturals day schedule in an adjoining clockshift room, was used as the control treatment.

For the next 34 days the experimental group was subjected to alternating rounds, 7 days In duration, of living on the natural day schedule and a 6 hour slow schedule. During each alteration the birds were given several flock and single tosses from different directions.

There were no significant differences in orientation or homing success between the control and experimental groups in their final test on August 31st. Due to the lack of time, this series was not continued.

PERMANENTLY SHIFTED: KEETON

In 1976-77 there were 21 tests at 7 sites of young: and yearling birds that had been raised as permanently shifted birds. Bar magnets were used in 13 releases, and 2 tests were under overcast conditions.

The results of many clock-shift tests support the Kramer model of a time-compensated sun compass system. See the CS section. The PSW tests of young, permanently shifted pigeons demonstrate that the sun compass is not innate, but is learned and can be recalibrated. Wiltschko et al. 1976.

These results suggest that the orientation system may adjust from one time phase to another, perhaps by combining a recalibration of their sun compass with an alteration of their cue-weighting scheme (e.g., elevating the importance of magnetic cues). The PSK series explored the role of magnetic cues in the readjustmerit process.

Young pigeons were weaned into the clock-shifting rooms on May 7, 1976, While the control birds lived on a natural day schedule in an adjoining room, the experimental group was raised and trained while living under a clock-shifted schedule that was 6 hours later than the natural day, The control and experimental groups, trained together, were given approximately 40 flock tosses of up to 15 miles in all directions before the 3 preliminary orientation tests. Following these tests the time-phase of the experimental group was changed to be in synchrony with the natural day.

There were no training flights while the experimental birds were being clock-shifted to the natural day schedule, a process which began July 10th. Because results from the following 3 tests of the normalized birds indicated that the recalibration process was still incomplete, the normalized birds and the controls were given 10 additional flock tosses up to 20 miles in all directions before the bar magnet tests of normalized birds were begun. During the magnet series, the birds were given 1 or 2 training tosses between tests.

In October, the controls and the experimentat! PSK birds were moved into a normal pen for overwintering. After a few flock tosses in the spring of 1977, they were tested as permanentlyshifted birds that had been normalized for a prolonged time.

NORMALIZED PERMANENTLY-SHIFTED

In 1975-77 there were 14 releases from 12 sites of permanently clock-shifted pigeons that had been normalized for a prolonged time.

In 197476 young pigeons were raised on a permanently clock-shifted time that was 6 hours later than the natural day. The birds were tested in their natal year both as permanently shifted birds and then as recently normalized birds. (See the PSK and the PSW series) To re- investigate possible long-term effects of rearing and testing young pigeons under conditions of changing circadian rhythms, tests of the previously manipulated birds continued to observe orientation behavior.

The results of the PSW series demonstrated that the pigeon sun compass is learned, raising the question of what reference cue was being used in this learning process; might that reference cue be the magnetic compass? Do young pigeons that have been made to couple and re-couple sun information in response to repeated changes of their circadian rhythm also learn to alter the ranking or the integration of cues?

In the PSN series, the former permanently shifted birds and their controls (from either the PSW or the PSK series) continued to be tested as normalized birds after being overwintered on a natural day schedule in a regular pen. Bar magnets were attached to the birds just prior to release in 7 tests, and two of these tests were conducted under overcast conditions.

PERMANENTLY SHIFTED: WILTSCHKO

In collaboration with R. and W. Wiltschko in 1974-76 and 1960 there were 78 releases from 20 sites of pigeons that had been living on a permanently clock-shifted schedule. See Wiltschko et al. 1976.

The results of standard clock-shift tests (see CS section) are consistent with Kramer's model of avian navigation, a model including a time-compensated compass that is coupled with information from the sun's azimuth. The PSW test series investigated the development of this sun-derived compass: How is the relationship between the internal clock, the sun azimuth and geographic direction formed? Is the sun compass innate or must It be established by experience? If it is learned, can it be re-calibrated to a changed circadian rhythm?

The 1974-76 PSW tests used birds that were raised and trained under a permanently clock-shifted regimen that was 6 hours later than the natural day. Upon completion of a pretest training schedule of afternoon homing flights, the experimentals were first tested as permanant1y shifted birds and later, as normalized or normaIized and reshifted birds.

In 1975 and 1976 there were also tests of the experimental birds remaining from the previous year, but that had been living on a natural day schedule in a normal pen for almost a year. In 1975, these were re-shifted once again to the 6 hour-slow phase under which they were reared and were now tested as yearlings. In 1976 there were two tests of pigeons that had been reared and previously tested as permanently shifted young birds, then lived on natural since the previous fall and were tested in the spring as normalized bIrds.

Yearlings that had been initiallIy raised and trained as normaI birds were used in the 1980 PSW series. To see if this group of yearlings had developed alternative compass systems, samples of PSW birds, before they were permanently clock-shifted, were first tested at sites under overcast, and subsequently as standard clock-shifted birds under sun.

On May 4, 1980 the yearlings commenced living on a permanentIy cIock-shifted day that was 6 hours later than the natural day. Permanently clock-shifted (PS) and normalized PS birds were tested at 14 sites that were in and outside of their training range. Normalized PS birds were used in 27 tests that included 5 releases in which the orientation of the normalized group was compared to that of standard clock-shifted birds.

In all PSW tests the control treatments were comprised of samples of the same group of birds that was used for the experimental treatment. The controls lived in an adjoining clock-shift room in synchrony with the natural day. In all other respects, including access to the outside aviaries and training, the groups were treated identically.

RANDOM ACTIVITY

In 1972 there were 6 releases from 2 sites of pigeons that had been living on a constant light regime. Bar magnets were used in 1 release.

Kramer (1951) demonstrated that the birds' use of the sun as a compass depended on an internal clock that enabled them to compensate for the sun's changing azimuth, and he later (1953) suggested that homeward navigation of pigeons might depend on a coupling of the sun compass with map information concerning the home direction.

In his clock-shift tests under overcast conditions, Keeton (1963) found that the sun was not essential for accurate homeward orientation by experienced pigeons, results that suggested an alternative compass mechanism and that raised other questions: If the sun compass is not an essential element in the navigation process, does this mean that the map is capable in itself of providing sufficient information for true navigation, and does the sun compass simply function as an accessory check mechanism? Or can the map-and-compass model be retained intact by assuming that the birds have alternative compasses? (see Keeton, 1974a)

If the use of solar information by pigeons, even under sunny conditions, could be circumvented, other non-time compensated navigational strategies could be studied. One approach to this experimental design is to interfere with the time compensation component of the sun compass mechanism.

In the pilot RA study, experimental pigeons were kept under continuous bright or dim light in a closed clock-shift room until their circadian rhythms were either randomized or made free running, respectively. Throughout the incarceration period, the feeding and general maintenace procedures were randomized. Activity levels were monitored by microswitches attached to their water dish, feeder, and perches, as well as by a photo electric cell at floor level; an Esterline event recorder was used to record activity. The control birds lived on a normal schedule in their regular pens.

When the charted activity levels indicated that the normal circadian rhythm was either free running or randomized, the manipulated birds were flown under sun to see how they would respond to sun cues, and whether they would compensate for their inability to read the sun compass accurately. In an attempt to interfere with the orientation of the manipulated birds, bar magnets were used in 1 test.

Although 11 tests were conducted, only 6 resulted in sufficient data to qualify for inclusion in the Keeton Index. Attrition of data points was mainly due to the frequent tendency for the continuous light birds to land or to remain in close proximity to the release site until they could later join another test bird.

REPEATED CLOCK-SHIFTS

In 1973 previously clock-shifted pigeons were clock-shifted and tested again at Weedsport, a site familiar to some of them.

Results from early clock-shift tests conducted at Cornell indicated that although most shifted birds seldom return to the loft on the day of release, they often return the next day. The CSN (Clock-shift Normalization) series indicated that the effects of tbe clock-shift could still be seen in the birds orientation behavior for several days (see Alexander, 1975 and the CSN series); thus, rapid re-entrainmeht to normal time was probably not the explanation for clock-shifted birds to return home the day after release. Furthermore, in almost every clock-shift test there are 1 or 2 experimental birds that regardless of their initial orientation at the test site, do home on the 1st day, often within the mean horning time of the control birds.

Some possible explanations for this behavior could include the following: a mechanism for position correction, derived from the map component of the navigation system; or some birds may cease using the sun compass, reorienting themselves by other means; or perhaps the birds use the same reference cue they used as youngsters (when they first calibrated the sun compass) to recalibrate so that they can read the sun compass correctly even though their clock is 6 hours slow or fast. Would repeatedly clock-shifted pigeons become more adept at using such strategies? Is the clock-shift response affected by familiarity with a site? Does the distance flown by a clock-shifted bird affect subsequent sun compass orientation?

The pilot tests in the Repeated Clock-Shift Series were an early attempt to evaluate these questions.

A large group of young pigeons was clock-shifted and tested at one of three sites, 9.6, 33, and 45.6 miles distant. The returning birds were normalized and trained before being clock-shifted again. The final test of this series compared the orientation of clock-shifted birds that were new to the site to that of birds that were familiar to the site.

RANGING FIRST-FLIGHTS

From 1975 through 1980 there were over 29 releases at 3 sites of clock-shifted young first-flight pigeons that had ranged before they were tested.

Preliminary tests (see the FF series) demonstrated that the orientation of young first-flight pigeons could be affected by pre-test ranging flights away from the loft, a behavior frequently seen in young birds during their routine exercise flights. Groups of exercising birds that remained out of the observer's sight for 20 minutes or more were designated as Ranging.

A single test in 1975 compared the sun-compass responses of young inexperienced pigeons that had ranged to those that had not. In another clock-shift tests, the orientation of inexperienced birds that had ranged extensively was compared to the orientation of those that had minimal ranging experience.

In a 1977 test, 9-10 week old ranging first-flights were clock-shifted and flown with either bar magnets or brass bars.

To compare the effects of age and ranging experience on the sun compass orientation of young, inexperienced birds, J. Jones (Undergraduate Research, 1978) conducted a series of 21 clock-shift releases of pigeons ranging from 6 to 19.5 weeks old; birds that had ranged were used in 12 of the Jones' tests.

RETURNED RESET

In 1975-77 and 1979-1980 there were 11 releases from 9 sites of clock-shifted pigeons that were successful homers from a test conducted on the previous day.

Experiments conducted by Kramer (1953), Hoffmann (1954). Schmidt-Koenig (1960), and others conclusively demonstrated that the avian navigation system includes a time-compensated sun compass. When flown on a sunny day, horning pigeons whose internal time sense has been changed by 6 hours usually give vanishing bearings that are deflected about 90 degrees from those of the control birds. Such clock-shifted birds not only vanish in a non-homeward direction but many never return home.

However, despite the fact that their circadian rhythms have been reset and regardless of the direction of their vanishing bearings, a few clock-shifted birds do return home on the day of the test, frequently within the homing times of their controls. Rapid re-entrainment to normal time is probably not the explanation for this phenomenon (see the CSN series).

The successful horning of clock-shifted pigeons has several possible explanations: there may be individual differences in response to the clock-shifting manipulation; the successful homers may be either correcting for position, possibly using a mechanism derived from the map component of the navigational system; or such birds may be recalibrating the sun information to their new time sense by reverting to the reference cue used when they initially calibrated their sun compasses. There is also the possibility that a non-solar compass may be used. Would repeatedly clock-shifting the same pigeons make them more adept at using such alternative orientation strategies? Do distance or familiarity of the release site affect sun compass orientation?

The Returned Reset series was an attempt to evaluate these paradigms and to perhaps contribute to the understanding of the way in which cues are integrated. By repeatedly testing the same pigeons, the suggestion that unusual clock-shift responses are a result of individual differences could also be investigated. Were these differences site or time dependent and were they consistently recurring behaviors?

METHODS

A clock-shifted bird that homed on the day of the test and within the overlap period of time between the natural day and the clock-shifted day, would be immediately returned to its clock-shifting room; no pigeons returning after the onset of the artificial night were included. Although they now had experienced one homing flight under sunny conditions, the returning clock-shifted birds continued living on a day 6 hours In advance of the natural time until they were retested on the next sunny day,

Information about the related previous clock-shift release for each group of RR birds can be found in the test comments.

SUN COMPASS ONTOGENY

To study the ontogeny of the sun compass 6 to 62 week old inexperienced and specially trained pigeons were clock-shifted and flown in over 60 releases from 6 sites in 1971-73 and 1975-1980.

Kramer's (1953) model of an avian time-compensated sun compass has been well demonstrated by many tests using clock-shifted pigeons; when experienced pigeons whose internal timesense has been changed by 6 hours are released under sunny conditions, they generally choose vanishing directions that are deflected approximately 90 degrees away from home. By subjecting young, trained pigeons to a permanent clock-shift, Wiltschko et al. (1976) demonstrated that the sun-compass is not innate, but rather is learned and that it can be recalibrated (see the PS series).

However, Alexander (1975) did not always find the predicted orientation response to clock-shifting in her tests of inexperienced pigeons; although control treatments of untrained pigeons were well-oriented, their clock-shifted counterparts frequently were not, suggesting that inexperienced birds integrate orientational cues differently than experienced birds.

The SCO tests investigated the age, experience, seasonal, and training conditions prerequisites for the acquisition of the sun compass, and hundreds of inexperienced and specially trained birds, ranging in age from 6 to 62 weeks, were clock-shifted and tested at different times of the year. The older birds included in the SCO series were over-wintered as either untrained or specially trained pigeons and then tested as yearlings in the early spring. Comments in the test index describe the special training. See Brown et al. (in press)

Some of the special training protocols included comparing the effects of a single preliminary homing flight under sun or under overcast on the acquisition of the sun compass. Other tests examined the number of preliminary training flights necessary for young birds to acquire the sun compass (See Alexander, 1975; also the AC series). In other SCO tests, samples of the inexperienced birds that were tested in the Fall were given 1 or 2 short distance flock tosses before clock-shifting, and an untested portion of this specially trained group was over-wintered and flown the following spring.

To investigate the possibility that non-solar cues were being used by the inexperienced birds, bar magnets and brass bars were attached to the clock-shifted pigeons in 4 tests in 1977-78, and 1980, and because of apparent orientational differences between young and yearling clock-shifted pigeons, a representative sample of each age category was also tested under overcast in 1977. (See the NSK and NSW series for other overcast releases of inexperienced birds.)

In 1978 J. Jones conducted a comprehensive series of 21 clock-shift tests at South Danby V to investigate the effects of age and ranging experience on the development of the sun compass in inexperienced birds. (Undergraduate Independent Research)

METHODS

Upon weaning (at about the age of 4 weeks), young pigeons are routinely encouraged to leave their lofts for daily exercise flights. After several short exploratory ventures, these develop into longer and longer flying sessions lasting from 20 minutes to over an hour and usually within sight of observers at the loft.

For reasons of convenience, most exercise flights are in the morning hours; however, some afternoon flights are also included, and the inexperienced birds have opportunities to fly under a variety of weather conditions. By definition, inexperienced (or first-flight) birds are never taken away for any training flights, the only exception to this being the occasions when they range away.

Inexperienced birds are determined to be physically ready for testing if the group of 50 to 100 birds form a distinctive flock or kit while they are exercising around the loft and when all members of the kit are uniformly sustaining vigorous flight for a minimum of 20 minutes. Alternatively, if kit ranges away from the loft area, staying out of sight for 20 or more minutes, it is also presumed ready for testing or, as in the case of the SCO tests, ready to be put into the clock-shift rooms. The age at which young birds are ready for testing by these criteria varies considerably and may be a function of the weather conditions to which the young hatchlings and weaners are subjected.

In order to examine the relationship of different maturity levels to sun compass responses, some groups continued their daily exercises around the loft until they had reached a specified age. In cases where untrained birds were overwintered and then tested as yearlings, daily loft exercises ceased about mid-November and then resumed at least 1 month prior to their spring tests. All clock-shifts were 6 hours fast, and the birds were kept in the shifting rooms for at least 5 days before being tested. Whenever a test was discontinued because of weather conditions, the remaining untested clock-shifted birds were returned to the shifting rooms before the end of their subjective day.

CLOCK-SHIFT WITH EXERCISE

From 1970-76 and 1978-79 there were 69 releases from 16 sites of clock-shifted birds that had been exercised during their clock-shifting period. Included in this series are 25 tests in which the birds were exercised inside of cages. Bar magnets were attached to the birds in 16 releases. Alexander, 1975; Edrich and Keeton, 1978.

Since 1953 when Kramer first proposed a time-compensated sun compass as part of the avian navigational system, scores of clock-shift tests have demonstrated that sun information, although not essential in the case of experienced pigeons, is preferentially used by them for orientation. When pigeons whose internal time sense is changed by 6 hours are flown under sunny conditions, their vanishing bearings are deflected by approximately 90 degrees from the home direction. Matthews (1966) argued that, since the incarceration associated with clockshifting deprives birds of important information about the daily changes in the sun's position for 5 or more days, test birds could interpret a clock-shift as a longitudinal displacement from home, and therefore sun Information was not necessarily being used as a compass.

But Alexander and Keeton (1972a) found that clock-shifted pigeons continued to use the sun in a manner consistent with the Kramer hypothesis even though they had opportunities to observe the sun from their aviaries during the entire clock-shifting period. See the AR series; also Alexander, 1975.

One explanation of the normal clock-shifted orientation shown by the aviary-exposed birds in the AR tests is that, because the aviary birds were not allowed to fly, the position of the sun was of no significance to them; thus they paid no attention to the daily changes.

The suggestion that flight acitivity may facilitate the use of solar cues comes from the results of the Nearby Clock-Shift series (see Alexander,1975? and NRBY). Clock-shifted birds choose vanishing bearings In the predicted deflected direction when they are released from sites within view of the home loft, evidence that their navigation system is being influenced by sun cues even though they are confronted with landmarks as familiar to them as their own loft.

The initial SE design combined daily flying experience under sun with the clock-shifting manipulation in order to stimulate attentiveness to solar cues, presenting the exercising pigeons with conflicting information derived from their changing internal clocks and their daily appraisals of solar and other, famiIiar cues.

This treatment could have the following results when the birds were tested

homeward orientation would suggest that the time compensated sun cues were disregarded and an alternative compass was used or that the birds had been able to recalibrate, perhaps on a daily basis, the relation of the internai clock solar cues;

clock-shifted orientation would suggest that the birds were re-calibrating or updating the relation of the internal clock to solar cues on a daily basis

disorientation would suggest that individual birds were using different compensatory strategies or were weighing substitute cues differently

To demonstrate that it was the daily exposure to solar information that was the responsible for any changes orientation, 4 tests were conducted in 1971-72 using clock-shifted pigeons that had been given similar daily exercise flights under total overcast instead of under sun conditions.

To test the possibility that young birds used in the SE tests were downgrading the sun compass while elevating the magnetic compass, bar magnets were attached to the exercised clock-shifted birds before they were released in 16 tests in 1974 and 1976.

There were also 7 tests of clock-shifted birds that compared the orientation of birds that were exercised under sun to those that merely experienced a passive sun exposure in aviaries during the clock-shifting period. Other tests incIuded a treatment of standard clock-shifted birds that had remained incarcerated and saw no sun at all throughout the shifting period.

In 1974-75 and again in 1978-79 there were collaborative tests with W. Edrich in which the exercise of the clock-shifted birds was restricted to forced flights within long cages. See Edrich and Keeton, 1978 and the EC series.

METHODS

Beginning on the first morning after pigeons were placed in the clock-shifting rooms, the control and shifted treatments were taken out of the rooms each day and allowed to fly together around the loft. With each day of the shift, both the controls and shifted birds became increasingly reluctant to fly and had to be vigorously flagged for the predetermined minimum of 20 minutes. To take advantage of available sun, the times of these exercises varied, but the exercises were always conducted during the overlap period between the natural and the clock-shifted days. Following most of the exercise sessions, the birds were returned to their closed, artificially lit clock-shifting rooms where they were fed. However in the Alexander series (AC tests), the groups were allowed to sit in their aviaries for an additional 8 hours of sun exposure. In the Edrich cage series, the birds were intermittently forced to fIy back and forth for periods of 10-15 minutes and then allowed to sit on perches at either end of the long exercise cage in which they remained throughout the overlap period between the natural and the clock-shifted day. (see the EC series)

If weather conditions permitted, the groups were tested after a minimum of 4 consecutive days of exercising under sun, but in all cases, they were always tested on a day following a sun exercise. Information regarding the number of sun exercises and the number of days in the clock-shift rooms appear in the test comments or in the literature.

MAGNETISM

The idea that animals might use the earth's magnetic field in navigation was suggested almost a century ago. Despite repeated attempts to test this hypothesis, there was no convincing data of such magnetic effects on birds until the I960's when German scientists, using caged robins, observed behavioral changes that correlated with alterations of the magnetic field (Merkel and Frornme, 1958; Merkel et al., 1964; Merkel and Wilschko, 1965). Since then a wide range of experiments both in the laboratory and with free-flying birds, has led to a steady accumulation of evidence supporting the theory of magnetic influences on the navigation systems of birds. Using homing pigeons as his experimental birds, Keeton began looking for the basic components of the avian navigation system, a quest that led not only to new discoveries about the effects of magnetic manipulations, but which also stimulated others to continue similar searches within the framework of a hierarchal and redundant cue system that included information derived from the earth's magnetic field.

From his earlier work (Keeton, 1969; Keeton and Gobert, 1970), Keeton determined that, in the absence of the sun and familiar landmarks, pigeons could still orient towards home, results suggesting the use alternative cues. This assumption served as the stepping stone to the first repeatable demonstration of magnetic interference on the orientation of free-flying homing pigeons (Keeton, 1971, 1972). The results of these early experiments, using simple bar magnets on birds of varying ages and experience, soon found support in the tests of other investigators using miniature Helmholtz coils (Walcott, 1972, 1977; Walcott and Green, 1974). With these advances in the study of avian orientation, the question of magnetic effects on orientation was reopened, but more importantly, there was a new recognition and emphasis on controlling for such variables as the age and experience of birds, the availability of celestial information, and the familiarity with release sites gained new importance in experimental design.

