treatment was initiated. Six animals were treated with four melatonin implants inserted consecutively at weekly intervals while five were given beeswax implants. Molting from the dorsal surface, growth of brown hair, and testicular enlargement ceased 20 to 30 days after treatment was begun. Molting from the ventral surface, growth of new white hair, and testicular regression was evident 10 to 20 days later. Molting ceased and the testes became completely regressed 60 to 70 days after treatment. The hair on the dorsal surface was not shed in most animals, so that the weasels were white with brown patches on the back. Controls molted, grew a new brown pelage, and developed enlarged testes.

Pituitary autografts were made under the kidney capsule in three brown and four white weasels (group 3) in November. Hair growth was initiated by plucking on the day the autografts were made. Melatonin treatment was started 14 to 20 days after surgery when new brown hair appeared in the plucked area. Five implants were inserted at consecutive weekly intervals, and hair was plucked after each implant was made.

Animals molted after the pituitary autografts were made. Some additional shedding was noted in these animals after the melatonin treatment was initiated, but in all cases the hair that grew after molting or plucking was brown (Table 1).

Melatonin appeared to have an inhibitory effect on the initiation of hair growth in some weasels in groups 2 and 3. The time between the implants and the appearance of hair ranged from 24 to 51 days in some treated animals, whereas the tips of new hairs could be seen in all control and most treated weasels 14 to 20 days after plucking.

Melatonin inhibited the effect of the long-day photoperiod and induced the fall molt, growth of the white pelage, and testicular regression in weasels in group 1. Melatonin also stopped and reversed the effects of increased day length in the weasels in group 2, as indicated by molting, growth of white rather than brown hair, and a decrease in the size of the testes.

The inhibition of hair pigmentation observed in intact weasels treated with melatonin indicates that the pineal gland is involved in the seasonal control of hair color. The central nervous system exhibits an inhibitory influence over the production and secretion of

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MSH in the weasel (3). Since weasels with pituitary autografts grew brown hair when treated with melatonin, it is probable that melatonin does not act directly on the pituitary gland to inhibit MSH secretion.

The MSH-release-inhibiting factor has been demonstrated in the rat and other animals (5, 6); it decreases the content of MSH in the plasma and elevates that in the pituitary (15). On the basis of our data and those cited, we postulate that melatonin acts on the hypothalamus causing the release of this inhibitor in the weasel.

The inhibitory effects of melatonin on reproduction in the rat have been documented (16, 17). The regression of the testes observed in intact weasels treated with melatonin suggests that the pineal gland may also be involved in the regulation of seasonal reproductive changes in addition to pelage cycles.

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- 24 April 1969; revised 26 June 1969

## **Orientation by Pigeons: Is the Sun Necessary?**

Abstract. Although most recent hypotheses of pigeon homing have assigned an essential role to the sun, there has been some evidence suggesting that the sun is not essential. Two series of releases were designed to examine the question more carefully. Birds whose internal clocks had been shifted 6 hours were used in the critical tests. Under sun, the vanishing bearings of the clock-shifted birds were deflected in the direction predicted by a hypothesis of use of the sun as a simple compass. By contrast, under total overcast the bearings of both the clockshifted and the control birds were homeward oriented and there was no difference between them, even at a release site the birds could never have seen previously. Therefore it is concluded that the sun is used as a compass when it is available. but that the pigeon navigation system contains sufficient redundancy to make accurate orientation possible in the absence of both the sun and familiar landmarks; the orientational cues used under such conditions do not require time compensation. This conclusion is in complete disagreement with the Matthews sun-arc hypothesis of pigeon navigation, and it makes necessary a major reformulation (at the very least) of the other principal hypothesis, that of Kramer.