Within three years of the first reports of magnetic effects on homing pigeons, the Keeton research group found a consistent correlation between day-to-day changes in the initial bearings chosen by pigeons and geomagnetic disturbances of, frequently, less than 40 gamma; they also found that the effect could be masked by attaching bar magnets to the test birds (Keeton et al.,1974; Larkin and Keeton, 1976). Moreover, these small geomagnetic changes measureably affected orientation even on sunny days suggesting either an integration of sun and magnetic cues for the compass portion of the navigational system or perhaps, that the magnetic field contributes in some way to the ellusive map hypothesized by Kramer (1933).

The wide spectrum of experimental designs that was spawned by these early discoveries probed not only the possible interaction of sun and magnetism, but also the relationship of magnetic information to other known sensory capabilities of pigeons. Bar magnets were attached to night-flying pigeons, to pigeons raised without ever seeing the sun, and in tests of a possible inertial navigation system, to pigeons being transported on a spinning wheel. Pigeons wearing frosted lenses or ear plugs, and pigeons that were clock-shifted were also flown with attached bar magnets, and sometimes the bar magnets were worn for long periods of time before a test was conducted. In other experiments homing pigeons were raised in an altered magnetic field or were deprived of magnetic information on their outward journey to release sites. A total of more than 500 test releases from over 50 sites involve some kind of magnetic manipulation.

At the 1970 NASA Symposium on Animal Orientation and Navigation (Keeton, 1972), Keeton spoke of the perplexing variability in results of many tests involving magnetism. The variability persisted over the years even when weather conditions, experience of test birds, and all other readily apparent variables could be held constant. Although the precise role of magnetism in avian navigation is still not clearly understood, the pioneering research conducted at the Keeton research facilities at Cornell University helped to lay aside the old beliefs that birds cannot detect a magnetic field as weak as that of the earth's, and that homing pigeons can not use geomagnetism in some orientational capacity.

TESTS RELATED TO MAGNETISIM

ACC A battery powered coil induced an alternating current around the head of a flying pigeon.

FAR Faraday cages screened out rapidly moving E.M. fields during the outward journey of test pigeons.

FF+ Untrained young and yearling pigeons were subjected to various magnetic manipulations.

K The orientation of pigeons, repeatedly released from the same site, was compared to geomagnetic fluctuations and the lunar cycle.

M Miscellaneous magnetic manipulations such as wing or head magnets, eyecoils, and iron transport boxes were used in pilot tests of their effects on pigeon orientation.

MB Bar magnets were attached to the backs of pigeons in the following series of tests:

MNS The magnetic polarity was alternated.

MSH Bar magnets were attached to one group of pigeons while still at the home loft and to another group at the release site.

PBK Permanently attached bar magnets were worn by young pigeons for a prolonged time prior to testing.

PBS Old birds wore permanently attached bar magnets and the polarity was rotated daily.

PBW Young birds wore permanently attached bar magnets and the polarity was rotated daily.

MC Pigeons were held in an artificially altered magnetic field while being transported to release sites.

MS Pigeons were reared in a loft surrounded by coils that shifted magnetic north in a clockwise direction.

VW Pigeons were transported to release sites in the rear of a VW station wagon.

ALTERNATING CURRENT COILS

The effects of an alternating current on pigeon orientation and homing was investigated by M. Kreithen and H. McIsaac in a series of 7 tests from 7 release sites in 1977-78. This series is being continued by the same investigators at the University of Pittsburgh.

Battery-powered single coils were attached to the tops of pigeons' heads. When the power connection was made, a small electronic device produced a 60 cycle alternating current around the heads of the experimental birds. Control birds wore identical apparatuses, including live batteries, but because they were flown with a disconnected circuit, there was no current flowing through their head coils.

Veterinary branding cement was used to attach the coils and battery packs to the skin on the heads and backs of the birds at the test sites, immediately prior to each bird's release.

FARADAY CAGE

In 1980 there were 8 releases from 6 sites of pigeons that had been transported to the test site inside of a Faraday cage.

Results from outward journey tests (Papi et al. 1973; Wiltschko et al.,1978) suggest that relevant orientational information may be available to pigeons on their outward journey to release sites. The pilot Faraday cage tests investigated the effects of separating geomagnetic and electrical cues by using Faraday cages to transport birds.

The 3.5'x2'x2' Faraday cages were constructed of aluminum window screening over a wooden framework and were large enough to accommodate a regular-sized pigeon carrying basket. Aluminum screening, when tightly joined, effectively screens out rapidly moving E.M. fields, but has no effect on the normal geomagnetic field within the cage. The experimental birds always rode to the release site inside of a tightly-closed Faraday cage, and the control birds, transported in the same pick-up truck, traveled in a normal basket.

Upon arrival at the site, both groups of birds were removed from the truck and placed on the ground where they waited until every bird was flown. In some tests, half of experimental group remained in the Faraday cage while the other half was placed in a regular basket for the waiting period.

The Faraday cage design was also used in conjunction with some of the outward journey detour tests.

FIRST FLIGHTS WITH MAGNETS

In 1969–71 and 1973–78 there were 50 releases of untrained, or first-flight pigeons that were subjected to some kind of magnetic manipulation.

From the results of his early overcast tests, Keeton concluded that in the absence of sun information, older, experienced homing pigeons could use redundant cues in order to orient. (Keeton,1969). However, the navigation systems of younger, inexperienced pigeons appear to need both sun and magnetic cues (Keeton, 1971) suggesting that naive birds have limited navigational information available to them and, possibly because they have not had extended flying experience, they lack the cue redundancy of their more experienced counterparts.

One approach to teasing apart the integrating components of the avian navigation system is to study the ontogeny of orientation behavior in young, inexperienced birds before their cue repertoire becomes more complex by extended flying experience. As a rule, all homing pigeons require some flying experience to enhance their homing capabilities both from the viewpoint of physical development and of knowledgeability of their home environments. Traditionally, this flying experience is accomplished by first giving groups of young birds flights around the home loft area and, after several days of loft flights, when they performing well, taking the entire flock of young birds away to increasingly more distant locations for flock homing flights. The inexperienced birds in the FF series were exclusively exercised around the loft area and their first homing flight was solo.

First-flight pigeons were used in tests that examined the role of geomagnetism in the development of compass mechanisms; the influence of the earth's magnetic field on the calibration of the sun compass and on the sun compass response in young birds; the role of magnetic cues available on the outward journey; the effects of reversed magnetic polarity. These tests are cross-referenced with the following codes: CS, MB, MS, MC, MNS, NSW, VW.

GEOMAGNETIC FLUCTUATIONS

In1970, 1972–75, and in 1978 there were 225 tests from 6 locations of experienced birds that were repeatedly released from the same site. The 6 years of tests explored the relationship between the vanishing directions of pigeons and the natural fluctuations of the earth's magnetic field, and in two of these series, the lunar synodic cycle. Clock-shifted K birds were flown in 6 tests.

The results of tests using bar magnets (Keeton 1971, 1972) suggested that magnetic information could be a component of the pigeon navigation system. The work of Wiltschko and Merkel (1971) and of Wiltschko (1972, 1974) indicated the both European Robins and two species of European warblers respond behaviorally to relatively small magnetic changes. Southern (1971), working with gull chicks, presented data that also suggest sensitivity to very small geomagnetic fluctuations. The K tests investigated the their effects on orientation.

In an attempt to control for variability resulting from individual bird and site differences, the same group of experienced pigeons was released exclusively from the same site until a series was completed. Although some overcast tests were conducted, only data obtained under sunny conditions was used in the published analysis. Vanishing bearings were compared to indices, the measures of magnetic disturbance prepared by the Fredericksburg (VA) Observatory.

Results of the 1970 and the 197-73 tests at Weedsport (45 miles north) and Campbell (40 miles west) are reported in Keeton et al. (1974).

In 1970, bar magnets and brass bars were attached to pigeons in some of the Weedsport tests that are reported in Keeton (1972). The bar magnet tests of K birds were replicated in 1973-74, suggesting a magnetic basis for the relationship between the variations of the vanishing directions and the fluctuations of the geomagnetic field (Larkin and Keeton, 1976).

Because significant correlations between vanishing directions and geomagnetism were found, even on sunny days when presumably the birds were using sun cues for orienting, a sun-magnetism relationship is suggested. To test for this possibility as well as to explore the effect of repeated flights from the same release site on the sun compass response, the K birds were clock-shifted at the end and at the beginning of their yearly test series at Weedsport in 1973, 1974, and 1975.

For the five different years of tests, a measureable counterclockwise shift of initial bearings was found to be correlated with high values at two release sites of 40 or more miles distant from the loft. To test for the effect at other distances and directions, 50 synchronous tests were conducted in 1978 from sites 17 miles west and 19 miles south. There were also tests at a 8 site miles east.

Often when animals have shown clear responsiveness to magnetic stimuli, they have been simultaneously responding to gravity (e.g. Lindauer & Martin 1966; Wehner & Labhart 1970; Wiltschko & Wilschko 1972). To determine if gravity cues might play some role in pigeon orientation, especially in situations where the birds are known to be responding to magnetic information, data from the K tests of 1970, 197, 1973 and 1974 were compared to the lunar synodic cycle. The results of this analysis are found in Larkin and Keeton (1978).

The birds used in the K tests were included in two other series. In 1973, half of the K birds were transported to their Weedsport release site via a west detour route while the other half was driven there via an east detour route. The results of these tests are reported in Keeton (1974). At the end of the test season in 1974, a release at the Castor Hill Fire Tower compared the orientation of K birds that were repeatedly released from Weedsport, a north site to that of birds repeatedly released from Orwell, a south site.

MISCELLANEOUS MAGNETIC MANIPULATIONS

Several pilot tests investigated the effects of magnetic distortions produced by methods other than bar magnets and large Helmholtz coils.

Some tests in 1970-71 and in 1976-77 used alternative methods for masking or disturbing the natural geomagnetic field. These methods included plastic magnetic strips attached to wings of flying pigeons; a large, rotating magnet that was suspended over a basket of pigeons during transport; and Heimholtz-1ike head coils around the eyes of test birds. There were also three tests that employed small, cylindrical head magnets. Two tests in 1977 transported birds in an iron box and included either an odor deprivation treatment or an outward journey detour design.

Details of the designs used in this series are found in test commentary.

BAR MAGNETS

From 1969 through 1980 Cornell pigeons wore bar magnets in over 3 tests from 53 sites of 1 to 465 miles in distance. Sixty of the releases were under overcast skies. A discussion of the early MB tests appears in Keeton (1971 and 1972). The use of bar magnets in the series is reported in Larkin and Keeton (1976).

In 1973 and all subsequent years, the bar magnets used in the MB tests were made of Alnico alloy manufactured by the Permag Corporation of Jackson Heights, NY. Weighing approximatedly three grams, they were cut to the standard size of 2.5 x 0.6 x 0.3 cm, and they were calibrated to a field strength of 1400 guass at the tip of the bar. When a bar was in position on a pigeon's back, the field strength around the bird's head was approximately 0.5 guass. The brass bars used on control birds were cut to the same dimensions as the magnets.

A brass or magnet bar was normally applied to a test bird at the release site, immediately prior to its release. A small dab of non-irritating glue, such as Veterinary Branding or Tag Cement, was used to attach the tip of a bar to the dorsal skin at the base of the neck. After the glued bar was firmly pressed down, the parted dorsal feathers were smoothed back into place covering the bar and allowing the bird to fly in as natural a condition as possible. Except in the permanent bar series, all bar magnets were removed from the test birds upon their return to the loft. Between tests, the bar magnets were carefully stored in accordance with the manufacturer's instructions, and any bars that were suspect were sent to the manufacturer for re-calibration.

When glued on the birds, the normal polarity alignment for the magnet bars was in the north-forward position, that is, the north-seeking pole was towards the pigeon's head.

Bar magnets were used in conjunction with some sun compass tests (see CS, RA, SE, NSW, PSK, PSN, RR) and some sensory tests (see LENS,IW, COC, EP|K); they were also used in the Castor Hill and Jersey Hill Fire Tower tests (CH,HO), in tests of night-flying pigeons (NF), and in many first-flight (FF) releases.

N-FORWARD AND S-FORWARD MAGNETS

1971, 1973–74, and 1977 there were 6 releases from 6 sites Of pigeons that wore bar magnets aligned in either the north-forward or south-forward position. Six tests were under overcast conditions.

When a bar magnet was in the north-forward position, the north seeking pole was towards the pigeon's head.

Walcott and Green (1974) published the results of tests in which the polarity of the magnetic field, produced by Helmholtz-type coils worn by the test birds while in flight, could be altered; under overcast conditions there were significant changes in orientation when the polarity was reversed.

No attempt was made to control for polarity in the initial bar magnet tests conducted at Cornell (Keeton, 1971, 1972). Eight subsequent releasee in 1971 of young first-flight, second-flight, and experienced birds compared the effects on orientation of wearing bar magnets in either the north-forward or south-forward position. Sixteen additional bar magnet tests continued to investigate the effects of polarity reversal on pigeon orientation, and these included 6 releases of K birds wearing bar magnets in either the north-forward or south-forward position. (Larkin and Keeton, 1976).

MAGNETS APPLIED AT HOME OR AT RELEASE

In 1976–79, there were 10 releases from 6 sites that compared the orientation of pigeons that wore magnets during the outward journey to that of pigeons whose magnets were attached at the release site. Seven tests were conducted under overcast condii;ions.

Young pigeons were disoriented when they were subjected to an artificially altered magnetic field during transport to the release site (Wiltschko et al. 1976). These results suggest that magnetic information available to pigeons on the outward journey may be navigationally important. Reports from investigations of other organisms indicate that there may be a time lag in responding to magnetic stimuli, suggesting that sufficient time must be allowed for a magnetic manipulation to be effective. (Lindauer and Martin, 1966,197; Brown, 1971; Wiltschko, 1972).

The MSH tests examined the possibility that magnetic responsiveness may be influenced by either route related magnetic cues or the length of time allowed for a test bird to process magnetic information. The orientation and homing success of pigeons that were exposed to bar magnets from the time they left the home loft until they returned to it were compared to the orientation and homing success of pigeons that wore bar magnets only for the flight home.

The two experimental groups were transported to release sites in separate baskets. While bar magnets were glued to the birds before the left the loft in one treatment, the bars were applied just prior to release in the other treatment.

A third basket held the controls, and brass bars were normally attached to these at the release site.

PERMANENTLY ATTACHED MAGNETS: KEETON

Homing pigeons that had worn magnet or brass bars for an extended time were flown in 19 releases from 7 sites in 1969 and 1970.

Keeton's experiments with clock-shifted pigeons demonstrated that experienced pigeons can orient at unfamiliar places under total overcast (Keeton, 1969), suggesting that alternative orientation cues were being used in the absence of the sun. Additional experiments with experienced birds had shown that bar magnets cause disorientation under overcast (Keeton, 1971). Taken together, the results of these two series of tests suggest the possibility that experienced pigeons are able to use magnetic cues as an alternative navigational strategy under overcast conditions, and that bar magnets somehow interfere with orientation when the sun is not visible.

To test the possibility that pigeons could be prevented from learning about magnetic cues, bar magnets were permanently attached to very young birds before they could fly. Because training flights, which expose pigeons to cue learning opportunities, may enhance their use of magnetic information, the bar magnets were left attached throughout the training period, presumably masking available magnetic information at a developmental stage important for learning navigational cues. Another group of pigeons wore brass bars and shared the same pen with the experimental birds. The two groups were flock-tossed together and were given single-toss training with the bars in place. The bars were removed immediately prior to each bird's release at the test site. The results of the PBK series are found in Keeton (1971).

Because the results of the second PBK series showed little effect of the magnetic manipulation, a third series of permanent bar tests was conducted in the same year. In this series, the two groups of birds lived in separate pens ensuring that the control birds were not being altered in any way by an exposure to the magnetic field created by the bar magnets that were attached to the experimental birds. Otherwise, the groups were trained in the same manner as above, and three tests, including one under overcast, were conducted at the Weedsport and Auburn release sites, 40 and more miles north of the loft.

In all PBK tests no attempt was made to control for the alignment of polarity of the bar magnets.

Note: The first 3 bar magnet tests in 1969 used experienced birds that had worn their magnets since May 16th. The results of these tests are also found in Keeton (1971).

PERMANENTLY ATTACHED MAGNETS: SLACK

In 1976 there were 14 tests from 4 sites of experienced pigeons that continuously wore bar magnets. This was an Undergraduate Independent Study Project conducted by D. Slack.

The earth's magnetic field may be a source of compass or map information for navigating birds. (See the PBW series for background information). Navigationally important information may be available to the birds either at the release site or during the outward journey (Wiltschko et al.1976). How birds learn to use magnetic cues is not known.

Training flights and tests from certain locations, usually to the west of the Cornell loft, frequently result in poor orientation, poor homing, or both. One possible explanation for this decrement in performance is that a yet unidentified magnetic distortions at these locations may interfere with the navigation system, making it difficult for birds to get compass information under overcast conditions or map information or both, if there is an integration of the sun and magnetic cues. If pigeons could be trained to ignore or downgrade magnetic cues, thus forcing them to rely on more dependable information, their performance from problem locations might improve.

Keeton and and later Weiler attempted to prevent young pigeons from learning magnetic cues by masking available geomagnetic information with an artificial magnetic field created around the pigeons by permanently worn bar magnets (see the PBK and PBW series). The Slack modifications of the original permanent bar design included using older, experienced birds; changing the magnetic polarity of the bars each day; giving the birds directional training; and testing the birds, both with bars left on and taken off, from sites known to adversely affect the orientation of normal pigeons.

Bar magnets attached to the backs of the experimental pigeons with strips of Velcro were rotated every day to one of four alignments of polarity as determined by a random number table for each bird (see the PBW series for details). Another group of normal birds, with no bars attached, lived in a separate pen and were used, on an alternating basis, as one or more of the other treatments for each test. Any controls that were not used in a test were flock-tossed from the site, keeping the flying experience equivalent for all.

Control and experimental birds, with their bars attached, were trained together, and before the first test at the Jersey Hill Fire Tower on June 23rd, all had flown in 21 sun and two overcast flock tosses of up to 60 miles exclusively from the west. With the exception of the five releases from West Groton, the PBS birds were flown only from the west. The experimental birds wore their rotated bar magnets for the outward journey to test sites. In some tests the bars were left on, while in other tests the magnets were replaced by brass bars just before release.

To control for route-based as well as site-based magnetic cues some of the other treatments used in the PBS tests included the following: birds that were brought out to the test site and flown home with brass bars on their backs; birds that were brought out with brass bars but flown with standard bar magnets; birds that were brought out with standard magnets and flown with them; birds that were brought out with standard magnets and flown with brass bars.

PERMANENTLY ATTACHED MAGNETS: WEILER

In 1976–77 there were 8 tests from 6 sites of the same group of pigeons that had continuously worn bar magnets. Five of the releases were under overcast, and in other tests, the PBW birds were clock-shifted. This Undergraduate Independent Research Project was conducted by M. Weiler.

Results of bar magnet tests (Keeton, 1971) and head coil tests (WalcOtt and Green, 1974) give evidence that magnetism may be a source of compass information for orienting birds. Other studies of the relationship of geomagnetic fluctuations to orientation suggest the possibility that pigeons may use magnetic cues for the map component of the avian navigation system as well; or it is possible that there is an integration of sun and magnetic cues.

In an attempt to separate sun from magnetic cues, the Weiler tests used birds that were reared with permanently attached bar magnets, presumably preventing them from learning the true geomagnetic field. To preclude the possibility that pigeons could somehow adjust to or factor out a fixed, artificially imposed magnetic field, the positions of the bar magnets was changed daily.

Strips of Velcro were glued to both the bar magnets and to the skin of the experimental pigeons (see MB for more details). This method allowed the bars to be easily rotated each day to 1 of 4 positions determined by a table of random numbers. To control for possible variability between magnets, the bars were periodically interchanged among the test birds, and the distance of the tip of the magnet to the pigeon's head was also varied thus changing the field strength as well as the polarity of the magnetic field surrounding the test birds.

Magnet birds and the birds with permanently attached brass bars lived in separate pens, but the two groups were flock-tossed together in all directions to distances of five miles under overcast and 15 miles under sun. Experience to the west, however, was limited to one 15 mile flight under sun. On all test days, the bars on the habituated magnet birds were aligned to the north-forward position before they left the loft.

Weiler reported that during the early training period more permanent magnet birds were lost than permanent brass birds, possibly resulting in some pre-test selection.

For the period of 4 months between field seasons, the permanent bars were removed, and the habituated magnet birds were over-wintered in a small loft surrounded by a pair of Helmholtz coils that produced a randomly changing magnetic field. In mid-March 1977, the bar magnets were rettached to the experimental group before they were returned to their home loft, and regular procedures as described above were resumed.

For clock-shift tests of these birds, see CSW.

MAGNETIC COIL TRANSPORT

In 1974–76 there were 26 releases at 6 sites of homing pigeons that were exposed to an artificially altered magnetic field while they were being transported to release sites. Fifteen of the tests are published in Wiltschko et al.,1976.

Kramer's (1950) model of the avian navigation system includes compass and map components. Subsequent research has shown that the sun (Kramer,1953; Schmidt-Koenig,1956) and the geomagnetic field (Keeton, 1971; Walcott and Green, 1974) may be sources of compass information for orienting birds.

Some early hypotheses assumed that map information was derived from site-specific factors (Yeagley,1947; Matthews,1953) or outward route information (Barlow, 1964). In 1973 Papi and his colleagues proposed that olfactory information available during the journey to a release site played some role in the navigational process. A chance observation in 1974 that young pigeons, transported in a distorted magnetic field (see VW series), could not orient, led to subsequent investigations of possible route-based magnetic information.

Experimental birds in the MC series were transported in a regular pigeon basket that was placed between a pair of Helmholtz coils powered by the battery of the closed van used to transport the birds to the release site. A basket of control birds, travelling the same route, was transported in another vehicle, usually a carry-all. Upon arrival at the site, each basket of birds was normally removed from its transport vehicle and placed on the ground for the duration of the release. In some tests, however, the experimental birds remained in the altered magnetic field until they were flown. In another design, normally transported birds were put into the magnetic field either immediately upon arrival or two hours later.