For roughly the last 20 years, there has been much emphasis on the sun in research on pigeon homing. In a series of papers, Kramer and his colleagues (1) showed that both wild migrant birds and pigeons can use the sun as a compass to choose a direction in a circular cage. Matthews (2, 3) went further, erecting a hypothesis of complete navigation by the sun. He suggested that a pigeon displaced from home could determine its latitudinal displacement by extrapolating the sun's arc at the release point to its highest (noon) position and comparing its altitude with the remembered noon altitude of the sun at home. According to Matthews, the bird could determine its longitudinal displacement by, in effect, comparing sun time at the release point with home time, as indicated by the bird's internal sense of time, or "internal clock." With information about both its latitudinal and its longitudinal displacement, the bird could then determine the direction it must fly to get home. Although the results of many investigators have appeared to support the idea that pigeons



Fig. 1. Release under total overcast at Fleming, 17 May 1968. Home bearing, 164°; mean bearing, 156°; wind from 270°, strong (25). (In this figure and in all later figures, the home bearing is indicated by a dashed arrow, the mean bearing by a solid arrow, labeled M, and true north by a thin line at the top of the circle. Each symbol on the periphery of the large circle indicates the bearing of one bird.)

are indeed capable of true navigation, both theoretical considerations (4, 5)and experimental evidence have failed to support Matthews' hypothesis or other sun-navigation hypotheses, for example, Pennycuick (6), and they have not gained wide acceptance.

Perhaps the most damaging evidence against Matthews has come from experiments in which the vanishing bearings of clock-shifted pigeons released at a site distant from home are compared with the vanishing bearings of control birds (that is, ones whose internal clock is on normal home time). Schmidt-Koenig (7, 8) and Graue (9) have shown that shifts of pigeons' internal clocks result in deflections of the birds' vanishing bearings in a manner consistent with their use of the sun as a simple compass but not consistent with Matthews' hypothesis of bicoordinate navigation by the sun. These results have appeared to support the proposal of Kramer (10) that orientation is a two-stage process, involving a "map" step in which the geographic position of the release site and the "theoretical" homing direction are determined, followed by a "compass" step in which the deduced homing direction is ascertained in the field. The clockshift experiments have been interpreted as indicating that the second step depends upon a sun compass, a compass that requires time compensation at an average rate of 15° per hour because of the sun's changing position during the day.

Reports by several workers (3, 4, 29 AUGUST 1969

11) that pigeons cannot orient well under total overcast have seemed to support this conclusion. However, the map component of Kramer's map-andcompass hypothesis has never been clearly defined, nor have the environmental cues and sensory modalities on which it might depend been elucidated.

During the last 2 years, my colleagues and I have conducted several hundred series of releases of pigeons from the Cornell lofts at Ithaca, New York. More or less by chance, some of these releases have been made under total overcast, from distances of 20 to 100 miles (32 to 160 km), and from points north, east, and south of Ithaca. The vanishing bearings from these overcast releases have been consistently nonrandom and homeward oriented. differing little from those of releases under sun at the same locations. In view of these results, we were not convinced that the sun is an essential component of the navigation of pigeons. Consequently, we carried out a series of experiments designed to test more rigorously the importance of the sun in pigeon orientation.

The birds used in these tests were of the Morris Gordon, Whitney Huyskins-Van Riel, and Nemechek Trenton strains. All birds used in any one series of releases were of similar age, were housed together in the same pen, fed the same grain mixture at the same time of day, and exercised together. They were routinely given exercise flights at the loft on overcast or rainy days and were also given occasional short training flights under such conditions; thus the birds became accustomed to flying in inclement weather.

Birds were carried to the release sites in closed vehicles, and usually in individual, closed, basket compartments. They were tossed individually from the hand, the directions in which they were pointed at the toss being randomized. Whenever control (C) and clock-shifted (S) birds were being compared, individuals from the C group were randomly paired with S individuals, and the tosses followed the sequence C,S,C,S, and so forth; thus differences in exposure of the two treatments to changes in the weather or to other temporally varying parameters were minimized.

Each bird was observed with  $10 \times 50$  binoculars until it vanished from sight, and a compass bearing for the vanishing point was recorded to the nearest 5°. The interval between toss and vanish was timed with a stop watch.