A magnetometer was used to measure the coil field while the van was parked near Langmuir Laboratory. Measurements were taken at the center of the pigeon basket that was placed between the two coils. Values given in the following table are of the measured, and not the calculated, field.

	Inside of Van		Outside of Van
	1 Amp	2 Amps	
Horizontal	0.012	0.1704	0.2210
Z	0.199	0.1944	0.4751
Total Intensity	0.199	0.2585	0.5400
Inclination	67	46	65

Young non-ranged and ranged[1] first-flight pigeons aged 6 to 19 weeks as well as young birds with short distance training and experienced yearlings were used in the MC tests.

MAGNETIC SHIFT

In 1974–76 and 1980 there were 32 collaborative releasee from 16 sites of young pigeons that had been reared in a shifted geomagnetic field. Three releases were under overcast. See Wiltschko et al. (1983).

Many experiments testing clock-shifted pigeons under sunny skies demonstrate that pigeons use the sun as a compass. Further investigations discovered that the sun compass system is not innate, but rather that it is learned (W. Wiltschko et al.1976). By allowing very young pigeons to observe the sun only when they were in an artificially shifted magnetic field, the MS series attempted to test whether or not the sun compass is calibrated by the earth's magnetic field.

A pilot test in 1974 used experienced yearlings that had lived in the magnetic shift loft for six to eight weeks prior to testing. In all other tests, young homing pigeons were either born in the special magnetic shift loft or were weaned into it before they could see the sun.

The loft, a white fiberglass and wood structure measuring 5 x 4 x 4.5 feet, and its rooftop wire avairy were surrounded by a pair of 6.5 foot (diameter) Helmholtz coils aligned on a NE-SW axis. The coils were powered from an electrical source in a nearby building. In the 1974-76 tests, magnetic north was shifted clockwise by approximately 70 degrees; in the 1980 series, the geomagnetic field was shifted clockwise by 120 degrees. (The measurements of these deflections were determined by reading a magnetic compass placed in the center of the loft floor.)

Control birds, usually nest mates of the experimentals, lived in another loft under naturally occurring magnetic conditions. The controls and the exprimentals were exercised together only under overcast conditions.

In the 1974–76 series, the birds were tested either as first-flights or as birds with shortdistance flock-toss training under overcast.

In 1980, the experience of the test birds was varied and increased with each test release.

VOLKSWAGON TRANSPORT

In 1974 and 1976-77 there were 13 tests from 4 sites comparing the orientation of pigeons that were transported in the back of a Volkswagon station wagon to that of birds transported in regular loft vehicles. One test was under overcast.

Kramer's (1950) model of the avian navigation system includes both compass and map components. Experimental evidence points to the sun (Kramer, 1953; Schmidt-Koenig. 1958) and the geomagnetic field (Keeton,1971; Walcott and Green,1974) as sources of compass information. Early hypotheses assumed that map information was derived from site-specific factors (Yeagley,1947; Matthews, 1953) or outward route information (Barlow,1964). More recently Papi and his colleagues (1973) reported evidence that olfactory information collected during displacement played some role in the navigation process.

The June 1974 discovery at Cornell (see note in Wiltschko et al.,1978) that young first-flight pigeons transported in a VW, could not orient, led to a series of tests designed to explore the effects on orientation of an outward journey in the distorted magnetic field generated by a VW engine.

In all tests, the basket of experimental birds was placed over the engine in the rear of a 1972 VW Squareback for the outward journey to the release site. Magnetic measurements, made when the engine was running at idle speed, indicated that severe, high-frequency distortions, in the order of 1.6 gauss within the period of the charge-discharge cycle of the spark coil, were being generated. There were also substantial distortions in the vertical component when the engine was turned off; using a moving probe, measurements were taken at nine places, and values ranging from 0.72 to 0.456 gauss were found on the rear floor.

Control treatments, travelling the same route as the experimentals, were transported in one of the regular loft vehicles. Upon arrival at the site, the experimental and control treatments were removed from their vehicles, and the baskets were kept on the ground until all birds were flown. In the one exception to this design (August 18, 1976), the experimental birds remained in the VW while the engine continued running until they were all released.

Young first-flight birds from 6.5 to 15 weeks of age were used in 11 tests; in six of these tests, the birds had never ranged away from the loft. Two other tests used either experienced yearlings or old birds. First-flight birds that flew away out of sight of the loft observer for more than 20 minutes during some of the daily exercises around the loft.

1 Non-ranged first-flight birds are those that never flew away from the immediate loft area during their daily exercise flights; first-flights that flew out of sight of loft observers for more than minutes are defined as ranged birds.

MAP STUDIES

For the past three decades scientists have used a compass and map model of avian navigation as a basis for interpreting the results of hundreds of orientation tests of migratory birds and homing pigeons.

It was Gustav Kramer (1950, 1951) who first suggested that birds, in order to navigate successfully, must be able to combine position or map information with compass information. Several sources öf compass information have been proposed, and current evidence supports possibly redundant solar and magnetic compasses. A compass alone, however, cannot tell a bird where it is, nor in which direction it must fly to reach a particular destination. But despite years of investigations, the avian map component of Kramer's model remains a mystery.

Some investigators have felt that insights to the enigma of the map might be found by studying the orièntation behavior of homing pigeons at certain release sites where they regularly choose departure directions which are deflected from true home (Kramer, 1956; Hoffman, 1959; Walraff, 1959; Schmidt-Koenig, 1961; Keeton, 1973). These predictable delfections, or site biases, do not appear to be a function of any known or suspected compass system, and variables such as age, experience, and the time of day or year do not seem to affect these biases. Because test birds repeatedly make the same orientâtional error when flown from such locations, the influence of some property of the test site suggests itself as an important element of a navigational map.

Other investigators (Wallraff, 1967» 1970; Schmidt-Koenig, 1963) have suggested that it may be the location of the home loft that plays an important role in influencing the departure directions. Thus, when birds living in different loft locations are tested at various sites, their orientation is interpreted as being a loft-related or due to a preferred compass direction; these orientations are derived from, or in part modified by, the navigational information available to birds around their particular home environment.

Because he was convinced that clues of fundamental importance lay undeciphered in orientation biases, much of Keeton's avian map research at Cornell was designed to study every possible aspect of homing pigeon behavior at dozens of release sites, and especially at those which were known to produce predictable deflections or disorientation in the departure directions of homing pigeons. Some of Keeton's early tests examined biases to see if they could be the result of differences in the ages, experience or the previous training; or perhaps, if particular sensory information was involved at certain sites. He also wondered if the observed variation in the magnitude of clock-shift deflections might also be site-dependent. With this in mind, he set out to fly clock-shifted pigeons in tests, frequently synchronously from two sites, from varied distances arid directions.

Other tests were conducted with different strains of homers or with pigeons borrowed from pigeon fanciers whose lofts were north, east, south, and west of Cornell. There were experiments in which Cornell birds were held at release sites overnight or for a few days before they were flown while still other test designs called for raising Cornell-bred pigeons in localities near the release sites that were under investigation; the orientation of these birds was later compared to the orientation of similarly aged and trained pigeons native to the test area. In another study over a span of two years, the effects of changing some of the environmental factors around one of the home lofts was investigated.

When a map of induction vectors, plotted for the northeastern section of the US, came to Keeton's attention, he noticed that some of the station vectors bore an intriguing resemblance to the general orientation pattern of Cornell pigeons, and he wondered if the electro-magnetic information represented by this map could be of some relevance to the avian map used by his pigeons. Consequently, in twelve of the many tests conducted in 1978 and 1979, birds were flown from several new release sites that were suggested by this induction survey.

By studying a wide-grid pattern of similarities and differences in orientation responses of pigeons over a large geographic area, Keeton hoped that some corresponding geophysical characteristics could be delineated, characteristics that could serve as the basis for the avian map. Experiments to attain this goal, frequently in conjunction with other investigations, took Cornell pigeons near and far to more than 200 release sites in the states of New York and Pennsylvania and to a few points in New Jersey, Maryland, Washington, DC, and North Carolina. And, using birds that were unfamiliar and familiar to the sites, pigeons continued to be released from many of the same locations, year after year, so that any possible long-term variations in orientation biases could be documented.

There were also series of tests that methodically mapped out the extent of the curious orientation behavior observed at two locations, the Jersey Hill and the Castor Hill Fire Towers. And finally, in an effort that was to be tragically interrupted during the summer of 1980, the vanishing bearings of hundreds of Cornell pigeons, flown in 80 tests, provided the additional data points needed to expand upon the orientation characteristics of at least two broad areas surrounding the Cornell lofts. The results of this detailed exploration gave form to a unique "Pigeon Map of New York State"; these data, in addition to the accumulation of data from earlier Keeton research, became the basis of another hypothetical avian map of arcing lines perceived by Bruce Moore (unpublished manuseript, 1982).

Keeton's diverse and extensive investigations, not only of the more general orientation pattern that typifies a large geographic area, but also of the nature of biases at individual release sites, have left hundreds of data points, often cross-indexed with exploratory manipulations, to be analyzed by others in their pursuit of the elusive map that is intrinsic to solving the mystery of avian orientation.

CA CAMPBELL (NY). Releases were conducted from Campbell, a site 40 miles west of Cornell, at which Cornell homing pigeons exhibit a pronounced counter-clockwise orientation bias. One series of K tests was also conducted here.

CH CASTOR HILL. Releases were conducted from the Castor Hill Fire Tower, a site 90 miles north of Cornell that is known for its pronounced clock-wise bias. Tests were also conducted at 15 other sites in the Castor Hill region. Test manipulations included the use of frosted lenses, walking pigeons, bar magnets, clock-shifts, ear plugs, olfactory deprivation, and special trailing proceedures.

CR CROSS RELEASES. The orientation of pigeons from other lofts was compared to that of Cornell birds at the Castor Hill and Jersey Hill Fire Towers, at Campbell, and 23 other sites.

CS CLOCK-SHIFT. Clock-shifted pigeons, sometimes wearing bar magnets, were flown from 45 release sites.

DD DIRECTION AND DISTANCE. An early study of the effects of direction and distance on orientation.

EP EAR PLUG. Tests to observe the orientation of birds with attentuated hearing at sites with unusual biases. Bar magnets were sometimes used.

EQ EQUINOX. To test Matthews' sun-are hypothesis, Cornell pigeons were flown during the vernal and autumnal equinoxes.

FF FIRST FLIGHT. Young and older inexperienced birds were flown from sites known to produce orientation biases.

HO HORNELL (NY). Tests, including bar magnets, walkers, ear plugs and clock-shifts, were conducted at the Jersey Hill Fire Tower, a site 75 miles west of Cornell àt which Cornell pigeons are almost always disoriented. There were also releases of pigeons raised in the Hornell area, and releases of these and of Cornell pigeons from six other sites in this westerly region.

IVS INDUCTION VECTOR SURVEY. Cornell pigeons were flown from new sites that were suggested by information found on a map of induction vectors.

K K TESTS. A series of tests that compared small changes in the vanishing directions togeomagnetic fluctuations. Some tests were conducted at Campbell and Cayutav!lie, sites known for their counter-clockwise bias.

MB MAGNET AND BRASS BARS. Bar magnets were attached to pigeons tested at sites known for unusual biases or random orientation.

NB NO BIAS BIRDS. Birds that did not exhibit the expected bias at the Castor Hill Fire Tower were tested at several locations in the Castor Hill region as well as at sites in other geographical regions.

OJ OUTWARD JOURNEY. Pigeons were transported to release sites while being deprived of potential orientation information during the outward journey.

OLF OLFACTORY TESTS. Tests to determine the effects of olfactory deprivation at sites with known biases as well as at other locations.

RL REVERSED LOFTS. Aviaries on two adjoining lofts were reversed from each other, altering some of the perceived environmental information normally available to pigeons,

RT RADIO TRACKING. Pigeons were radio tracked at some sites with unusual orientation patterns.

SC SITE CHECKS. Pigeons were flown from many new sites to determine the orientation characteristics of the sites as well as the general orientation pattern of a region.

SW SWALLOWS. The orientation of a species other than Columba livia was studied at the Castor Hill Fire Tower, at Campbell, and at several other sites.

TB TRAINING BIAS. Pigeons that had extensive flying experience in a single direction were flown from the Castor Hill and Jersey Hill Fire Towers and at some other sites.

WDP WINDSOR DIRECTIONAL PREFERENCE SURVEY. Over 100 releases examined the extent of the regional expression of known biases.

WG WEST GROTON. A series of tests examined the unpredictable pattern of orientation seen at West Groton, NY, a site 12 miles north of the Cornell loft.

WT WEST TRAINED BIRDS. Pigeons with repeated west training were flown from many sites west of the Cornell Lofts and in some other locations.

CAMPBELL TESTS

From 1969 through 1980, there were 74 releases at Campbell, NY, a site with a predictable counter-clockwise bias that is approximately 40 miles west of the Cornell lofts.

One approach to the elucidation of the avian map is to thoroughly study the phenomenon of release-site biases, the fact that at many release sites the deviation of initial bearings from the true home direction is usually consistent for releases of birds from a given loft. Results of such investigations suggest that these site-specific biases are not a function of a compass mechanism. Hence it is plausable that the biases are related to some geophysical properties that may provide at least a part of the map information as hypothesized by Kramer. By observing the orientation of pigeons of varying ages and experiences, and by subjecting birds to manipulations which may interfere with the perception of certain site specific cues, a clue to the avian map may be discovered. See Keeton (1973).

Other models of position-finding include the one, proposed by Wallraff (1967,1970) and Schmidt-Koenig (1973a), that attributes importance to the information pigeons learn at the home loft. On the other hand, results of experiments conducted by Wiltschko, et al. (1978) suggest that map information may perhaps be acquired on the outward journey to a release site. To test these possibilities, pigeons living in four locations other than Cornell were flown from Campbell. There were also releases of pigeons that were raised in two Cornell lofts that faced in opposite directions, thus changing some of the perceived loft information. In another design, birds were transported to the release site while they were anosmic, or being randomly spun, or while they were wearing bar magnets, manipulations that were intended to distort some of the route information presumably available to pigeons during transport to a test site.

In one of the CA tests, pigeons were radio-tracked and in another test, the orientation of another avian species (swallows) was observed. There were other tests that were conducted under overcast conditions; and there were tests of first-flight birds, NB birds (birds with no bias at the Castor Hill Fire Tower), of birds with special directional training, of anosmic pigeons, of pigeons prevented from hearing infrasound or smelling odors; and there were bar magnet tests that compared the effects of different magnetic polarities on orientation. Some test designs included permanently shifted pigeons, and there was one clock-shift test.

The CA database also includes the results from tests of walking pigeons and from the 37 releases conducted in 1974 that were used in the analysis comparing vanishing bearings to the fluctuations of the geomagnetic field. (see Keeton et al», 1974) See CR, CS, DD, EP, FF, IW, K, MB, MNS, NB, OJ, OLF, RL, RT, SW, TB, W, WT.

CASTOR HILL FIRE TOWER

An early series of 24 tests conducted from 1968 to 1972 at the Castor Hill Fire Tower confirmed the predictability of the pronounced clock-wise bias at this site 90 miles north of Cornell; the results suggested that the biasing effect was not compass-related. (Keeton, 1973) The subsequent 103 CH releases from 1972 to 1980 continued examining the bias at the original site and began defining the geographical extent of the bias by releasing pigeons at 17 other sites within a 40 mile radius of the Castor Hill Fire Tower.

Keeton (1973) hypothesized that some environmental factor basic to the homing process is rotated clock-wise at the Castor Hill release site, and that biologically the birds are not making an an orientation error, but rather are reading correctly a distorted map. He proposed continuing the study of the Castor Hill bias by examining the effects of various sensory manipulations on the orientation of pigeons flown from here and by conducting an intensive investigation not only of the bias at the original release site but also of the more general bias characterizing the area. By delineating the geographic extent of the general bias and, perhaps, some of the sensory modalities involved in orientation at sites with such biases, some important clues to the map might emerge.

Although the initial departure directions at Castor Hill indicate that the birds are making a 60 to 90 degree error at this site, they apparently are soon able to make course corrections as they home successfully. To determine whether or not pigeons are integrating information over some time interval or some distance, and then making their correction when they have accumulated enough information, the flight paths of test birds were aerially radio-tracked in 1970 and in 1972.** This collaborative research with C. Walcott identified the geographic points at which Cornell pigeons, whose initial bearings showed the expected clock-wise deflections, turned homewards (Keeton, 1973). Several subsequent releases of pigeons from the sites suggested by the aerial survey, confirmed the locations of such turning points, and further, identified pairs of sites at which the characteristic Castor Hill clockwise bias and homeward orientation of Cornell pigeons are found within a few miles of each other.

Over the 13 years of investigations in the Castor Hill region, Cornell pigeons of different ages and histories, and sometimes with different or special directional training, were flown in morning and afternoon tests and at various times of the year. The orientation of very experienced birds that had a history of releases in the Castor Hill area was compared to young, inexperienced first-flight birds. Groups that had been flown exclusively from the north and from the south were tested at the fire tower; the west-trained veterans of many Hornell experiences were also used here. There were tests in which pigeons were held at the site over night, and one test, suggested by F. Papi, in which pigeons, while deprived of olfactory, visual, and magnetic cues, were transported from Cornell to an intermediate destination that is 30 miles north of the fire tower; at this point they were transferred to the regular carrying baskets and driven south to the Castor Hill release site where their orientation was compared to that of pigeons approaching the release site in the normal way. Homers from 5 other lofts, feral pigeons and swallows were flown from the Castor Hill Fire Tower; some groups of birds were clock-shifted, and others were flown with bar magnets or with various impairments of their hearing, vision, or sense of smell. See COC, COM, CR, CS, EP, FF, IW, LENS, MB, OLF, OJ D, SW, TB, W.

One unusual group of experienced birds (the NB birds), first flown at Castor Hill Fire Tower in 1974 as part of a larger sample, repeatedly showed a reduced bias here and at other sites in the Castor Hill region. Intensive directional training in 1976 had no significant effect on their comparatively unbiased orientation. When the NB birds were clock-shifted, they (like the birds used in earlier clock-shift tests at the Castor Hill Fire Tower) exhibited the normally expected deflection. In one test, they were flown with bar magnets. In 1979 some of their existing progeny (of various ages and test backgrounds) were also flown from this site; another group of progeny, this time intentionally raised for additional tests, was used here in 1980. See NB tests.

** Aerial radio-tracking was conducted on August 4, 1970 and on August 11, 1972; the latter test used clock-shifted birds. As the data from these tests exists in a format other than the one used in this Index, the aerial radio-tracking results are not reported here.

CROSS RELEASES

In 1968 through 1974 and in 1980 pigeons were flown from 26 sites in 83 tests that compared the orientation of pigeons raised at Cornell to that of pigeons raised at 13 other locations.

Pigeons raised in different localities may differ in orientation behavior as a result dissimilar navigational information available to them at their home lofts. This model of orientation assumes that something about the loft location imposes a strong directional preference on pigeons, and that at release sites the birds choose initial bearings that are a compromise between the loft-specific preferred direction and the true home direction (Wallraff, 1967, 1970). If this preferred compass direction is independent of any influencing characteristics of the release site or of the strains of pigeons raised in various sections of the country, then cues obtained at the home loft would play an important role in formulating the navigational map for pigeons.

With the cooperation of New York State pigeon fanciers from Fredonia, Hornell, Schenectady and Syracuse, as well as those from Boston, MA, Chicago, IL, Lancaster, PA and Roanoke, VA, the orientation of birds from other, sometimes more distant, locations was compared to that of Cornell birds at sites with unusual biases such as Castor Hill, Jersey Hill, and Campbell as well as at other frequently used sites. There were also tests that included pigeons raised in 4 other lofts in the Ithaca area. The birds borrowed from fanciers were of several different strains and most had histories of long distance racing.

Other series of cross-releases were conducted with Cornell birds that, while they were still very young, were settled in the Mulligan and Gray lofts near Hornell, NY and at the MacCoy loft at Trumbull's Corners near Ithaca. The young birds were raised, trained, and kept in their new locations until they were tested. The MacCoy birds were frequently trained with Cornell Loft birds but were also used as race birds by their owner; the Mulligan and Gray birds were not raced and received training around the Hornell area that was similar to the training usually given to Cornell birds. Because of the handler's lack of experience with pigeons, many of the Mulligan birds were lost during training resulting in small sample sizes. The orientation of the Gray and Mulligan birds was compared to that of Cornell birds at the Jersey Hill Fire Tower, and the Gray loft birds were tested at several other sites including one test at Auburn, NY, a site some distance away from the Hornell region. Gray birds were also used in Walker tests at Trurnansburg, NY. The MacCoy birds were flown from some sites north of Cornell, including the Castor Hill Fire Tower, and two sites in the northwest.

There were also two outward journey-detour tests at Lyons, NY, that included birds raised in the French loft in Ithaca.

A list of non-Cornell lofts and their locations can be found elsewhere in this manual.

CLOCK-SHIFT

Clock-shifted birds of various ages and experiences were flown in over 300 tests from 45 sites in 1967 through 1980. Bar magnets were attached to birds in some tests.

When tested on a sunny day, pigeons whose circadian rhythms have been changed by 6 hours usually give vanishing bearings that are deflected by about 90 degrees from the bearings of control birds living on normal time, a well-documented behavior demonstrating the sun-compass. However, many such clock-shift tests performed with Cornell pigeons have resulted in deflections of considerably more or less than this prediction. Some release sites appear to produce larger clock-shift deflections than others, results suggestive of an integration of cues that may be site-related.

To control for possible temporal variability, some paired clock-shift tests were conducted synchronously, frequently from equidistant locations. There were other clock-shift tests in which bar magnets were used on both control and shifted birds. Series of 4 or more clock-shift tests at the same site were conducted at the following places: Auburn, Caroline I, Castor Hill Fire Tower, Catatonk II, Enfield IV, Game Farm Road, Hunt Hill Road, Langmuir Lab, Liddell, Locke I, Marathon II, Richford, South Danby V, Weedsport, and West Groton. Of particular interest is a series of three clock shift-tests conducted at the Jersey Hill Fire Tower, a site known for its disorienting effects on Cornell homing pigeons.