Fig. 2. Preparatory release 6 June 1968, under sun at Marathon, 20.8 miles. Home bearing,  $269^{\circ}$ ; mean bearing,  $287^{\circ}$ ; wind from  $300^{\circ}$ , strong.

An associate at the loft recorded the time of arrival for each bird, so that homing speeds could be calculated (based on elapsed time between vanishing from the release site and arrival at the loft).

Six-hour clock shifts were effected by holding each group of birds for at least 5 days in a wire cage [6 by 6 by 6 feet (1.8 by 1.8 by 1.8 m)] in a wellventilated, light-tight room, with lights regulated by an automatic timer. The light period was of the length appropriate to the date. The cages and rooms used for control and clock-shift groups were identical, except that the lights for the controls were turned on and off in synchrony with exterior conditions, whereas those for shifted groups were turned on and off 6 hours earlier or later.



Fig. 3. Clock-shift (6 hours slow) tests under sun from Marathon, 20.8 miles. Home bearing, 269°; wind 21 June, from 310°, light to moderate; wind 22 June, from 260°, strong.  $\bigcirc$ , Control cocks, 21 June (mean 280°); O, clock-shifted cocks, 21 June (mean 349°);  $\bigtriangleup$ , clock-shifted hens, 22 June (mean 267°);  $\bigstar$ , clock-shifted hens, 22 June (mean 19°). Mean bearing of combined controls (*MC* arrow), 274°; combined clock-shifted birds (*MS* arrow), 3°.

The circular mean for each group of vanishing bearings was calculated by vector analysis, following the procedure outlined by Batschelet (12). Bearings were tested for randomness by the V test (13). This may also be considered a test of whether the bearings are at least roughly oriented in some predicted direction; for the releases described in this report, the predicted bearing for normal, control, and clock-shifted birds under overcast was the home direction, and that for clockshifted birds under sun was 90° to the right or left of home, depending on the direction of the clock shift (14). In releases where both control and clockshifted birds were used, the two sets of bearings were compared by means of a distribution-free, two-sample test on a circle proposed by Wheeler and Watson (15). The vanishing intervals of control and clock-shifted birds were compared by means of the Wilcoxon matched-pairs, signed-ranks test (16); in only one case (A versus B birds at Marathon) was the difference significant. The same comparison was made of homing speeds whenever the number of returns warranted it.

For the first series of releases, in June and July 1968, a flock of birds hatched in the late summer of 1967 was used (17). These birds had been trained up to 30 miles. One of their releases had been under total overcast from Fleming, New York, 30.4 miles north of the loft (Fig. 1). The birds had vanished nonrandomly in the homeward direction (P = .002), and all birds had returned home on the day of release [mean speed, 27 miles/hour (43 km/hour)].

After the birds had raised one clutch of youngsters, the sexes were separated in order to minimize differences that might result from individuals being in different stages of the reproductive cycle. The past flight records of all the birds were analyzed, and those with experience only from the north or south were designated group A; those with some experience also from east or west were designated group B.

The test releases in this series were conducted from Marathon, New York, 20.8 miles east of the loft. The birds of group A were first given a series of flock releases from 10 miles east. The birds of group B were given a series of flock releases from Marathon, followed by three single-toss preparatory releases (3, 5, and 6 June) under sun, which established a base line for the normal behavior at this locality. In each of the three single-toss releases, the vanishing bearings (Fig. 2) were nonrandom homeward (P < .001). The three means differed among themselves by less than 2°.