DISTANCE AND DIRECTION

From 1967 through 1971 there were over 200 releases of pigeons at 38 sites from 4 to i£ø miles north, east, south, and west of the Cornell lofts. The analyses of 172 of the releases conducted in 1968-69 are published in Keeton (1970c).

Matthews (1955, 1963), Schmidt-Koenig (1964, 1966, 1968), and Wallraff (1967) have reported that the orientation of pigeons is affected by the distance of the release site. If the distance effect is a general characteristic of pigeon homing, it has important implications for the nature of the navigation system used by these birds. Results demonstrating the distance effect have been used in support of Matthews' sun-arc hypothesis (1955, 1963); this argument assumes that pigeons can extrapolate the sun's zenith position more accurately at distant release sites, and that pigeons would use landmarks for navigation at closer distances; intermediate distances, being without either of these navigational aids, would therefore pose the most problems for orienting homing pigeons.

The D & D tests were conducted with normally trained Cornell pigeons that had homing experience from all directions; a minimum of 3 different groups of birds were flown from each site. This initial test series that was published in 1970 was later expanded. See WDP and SC series.

EAR PLUG

In 1977 there were 15 releases at 10 sites of pigeons that could not perceive infrasound. Six of the tests included bar magnets and were conducted at sites known for their unusual biases or for disorientation.

A new orientation possibility was introduced when it was discovered that homing pigeons are able to detect infrasound (Yodlowski et al., 1977) and to distinquish between different infrasonic frequencies (Kreithen and Quine, 1979). Potentially, pigeons have the capability to monitor distant infrasonic sources and use the sound beacons generated by them to determine their position relative to home.

Results of past research suggest that pigeons can integrate orientation cues in a variety of ways depending upon the birds' age, experience, and on weather conditions as well as geographic locations of the release sites and home lofts. By simultaneously depriving test birds of more than one source of information (i.e. familiarity with the site, magnetic and infrasonic cues), some of the characteristics of a release site that are important to avian orientation may be elucidated.

Using a non-surgical method, infrasound perception was attenuated in the test birds (See the EP series for details). Bar magnets were attached to the birds in 6 tests conducted from the Castor Hill region and from the Jersey Hill Fire Tower.

EQUINOX TESTS

Matthews' sun arc hypothesis was tested in 1969-70 and 1972 when there were 7 releases from 4 sites of pigeons that were prevented from seeing the sun at the time of the vernal and autumnal equinoxes. Keeton (1970b).

One of the principal hypotheses of pigeon navigation a few decades ago was that of Matthews (1951, 1953), who proposed that birds, when taken to a new location, used information extrapolated from the sun's path as remembered at the home loft. The difference between the noon altitudes of the sun at the two locations could provide the test birds with information about their latitudinal displacement, and the difference in local sun time at the two sites, the longitudinal placement. Although other investigators could not replicate Matthews' results, he used his sun occlusion experiments to support his sun-arc hypothesis.

Keeton's first series of sun occlusion tests used experienced birds, released from the south, and were conducted in the autumn. Keeton (1970b). Subsequent occulsion experiments were from north sites, used both experienced and inexperienced pigeons, and were conducted in the spring. Keeton (1974a).

FIRST FLIGHT

From 1968 through 1980 there were 218 tests at 32 sites that used inexperienced or first-flight birds. Ten of the tests were conducted in the Castor Hill region.

The orientation performance of inexperienced or first-flight pigeons differs from that of old, experienced pigeons in several ways: young first-flight pigeons require the sun for accurate homeward orientation, whereas experienced pigeons do not (Keeton and Gobert, 1970); first-flight pigeons are usually disoriented by bar magnets even under sun and at short distances, whereas experienced birds are not (Keeton, 1971, 197£); older first-flight birds respond to six-hour clock-shifts by vanishing randomly whereas older experienced birds choose non-random bearings that are deflected roughly 90 degrees from the controls (Alexander, 1975); at some release sites first-flight birds choose non-random bearings that differ significantly from those of experienced birds (unpublished data; see Auburn, Weedspört, and West Groton). Furthermore, by doing simultaneous releases of first-flight birds at two neighboring sites, markedly different site-dependent orientation patterns emerge, patterns that are not replicable with older, experienced birds (Windsor, 1972).

It appears, then, that for successful orientation, first-flight pigeons may require more cues than do more experienced birds; or perhaps such naive birds have not yet settled on a hierarchial weighting system making it difficult for them to choose which cue to use when there is confiiciting information. These developmental differences offer an opportunity of looking at differing utilizations of what may be the same fundamental set of cues, and thereby getting a better idea of the relationships and interactions of the cues involved in orientation. Comparing the orientation behavior of experienced pigeons to that of first-flight pigeons at sites with unusual biases could lead to an important clue to the map component of the avian navigation system.

First-flight birds were flown in 10 tests in the Castor Hill region and in 5 tests from the Campbell release site. There was also one test from the Jersey Hill Fire Tower and 20 tests from

West Groton, a site at which first-flight birds regularly deviate markedly from true home direction. (Keeton, 1974).

See FF for definitions pertaining to first-flight pigeons.

HORNELL, NY

The 66 HO tests conducted in 1968-1970, 1972-1973, and 1977-1979 included 29 releases of flying pigeons and 11 tests of walking pigeons at the Jersey Hill Fire Tower, a site approximately 75 miles west of Ithaca where Cornell pigeons are usually disoriented. There were also 25 tests from 8 other sites in the Hornell region. An additional flying release was done at Auburn, and a walking test was done at Trumaneburg; veterans of Jersey Hill Fire Tower tests were used at these two sites as well as at several others.

Preliminary tests in 1968 at the Jersey Hill Fire Tower confirmed that well-trained, experienced Cornell pigeons, even when familiar to the site, are disoriented here (Keeton, 1970c, 1974). Similar sites known for their disorienting effect on pigeons have also been reported elsewhere (Schmidt-Koenig, 1971).

Orientation may be a function of the map information available at release sites or may be related to a preferred compass direction resulting from cues learned at the home loft (Wallraff, 1967, 1970). If route information (Wiltschko et al. 1978) provides important navigational cues, then the outward journey to a release site may also have some effect on orientation behavior.

A release site that regularly causes disorientation of normal, experienced pigeons raised at Cornell may have some map cues that are conflicting or distorted, but the problem may be one for exclusively Cornell pigeons; if this were so, it would support the loft-inforrnation model propsed by some investigators. On the other hand, it is equally possible that some important map determinant, which may be effectual on the outward journey to such a release site, is insufficient or ambiguous for Cornell birds.

One thrust of the investigations of the Jersey Hill site attempted to determine if the disorienting effects on pigeons are a result of local environmental peculiarities or whether they are a reflection of more widespread irregularities that can be matched to some geophysical characterisitic of a broader area. Other tests were designed to determine the effect of training, experience, and familiarity on the orientation behavior of Cornell pigeons flown from here; and still other experiments investigated the roles of some sensory modalities that may be involved.

An anectodal account of an elderly ex-pilot, who maintained that his compass frequently malfunctioned when he was flying over the Hornell area in the 1930's, stimulated a concentrated perusal of magnetic maps of the region, including (through a special courtesy) some aeromagnetic maps that had recently been compiled for the petroleum industry. A rough magnetic pilot survey around the Jersey Hill Fire Tower was also conducted, but no dramatic magnetic distortions were found. (Keeton, 1971)

Initial releases of Cornell pigeons from several sites within a 40 mile radius of the Jersey Hill Fire Tower nevertheless confirmed that there is a considerable portion of western New York from which Cornell pigeons do not orient properly. But numerous racing pigeons are able to navigate successfully to their home lofts located within this region; thus some loft-specific or natal-area specific disorienting factors become suspect.

One test design used Cornell birds that, before they were flown, were held at the release site overnight or that had lived for 5 days in a loft near the Jersey Hill release site. Still other tests included young birds from Cornell stock that were raised and trained in two locations near the Jersey Hill Fire Tower, in the Mulligan and Gray lofts. There were tests of birds borrowed from the Fredonia, NY area; and there were also releases that compared young first-flights that had very little flying experience around the Cornell lofts to old experienced birds. In collaboration with C. Walcott, Cornell pigeons were radio-tracked aerially[2], and in other releases, pigeons were flown on days that were totally overcast.

Although intensive west training and familiarity with the Hornell area enhanced homing success of Cornell pigeons, there was no analagous improvement in their orientation. Starting with 1973, many tests in the Hornell area used birds that had been purposely west trained (see WT) before their first release from this location and, because they were successful homers, continued to be flown in many subsequent tests from the Jersey Hill Fire Tower. The orientation of these Hornell birds was investigated elsewhere, at other sites out of the Hornell region, and a subset of one of these groups was discovered to have a greatly reduced bias at Castor Hill (See NB). The orientation of this subset was compared to the orientation of the Gray Loft birds at Auburn, a site north of Cornell. Other groups of Hornell birds were also flown at Castor Hill, Campbell, and Burdett; some others were clock-shifted and flown at Cayutaville I where their orientation was compared to experienced birds with no west training.

West-trained birds, birds from a loft 75 miles west of the site, birds with permanently worn bar magnets, birds that wore magnets only on the outward journey, and birds with plugged ears and bar magnets, as well as tests of walking pigeons were tried at the Jersey Hill Fire Tower. The test results from clock-shifted pigeons that were flown from Jersey Hill with bar magnets suggested a puzzling relationship of sun and magnetic cues and led to overcast tests of magnet-weaving birds. See CR, DD, CS, EP, FF, MB, PBS, NB, RT, W.

2 Because aerial radio-tracks are not in the format used in this Index, aerial data has been omitted.

INDUCTION VECTOR SURVEY

In 1978 and 1979 there were 12 tests at 7 release sites that were chosen on the basis of the locations of certain induction vectors appearing on a survey map.

Keeton was intriqued by the pattern of orientation biases, some of them extreme, that he saw developing as a result of testing homing pigeons at many new sites. He felt that such biases could be related to some geophysical property of the release sites and could therefore be clues to the source of information used by pigeons to find home direction.

A geophysical survey map[3] of deep, subsurface magnetic properties showed induction vectors that appeared to correspond with some of the known orientation biases of Cornell pigeons. Several vectors of special interest were located in the Castor Hill and Jersey Hill areas. To further study this apparent relationship, pigeons were released from 7 new locations that were suggested by the information on the survey map. At least three different groups of birds were flown at most sites.

GEOMAGNETIC FLUCTUATIONS

Six years of tests explored the relationship between the vanishing directions of experienced homing pigeons and naturally occurring fluctuations of the earth's magnetic field, and in two of these series, the lunar synodic cycle. Over 300 releases were conducted in 1970, 1972-75, and in 1978 from 6 locations including sites with known orientation biases.

Tests at many release sites demonstrate that Cornell pigeons exhibit not only site-specific biases, but frequently day-to-day orientation changes at the same site, a behavior suggestive of some variable environmental parameter that is involved in avain navigation. Results of bar magnet tests reported earlier led to the consideration of magnetic information as a component of the pigeon navigation system (Keeton, 1971, 1972). The results of subsequent K tests demonstrate that pigeons are capable of detecting very small changes of magnetic intensity, a range of sensitivity that is potentially capable of extracting relevant orientation information from the earth's magnetic field (Keeton, et al. 1974). As all the published K tests were conducted under sunny skies (when the pigeons were presumably using the sun compass), this responsiveness to geomagnetic fluctuations suggests an effect on some non-compass, possibly map-related, use the birds make of magnetic cues. (Larkin & Keeton, 1976). A 1976 computer analysis of magnetograms attempted to determine which component of the earth's magnetic field appeared to be orientationly relevant in the K series. Preliminary results of this analysis hinted that the best predictor of pigeons' orientation behavior is declination, a parameter of the magnetic field that varies geographically as a rough analog of longitude and that could possibly serve as a navigational coordinate (Larkin & Keeton, unpublished data). For declination to be navigationally useful, however, true north determination is necessary; this determination could potentially be made by detecting the north-south gravitational gradient; Keeton, therefore, felt that sucn a possibility made gravity an important navigation variable to consider.

Frequently, when animals have shown a responsiveness to magnetic stimuli, they have been simultaneously responding to gravity (e.g. Lindauer & Martin 1968; Wehner & Labhart 1970; Wiltschko & Wiltschko 1972). When the data from four years of K tests was analyzed, a linear correlation was found between the pigeons' mean vanishing bearings and the day of lunar month (Larkin & Keeton, 1978), suggesting the influence of gravity. The periodicity that was discovered may be a hint that information from such geophysical parameters of the environment as gravity may be contributing to the formulation of the pigeons' map.

To investigate the effects of distance and site-specific temporal changes on the K-orientation correlation, the 1978 K series included synchronous releases at two sites south and west of the Cornell lofts; a third site was also frequently-used, although not at the same time of day. All three sites were at shorter distances from the loft than the locations of previous K tests. For details of the K series, see the Magnetism section of this Index.

BAR MAGNETS

Starting with 1969 there were over 300 releases from 53 sites of pigeons wearing bar magnets.

Although the concepts of Kramer's hypothetical avian map have remained hazy, Keeton (1974a) felt that possible clues to it could be found in the geographic and temporal deviations from predicted orientation behavior observed at some sites.

Results from his early research (Keeton 1969, 1970, 1971, Keeton and Gobert, 1970) suggested to Keeton that the pigeon navigation system involved a hierarchy of multiple cues including solar and magnetic information. Subsequent investigations indicated that pigeons were sensitive to very small changes in the geomagnetic field, even in the presence of the sun, implying an integration of these cue systems. (Keeton et al.1974)

How important and how predictable is the role of the magnetic field in the navigation system? In an attempt to answer these questions and to decipher the basis of the orientation patterns at many sites, bar magnets (sometimes worn for long periods of time) were attached to pigeons that were flown from sites known to produce unusual orientation responses. See Castor Hill and Hornell. Also see the Magnetism section of this Index for additional information about various magnetic manipulations.

3 The map of induction vectors was developed by Professor John Greenhouse, University of Waterloo.

NO BIAS

From 1973 through 1980 the No Bias birds were flown in 41 releases from 10 sites in the Castor Hill region. There were also over 70 releases at 19 other locations.

Keeton (1973) reported that pigeons flown from the Castor Hill Fire Tower predictably choose departure directions that are skewed 60 to 90 degrees away from home. From the results of his tests he concluded that at this site there is a clockwise rotation of some fundamental map cues that are important not only to pigeons from several lofts but also to swallows.

However, one group of Cornell birds exhibited no clockwise bias when released from the Castor' Hill area, but instead persistently oriented towards the home direction. Were these No Bias birds using different cues or were they weighting available cues differently? Was this orientation behavior learned or innate, and did it affect the NB birds' orientation at other sites? Numerous tests explored these questions. See the NB (in the Miscellaneous Tests Section) for more information.

OUTWARD JOURNEY

In 1969-70 and 1972 through 1980 there were over 180 releases of pigeons that had been deprived of some potential navigational cue while being transported to release sites.

Despite considerable attention given during the last decades to the problem of pigeon navigation, it is not yet clear when or where the birds obtain information from which they derive the home direction. There is a possibility that the compass systems normally used by birds may also serve as a reference for a route reversal mechanism. Wiltschko et al.(1978).

To test whether map information gained during the outward journey is incorporated in directional determinations at release sites, pigeons were driven to test locations while potential cues were being manipulated. Included in the OJ tests were interferences of auditory, inertial, magnetic, and olfactory inputs during transport. See the following Index sections: COC, EP, IW, MB, OLF, PBS.

OLFACTION

From 1973 through 1980 there were over 200 releases from more than 25 sites of pigeons that had undergone some type of olfactory manipulation.

Papi et al. (1972) put forward an olfactory navigation hypothesis which proposed that young pigeons at the home loft would learn to associate particular odors with certain directions. Pigeons would then use this association at the release site to assess their position relative to home. Olfaction could, therefore, be an important factor in the map step suggested by Kramer.

Numerous olfactory-type experiments conducted in Italy appear to support this hypothesis, but replications of these tests in upstate New York frequently produced contraditory results. See Papi et al. (1978). Also see the OLF section of this Index for details of the Cornell olfactory tests.

REVERSED LOFTS

In 1978 and 1979 there were 31 tests at 11 release sites that compared the orientation behavior of pigeons living in two opposite-facing lofts.

Pigeons raised in different locations frequently show differences in initial orientation at a given release Site (Wallraff 1967, 1970; Schmidt-Koenig, 1963). This preferred compass direction (Wallraff, 1978) appears to be independent of the release site location, suggesting that information derived at the home loft may be an important component of the avian navigational map. (Papi et al. 1972; see also Papi, 1976) propose that wind-borne odors, present in the loft area and learned by resident birds, constitute the basis of this map component.

However, many of the olfactory-type experiments that were conducted at Cornell did not replicate the results of the same experiments when these were performed in Italy (Papi, et al. 1978). The difference in loft arrangements at the two research facilities may have contributed to this descrepancy. The Italian lofts have very large aviaries that are open to air currents blowing in from all directions. By contrast, the Cornell lofts have smaller aviaries that always face south so that they are shielded from the prevailing northwesterly winds. Could these differences of exposure to possible wind-borne cues result in different orientation behavior?

Furthermore this imposed limitation of exposure to wind-borne cues could be a contributing factor to the orientation biases frequently exhibited by Cornell birds, biases that often send pigeons off in directions deviating markedly from the true home direction.

To determine whether the orientation of Cornell pigeons could be the result of their asymmetric exposure to home loft cues, one loft building was turned by 180 degrees so that its aviary faced north. A group of 100 young pigeons, divided by siblings, was weaned into this loft and into an adjacent control loft (with the standard south facing aviary). Both groups received identical feeding and care, and they were exercised and trained together. The orientation of the two groups was compared in tests, frequently synchronous from two directions, at release sites located 10 to 55 miles from Cornell.

RADIO TRACKING

From 1969 through 1977 and again in 1980 there were 151 releases from 75 sites of pigeons wearing radio transmitters Sixty-eight RT releases in the WDP series investigated the spatial extent of directional tendencies of orienting homing pigeons. Another 51 RT tests were of night-flying pigeons, and in 25 of these test birds wore bar magnets. Radio-tracked bearings were compared to visual bearings in 16 tests. Windsor, 1972,1975; Goodloe, 1974; Keeton, 1973a, 1974. Also see CH, NF, WDP, and West Groton series.

The study of site biases and the effects of distance and direction on the orientation of homing pigeons may provide clues to the avain map. Because a greater portion of the flight path can be monitored when radio telemety is used in orientation studies, this technique can add important information about navigational or reorientation strategies used by pigeons once they have left the release site and are out of range of visual observers.

In 1969-71, an early (collaborative with J. Downhower) series of 13 releases of pigeons from 11 sites, including some with pronounced orientation biases, compared final radio-tracked to visually-tracked vanishing bearings. With the cooperation of C. Walcott, Cornell pigeons were also aerially radio-tracked from the Jersey Hill and the Castor Hill Fire Towers, yielding additional information about the test birds' behavior after they flew out of range of either-visual observers or ground radio stations.[4]

To test the assumption that the directions chosen by departing test birds and the magnitude of their deflections from home direction are a region-wide phenomena, D. Windsor plotted the orientation of Cornell homing pigeons from a systematic gridwork of release sites in all directions from the Cornell loft. Because visual tracking would limit the choice of release sites, the radio tracking technique was employed. Five of the Windsor RT releases were under overcast conditions. See the WDP series.

Radio-tracking was also used by L.Goodloe who studied the navigational capabilities of homing pigeons that were flown at night. Goodloe's 42[5] releases from 1969 to 1972 were conducted from 7 locations in the four cardinal directions at both new and familiar sites; in some tests the birds wore bar magnets. With the assistance of L. Venezia, this study was expanded by W.T. Keeton in 1974, when an additional 19 night releases were radio-tracked. See the NF series.

In 1975-76 Cornell pigeons were also radio-tracked from three sites in the Castor Hill region, determining the location of at least one turning point where test birds re-oriented towards home. See the CH series.

In the 1977 collaborative olfactory series, the effects of anosmia on the navigational capabilities of pigeons at familiar and unfamiliar sites was compared. With the cooperation of C. Walcott, aerial radio telemetry* was used to determine the flight paths of some of the test birds at Lyons, NY. See Papi et al. (1978). Also see the OLF TU series.

4 Because a different format is used in recording the data from aerial radio-tracking, these data are not present in the Index.

5 The Goodloe thesis cites 10 NF releases in 1970 including those from Kellogg Fire Tower, a release site 53 miles south of Cornell. These releases are not included in the Index because the original data sheets are not available.

Three radio-tracking tests were conducted by B. Moore in 1980 to determine the homing flight paths of Cornell pigeons as they approached their home loft, returning from release sites situated west of the Cornell lofts.

RADIO TRACKING AS A TECHNIQUE

Traditionally, visually monitored vanishing bearings have been emphasized in experiments on homing, and such observatione provide much valuable information about the earliest stage of the homing process. But they also have several shortcomings: (1) there can be considerable noise in the data at even the most carefully selected release sites due to the loss of birds behind distant trees, other obstacles or varying degrees of haze; (2) visually taken initial bearings represent only a small portion of the homeward flight and give no information about reorientation along the flight path, which is interesting especially in cases where successfully returning pigeons' departure bearings show considerable deflections from the true home direction; (3) the selection of release sites becomes limited, not by the experimental design, but rather by topography (or the location of a fire tower) that permits good visibility in all directions. In conducting a wide-grid orientation survey (such as the WDP series) radio-tracking becomes a preferred method of collecting data since it allows for the flexibility needed to choose release sites at specified distances and directions. And, of course, to study night homing, radio telemetry is essential.

Drawbacks of the radio-tracking technique include the outlay of both time and capital necessary to obtain, maintain and replace the various components of the system; it is also a more time-consuming way to get orientation information, and it inevitably results in smaller sample sizes in a given period of time. Unless the triangulation method is used, radio-tracking does not provide much information about the distance travelled by a test bird within the first few minutes after release, nor does it offer the additonal behavioral information that can be noted by an observer watching with binoculars. Used in conjunction with aircraft, as it was in the CH series, radio-tracking can reveal details of the flight paths and reorientation strategies of pigeons that initially appear to have incorrect departure bearings.