Then the cocks were randomly divided



Figs. 4 to 6. Clock-shift (6 hours fast) tests from Marathon, 20.8 miles. Home bearing, 269°. Open symbols, controls; solid symbols, shifted birds. Fig. 4. Release, 11 July 1968; total overcast; no wind. Mean bearing of controls, 291° of clock-shifted birds, 276°. Fig. 5. Releases, 17 July (circles) and 5 August 1968 (triangles); sun; wind 17 July, from south-southeast at start, shifting to northnorthwest by end of release, very light; wind 5 August, from 190°, light. Mean bearing of combined controls, 277° (17 July, 276°; 5 August, 278°); of combined clock-shifted birds, 202° (17 July, 152° August,  $234^{\circ}$ ). Fig. 6. Release, 24 July 1968; total overcast; wind from 140° light. Mean bearing of controls, 280°; of clock-shifted birds, 277°.

into two groups, one to be clock-shifted 6 hours slow (counterclockwise) and the other to serve as controls; the hens were treated in a similar manner. After shifting, the cocks were released on 21 June, and the test was replicated with the hens on 22 June; both releases were under sunny conditions. The vanishing bearings of the controls in both releases were nonrandom and oriented westward, toward home (cocks, P = .001; hens, P < .001), deviating from the home direction by less than 10°. In both releases, the mean bearing of the shifted birds was northward (shifted clockwise from home) as predicted (cocks, P = .016; hens, P =.027; combined, P = .002), the mean of the combined cocks and hens deviating from the mean of the combined controls by approximately 89° (Fig. 3). In both releases, the difference between the bearings of the control and clockshifted birds was significant (cocks, P =.043; hens, P = .017).

The differences in vanishing intervals (Table 1) between control and shifted birds were not significant; similarly, differences between the vanishing intervals for these releases and the vanishing intervals for the same birds in the 6 June preparatory release were not significant for either control or shifted birds, thus indicating that confinement in the light-control rooms had not measurably affected this behavioral parameter. In both the cock release and the hen release, there was a striking difference between control and shifted birds in homing success; all but one of the 12 control cocks and all 11 control hens returned the day of release, whereas only five of 12 shifted cocks and none of 11 shifted hens returned the same day, and two of the five cocks arrived with control birds that may have led them.

When the combined results of the 21 and 22 June releases were analyzed in terms of the previous experience of the birds (that is, group A, which had never previously been released at Marathon, and group B, which had had many previous releases at this site), it was clear that clock-shifting had deflected the bearings of both groups. The bearings of the clock-shifted group A birds were nonrandom and oriented northward (P = .024), their mean being  $102^{\circ}$ clockwise from the mean of the A controls. The bearings of the shifted group B birds were nonrandom northward (P = .016), their mean being 68° clockwise from the mean of the B controls. In both cases, the difference between

the bearings of the control and clockshifted birds was significant (group A, P = .003; group B, P < .001). It is not clear whether the difference in the magnitude of the deflections in the two releases is significant, but it does seem evident that extensive previous experience at this site, with all the attendant opportunity for learning landmarks, had not prevented clock-shifting and the resulting erroneous interpretation of solar information from sending the birds in an incorrect direction. Surprisingly, the less experienced group A control birds had significantly shorter vanishing intervals (P = .01) and faster homing speeds (P = .05) than the more experienced group B controls. No such differences were apparent in a comparison of A and B clock-shifted birds.

The birds that returned from the 21 and 22 June releases, plus some additional birds from the same original flock, were again segregated by sex and each sex divided into two groups, one to be clock-shifted 6 hours fast (clockwise) and the other to serve as controls. After shifting, the cocks were released under total overcast and light rain on 11 July (Fig. 4). Both the control birds and the shifted birds vanished nonrandomly in the homeward direction (control, P = .001; shifted, P < .001); the difference between the bearings of the two groups was not significant. It was clear that the bearings of the birds with shifted internal clocks were not deflected southward. That there was no difference in the behavior of control and shifted birds was further indicated by the fact that 11 of 11 control birds and eight of ten shifted birds returned the same day, with comparable speeds.

The day after they returned to the loft, the birds used in the 11 July release were again put in the light-control rooms and held until 17 July, when they were again released at Marathon, in the same order as on 11 July, but this time under sun. The results were dramatically different from those of 11 July. The controls vanished nonran-

Figs. 7 to 9. Preliminary tests under sun from Petersberg, 102 miles. Home bearing, 263°. Fig. 7. Release, 17 October 1968; wind from southwest, moderate. Mean bearing, 303°. Fig. 8. Release, 20 October 1968; wind from west, very light. Mean bearing, 293°. Fig. 9. Release, 31 October 1968; wind from west-northwest, moderate but with intermittent strong gusts. Controls (open circles) not significantly different from random; mean bearing of clock-shifted (6 hours fast) birds (solid circles), 200°. domly toward home (P < .001) (Fig. 5), and the shifted birds vanished nonrandomly southward (P = .023) as predicted; the difference between the bearings of the control and clock-shifted birds was significant (P < .001). Furthermore, ten of ten controls returned home in less than an hour, whereas only two of ten shifted birds returned the same day and one of those took more than 5 hours.

Taken together, the 11 July and 17 July releases seemed to indicate that when the sun is not visible both clock-



shifted and normal birds can orient accurately toward home, whereas under sunny conditions the same shifted birds give vanishing bearings deflected in a predictable direction. That these results are repeatable was demonstrated by a replication of the tests, this time with the hens. The birds were released on 24 July under total overcast and steady light rain. Once again, both the control and the shifted birds vanished nonrandomly homeward (P < .001 for each). The mean bearings of the two groups differed from each other by less than 3°, and each differed from the home direction by less than 11° (Fig. 6). Unexpectedly, the controls did have better homing success (nine of ten birds back the same day) than the shifted birds (three of ten); this difference may have resulted from a short period of sun that developed near the loft while the birds were en route.

As with the cocks, the hens of the 24 July release were returned to the lightcontrol rooms the next day after they arrived home and were held there until 5 August, when they were again released at Marathon, in the same order as on 24 July, but this time under sun. Again, with the same birds, the results under sun differed markedly from those obtained under overcast. The controls vanished nonrandomly toward home (P < .001) (Fig. 5), and the shifted birds vanished nonrandomly southward (P = .027) as predicted; the difference between the bearings of the control and clock-shifted birds was significant (P = .002), although the deflection of the mean of the shifted birds from that of the controls was not as great as in the 17 July release.

The releases described above demonstrated that when the sun is visible, pigeons use it as one component of their guidance system, but that when it is not visible they can orient toward home by means of cues that do not require use of their internal clock. What might those other cues be? The most obvious possibility for the Marathon releases was that, in the absence of the sun, the birds relied on familiar landmarks, since the release site was only 20.8 miles from home and all birds had been there previously. To test this possibility, a second series of releases was performed from the Petersberg Fire Tower, near Warnerville, New York, 102 miles east of the loft.

Except for the first release, the birds used were unmated youngsters, 6 to 7 months old. The birds had been given only short-distance training, consisting

Table 1. Data from releases.

	Release	Number of birds*	Mean bearing (deg)	P (V test)	Mean vanis'ing interval (minutes)	Birds home same day	Mean speed of day birds (miles/hour)	Birds home later
Provine			First	series (home	269°)		······	
3	June	20	286	< 0.001	7.5	20	25.3	
5	June	21	287	< .001	4.4	21	30.9	
6	June	19	287	< .001	3.5	19	28.3	
21	June (control)	12	280	.001	3.2	11	29.6	
21	June (shifted)	12 (11)	349	.016	4.0	5	15.4	2
22	June (control)	11	267	< .001	4.1	11	19.7	
22	June (shifted)	11 (9)	19	.027	2.9	0		5
11	July (control)	11	291	.001	4.7	11	19.0	
11	July (shifted)	10	276	< .001	4.0	8	18.8	1
17	July (control)	10	276	< .001	2.5	. 10	31.2	
17	July (shifted)	10	152	.023	2.6	2		5
24	July (control)	10	280	< .001	5.7	9	16.1	1
24	July (shifted)	10 (9)	277	< .001	5.0	3		7
5	August (control)	11	278	.001	4.0	11	35.2	
5	August (shifted)	10 (9)	234	.027	3.4	5	28.3	3
			Second	series (home	e 263°)			
17	October	17	303	< 0.001	2.6	14	24.0	2
20	October	10 (8)	294	.007	4.4	5	25.7	0
31	October (control)	7	260	.089	2.8	1		4
31	October (shifted)	9	200	.007	3.6	0		6
3	November (control)	12 (10)	301	.024	4.3	0		4
3	November (shifted)	13 (11)	280	.008	4.5	0		7
29	November	11 (9)	286	.013	5.0	0		6