EQUIPMENT:

Adapted from Cochran (1965), the 2.5 x 1.0 x 0.5 cm miniaturized-component transmitters used in Cornell tests weighed between 4.4 and 9 grams, depending on battery size. Immediately prior to the release of a test bird, a transmitter was slipped into a plastic envelope that was semi-permanently attached to the dorsal skin with branding cement, a method that not only protected the transmitter but also allowed for the convenient, repeated use of the same bird without additional feather removal or handling of the branding cement.

The receiver used, an AVM Model LA 11, was constructed by Cochran, and could be tuned to 12 frequencies from 148.000 to 148.220 megacycles. The fundamental frequencies varied from 44.400 to 44.466 megacycles.

A two-meter directional, dipole aluminum antenna was normally attached to a vertical mast which could be fitted through a small port in the roof of the tracking vehicle. A compass rose, aligned with a hand-held compass for each release site, rested at the base of the antenna.

The range over which pigeons could be radio-tracked was influenced by meteorological and topographical features, the power of the transmitters, proper tuning, and the height at which the birds flew. Line-of-sight tracking tests of equipment indicated a probable range of 4 to 10 miles from the release site. Birds were usually tracked until the signal could no longer be heard, but the compass position of each pigeon was continuously monitored at one minute intervals. The RT vanishing bearings reported here are the final bearings for each bird.

SITE CHECKS

From 1967 onwards, experienced Cornell pigeons were flown from over 100 locations in an attempt to determine the orientation properties of release sites in the experimental area.

Because Keeton felt that clues of fundamental importance to the avian map could be found by studying the orientation patterns of pigeons released from sites over a large area, Cornell birds were regularly flown from new locations. Early releases in 1967 through 1971 are found in the DD section, a series that was later expanded upon by D. Windsor (see the WDP section).

Studies pertaining to particular regions of specific orientation interest, such as the Castor Hill and Jersey Hill areas, can be found under codes related to that area, e.g. CH and HO.

The 80 SC releases conducted in 1980 included tests from 21 new sites located east, northeast, southwest, and northwest of the Cornell lofts. In some cases, the new sites were selected with the intention of integrating the orientation patterns suggested by previous tests conducted from widely separated test sites. Some tests merely confirmed results of a previous, single test at that site. Other tests explored totally new regions. At least three releases were conducted on different days at each new site using pigeons of varying ages and experiences. To examine whether or not loft locations were a factor in determining the directional preferences of homing pigeons, some site checks included birds borrowed from the French loft in Ithaca or the Cornell-stock birds raised in the MacCoy loft, southwest of Ithaca. Temporal variability was also considered, and synchronous tests at two or three release points were conducted whenever it was possible.

There were also site checks at previously used sites. Some sites known for erratic orientation results (e.g. Locke I, Canastota II, Enfield IV) were routinely checked each year, whenever it was convenient to do so. Other site checks involved the release of pigeons from a location that either had not been used for several years or that was undocumented, before that particular site was to be used for critical tests.

SWALLOWS

A study of the orientation of bank swallows in 1969-70 included 14 tests at 9 release sites. Swallows from five colonies were used. Downhower and Windsor (1971).

Studying site biases, such as the pronounced clock-wise bias found at Castor Hill, may yield clues to the avian map. When bank swallows from the Cornell area are released at Castor Hill, most depart in the same directions that are chosen by Cornell pigeons. Thus it appears that two different avian species agree on the appropriate homing direction, strengthening the suggestion that some environmental factor fundamental to the avian homing process is rotated clockwise at Castor Hill. Keeton (1973).

Analagous investigations were conducted at other release sites, especially sites that are characterized by the biased or disoriented behavior seen in Cornell pigeons when they are flown from them. The orientation of bank swallows was compared to that of pigeons in 8 of the 1970 swallow releases including the tests at the Jersey Hill Fire Tower, Burdett and Campbell

TRAINING BIASES

In 1967-70, 1972, 1974, and 1976-77 there were over 70 releases of pigeons that had repeated single-direction flying experinece previous to testing. The effect of special training on the orientation of young, inexperienced pigeons was also examined.

Numerous investigators have reported that when pigeons that have been trained from a single direction are released at a site off the training line, they take up initial bearings that reflect the original training direction even though that direction is no longer appropriate. If true, these observations have important implications regarding the formulation of the avain map. (See Keeton, 1974a for bilbliographic references).

To test this hypothesis, 47 releases were conducted at 10 sites in 1967-69. See Alexander and Keeton (1972). This study also appears in a Master of Science Thesis by J. Alexander, 1970.

D. Windsor, who was investigating orientation preferences in homing pigeons, expanded his WDP study to include young, inexperienced birds which he flew from West Groton, a site at which experienced birds and first-flight birds orient very differently. By giving groups of first-flights their first training tosses from another northerly location, Windsor demonstrated that the change of directional preference at a given release point was not dependent on young pigeons gaining site-specific information; information gained from homing experience alone, even when it was from other sites, appeared to be sufficient to correct initial orientation to a more appropriate direction. See Windsor (1972).

Windsor also wondered if the directional preferences of inexperienced young birds could be attributible to the presence or absence of solar cues on their first flight away from home. Five tests at West Groton compared the orientation of second-flights that had their first training as singly tossed birds from a northerly site under either sun or overcast conditions.

In 1972 Keeton continued investigating the effects of tnaining biases on young, inexperienced birds at West Groton. In a series of 5 tests, young homing pigeons were given their first flying experience away from home as single tossed birds from either a northerly or a southerly direction; their orientation as second-flights was then compared to that of experienced birds and of first-flights first flown at the West Groton site.

Other tests of older, experienced birds attempted to evaluate the relationship between previous directional experience and the observed site biases which Keeton felt were important clues to the avian map. Could special training alter the interpretation of available map information at sites like the Castor Hill Fire Tower? Could a site bias be unlearned through rigorous training? What is the orientation response of old experienced pigeons, successful homers from many tests in the Hornell area, when they are confronted with the rotated map found at the Castor Hill Fire Tower? Were the clock-shifted birds flown from the Jersey Hill Fire Tower integrating navigational cues differently, and would they continue to do so if clock-shifted again and tested elsewhere? A test at Cayutaville I compared the orientation of such birds to the orientation of another group of clock-shifted pigeons that had extensive north training.

In another series of collaborative (with W.Edrich) investigations designed to explore the relationship between the sun compass and map information, clock-shifted birds were given directional training during their overlap time. For details, see SE tests in the Sun Compass section.

In an experimental design suggested by F.Papi, the effect of olfactory deprivation on line-trained pigeons was examined at Lyons and New South Berlin. See Papi et al. (1978). See also AB, NW, and WT.

DIRECTIONAL PREFERENCE: WINDSOR

From 1970 through 1972 D. Windsor conducted 144 tests in which Cornell pigeons were radio-tracked,from 65 release sites. Also included under the WDP code are 16 Windsor tests using first-flight pigeons, 15 Windsor K tests with bar magnets, parallel tests from nearby sites, tests comparing orientation behavior under sun and overcast conditions, and a study of the effects of initial training on the orientation of young birds. (Windsor 1972,1975; Keeton, 1974a)

The earlier DD study examined the accuracy of pigeon orientation as a function of distance and direction (Keeton, 1970c). Using both visual and radio tracking techniques, D. Windsor expanded on the DD series with over 100 releases from all directions testing the assumption that the directions of vanishing bearings, as well as the magnitude of orientation preferences, are region-wide phenomena.

In addition to this spatial study of orientation behavior from a gridwork of release points, the WDP series includes the following: a series of releases from a single release site which monitored day-to-day and within-day orientation variations of the same group of birds (see Keeton, 1972); a study comparing orientation results of eleven overcast tests at 7 sites to the results of tests conducted at the same sites under sun; tests of first-flight and inexperienced pigeons which suggest that the directional tendencies of such birds are a discontinuous spatial phenomenon that can vary dramatically at two nearby release points, evidence that individual release site characteristics must be navigationally important to such inexperienced birds; the investigation of effects of first training flights (under sun or overcast; as singles or as flock members) on the orientation of young birds on their second flight; a series of 12 releases comparing the orientation of inexperienced birds to that of experienced birds at West Groton, a site 10 miles north of Cornell where first-flight birds exhibit unusual orientation. See FF, RT, and West Groton.

WEST GROTON

In 1967,1971-73, 1977-78, and in 1980 there were 37 releases at West Groton, a site about 12 miles north of the Cornell lofts, where inexperienced birds exhibit markedly different orientation patterns from those observed in experienced birds.

One approach to the elucidation of Kramer's map component of the avian navigation system is to investigate release-site biases, that is, at each release site the deviation of pigeons' initial bearings from the home direction is usually remarkably consistent for pigeons from a given loft. It is plausible that these biases are related to some geophysical property of the site and therefore may be a clue to at least part of the map information hypothesized by Kramer. At West Groton, however, tests comparing inexperienced and experienced birds suggested that experience may affect which cues are used, or perhaps how pigeons weight the cues available to them at a release site. Is it important for young, naive pigeons to learn the site-specific information before they can orient appropriately at that release site? Or can necessary information be gained from general flying experience? If the latter is true, does the direction or distance of the first independent flight influence the subsequent orientation of pigeons at a site like West Groton? Is the West Groton effect restricted to a very small area or is it part of a regional discongruity? Were the observed orientation patterns temporal?

To answer these and other questions about the characteristics of the West Groton site, tests were conducted using first-flight birds of various ages, relatively inexperienced young birds with special directional training, clock-shifted birds, birds wearing permanent bar magnets, and birds transported to the site while being spun on a rotating wheel. There were also tests comparing the orientation of similar groups of pigeons released synchronously at West Groton and at a site less than 6 miles away. See D. Windsor (1972). In 1978 there was a West Groton release done synchronously with tests at Richford and Dryden III. Another test involved releasing birds of Cornell stock that were reared in the MacCoy loft. See also the , CR, FF, IW, PBS, RT, TB, WDP, and the WT series.

WEST TRAINING

From 1973 onward there were over 50 releases of pigeons that had been given intensive west training before being used in tests from sites to the west of the Cornell lofts.

The deviation of pigeons' initial bearings from the true home direction appears to be a site-specific phenomenon, and this bias is remarkably consistent for pigeons from a given loft. It is possible that such orienttional biases are related to the geophysical properties of various sites and may therefore may be a clue to at least a part of the map information hypothesized by Kramer.

However, some investigators have found that directional training also has an effect on the orientation of pigeons. See the TB series for information about directional training experiments.

Some early releases of young pigeons from the Hornell area, about 75 west of Cornell, resulted in unusually poor returns. Subsequent orientation and homing results from tests using more experienced and older birds confirmed that the west was a difficult direction for normally trained Cornell pigeons. Even when they are flown from some west sites that are less distant, Cornell pigeons exhibit unpredictable orientation patterns.

In 1973 a group of 100 young birds was assigned to a number of tests at sites west of Cornell including Campbell and the Jersey Hill Fire Tower. With the intention of reducing early losses, the pigeons were given additional west training after the all-direction training to which all test birds at Cornell are normally subjected. When tested at the Jersey Hill Fire Tower, the homing success of this group was excellent. (Some of these 1973 west trained birds subsequently became the No Bias group. See the NB series.)

Because there was a continuation of the Campbell series in the following year, a second group of young birds, after their normal all-direction training, was also given the same special west training prior to their 1974 tests from this site. In the first test from Campbell, the orientation and homing performance of birds having both flock and single toss training or only flock toss training, both from the west, was compared to the orientation and homing success of similarly aged birds that were trained in the normal (all direction) way.

Since many test designs called for repeated releases of birds familiar to the Hornell area, subsequent training regimens for birds to be used there always included additional west training.

West trained birds were also tested at other sites such as Castor Hill. Their orientation and homing performance was compared to that of north trained birds at Enfield IV and Cayutaville I; the latter test involved clock-shifting both groups.

SENSORY STUDIES

The early work of Gustav Kramer (1950b, 1951) demonstrated that solar cues played n important role in avian orientation. Subsequent research by Schmidt-Koenig (1960), Hoffman (1960), and Keeth and Gobert (1970) gave support to the idea that the sun compass is a indeed a preferred orientation cue for pigeons and probably for other diurnal birds as well. However, results from other experiments by Keeton (1969, 1971) documented that pigeons could also orient in the absence of the sun, and that magnetic cues too played a role in the avian orientation system. It was because of this experimental evidence that Keeton (1974a) viewed the avian orientation system as one of a variety of different hierarchies or weighting schemes of components that could be combined in different ways depending upon such variables as age, experience, and prevailing environmental conditions. Much of the Cornell research that followed these early pionreering years was guided by Keeton's multi-cue concept and was concerned with the search for and the testing of non-solar, non-magnetic sources of navigational information.

Impressed by the fact that in many studies animals shown responsiveness to magnetic stimuli had simultaneously been responding to gravity, Keeton sought to determine whether gravitational cues might also play a role in pigeon homing. By looking for an influence of the natural monthly gravitational cycle caused by the moon's changing position a significant correlation was found between the pigeons' mean vanishing bearings and the day of the lunar synodic month (Larkin and Keeton, 1978). In another study of gravitational influences, pigeons were exposed to distorted gravity cues while being transported to release sites.

The importance of vision in pigeon homing was elucidated by K. Schmidt-Koenig (1972, 1977) who conducted many of his tests using frosted lenses on Cornell pigeons. The results of this collaborative work effectively demonstrated that detailed visual information is not necessary for accurate orientation.

Still other investigations of non-solar, non-magnetic cues were stimulated by the discovery of new sensory capabilities of homing pigeons, results of the laboratory research in progress at Cornell, (Kreithen and Keeton, 1974a, b,c; Yadlowski et al. 1977; Kreithen and Eisner, 1978; Kreithen and Quine, 1979). The possibility that infrasound could be utilized by pigeons was tested by flying decochleated pigeons under overcast conditions. This auditory discovery and the need to conduct tests with flying pigeons also prompted the development of a non-surgical method of attentuating sound perceived by test birds. The consideration of polarized light as a potential navigational aid led to the design of special, light-altering panels on lofts in which test birds lived (Phillips and Waldvogel, 198S).

At the same time scientists in Italy were reporting the results of their many tests of the olfactory hypothesis proposed by F. Papi (1972, 1976). The largest effort ever undertaken by the Keeton group to replicate the experiments of others involved testing the role of olfaction in the Ithaca area; the effort culimnated during the summer of 1977 when over 50 collaborative releases, directed by F. Papi and his colleague S. Benvenuti, were conducted at Cornell. A variety of techniques was used to deprive pigeons of olfactory information. Birds were tranported to the release site with nasal plugs or nasal tubes, and in some cases, released with the devices still in place. The olfactory nerve was sectioned in another group. In a series of detour tests, pigeons were taken to the release site by circuitous routes to give then a confusing olfactory picture of their outward journey. And, in replications of the Papi deflector experiments, birds were raised in specially constructed lofts which deflected the directions of wind-borne odors. Two papers emerged from this collaborative work and although there was general aggreement among the authors regarding the results of the many experiments, separate interpretations were presented by the Italian and American teams. See Papi et al.(1978).

Follow-up investigations on some of the Papi tests continued. As part of his doctoral research, J. Waldvogel found that the orientation of birds that had spent as little as five days in the deflector lofts was also affected (Waldvogel 1981; Waldvogel et al.1980). Tests of deflector birds under overcast conditions, and still other tests of birds living in the lofts with light-modifiying deflector panels, suggest that the orientation behavior originally reported may not be due to olfaction alone (Waldvogel and Phillips,1982).

The outward journey detour tests were also continued, adding to the original Papi design by including treatments transported in Faraday cages, screening out rapidly moving E-M fields but that not interferring with the perception of such potential route-cues as odors, light, or magnetism. There were also some detour tests in which a a treatment of birds transported by a direct route was added.

Other series of tests explored the possibility that pigeons might use inertial information to trace back their outward journey. In one series the normal inertial information was masked by by transporting birds on a spinning wheel, and in another test, pigeons with no saccular otolith, a possible acceleration detector, were flown.

It has become increasingly apparent in recent years that avian navigation systems are extremely complex. The possibility now exists that birds could use not only the more traditionally studied cues of sun and stars, along with such previously known but largely ignored cues as odors, but also a host of cues they were previously not known to detect: the earth's magnetic field, barometric pressure, ultraviolet light, the polarization of light, and infrasound. Much of Keeton's energy was devoted not only to investigating the ever-expanding repertory of available navigational information but also to determining how the many cues are integrated. His catalog of sensory tests is a tribute to this dedication.

AP ALPHA-PINENE. Alpha-pinene was applied to pigeons' beaks prior to release.

COC COCHLEA. Pigeons with cochleae removed were flown under sun and overcast.

D DETOUR. In order to give test birds a misleading olfactory picture of their displacement route, they were transported to test sites via circuituous routes.

DEF DEFLECTOR LOFTS. Pigeons lived in special lofts equipped with delfecting wings that changed the directions of incoming wind-borne odors.

EP EAR PLUG. A non-surgical/method produced auditory attentuation in test birds.

FAR FARADAY CAGE. Experimental birds were transported to test sites inside of a Farady Cage.

GA GRAVITATIONAL CHANGES. Gravity was altered by buidling a wall of lead bricks around experimental birds while they were being transported to a release site.

IW INERTIAL WHEEL. Test birds were subjected to randomized angular rotations on the outward journey to the release site.

LC LUNAR CYCLE. Vanishing bearings were compared to the day of the lunar synodic month.

LENS LENS. Experimental birds wore frosted lenses which impaired the visual resolution of landmarks.

OJ OUTWARD JOURNEY. Various potential navigational cues were manipulated during the journey to the test site.

OLF OLFACTION. The role of olfactory information was investigated in a variety of experimental designs.

ONS OLFACTORY NERVE SECTION TESTS. Pigeons were made anosmic by sectioning their olfactory nerves.

PL PLUGGED NOSTRILS. The nostrils of experimental birds were plugged to prevent the birds from using olfactory information.

QOT OLIVE OIL AND TURPENTINE: QUINE. Pigeons were raised in special structures in which they learned to associate compass directions with the odors of olive oil and turpentine.

SAC SACCULAR OTOLITH EXTIRPATION. The saccular otolith was removed in the experimental pigeons.

TC CLOSED CONTAINERS. To prevent birds from using olfactory information on the outward journey, they were transported in closed containers.

TU OLFACTORY TUBES. Plastic tubes that by-passed the olfactory mucosa produced anosmia in experimental pigeons.

X XYLOCAINE NASAL SPRAY. Experimental birds were made anosmic by spraying Xylocaine into their nostrils.

ALPHA PINENE

Alpha pinene, topically applied near the nostril area, was used to mask olfactory cues available to homing pigeons. This method was used to test the olfactory hypothesis in 3 releases from 8 sites in 1973-75 and in 1977.

The 1973-75 series of alpha pinene tests attempted to replicate the experimental design reported by Benvenuti et al. (1973). See Keeton and Brown (1975).

Because the results of the Cornell alpha pinene tests were not in agreement with those published by Benvenuti, another alpha pinene series was conducted at Cornell in 1977 in collaboration with F. Papi and S. Benvenuti. See Papi et al. (1978).

COCHLEA

In 1973-75 there were 15 releases from 6 sites of pigeons that had undergone bilateral extirpations of their cochleae. Eight of the tests were conducted under overcast conditions, and in five releases the experimental birds also wore bar magnets.

Wallraff (1972) had reported no detectable decrement in the homing ability of pigeons whose cochleae and lagenae had been removed, but his tests were conducted when the sun was visible, a condition that could have provided the experimental birds with alternative navigational information.

In 1973, G. Manley (then of MCGill University, Montreal, Canada) suggested that the pigeon cochlea, elongated across the flight path, would appear to be a logical site for magnetic reception (personal communication). He proposed collaborative experiments using de-cochleated Cornell pigeons that would be flown under overcast.

The results of the three 1973 pilot tests of decochleated birds were sufficiently encouraging to warrant further investigation, and Manley returned to Cornell the following spring when he extirpated the cochleae and lagenae from a larger sample of pigeons[6]. This group of trained yearlings was used in the 7 releases conducted in 1974 and the 5 tests in 1975. The latter series included 3 releases from sites in the Castor Hill region, an area known for its exaggerated clockwise orientational bias.

6 Surgical proceedures: Using Equithesin as an anesthetic, the cochleae and lagenae of both ears were removed in the experimental (E) birds. A second group of operated birds (ME) had the columellae bisected, but the cochleae remained intact; this procedure eliminated direct sound conduction between the tympanum and the oval window. Control birds (C), which were randomly selected penmates of the experimental groups, underwent similar anesthetic proceedures but experienced no surgical interventions.

The discovery in 1975 that pigeons could detect infrasound led to the laboratory testing of the auditory capabilities of the decochleated birds. See Yadlowski, et al. (1977).

DETOUR

In 1973-74 and 1977-80 there were 43 releases at 8 locations of pigeons that were transported to the test site by two widely diverging routes

In Italy, Papi et al. (1973) reported an olfactory effect of outward journey detours on the initial orientation of homing pigeons. Because these results were at variance with those obtained by other investigators, and since the proposed orientation effects of different routes have important theoretical implications for the hypotheses concerning the mechanism of pigeon homing, 15 detour experiments were performed at Cornell in 1973-74. See Keeton (1974c).

Two pilot tests using very young first-flight pigeons were conducted on June 4 and 5, 1974 at Langmuir.

In a series of 15 tests using experienced birds, Keeton (1974c) found no orientation effect from transporting pigeons to release sites by different routes. This and other discrepancies between the results obtained by American and Italian investigators led to the 1977 collaborative olfactory hypothesis investigations, which included detour tests using Cornell pigeons released at sites, one from the east and the other from the north. See Papi et al. (1978).