<sup>\*</sup> For any release in which bearings were not obtained for all birds (because the bird landed, or was lost before the binoculars could be focused on it, and so forth), the number of birds for which bearings were obtained is shown in parentheses.

of a series of 1- to 4-mile flights from all directions, followed by single 30mile flights from the north and south, and single 20-mile flights from the east and west. Our records indicated that on these flights most of the birds had not been out of our sight long enough to have had an opportunity to be in the vicinity of Petersberg Tower. No bird was used in more than one test in this series.

In order to determine, as a basis for later comparisons, what behavior could be expected from experienced birds at this release site, a first release was performed under sun on 17 October with birds that had had many releases in all directions from the loft but that had not previously been released at Petersberg. The birds vanished (Fig. 7) non-randomly homeward (P < .001).

Ten of the relatively inexperienced birds were given a test flight under sun from Petersberg on 20 October. Two birds were chased by hawks and no reliable vanishing bearings could be obtained for them. The vanishing bearings of the other eight (Fig. 8) were nonrandom and oriented homeward (P = .007), the mean bearing differing from that of the experienced birds of the 17 October release by only approximately 9°.

On 31 October, a third release was

performed under sun with two groups of the relatively inexperienced birds, one a control group and the other clock-shifted 6 hours fast (clockwise). Unfortunately, unavoidable delays during the drive to the release site made it impossible to release all the birds, and the sample sizes were consequently small, bearings being obtained for only seven control and nine shifted birds. Six of the seven controls vanished in the homeward half of the circle (Fig. 9). Nevertheless, the bearings were not statistically different from random (P = .089). The shifted birds vanished nonrandomly southward (P = .007) as predicted. This test was not conclusive. since the control bearings did not provide a reliable basis for comparison with the bearings of the shifted birds. However, the bearings of the shifted birds, when compared with those of the normal birds used in the 17 and 20 October releases (Figs. 7 and 8), were consistent with the expectation that under sun at Petersberg relatively inexperienced birds clock-shifted 6 hours fast would vanish southward.

With the results of the three sun releases of 17, 20, and 31 October providing a basis for comparisons, two releases were performed with relatively inexperienced birds at Petersberg under total overcast. The first such release

was conducted on 3 November, using two groups of birds, one a control group and the other shifted 6 hours fast (clockwise). As in the releases under overcast at Marathon, the vanishing bearings (Fig. 10) of both groups were nonrandom homeward (control, P =.024; shifted, P = .008; combined, P =.001). There was no evidence that the shifted birds had been deflected by their treatment, thus assuring us that the sun had indeed not been visible to the birds. Yet despite the fact that the sun was not visible and that familiar landmarks were not available, the mean bearings obtained on this release (controls, 301°; shifted, 280°; combined, 290°) were remarkably similar to those obtained on the 17 and 20 October sun releases (303° and 294°, respectively).

In an attempt to replicate the Petersberg overcast release, two more groups of the relatively inexperienced birds were put in the light-control rooms. However, the group to be clock-shifted became sick, and when the release was conducted on 29 November, only the group intended as controls could be used. We thus had no direct proof that on this day the birds could not detect the sun's position, although there seems no reason to doubt that this was the case since the day was very dark and a light rain was falling; if anything, the overcast was heavier than on the releases of 11 July, 17 July, and 3 November, when the lack of deflection of shifted birds' bearings had demonstrated that the birds were not using the sun compass. A total of 11 birds were used in this release, but bearings were obtained for only nine (Fig. 11). These were nonrandom homeward (P = .013). The mean vanishing bearing (286°) was very close to those obtained in the previous releases.

Our tests confirm the findings of Schmidt-Koenig (7, 8) that when clock-shifted birds are released under sun their bearings are deflected in a predictable direction from the bearings of control birds. It follows that the sun must be used, when available, as one source of information in the pigeon orientation system.

Our results, like those of Schmidt-Koenig, are consistent with the conclusion that the sun is used as a simple compass, not as the basis for a bicoordinate navigation system as proposed by Matthews (2, 3). In our releases of 21 and 22 June, the Matthews hypothesis would have predicted that the birds with their internal clocks 6 hours slow would orient westward (18); but our birds actually vanished northward, as predicted by the Kramer map-andcompass hypothesis (10). Similarly, in our releases of 17 July and 5 August, the Matthews hypothesis would have predicted that the clock-shifted (6 hours fast) birds would orient eastward, but they actually went southward as predicted by the map-and-compass hypothesis.

Matthews (19) has recently attempted to discount the similar results of Schmidt-Koenig's clock-shift experiments on the basis of the confusing way the data were presented and the large deviations from the true homeward direction of the mean vanishing bearings of Schmidt-Koenig's control birds. The disagreement between the results reported here and the predictions of the Matthews hypothesis do not seem subject to either of these criticisms. Matthews has also objected that most of Schmidt-Koenig's releases were either at distances so short (5 to 14 miles) that orientation would be by landmarks, or at intermediate distances (19 to 43 miles) where, according to the "distance effect" reported by Schmidt-Koenig (20) and by Wallraff (21), orientation toward home would be poor. Although none of the releases reported here were in the inner "landmark zone," Marathon is in the intermediate so-called "disorientation zone." However, as will be reported in a separate paper, we have conducted hundreds of releases at many distances from all four cardinal directions in an effort to detect a "distance effect," and can find none. The good orientation shown at Marathon is consistent with the good orientation we routinely see at similar distances in other directions. At any rate, Petersberg is far enough away from our loft to be in the "zone of navigation," and hence our results there are not subject to Matthews' obiection.

Our results at Marathon are in agreement with those of Graue (9) that clock-shifted pigeons released under sun give deflected vanishing bearings even at release sites where they have been many times previously. It appears, therefore, that sun information, when available, takes precedence over use of landmarks, if indeed landmarks are used at all by pigeons at distances as great as 20 miles.

Although our results indicate that the sun plays an important role in pigeon navigation, they also demonstrate that the navigation system contains

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sufficient redundancy so that the sun is not essential for homeward orientation, even at unfamiliar locations. The fact that there was no difference in the orientation of control and clock-shifted birds under total overcast indicates further that whatever guidance system is being used under such conditions does not involve the birds' internal clocks, and hence must not require any time compensation.

We have found that the mean vanishing bearings for releases of our birds at a given release site are usually remarkably consistent and usually close to the true home direction, but seldom directly homeward. This is true even of releases in which birds of different ages and training are used, and even if the releases are made at different times of day or in different years. For example, mean bearings at Marathon are usually between 5° and 20° north of the true home direction (Fig. 2), and mean bearings at Fleming are usually slightly east of the home direction (Fig. 1); there is no obvious relation





between these biases and local topographic features. Such release site-specific biases have been reported by other investigators (8, 22). The important point here is that the same biases are exhibited by birds under overcast and under sun (compare Figs. 4 and 6 with Fig. 2, and compare Figs. 10 and 11 with Figs. 7 and 8), which suggests that the same fundamental guidance system is being used in both cases. Perhaps the normal role of the sun is simply as some sort of check mechanism.