One unpublished 1977 detour test was conducted at the Castor Hill Fire Tower, a site 90 miles north of Ithaca where orienting pigeons regularly exhibit a pronounced clockwise bias. The experimental birds left Cornell simultaneously in two vehicles, following the regular northward route along I-81 for the first and longest legs of their outward journey. However, one group of experimental pigeons was deprived of olfactory, visual, and magnetic cues on the northern leg of their journey, and their journey northward was extended to Watertown, a city approximately 20 miles north of the fire tower. At Watertown, they were taken out of their various containers, placed into ordinary pigeon baskets in the back of the pick-up truck and then driven south to the release site. The control group, in regular pigeon baskets, was transported in the project's metal-body carryall which was driven northward to the Pulaski exit. At Pulaski the journey continued eastward to Redfield, and from there continued, approximately 7 miles in a north direction to the fire tower. Thus, the immediate approach pattern to the release site of the control birds was from a southerly direction instead of the normally used west-to-east route from the Lacona exit. A group of No Bias birds also travelled in the carryall.

The published 1977 detour series was continued from 1978 through 1980 using the same routes and the same north site, Lyons, except for releases which were conducted at a nearby drumlin, Clyde, when Lyons was temporarily unavailable. The pre-test training procedures also followed the original Papi design[7]. In these 20 continuing tests, pigeons were transported in both regular open baskets with normal access to fresh air and in closed containers which were supplied with either pumped-in fresh air or with bottled pure air that was devoid of any odors. The containers were air-tight and opaque preventing the pigeons from using any visual or solar cues. The two containers used for each test were also constructed of dissimilar materials; whenever the information is available from field data sheets, the type of container (aluminum or wood box) is noted in the test comments.

In all cases, the birds travelled in the backs of the loft pick-up trucks, both groups leaving from the Cornell loft simoultaenously and arriving at the release site within 15 minutes of each other. When buttles of compressed air were used, the bottles were placed towards the cab of the truck leaving sufficient space towards the rear for the containers and baskets of test birds. The open baskets rode next to the tailgate.

The first 6 releases in 1979 should be considered as 3 pairs of tests. The first release of each pair of tests consisted of birds that are new to site, with the exception of the July 20th test which included some individuals that had been flown from the Lyons site in 1977 or 1978. The second release of each pair of tests consisted of the previously flown birds, but the groups now travelled in the direction reversed from that of their first journey, i.e. the former east group was now detured to the west, and vice versa.

Preliminary analyses of the Cornell detour tests suggested that the orientation deflections observed at the Lyons site were principally due to the vanishing bearings of the birds transported via the west route. To determine if non-olfactory route information may be involved, tests were conducted in 1980 of pigeons that were transported to the test site inside of Faraday cages. See FAR for more information.

To determine if the home loft location could be a factor in the detour effect, pigeons from the French loft in Ithaca were also tested at Lyons in 1980. There was only one treatment of the French birds because only a small number was available.

On May 15th and 16th, 1980 there were two detour tests conducted at Lyons that compared the orientation of birds with the Papi-type training to that of birds with regular, all-direction training.

7 Because the intention of the Papi pre-test training was to familiarize the test birds with odors along the initial segments of the two detour routes, all the detour test birds (after their normal all-direction training) were given a number of east and west flock tosses of up to miles in each direction. After the completion of the east-west training and just prior to testing, there was one last flock toss from a point 40 miles north.

DEFLECTOR LOFT

The olfactory hypothesis was tested in over 100 releases of pigeons that lived in lofts designed to alter the direction of perceived wind-borne odors. The tests were conducted at four sites from 1977 through 1980.

Baldaceini et al. (1975) reported that pigeons exhibit predictably deviated mean vanishing bearings after prolonged exposure to deflected wind flow. Papi's olfactory hypothesis predicts that young pigeons learn an olfactory map at the home loft and later use this information when orienting from unfamiliar sites. By rotating the directions of wind-borne odors that are perceived by pigeons at the home loft, the initial orientation of such pigeons will show an analagous rotation, reflecting the learned, skewed olfactory map.

The 1977 Collaborative tests in the Ithaca area included young Cornell birds raised rn specially constructed deflector lofts[8]. See Waldvogel et al. (978).

The continuing 4 deflector loft experiments in 1978 involved releases of the deflector loft yearlings and additional young birds. Some of these permanently housed deflector birds were tested under overcast conditions. See Waldvogel and Phillips (1982). Another set of 3 tests investigated the effects on orientation of normally raised, experienced yearlings that were kept in the deflector lofts for only short periods of time. See Waldvogel et al. (1980). The short-term residency technique was also used in 6 releases of pigeons that had undergone olfactory nerve surgery.

In 1979 there were 32 DEF releases using both permanent and short-term resident birds. Keeping the itegrity of the original wind-rotating design, two new deflector lofts were constructed. Although wind and odor patterns in the new lofts remained the same, a modification of the glass panels altered the perceived ambient light thus pitting olfactory cues against light cues. See Phillips and Waldvogel (1982).

There were 44 releases in 1980 using both types of birds housed in the standard and the alteredpanel lofts, and 5 overcast releases of permanent residents were conducted. The results of many of the 1980 tests are included in the 198 papers cited above.

The unpublished DEF research, as well as the results from subsequent DEF experiments, is currently being analyzed by J. Waldvogel and J.Phillips.

EAR PLUG

In 1977 there were 15 releases at 15 sites of pigeons that could not perceive infrasound. Six of the tests included bar magnets and were conducted at sites known for their unusual biases or for disorientation.

A new orientation possibility was introduced when it was discovered that homing pigeons are able to detect infrasound (Yodlowski et al., 1977) and to distinquish between different infrasonic frequencies (Kreithen and Quine, 1979). Potentially, pigeons have the capability to monitor distant infrasonic sources and use the sound beacons generated by them to determine their position relative to home.

To determine the location of the receptors responsible for infrasound detection, Yodlowski et al. (1977) tested five pigeons from which the cochleae and lagenae had been surgically removed. (For details of the cochleae extirpations, see the COC section.) The results of these tests suggest that the receptors for infrasound are in the inner ear.

Using Cornell homing pigeons, D. Feinstein (Cornell Senior Honors Thesis, 1978) was successful in developing a nonsurgical technique that attenuated infrasound detection but which left the experimental birds physiologically intact. Desired levels of sound attenuation were accomplished by the insertion of vaseline-coated plugs into the external meatus of each ear followed by an additional application of vaseline directly into the ear canal. The effectiveness of this procedure in attenuating sound was evaluated by classical cardiac conditioning methods. Randomly selected birds with plugged ears, tested at frequencies ranging from to 45 Hz, were found to have an average sound attenuation of 35 dB.

To determine the effect of infrasound attenuation on the orientation of homing pigeons, Feinstein conducted releases from sites known for producing preditable biases or disorientation.

Ear plugs were inserted into both ears of experimental birds at the loft, and because the procedure was time-consuming, usually on the evening before a test unless otherwise stated in the test comments. Additional vaseline was applied at the release site immediately prior to the release of each test bird. Untreated pen mates of the experimental birds were used as controls. After each test, the ear plugs were removed from the successfully homing birds, and their ears were thoroughly cleansed using cotton swabs and warm water. The pigeons assigned to the EP series were regularly rotated through all the inclusive treatments.

Bar magnets were attached to EP birds in 6 tests including those conducted at the Jersey Hill Fire Tower, a site where Cornell birds are inexplicably disoriented.

FARADAY CAGE

In 1980 there were 8 releases from 6 locations of pigeons which were shielded from rapidly moving E-M fields during their outward journey to the test site.

8 The Cornell deflector lofts were constructed in art open field adjacent to the Liddell Laboratory about miles north of the main loft. Therefore, the pigeons used in the DEF tests homed to Liddell if they were pemanent residents, or they homed to the regular Cornell lofts on Turkey Hill Road if they wore short-term residents.

Results of outward journey tests (Papi et al. 1973; Wiltschko et al. 1978) suggest that relevant olfactory or magnetic orientation information may be available to pigeons on their outward journey to release sites. The suggestion that navigational cues may be available on the displacement route has important theoretical implications for the hypotheses concerning the mechanism of pigeon homing.

Keeton (1972a) wrote of the perplexing variability in results of many tests, a variability which persisted over the years even when weather, experience of test birds and all other readily apparent variables could be held constant. Although the idea of navigational interference from electrical emmissions is not new, the continual proliferation of electronic devices that now dot the countryside resurrect the question in a contemporary context. Could E-M emmissions along displacement routes be a contributing factor to the inexplicable changes observed in the orientation of pigeons? See Keeton, (1974a).

The FAR tests investigated the effects of separating geomagnetic and electrical field cues by transporting test birds to release sites inside of Faraday cages.

The 3.5 x 2 x 2 foot Faraday cages were constructed of aluminum window-screening stretched over a wooden framework, and each was large enough to accommodate a regular-sized pigeon carrying basket. When tightly joined, such aluminum screening effectively eliminates rapidly moving E-M fields (radio, TV and micro waves) but does not affect the normally occurring geomagnetic information within the cage.

The basket with the experimental treatment, which was always transported to the release site inside of a Faraday cage, and the basket of controls were transported in the same pickup truck. Upon arrival at the site, both groups of birds were removed from the truck and were kept on the ground until every bird was flown. In some tests, half of the experimental group remained inside of the Faraday cage and the other half was placed in a regular basket outside of the cage.

Preliminary analyses of the Cornell outward journey detour tests suggested that the orientation deflections observed at the Lyons site were principally due to the mean vanishing bearings of the test birds arriving via the west route. To determine if an E-M effect was involved, two detour tests included transporting pigeons to Lyons in the Faraday cages.

GRAVITATIONAL CHANGES

In 1976 there were 4 tests at 3 locations of pigeons that were surrounded by a distorted gravitational field during the outward journey to the release site.

Some of Keeton's earliest work involved the role of magnetism in avian navigation. (Keeton, 1971; Keeton et al. 1974).

Impressed by the fact that in many studies when animals had shown responsiveness to magnetic stimuli, they had simultaeneously been responding to gravity (Lindauer and Martin, 1968; Wehner and Labhart, 1970; Wiltschko and Wiltschko 1972), Keeton sought to determine whether gravitational cues were also involved in avain orientation system. Due to the geographic variation in the strength of the earth's gravitational field, gravitational cues could not only provide addittional topographic information, but if a bird could use the north-south gravitational gradient to determine true north, then magnetic declination might be readable. Declination is one of the very few environmental parameters that varies as a rough analog of longitude, and hence its usefulness would be very great indeed. (Keeton, 1979b)

The role of route-based navigational cues has been recently resurrected by several investigators including Papi et al. (1973) and Wiltschko et al. (1978). The possibility that pigeons may be integrating gravitational changes on their outward Journey and the results of the lunar cycle analysis (see the LC tests) suggested the GA tests.

On the outward journey, the basket holding the experimental birds was surrounded by 2 walls constructed of 12 lead bricks weighing 15 pounds each. The controls, with one exception, were transported in the same vehicle, but their basket was kept some distance away from the lead wall. For the release of October 12th the experimental treatment was brought to the site in a carryall while the controls were transported in a pickup truck.

INERTIAL WHEEL

In 1970-72 and 1979-80 there were 21 releases at 12 sites of pigeons that were subjected to randomized angular rotations on the outward journey to a release site. Nine tests were conducted under overcast conditions, and magnets were attached to the birds in 3 of the releases.

The possibility that birds might detect all the twists and turns of the outward journey and use these to calculate the route home was suggested as early as 1873 by Charles Darwin. More recently other scientists including Barlow (1964, 1966, 1971) have investigated the possibility of inertial navigation.

There are at least two ways that inertial cues might play a role in avian orientation: (a) birds exhibiting a strong homing tendency (e.g. pigeons) might detect their linear and angular accelerations on the outward journey and then integrate this information to determine the homeward direction; (b) having chosen a bearing using other cues, a bird might use inertial information to maintain his course even when the original orientation cues are no longer available.

The many previous tests of the inertial navigation hypothesis had produced mostly negative results. (For a review, see Keeton, 1974a.) To investigate the possibility that in the presence of alternative navigational cues, pigeons may ignore inertial information, a series of experiments was initiated at Cornell in 1970.

Designed and conducted by B. Covey (Brass Foundation Undergraduate Research Grant), there were 17 tests in 1970-72 in which the experimental birds were driven to a release site in a carryall while being spun on a hand-driven wheel. The experimental birds travelled in the individual compartments of a "widowhood" carrying basket made of aluminum walls and a plastic front. This basket was strapped on to a rotating turntable. A table of random numbers determined the R.P.M. and the length of time for the clockwise and counter-clockwise direction of rotation. The average speed of rotation varied from 4 to 16 R.P.M; the duration of rotation in one direction varied from 10 seconds to 1.5 minutes. A tape recorder, placed beneath the experimental birds, set on high volume masked road noises.

Control birds, riding in the same vehicle, were transported in regular canvas pigeon baskets and remained stationary throughout the outward journey. Upon arrival at the test site, all pigeons were removed from the vehicle, and the baskets were kept on the ground until the test was completed. The only exception to this procedure was the test of September 12, 1970 when all baskets were carried into the fire tower cabin.

Six releases were conducted under overcast. In two other tests, bar magnets were glued to the backs of the experimental and control birds before leaving the home loft. A third magnetic manipulation involved gluing small, cylindrical magnets to the heads of test birds.

The second series of 4 IW tests conducted in 1979-80 used an automated turntable designed by J. Willis (undergraduate assistant) which rotated at preprogrammed, randomized speeds ranging from 2.9 to 3.5 rpm; the randomized time intervals governing the change in the direction of rotation were also programmed.

In this series the experimental treatment was carried to the release site in a canvas basket, and a pick-up truck was used for transportation. Road noises were not masked. Three of the releases were conducted under overcast conditions, and in all 4 tests the birds had limited, short-distance training.

LUNAR CYCLE

Data from 6 separate series of releases that were conducted during 4 different years at 3 release sites were used to study of the relationship of gravitational accelerations to the orientation of homing pigeons.

The results of other investigations suggest that detection of magnetic and gravitational stimuli may be linked (Lindauer and Martin, 1966; Wehner and Labhart,1970; Wiltschko and Wiltschko, 1972). The LC series explored the possibility that gravitational changes across the synodic lunar month might influence the initial bearings of homing pigeons under conditions when naturally occurring fluctuations in the geomagnetic field have been shown to influence the birds' behavior.

The pigeon orientation research at Cornell had been concerned with the elucidation of the the causes of the small, day-to-day variations of vanishing bearings at sites with relatively stable orientâtional biases. The underlying reason for these frequently observed changes in orientation could facilitate an understanding of the pigeons' navigational map and about how the birds integrate the various components of their navigational system. Looking for possible effects of gravitational changes on orientation of free-flying birds was one approach to these goals. See Larkin and Keeton (1978). (The LC marker is not assigned to any data for this series. See the KTEST Series for data used in the LC analysis.)

CONTACT LENS

From 1971 through 1975 there were 17 collaborative releases from 12 test sites of pigeons wearing frosted lenses which impaired the visual resolution of landmarks.

One of the three types of animal navigation systems suggested by Griffin (1955) was piloting, or steering a course on the basis of familiar landmarks. Downhower and Windsor (1971) presented evidence that homing Bank Swallows respond to landmarks located five km or less from their home colony. Pigeon fanciers frequently allude to the importance of prominent landscape features which provide their race birds with easily recognized visual guidance to the home loft. Although pigeons may use landmarks under certain conditions, the concensus among researchers in the orientation field has been that mechanisms other than pilotage by familiar landmarks are being used.

The point that landmarks are relatively unimportant in pigeon navigation was demonstrated by the experiments, conducted in Germany, of Schlichte and Schmidt-Koenig (1971; Schmidt-Koenig and Schlichte, 197S; Schlicte,1973) in which pigeons wearing frosted contact lewses were hot only able to orient homeward from distant sites but were also able to home successfully.

Schmidt-Koenig continued this research in the United States, and in 5 years of collaborative work with Keeton, tests of Cornell birds wearing frosted lenses were conducted at release sites from all four direct ions.

Birds wearing frosted lenses were flown from the Castor Hill Fire Tower, a site which is known for its exaggerated clockwise orientation bias; the results demonstrated that vision is not a factor in the unusal orientation pattern observed there (Keeton, 1974a). Clock-shift tests also demonstrated that pigeons wearing frosted lenses continue to use the sun compass (Schmidt-Koenig and Keeton, 1977).

Other collaborative research, using bar magnets, explored the possible integration of magnetic information and vision; and in another test, the role of vision in the orientation of very young, inexperienced birds was investigated.

OUTWARD JOURNEY

Potential navigational information was masked during the outward journey of pigeons used in over 250 tests conducted from more than 30 sites in 1973 through 1980.

Although the older hypotheses of avian navigation by inertial guidance, based on information gathered on the outward journey, have received no experimental confirmation and have been largely discarded (for summary, see Keeton, 1974a), two recent lines of investigation have resurrected the possibility that outward-journey information may be important after all. Papi's group in Italy (Papi et al. 1973) reported positive results from their olfactory-based outward journey tests; and the encouraging results of investigations at Cornell (Wiltschko et al., 1978) suggest that route-based magnetic information may be important to the orientation of young pigeons.

With the discovery of additional sensory capabilities in pigeons (Kreithen and Keeton, 1974 a, b, and e; Yodlowski et al. 1977; Kreithen and Eisner, 1978; Kreithen and Quine, 1979), new potential sources of navigational information were added to the list öf possible cues whose roles in the avian navigation system needed to be be investigated, not only at the times of release but also during the outward journey of test birds. For additional information regarding tests that include the manipulation of cues during the outward journey, see the following codes: AP COC D EP FAR GA IW MB MC MSH ONS QUT PBK PBS PBW SAC TC TU VW X.

OLFACTION

From 1973 through 1980 olfactory information, available to orienting pigeons, was manipulated in a variety of ways in over 200 tests conducted from 29 sites. Some manipulations involved surgical intervention.

It was in 1972 that Papi et al. first put forward their olfactory navigation hypothesis which proposed that young pigeons at the home loft would learn to associate particular odors with winds from certain directions. This olfactory information, along with a compass system, could be the basis of the pigeon navigation system.

Results from a wide array of olfactory-type tests in Italy supported this hypothesis, but the Keeton group could not successfully replicate many of the experiments. In a collaborative research effort in 1977, Italian and American researchers conducted a host of tests with Cornell homing pigeons resulting in two joint papers: Papi et al. (1978) and Waldvogel et al. (1978).

Tests of the olfactory hypothesis continued at Cornell, and specific information about olfactory tests can be found under the following codes: AP D DEF OJ ONS PL QOT RL TC TU X.

OLFACTORY NERVE SECTION

In 1974 and 1977-78 there were 19 releases from 9 sites of pigeons whose olfactory nerves had been sectioned. In 1978 the ONS birds lived in the deflector lofts before being tested.

Papi et al. (1972) proposed a new model for an avian navigation system based on olfactory cues. To test this hypothesis, Italian researchers have conducted a variety of experiments (Papi, 1976) including flying pigeons with sectioned olfactory nerves (Papi et al., 1971).

The results of the first series of ONS tests conducted in 1974 plus the two long-distance tests (from Durham, NO in 1977 are reported in Hermayer and Keeton (1979).

Because the Cornell attempts to replicate the Italian tests had generally not been successfull, Italian-American collaborative investigations, including a series of ONS tests, were conducted at Cornell in 1977. (Papi et al., 1978; Waldvogel et al., 1978).

To determine if the clockwise and counter-clockwise orientation observed in the deflector loft pigeons was due to skewed olfactory information, a third series of two ONS experiments was conducted by J. Waldvogel in 1978. In these tests, pigeons were put into the deflector lofts (see DEF) a few days after they had undergone olfactory nerve surgery. The experimental birds were subjected to bilateral sectioning of the olfactory nerve by the method described in the above papers. Surgical intervention in the control birds was limited to the trauma of anesthesia and skull trepanation but the membrane was left intact.

PLUGGED NOSTRILS

In 1977 there were 4 tests from 2 sites of pigeons whose nostrils were plugged with dental mastic during the outward journey.

Papi et al. (1972) proposed"that homing pigeons use olfactory cues in order to home from unfamiliar sites. As potential olfactory-based navigational information may be available to pigeons during their outward journey, the nostrils of test birds were plugged with a silicone paste before they left the loft. The plugs were removed just before each bird was released. Results of these tests are reported in Papi et al. (1978).

QUINE OLIVE OIL AND TURPENTINE

In 1975-77 there were 19 releases at 4 sites of pigeons that were trained to associate compass directions with the odors of olive oil and turpentine.

Papi et al. (1972) proposed a new, olfactory-based model of the avian navigation system. Many olfactory-type tests were performed in Italy including those in which young pigeons were subjected for a prolonged time to the artificial odors of olive oil and turpentine originating from specified directions. When these pigeons were tested, their orientation was in agreement with the prediction based on the olfactory hypothesis (Papi et al., 1974).

Attempts to replicate this test design were initiated at Cornell by D. Quine in 1975. A special loft was constructed on the Liddell Laboratory grounds, approximately 2 miles north of the main loft. At the weaning age of about 4 weeks, nestmates (odd and even band numbers) were separated and each was settled into one of the 2 separated halves of the windowless loft. Each group of young pigeons had access to one section of a glass-enclosed, elongated aviary that was positioned on the loft roof on a SW-NE axis. The birds' only opportunity to experience the outside world was when they were allowed into their respective glass aviaries. When in these structures, the groups were subjected to odors dispersed by fans at velocities of 2-4 m/s. While the odd numbered birds were subjected to the odors of turpentine coming from the SW alternating with the odor of olive oil blowing from the NE, the treatment of the even numbered birds was reversed, e.g., the odor of turpentine came from the NE, etc.

On relatively calm days preceding the first test, both groups of pigeons were given 6 free flights around the loft area and 4 flock tosses from very short distances. The test dates were also determined by wind velocities which never exceeded 5 mph while the birds were being liberated.

The experimental birds were transported to the release sites in closed, plastic-lined cardboard containers; a CO2 absorbent material monitored the oxygen content during transport and while the birds were being held at the release sites. Immediately before being released, either olive oil or turpentine was painted on each bird's beak. There were also analagous treatments using normal birds from the main loft.

SACCULAR OTOLITH EXTIRPATION

In 1971 there were 3 overcast releases from 3 locations of pigeons that had undergone extirpations of the saccular otolith. As early as 1873 Charles Darwin had contemplated the possibility of birds using the displacement route information to calculate their return journey to their homes. However, results of tests designed to investigate such inertial guidance systems have not generally supported this hypothesis. (See Keeton, 1974a for a summary.)

Experiments involving surgical leisoning of the vestibular organs of birds, the putative principal detectors of accelerations, have also consistently produced negative results, but presumably these tests have been performed under sunny skies. Current awareness of the complexity in the pigeon navigation system reopened the question of the role of the vestibular organs and focussed on the need for varying several possible cues simultaenously. K.E. Money suggested collaborative tests under overcast conditions of pigeons whose sacculi have been removed.

Cornell pigeons were shipped to Ontaria, Canada, where Money performed the saccular extirpations. The surgery removed discretely and bilaterally the lagena from the inner ear of some of the birds and the saccule from others. Histological examinations following field tests indicated that the surgery had accomplished its objectives without unintended damage to surrounding delicate structures. For detailed information, Dr. Money may be contacted at the Defence and Civil Institute of Environmental Medicine, Downsview, Ontario, Canada.

TRANSPORT IN CLOSED CONTAINERS

From 1975 through 1980 there were over 30 tests at more than 5 locations of pigeons that were transported to the test sites in closed containers.

The older hypothesis of avian navigation by interial mechanisms and route-based cues received little experimental confirmation and has been largely discarded by researchers in the field of avian orientation, (for a summary, see Keeton,1974a). Two recent investigations of route-based navigation, however, have resurrected the possibility that outward-journey information may be of importance to orienting birds: Papi's group (Papi,et al. (1973) and Wiltschko et al. (1978) cite evidence that olfactory and magnetic cues, respectively, may influence the direction of departure bearings of homing pigeons.

This research, together with the current awareness of the complexity of the pigeon navigation system, has reopened the question of outward journey cues with its focus on the need for simultaneously controlling for several possible cues. By transporting birds in closed containers visual, light, olfactory, auditory, magnetic and other cues lay be selectively controlled during the displacement journey.

Explanations of the type of containers used in the Cornell experiments are found in the Test Description section, and sometimes descriptive comments are included with the test data, itself. Other references to transport containers may be found in narrative sections relating to the tests in which they were included.

OLFACTORY TUBES

In 1976-77 there were 27 releases from 11 locations of pigeons that were made anosmic by wearing plastic nasal tabes.

Papi et al. (1972) have proposed that olfactory cues constitute the basis of the navigational map hypothesized by Kramer (1953). The Italian investigators have performed a wide range of experiments designed to test their olfactory model including tests of birds with surgically sectioned olfactory nerves.

In an attempt to avoid the trauma and other non-olfactory effects associated with surgical intervention, a substitute method of making pigeons anosmic by inserting plastic tubes in their nostrils was developed at Cornell. This method was used in tests that are reported in Keeton et al. (1977) and Papi et al. (1978).

XYLOCAINE NASAL SPRAY

In 1977, as part of the continuing Cornell tests of the olfactory hypothesis, there were 3 releases at 3 sites of pigeons that were made anosmic by spraying Xylocaine into their nostrils.

Another method of inducing anosmia in pigeons is to locally anesthesize the olfactory mucosa. K. Schmidt-Koenig supplied the Xylocaine spray for these tests, and Xylocaine propellent was used as the control spray.

Miscellaneous Tests

Although the three major emphases of William Keeton's research centered around compass systems, the elusive map, and the sensory capabilities of homing pigeons, a wide spectrum of other topics was being explored concurrently.

Hundreds of field tests, frequently collaborative, were directed at such inquiries as the orientation capabilities of feral pigeons or the ability of homing pigeons to orient at night; the importance of social interaction in the leadership of orienting flocks and flock homing success; and the effects of directional training or of previous experimental manipulations on the subsequent orientation of experimental birds. Questions about subjects as diverse as the nutritional requirements of pigeons and test methodologies used in Cornell orientation studies were under investigation. A curious group of pigeons that did not show the customary deflected vanishing bearings at the Castor Hill Fire Tower was the subject of another long-term study which involved not only an analysis of the past behavior of these birds at release sites other than Castor Hill but also the orientation patterns of their progeny.

The behavior of homing pigeons during two solar eclipses was also observed, at Valdosta, Georgia in 1970 and at release sites in Nova Scotia in 1972. In another series of tests, the orientation of Bank Swallows was compared to that of homing pigeons, and, in still other investigations, the orientation behavior of different strains of pigeons was observed. While the hundreds of field tests using free-flying pigeons were going on, techniques for conducting trials with non-flying birds were being evaluated in the hope of developing an appropriate method to study pigeon orientation under conditions offering researchers more control over important influencing variables. The two attempts that can be reported here are of pigeons that were walked in an outdoor circular arena and of pigeons that were released through a multi-choice circular cage.*

The breadth of subject matter found in the "Miscellaneous Tests" section serves as an introduction to the diversity and inclusiveness of Keeton's research on homing pigeons at Cornell University from 1967 to 1980. The insights gained from these inquiries have added another dimension to the general knowledge of avian navigation as it is currently understood; hopefully, these contributions may someday become what Bill Keeton had intended them to be, helpful stepping stones for others who find themselves as challanged as he was by the mysteries yet to be unravelled in the field of avian navigation.

*DATA OMITTED FROM THIS INDEX: Several other types of cages were also tried, but because the resulting data exist in formats other than the standard vanishing bearings that are the basis of this Index, these tests cannot be included in this compilation of Keeton's research. Some of the designs tested include a square cage made of wooden dowels; a circular aluminum cage with an optionally induced magnetic field and an activity registration system consisting of microswitches wired to wedge-shaped floor sections (see G. K. Watkins, Masters Thesis, 1969, University of Kentucky); a cross-shaped cage of wood offering four escape tunnels and the option of inducing a magnetic field around the exiting test birds (design by M. Kreithen). W. Edrich conducted trial runs using his hemispheric cage in which orienting behavior could be video-taped.

Also omitted are data from tests conducted by J. Rems (Masters Thesis, Cornell, 1973) who investigated the homing pigeon eye sign, a system used by many racing fanciers to evaluate the quality of their birds. The Rems data are not presented here because the treatment categories involved the pigmentation and morphology of the pigeon eye, characteristics that cannot be accurately defined without the use of colored illustrations.

Two other omitted studies were undertaken as undergraduate honors' projects. D. Finkelstein conducted an histological study of the pigeon cere. L. Scafuri pursued an investigation of the rolling and tumbling phenomena found in certain strains of pigeons; he explored the roles of genetics, vision, training and age involved in this behavior and documented tumbling in a time-lapse film.

In addition to the on-going research already cited, there are also a number of studies that were in a developmental stage in 1980 and for which there is no extant data. A mobile loft had been constructed which would allow the same group of pigeons to home to several different loft locations from a given release site; this endeavor included early trials to establish the best method of training pigeons for the mobile loft experiments, and a group of Danzig HiFliers, pigeons with a distinctive flying behavior, were purchased especially for this new undertaking. Designed by W. Edrich, there was also a set of mobile clock-shifting rooms that were wired for activity-monitoring and which could be used to reset the internal time-sense of pigeons while the birds were in locations other than their home loft. There were movable exercise cages of various shapes and sizes (see SE test series) for exercising birds that were being clock-shifted and in which other types of experimental birds could be temporarily housed away from the familiar environmental parameters surrounding their home lofts.

A portable field electrometer was being developed by M. Kreithen with the assistance of M. Trulahr, an undergraduate engineering student; this device, when used at test sites, could monitor changes in vertical DC potentials during releases of experimental birds.

M. Kreithen also developed a tilt chamber that could be used to investigate the interaction of locomotion, magnetic information and gravity within 45 minute or longer time constants.

There are cabinet drawers full of gravity, magnetic, geological, aeronautical and topographic maps, testimonials to the investigations, past and intended, of various environmental parameters of potential importance to the navigational abilities of pigeons. And, within the accumulation of data folders there are lists of homecoming days over the years, dates that had been singled out by the unusual number of simultaneously returning lost pigeons who, frequently after long absences and for inexplicable reasons, had chosen these particular days to come back to the Cornell lofts. There are field notes listing dates and times when erratic changes of behavior of flying pigeons were observed or when losses were unexpectedly high.

The lists of intriguing data and experimental designs could extend even further, but the samples already cited suffice to convey the comprehensiveness of avian orientation studies at Cornell University during the past decade.

MISCELLANEOUS TESTS

AB ALEXANDER TRAINING BIAS. The effects of directional training on initial orientation of pigeons was examined.

COM COMMON (FERAL) PIGEONS. The orientation of feral pigeons was compared to that of homing pigeons.

EK SOLAR ECLIPSE. Pigeons were flown during two solar eclipses.

GV GROUND VS. VEHICLE. The orientation of test pigeons being kept on the ground while waiting to be released was compared to that of pigeons waiting on top of a truck.

LE LEADERSHIP. The orientation of flocks of exclusively naive birds was compared to that of naive flocks with experienced leaders.

NB NO BIAS BIRDS. The orientation of birds that predictably exhibited a reduced deflection at the Castor Hill Fire Tower was examined at this site and at several other locations. The orientation of their progeny was also investigated.

NF NIGHT FLYING PIGEONS. The ability of pigeons to orient and fly home at night was studied. Some tests included the use of bar magnets.

NP NUTRITION PROJECT. The effect of a new diet formula on the flying performance of pigeons was evaluated.

NW NORTHWEST BIAS. The orientation of pigeons that had been trained on a northwest line was studied.

OC ORIENTATION CHECKS. These tests examined the orientation of special categories of pigeons: very young pigeons, pigeons that had not been flown for a long time, newly acquired strains of pigeons, pigeons that had previously responded to some orientation-altering manipulation, subsets of pigeons that were to be tested at new release sites, etc.

RT RADIO TRACKING. The technique of radio telemetry was compared to visual tracking of homing pigeons and was also used in conjunction with other studies of orientation.

SG SINGLE BIRDS VS. GROUPS OF FOUR. The orientation of single pigeons was compared to that of small flocks.

SOL SOCIAL LEADERSHIP TESTS. The importance of experienced leadership in conjunction with social interaction to the orientation and homing of young pigeons was studied. was studied.

SW BANK SWALLOWS. The orientation of Bank Swallows was compared to that of pigeons.

W WALKING PIGEONS. Observations were made of the orientation of pigeons whose wings were restrained.

WC CIRCULAR CAGE TESTS. The orientation of pigeons released through a circular cage was investigated.

ALEXANDER TRAINING BIAS

To determine if directional trailing has any effect on the initial orientation, 47 releases at 10 sites were done in 1967-69. See Alexander and Keeton (1972). This study also appears in a Master of Science Thesis by J. Alexander, 1970.

COMMON (FERAL) PIGEON

Eleven releases from 6 sites were conducted in 1974-75 to determine if the orientation and homing behavior of adult and young feral pigeons are comparable to that of similarly aged domesticated homing pigeons. In one series of tests, feral pigeons were clock-shifted, and another series of tests used young ferais that were raised and trained together with similarly aged Cornell homing pigeons. See Edrich and Keeton (1977).

ECLIPSE

Cornell pigeons and racing pigeons from several other lofts were flown in 25 releases before and during the solar eclipses of 1970 and 1972.

There are numerous reports of avian behavior during solar eclipses including those of unexpected evening vocalizations and roosting activity. Researchers in Poland also investigated eclipse effects on the homing of racing pigeons and concluded that the observed deficits in homing success were eclipse-related, possibly due to electro-magnetic emissions that may interfere with the homing ability of pigeons. See R.J. Wojtusiak, (1960).

Because of two anticipated eclipses in 1970 and 1972, racing fanciers in North America were inquiring about the possible effects on their race birds of these two solar events. Arrangements were made with racing pigeon owners to assist in conducting tests in the United States and Canada at locations where there would be maximal eclipse totality.

On March 6th, the day before the 1970 solar eclipse, seven flocks of experienced racing pigeons belonging to six lofts in the Valdosta, Georgia, area were flown from Lenox, a release site about 40 miles north of the loft locations. A test flock was comprised of two or three birds from each of the six participating lofts, and the flocks were released at regular intervals from 10:25 to 13:25 EST. All the birds homed successfully. They were tested again from the same site on the next day, (the day of the eclipse) when the same flock of birds was flown at roughly the same time of day as on the previous test. The sun was totally eclipsed at 13:18, and totality lasted for 2 minutes and 40 seconds. The homing success of the flocks released during and after totality differed from the previous day.

The 1972 EK tests were conducted at four locations in Nova Scotia, Canada, either within or close to the predicted band of maximum totality; there were also parallel releases from two sites in the Ithaca, NY, region where the magnitude of eclipsing was approximately 80%. Preparatory releases at all six sites took place on each of the four days preceding the July 10th eclipse. All birds in these preparatory flights, and also on the actual eclipse day, were flown at regular intervals beginning approximately two hours before the time of maximum totality and continuing until one hour after the period of totality. In the Ithaca area the release times were between 14:40 and 18:40 EDST. In Nova Scotia, the release times were 15:40, 16:10, 16:40, 17:10, 17:38, 18:10, and 18:30 ADST.

The flocks used in the parallel tests conducted in New York state consisted of experienced yearlings or yearlings and old birds, all from Cornell stock.. The flocks used in the Nova Scotia tests included mostly young race birds from local lofts, from Buffalo, NY, lofts and from Cornell; the imported birds were settled and trained by several cooperating fanciers living near the four test locations. In addition to the special afternoon pre-test training, the initial training in each locality consisted of flock tosses that race clubs normally give to young birds. Because there were considerable pre-test losses of the imported birds at some lofts, the flocks used in the tests were made up as follows: at Hilden, mostly Buffalo stock; at Alton and Salt Springs, mixed flocks of imports and local birds; at Englishtown, mostly local strains plus 2 suriving Cornell birds.

On July 10th in Nova Scotia, the sun was totally eclipsed at 17:38 ADST, and totality lasted for 2 minutes and 6 seconds.

There were no significant differences in homing success in any of the tests.

GROUND VERSUS VEHICLE

A series of 44 releases from 13 sites in 1977 and 1979 compared the orientation of test birds that, prior to being flown, were held on the ground to the orientation of test birds that were held on top of a vehicle.

Laboratory tests have demonstrated that pigeons can perceive such environmental variables as polarized and UV light, infrasound, and very small changes in atmospheric pressure. These, and possibly other still not understood environmental factors, may affect the orientation of pigeons by acting either as a source of navigational information or by somehow interfering with the avian navigational system. If information relevant to orientation is perceived or integrated by pigeons at the release site during the period of time that they are waiting to be flown, then release site procedures should be kept constant for all tests. For example, baskets of test pigeons that are held inside of a metal van until they are flown, could be exposed to a different E-M field than baskets of test birds that are held on the ground at the same release site.

Because of the unexplainable, reccurring variability in the orientation of Cornell pigeons at some sites, test methodologies were regularly monitored. The GV series was designed to study the possible effects on orientation of three methods of holding test birds at the site while they were waiting to be released. Upon arrival at the site, one basket of test birds was always placed on the ground, about 10 feet away from the vehicle. The second basket of birds was placed either on the metal cab of the pick-up truck or on the wooden observation platform above the truck bed. The groups remained in these locations until all birds were released. The tests were frequently done synchronously at two different release sites, and sites known for their unpredictable orientation were investigated.

The GV tests were conducted in the early part of the field season, before the groups of test pigeons had been fully trained (i.e. flock tosses in all directions up to 15 miles and at least 2 single tosses). The pre-test special training for the birds in most of the GV tests consisted of 2 to 5 short-distance flock tosses after an inactive overwintering. The only recent single-toss experience in the GV test year was the experience of a previous GV test, and as differences between treatments seem to decrease at some sites after 5 or 6 single flights of increasing distances, new sets of pigeons were used in succeeding tests of that year.

LEADERSHIP

Exploratory tests in 1968, 1970, and 1974 examined the effects of different sizes of pigeon flocks on their homing ability, compared the orientation of flocks comprised of different ratios of clock-shifted and control birds, and in 1974, compared the orientation of naive flocks to similar flocks that were released with an experienced leader.

Although dominance relationships and social groupings are important in many aspects of the social behavior of birds, these attributes may not be correlated with the orientation abilities of pigeons. The SG series described in the Miscellaneous Tests Section demonstrated that the homing accuracy of homogenous flocks was comparable to that of single birds of the same age and experience. (See the SG series and Keeton, 1970).

In a 1968 collaborative (with S.T. Emlen) LE test from Appalachin, the effect of different sizes of flocks on homing success was examined. Because no vanishing bearings were taken, this test is not recorded in the Keeton Database. The original data sheet from a second test of this series in 1968, conducted at Fleming, NY, is not available at the time of this writing and is also omitted from the Database.

In the single 1970 LE test presented here, 5 flocks were released from Locke II. Each flock was comprised of four pigeons; in some flocks there were three control birds and one clock-shifted bird while in other flocks the treatment numbers were reversed.

Two release sites were used in 1974 for the two LE tests in which the orientation and homing of flocks of inexperienced pigeons was compared to that of inexperienced flocks which included an older, experienced leader that was familiar to the release site. In the four weeks prior to testing, the young inexperienced birds had been given 10 flock tosses from distances no further than 5 miles from the home loft. The leaders were birds that had been released regularly either of the test sites throughout the 1974 test season.

NO BIAS

Between 1973 and 1980, an unusual group of Cornell pigeons was flown in 41 releases from 10 sites in the Castor Hill region, an area known for its predictable clockwise orientation bias. The NB birds, however, repeatedly exhibited a greatly reduced bias from all sites in this region. In another 77 releases, they were also tested at 19 other sites.

An early series of 25 tests at the Castor Hill Fire Tower using Cornell pigeons as well as pigeons from five other lofts clearly demonstrated that pigeons flown from this site exhibit a pronounced clockwise bias in their departure directions suggesting that some important map factor was rotated for pigeons from Ithaca as well as from other geographical points. (see Keeton, 1973). But in 1973 one subset of young birds, first flown from the Castor Hill Fire Tower as part of a larger group, gave vanishing bearings that were closer to the home direction than would be expected for young birds that were new to the site. Further tests confirmed the unique orientation behavior of this group not only at the fire tower site, but from 9 other locations in the Castor Hill area as well. Clock-shifting, flying with magnet bars attached, or a summer-long regimen of rigorous directional training did not alter this groups' persistent reduced orientation deflection in the Castor Hill area.

The discovery of this unusual orientation behavior prompted a study of the geneologies and previous flying experiences of the No Bias (FO) birds, but no conclusive explanation of the development of this orientation preference was derived from these investigations. The original NB birds were raised and trained in 1973 using standard Cornell procedures; as young birds, some (those banded in the 6300 series) were used in clock-shift tests while others (the 6400 series) were west-trained and flown several times from the Campbell release site. The latter were also tested, as young birds, at the Jersey Hill Fire Tower.

In 1979, surviving offspring (FA and H1) of the original No Bias birds were identified. Veterans of various tests and living in several different lofts, these experienced yearlings and old birds were given the usual preparatory north training together with a group of similarly aged and experienced birds that were selected from the general loft population to be their controls. The orientation of these two groups was compared to the orientation of the NB birds in two tests at the Castor Hill Fire Tower.

A selective breeding program was attempted in 1980 in order to produce another generation of progeny (FB) from the original No Bias birds, and these young offspring were also tested at the fire tower. However, because of uncontrollable circumstances, some of the FB birds did not have the identical parentage of their 1979 predessors. (The progeny tests and breeding attempts were projects suggested and conducted by Scott Smith, loft manager 1978-1981).

NIGHT FLYING

In 1969, 1971-72, and 1974, fifty-two releases from 9 sites examined the ability of pigeons to orient and to home at night. Bar magnets were attached to the birds in some tests. See L. Goodloe, Doctoral Thesis, (1974) for all tests except those conducted in 1974.* (Also see Keeton, 1974a, p. 68 for a review of nocturnal homing.)

Although homing pigeons are normally diurnal, a number of researchers, the Army Signal Corps, and some race clubs have demonstrated that pigeons can be trained to fly at night. The orientation and navigation mechanisms used by night-flying pigeons in the absence of the sun and daytime landmarks are not clearly understood. If the sun compass is not an essential element in the navigation process, does this mean that the map is capable in itself of providing sufficient information for true navigation?

In the NF series, Cornell pigeons were flown from distances of 20, 30, and 50 miles; radio telemetry was used to ascertain the initial departure directions and to track the initial portion of the homeward flight pattern.

Preliminary training of the flocks of experienced birds was begun at twilight, and successive training flights were repeated at later times each evening until all birds were homing in total darkness. On nights of inclement weather, the night birds would often spontaneously exercise around the loft area. The high attrition rate resulting from both the preliminary group training and the early single flights of night tests progressively decreased sample sizes, and because of these losses, it became necessary to use the same individuals more than once in the continuation bar magent tests at some sites. In such cases, the birds were alternated between the two test treatments; if a bird wore a brass bar on the first night, a bar magnet was attached to it on the second release from the same site, and vice versa. Tests were conducted from sites which had established histories of diurnal orientation behavior.

The night-flyers were kept in a semi-darkened pen and had continual free access to an open, south-facing aviary. The birds lived on an extended-light regimen in order to accommodate the late, post-flight feedings. While a 100-watt bulb was used inside the pen, two 150-watt floodlights illuminated the landing board on the outside of the night loft.

*The Goodloe thesis cites 10 NF releases in 1970 including those conducted from Kellogg Fire Tower, a release site 53 miles south of Cornell. These releases are not included in the Index because the original data sheets are not available.

NUTRITION PROJECT

Five releases at different sites in 1975 compared the flying performance of homing pigeons raised on the regular feed ration to that of birds raised on a new feed formulation. This was an Independent Undergraduate Research Project conducted by L. Hunter, 1975.

Because of rising feed costs, a less expensive pigeon diet was formulated for the Cornell Lofts by Milton Scott, Professor Emeritus, Cornell Poultry Science Department. Before adopting the new feed ration, its effects on the homing performance of test birds was investigated.

One hundred siblings were evenly divided between control and experimental treatments. With the single exception of food rations, the groups were treated identically from the time they were weaned until the final test in this series. The controls remained on the standard 16% protein diet while the the experimentals were fed the new 13% + 2% added fat formula. After routine training the orientation, homing performance, weight loss and weight recovery of the two groups were compared. Additional long-distance flock tosses (not reported here) were also used to measure the performance of the two groups, and in 1976, the effects of the two diets on reproductive peformance of breeding pigeons were also evaluated by B. Dehm as an Independent Undergraduate Research Project. See Brown, 1983.

NORTHWEST BIAS

Twelve releases from 8 sites in 1972 examined the effects of repeated training from the direction of the preferred bias normally seen in the initial orientation patterns of Cornell homing pigeons.

There is general agreement among investigators who have worked with pigeons that homing success improves with experience. However, there is some disagreement on whether there is a similar improvement in initial bearings, or whether previous training flights affect the deflections from home direction that are normally found at most releasesites. (See Keeton, 1974a, p. 103).

When flown from most sites in the Ithaca, NY, region, pigeons reared in the Cornell lofts exhibit predictable deviations from home direction in their initial orientation. At release sites that are east of a hypothetical NNW-SSE line running through the Cornell lofts, the vanishing bearings of Cornell pigeons are deflected clockwise from the true home direction; when released from sites that are west of this line, Cornell pigeons exhibit a counter-clockwise deflection. See D.M. Windsor (1975).

In the NW series, flocks of Cornell pigeons were given intensive flying experience along a predetermined a training line to the northwest of the loft. Tests were then conducted from 5 release sites along this training line and at 3 other sites: Weedsport, Marathon and the Castor Hill Fire Tower, a site at which pigeons from several home locations normally exhibit an exaggerated northwesterly bias.

ORIENTATION CHECKS

From 1971 through 1980 there were 49 tests* at 17 sites of certain groups of pigeons whose orientation was being examined before they were used in subsequent tests.

The accuracy of the initial orientation of homing pigeons not only varies from site to site, but it can also be affected by other factors including long periods of inactivity, previous experimental manipulations, special training procedures, or possibly by genetic backgrounds (see the NB series) and loft locations of the birds (see Keeton, 1974a, p. 101). As any of these factors have the potential of inadvertently influencing test results, the orientation of any suspect groups of Cornell pigeons was first evaluated before such birds were included in test treatments.

The OC Tests cited in this section include the orientation behavior of pigeons that had been raised in the magnetic-shift loft or as No Sun birds and that had been living under normal conditions for some time after the original tests were concluded; gift pigeons from another area that were settled at Cornell and trained here; and some visual bearings of unmanipulated pigeons that had been released through the Kreithen cage.

* Without a substantial effort, it was not possible to include numerous other OC tests that, at compilation time, were not readily identifiable as orientation checks.

SINGLE TOSS VS GROUPS OF FOUR

In 1967 and 1968, a series of 15 releases from 8 sites, compared the orientation of singly flown trained birds of trained pigeons flown in groups of four. See Keeton, (1970a).

The SG series tested the assumption that vanishing bearings of flocks are more accurate than those of single birds. This assumption suggests a correlation of dominance relationships with orientation ability. For related tests see the LE and SOL series.

In 1971 D. Windsor released first-flight birds singly and in flocks of ten on two consecutive days from Langmuir Lab. A few days later, on July 26th, he re-tested these birds at Langmuir, examining the effect of the preliminary single versus flock experience on their orientation as second-flights.

SOCIAL LEADERSHIP

In 1977 there were fourteen releases from six sites that examined the roles of experience and social interaction in the development of leadership qualities relevant to homing pigeon orientation. This series was initiated by N.J. Demong and included some tests in which birds were clock-shifted. For related tests see the LE and SG series.

** As this series will be continued at Cornell, the use of any SOL data is restricted until further notice. Inquiries about the data presented here should be directed to S.T.Emlen, Cornell University.**

Experienced yearlings were divided into two groups designated as social leaders and non-social leaders. The social leaders lived in the same pen with young, inexperienced experimental birds while the non-social leaders lived as part of a yearling flock in an adjacent loft building. As preparatory training, the combined groups of leaders were given several 10 to 15 mile flock tosses and were also single tossed from the test site. Additionally, the social leaders were also flown with their young, inexperienced pen-mates whose pre-test training was kept limited to a series of short-distance flock tosses within 3 miles of the loft.

In the tests at Venice Center and Orwell, there were three treatments of pigeons: homogenous flocks of the specially trained young birds (F); flocks of specially trained young birds with one social leader (F2); and flocks of specially trained young birds with one non-social leader (F3) .

After this first series of releases, both groups of leaders were used in a number of clock-shift tests. A control and a shifted leader were flown in pairs comprised of either two birds from the same pen (S) or birds from the two different pens (D). If the birds vanished together, the pair was given a single bearing, either (S) or (D). If the pair separated while flying, individual departure directions were recorded for each member of the pair and a notation was made as to their original pairing, ie. CD marked a bearing of a single control bird that had separated from its clock-shifted test partner which was housed in a different pen.

Some of the birds returning from the clock-shift tests were put back into the clock-shifting rooms and re-tested the following day; for the results of these tests see the RR test series.

SWALLOWS

In 1969 and 1970 there were 14 collaborative releases of Bank Swallows from 9 sites. Swallows from five colonies were used. Locations of the colonies are given elsewhere in this Index. Gee Downhower and Windsor, (1971).

The orientation of Bank Swallows was compared to that of homing pigeons in 8 of the 1970 tests at sites that included the Jersey Hill and Castor Hill Fire Tower areas. See Keeton (1973) and Keeton (1974a).

NON-FLYING PIGEONS

Although almost all of the Keeton orientation data presented in this Index were derived from free-flying homing pigeons, there were also results from several techniques which attempted to elicit valid and quantifiable orientation behavior from non-flying birds. The capability of investigating orientatioral behavior in a cage or in a small arena could not only enhance control over potential orientation cues, but also, in some cases, enable more birds to be tested in a shorter period of time thus reducing some of the temporal variâtiabi1ity to which regular flying tests are subject. See Keeton (1974a) p. 115.

Although techniques other than those described below were also used, they are not discussed here because the resulting data are not available in the format used in this Index.

ORIENTATION OF WALKERS

The 127 tests of walking pigeons were conducted in 1968-1974 and 1976-79 at 23 sites including the Castor Hill and Jersey Hill Fire Towers. There were also walking cross-releases using pigeons from three other lofts and several tests of clock-shifted birds.

The wings of experienced pigeons were restrained by small leather harnesses that were attached to the test birds either at the home loft or at the release site. A single pigeon was then placed in the center of a 50 ft. circle (in tests before 1972) or a 25 ft. circle in tests after 1972. The circular arenas were set up on flat terrain, preferrably recently mowed grassy areas, in secluded locations that minimized interruptions by curious bystanders as well as visual and accoustical artifacts. As walking pigeons appear to be particularly influenced by the wind, most tests from 1970 onwards were conducted either at sunrise or just before sunset, both times when the winds are calm and the motivation level of pigeons is naturally high.

By reading one of the 36 marked stakes around circumference of the test circle, a vanishing bearing was taken wenever a bird walked from the release cage in the center of the arena to the outer edge of the circle. Test birds were given 5 minute trials in the larger circles, and 3 minute trials when smaller circles were used. Observers, who were sitting 10 to 15 feet away behind burlap or natural blinds, changed their positions several times during a test.

In some cases, a walking pigeon was allowed to fly home after a trial, and a visual bearing was taken In the usual manner.

CIRCULAR CAGE

Twenty-one tests at 6 sites in 1968 investigated the orientation behavior of homing pigeons released from a circular cage. Eight escape exits were evenly spaced around the upper portion of the vertical walls of a circular cage made of hardware cloth. The 2.5 foot high cage was approximately five feet in diameter, and during testing was placed atop a wooden framework, raising its floor elevation to five feet above ground level. Each escape exit was furnished with a wooden perch at the base of its interior-facing framework; the wooden perches were wired to an Esteriine recorder, and microswitches on the perches registered the pre-escape activity of test birds which were placed individually into the cage via an opening in the solid wooden floor. Regular pigeon loft bobs were hung on the outside of the escape exits.

TEST & TREATMENT CODES

Alexander Bias

- A Birds released at successive clockwise sites.
- B Birds released at successive counter-clockwise sites.
- C Controls.
- E East-trained birds.
- N North-trained birds.
- S South-trained birds.
- W West-trained birds.

Alternating current coils

- C controls wearing inactive coils.
- E birds wearing live coils.

Alpha-pinene

- A A-pinene applied at the site.
- A1 A birds transported to the site with both nostrils plugged.
- AH Substance applied at the home loft.
- C Controls: wattles smeared with vaseline.
- C1 C birds transported to the site with both nostrils plugged.
- C2 Birds transported to the site with plugged nostrils. No vaseline was applied before release.
- CH Vaseline applied at the home loft.

Aviary resets

- AR reset with standard exposure.
- C control without aviary exposure.
- FC control exposed in a field aviary near the main loft.
- FR reset exposed in a field aviary near the main loft.
- HR reset exposed in an aviary attached to its home pen.
- R reset without aviary exposure.

Cochlea surgery

- C sham operated birds.
- CB C birds wearing brass bars.
- E Decochleated birds.
- EB E birds wearing brass bars.
- EM E birds wearing magnet bars.
- ME Birds with Middle ear surgery only.

Commons

- C Controls: regular Cornell stock.
- F Ferals.
- FM Ferals from Mecklenburg.
- FW Ferals from Weedsport.
- FI Ferals from Interlaken.
- FR Reset ferals.
- FC Control ferals from CS test. Clock-shift
- C controls from shifting room on normal time.
- CB a CS control wearing a brass bar.
- CM a CS control wearing a M bar. (see MB)
- R resets.
- RB a CS reset wearing a brass bar.
- RM a CS reset wearing a M bar.
- RV Visual bearings from radio-tracked resets.
- RT Final radio-track bearings of resets.

Clock-shift normalization

- C control from shifting room on normal time.
- R normal reset.
- F a reset which had homed once since the start of normalization.

Outward journey detour

- AB transported in an aluminum box with bottled air.
- B transporetd in closed boxes, breathing bottled air.
- C controls transported by the direct route in open baskets.
- E transported along an east detour.
- EN birds with no Papi training, transported along an east detour.
- EP birds with Papi training, transported along an east detour.
- F transported in closed container with fresh air pumped in.
- l transported in an iron box.
- N transported along a north detour.
- S transported along south detour.
- O birds in openbaskets.
- W transported along a west detour.
- WF transported in a wooden box, with fresh air pumped in.
- WN birds with no Papi training, transported along a west detour.
- WP birds with Papi training, transported along a west detour.

Deflector lofts

- A clockwise standard loft.
- A1 standard loft with clockwise deflector panels.
- B counterclockwise standard loft.
- B1 standard loft with counterclockwise deflector panels.
- C controls.
- D clockwise loft with altered wings.
- E counterclockwise loft with altered wings.
- AC ONS controls from the A loft.
- AE ONS experimentals from the A loft.
- BC ONS controls from the B loft.

BE ONS experimentals from the B loft.

Edrich cage
- C controls.
- C1 controls exercised in E-W cages.
- C2 controls exercised in N-S cages.
- C4
- R standard resets.
- R1 resets exercised in E-W cages.
- R2 resets exercised in N-S cages.

Ear plugs
- B birds wearing brass bars.
- C controls.
- M birds wearing Magnet bars.
- E birds with plugged ears.
- EB E birds wearing brass bars.
- EM E birds wearing Magnet bars.

Equinox
- C birds with normal view of the sky.
- E birds incarcerated in clock rooms during the equinox.

Faraday Cage
- C transport outside of cage.
- OE transport in open baskets outside of cage by an east route.
- OW transport in open baskets outside of cage by an west route.
- T transport in cage.
- TE transport in cage by an east detour
- TS a T bird which remained in the cage at the site until release.
- TW transport in cage by a west detour.

Ground vs. vehicle
- G ground release.
- V top of vehicle release.

Inertial wheel
- C controls.
- CB controls wearing brass bars.
- CU C birds wearing magnet bars with unknown orientation.
- E experiMentals.
- EU E birds wearing magnet bars with unknown orientation.

K
- C normal birds.
- F0 k birds from the NB F0 generation.
- K birds used exclusively at one site.
- KB K birds wearing brass bars.
- KC controls from a K bird CS test.
- KE K birds transported along an east detour.
- KM K birds wearing magnet bars alternated between N-fwd and S-fwd.
- KN K birds with north training.
- KR Resets from a K bird CS test.
- KS K birds with south training.
- KU K birds wearing magnet bars with unknown orientation.
- KW K birds transported along a west detour.

Leadership
- F a flock of peers.
- L a flock with a leader.

Contact lens
- C birds not wearing lenses.
- K clear lenses.
- F frosted lenses.
- FC CS controls wearing frosted lenses.
- FR CS resets wearing frosted lenses.
- FB Birds wearing brass bars and frosted lenses.
- FM Birds wearing N-fwd Magnet bars and frosted lenses.

Magnet-brass
- B controls with brass bars.
- M magnet bars aligned with the north seeking pole forward, applied at the site.
- S South forward.
- CB a CS control wearing a brass bar.
- CM a CS control wearing a magnet bar.
- RB a CS reset wearing a brass bar.
- RM a CS reset wearing a magnet bar.
- HB birds with magnets applied at home but replaced by brass bars at the release site.
- H magnet bars applied at the home loft.
- U magnet with unknown alignment.

Magnetic coil outward journey
- C birds transported normally.
- L birds put in coil with unknow amperage two hours after arrival at the site.
- L1 L birds in 1 amp field.
- L2 L birds in 2 amp field.

- S birds put in coil with unknown amperage immediately after arrival at the site.
- S1 S birds put in 1 amp field.
- S2 S birds put in 2 amp field.
- T transported in field with unknown amperage.
- T1 T birds in 1 amp field.
- T2 T birds in 2 amp field.
- Z Birds transported in coil with unknown amperage and left in the field until the moment of release.
- Z1 Z birds in a 1 amp field.
- Z2 Z birds in a 2 amp field.

Magnets: N-fwd vs. S-fwd

- C controls: no bar.
- B brass bar.
- M N-fwd applied at site.
- S S-fwd applied at site.

Magnet shift loft

- C controls: raised in a normal loft.
- M experimentals.
- R no documentation.

Magnets on at the site vs. on at home

- B brass.
- M N-fwd magnet on at the site.
- H N-fwd magnet on at home.

No bias

- F0 birds with bands 63-6400
- FA offspring of two F0 birds.
- FB 1980 offspring with one F0 parent.
- H1 1979 offspring with one F0 parent.

Night fliers

- C birds without transmitters.
- T final bearings from radio tracked birds.
- TB T birds wearing brass bars.
- TM T birds wearing N-fwd magnet bars.
- TU T birds wearing magnet bars with unknown alignment.

Nutrition

- C controls fed on standard diet.
- E experimentals.

Normalized returned resets

- C controls.
- 1 former straight resets which had been deflected >= 90 degrees.
- 2 former straight resets which had been deflected <= 90 degrees.
- 3 former aviary resets which had been deflected 90 degrees.

No sun: Keeton

- C controls: normal sun exposure.
- CR shifted C birds.
- N No sun exposure.
- NC N birds which were clock-shift controls.
- NR shifted N birds.

No sun: Waldvogel

- 5, 7, 10, 15, 20: these birds first saw the sun at N weeks of age.
- AC 1978 no sun experimentals as CS controls.
- AR 1978 no sun experimentals as CS resets.
- BC 1979 no sun experimentals as CS controls
- BR 1979 no sun experimentals as CS resets.
- C CS controls, from DEF loft.
- DC 1978 no sun controls as CS controls.
- DR 1978 no sun controls as CS resets.
- EC 1979 no sun controls as CS controls.
- ER 1979 no sun controls as CS resets.
- NC no sun controls as CS resets.

No sun: Wiltschko

- C control: normal sun exposure.
- B a former N bird wearing a brass bar.
- CR a shifted C bird.
- M a former N bird wearing a N-fwd magnet bar.
- N no sun exposure.
- NB N bird wearing a brass bar.
- NM N bird wearing a N-fwd magnet bar.
- NR Shifted N bird.

Northwests training bias.

- C controls: all direction training.
- 1 experienced old birds.
- 2 yearlings with only first flight experience from 20 miles east before training.
- 3 yearlings with no experience before training, or only first flight experience from 40 miles north.

Olfactory nerve section

- AC controls from the A deflector loft.
- AE experimentals from the A deflector loft.
- BC controls from the B deflector loft.
- BE experimentals froM the 8 deflector loft.
- C unoperated bird.
- C1 sham operation without membrane rupture.

C2 sham operation with membrane rupture.
C3 sham operation with unknown technique.
CU unilateral surgery, normal nostril open.
E bilateral surgery.
EU unilateral surgery, normal nostril plugged.

Permanent bar: Keeton
B1 habituated brass, flown with brass.
B2 habituated brass, flown with no bar.
M1 habituated N-fwd magnet, flown with magnet.
M2 habituated magnet, flown with brass.
U1 habituated to magnet with unknown alignment, flown with magnet.
U2 habituated to magnet with unknown alignment, flown with brass.

Permanet bars: Slack
B brass bars.
M N-fwd magnet bars put on at the site.
HA abituated magnet, flown with magnet.
HB magnet for the outward Journey, flown with brass.
HD habituated magnet, flown with brass.

Permanet bars: Weiler
B brass bars.
C control.
HC habituated brass, flown with brass.
HS habituated magnet, flown with magnet.
RM CS reset, habituated magnet.
M N-fwd magnet
XM habituated magnet, flown with brass.

Plugged nostrils
C controls: no plugs.
PL experimentals: plugged nostrils.
AB outward journey in aluminum box with pumped-in bottle air.

Psuedo permanent shift: Edrich
C controls.
CE C trained on an E-W line.
CN C trained on a N-S line.
N normalized P birds.
P permanent shift.
PE P birds trained on an E-W line.
PN P birds trained on a N-S line.

Psuedo permanent shift: Wiltschko
C controls: no permanent shift.
N normalized P bird.
P permanent shift: 6 hours slow.
R reset C birds.

Permanent shift with exercise
C control.
EN normalized P birds, with training during period of overlap between shift and normal days.
P permanent shift: 6 hours slow.

Permanent shift: Keeton
C controls.
CB birds wearing brass.
N normalized P birds.
NB N bird wearing brass.
NM N bird wearing N-fwd magnet.
NR N birds shifted back to their original rhythm.
P perManent shift.

Permanent shift normalized
C controls.
CB controls wearing brass bars.
CM controls earing N-fwd magnets.
N permanent shift.
NB N birds wearing brass bars.
NM N birds wearing N-fwd magnet bars.

Permanent shift: Wiltschko
C controls: no perManent shift.
CR C birds, reset 6 hours slow.
N normalized P birds.
NR N birds, reset back to their original rhythm.
P permanent shift 6 hours slow.
R normal reset.

Quine: olive oil and turpentine
C controls: normal birds from the Main loft.
CO C birds, olive oil applied at the site.
CP C birds transported to the site in a closed container.
CT C birds, turpentine applied at the site.
CV C birds, vaseline applied at the site.
OO olive oil on odd band experimentals.
DE olive oil on even band experimentals
TO turpentine on odd band experimentals.
TE turpentine on even band experimentals.

Random activity
D birds in room with dim light.
L birds in room with bright light.
LU L birds wearing magnet bars with unknown orientation.

Returned resets

- C control.
- R normal reset.
- RR returned R whose deflection in the CS test was not noted.
- RB RR wearing brass bar.
- RM RR wearing magnet bar.
- 1 returned R whose CS deflection was = 90 degrees.
- 2 returned R whose CS deflection was = 90 degrees.
- 3 returned aviary reset whose AR deflection was = 90 degrees.
- 4 returned aviary reset whose AR deflection was = 90 degrees.
- 5 returned aviary reset whose AR deflection was = 90 degrees.

Radio track

- T final radio bearing.
- V final visual bearing from a T bird.

Sacculus

- C controls.
- E experimentals.

Shift and excercise

- C standard CS control.
- CB C with brass bar.
- CM C with magnet bar.
- B normal bird with brass bar.
- R standard CS reset.
- E resets exercised in free flight at the loft.
- Ex resets exercised for x days.
- RB R with brass bar.
- EB E with brass bar.
- EM E with magnet bar.

Singles vs. group

- C single.
- GT flock.

Social leadership

- C control.
- CD pair of controls from different pens.
- CS pair of controls from the same pen.
- D pair from different pens.
- F flock of similar birds.
- F2 flock with social leader.
- F3 flock with non-social leader from another pen.
- RS pair of resets from the same pen.
- RD pair of resets from different pens.
- S pair from the same pen.

Swallows

- C normal pigeon.
- S swallow.
- SM male swallow.
- SF female swallow.

Transported in closed container

- A transported in aluminum box.
- AF transported in aluminum box with pumped-in fresh air.
- B pumped-in bottle air.
- C control: transport in open basket.
- F pumped-in fresh air.
- I transported in iron box.
- IF transported in iron box with pumped-in fresh air.
- W transported in wooden box.
- WB transported in wooden box with pumped-in bottle air.

Olfactory tubes

- 1L tube in left nostril only.
- 1R tube in right nostril only.
- C control: no tube.
- E experimental: tubes in both nostrils.

VW tests

- C controls.
- VW birds transported in VW.

Walkers

- W walking pigeons.
- W1 walking hens.
- W2 walking cocks.
- CW W, CS control.
- RW W, reset.
- BW W wearing a brass bar.
- UW W wearing a magnet bar of unknown orientation.
- V visual bearing from W released afetr walking.

Windsor directional preference

- C control.
- GT group toss.
- K, KB, KU see K tests.
- T final radio-track bearing.
- V visual bearing from T.

West trained

- WT west-trained.

Xylocaine nasal spray

C	controls: no spray.
NX	sprayed: no xylocaine in spray.
X	sprayed with xylocaine.