Whatever the role of the sun, the Kramer map-and-compass hypothesis now must be radically amended because, if the sun compass component is not essential for navigation, it follows that what Kramer has called the map component must provide more than the "theoretical" home direction—it must be capable of providing, on its own, sufficient information for true navigation.

Since our second series of releases, at Petersberg, rules out familiar landmarks as the cues upon which pigeons depend in the absence of the sun, we may consider some other possibilities. One would be that in this region wind from a particular direction might often be associated with heavy overcast and the birds might have learned this; however, no such clear association between wind direction and overcast seems to hold. For example, in the two overcast releases at Petersberg, the wind direction differed by approximately 70°, yet the mean bearings of the two releases differed by only 3°.

It has sometimes been suggested (23) that pigeons may be better able than man to detect the position of the moon or planets during the day, and to use these as sources of navigational information. Our tests make this appear very unlikely. We have repeatedly found that the birds' ability to localize the sun is not appreciably better or worse than our own. For example, on one partially overcast day, when the sun was visible at some times and not at others, we released a series of clockshifted birds and found that we could accurately predict what the birds would do, depending on whether we ourselves could determine the sun's location; if we could locate the sun, a clock-shifted bird released at that time would give a deflected vanishing bearing, whereas if we could not locate the sun, a clockshifted bird would head toward home. It would seem reasonable to suppose that if a bird is no more able to locate the sun than we are, then it should be no more able to locate the moon or planets. At any rate, our birds released under heavy overcast surely could not see the moon or planets, yet they were able to orient.

Matthews (19, 24) has recently put great stress on so-called "nonsense" directional tendencies (that is, the tendency of some birds always to fly in a particular compass direction, which may bear no relation to the true home direction) and has criticized some results of Kramer, Schmidt-Koenig, and others of their group on the basis of an apparent northward bias of their pigeons. The good orientation we have obtained in overcast releases from the north and south (most not described in this report; but see Fig. 1) preclude interpreting the westward orientation obtained in the releases from the east as a manifestation of such "nonsense" orientation. That the ability to orient toward home under heavy overcast is not restricted to some one strain of pigeons is demonstrated by the similar performance of three unrelated and physically unlike strains of Cornell birds.

In view of the obvious preference for using the sun when it is available, we might expect to observe some evidence of confusion when birds are released under overcast. One measure of this might be the vanishing interval. However, there is no consistent difference in this parameter between birds released under overcast and birds released under sun (Table 1). Another measure would be the extent of scatter of the vanishing bearings, and there may indeed be slightly more scatter under overcast than is exhibited by normal or control birds under sun. However, clock-shifted birds, which usually exhibit much more scatter under sun than control birds do, may actually show less scatter under overcast. If anything, then, it appears that overcast is less confusing to birds than is clock-shifting. The increased scatter of clock-shifted birds, which Schmidt-Koenig (7, 8) also found, may indicate that individual birds respond differently to a conflict between the information provided by their fundamental guidance system and that provided by the check mechanism of the sun compass.

It may well be asked at this point why others have so regularly reported that their pigeons are disoriented under overcast (3, 11). One contributing factor may well have been the motivational state of their birds. Pigeons seldom voluntarily fly for long under adverse weather conditions, and if they have not regularly been forced to exercise under such conditions they may perform poorly when released at a distant point when the weather is bad. It is well known among pigeon fanciers that the birds often perform poorly when handled in an unfamiliar way or released under circumstances to which they are not accustomed.

We need not turn exclusively to explanations such as these for the results of others, because those results are not in as much disagreement with ours as might be supposed from reading Matthews' 1968 book (19). When claims are made that pigeons are disoriented under overcast, one of the principal references cited is the classic 1953 paper by Matthews (3) in which he argued strongly for sun navigation. In this paper. Matthews presented the results of five releases under overcast (his tests 4, 13, 20, 21, and 26) and claimed that the bearings were random. I subjected his data to the Rayleigh test for randomness on a circle (12), and found that only two of these (tests 20 and 21) were actually random; one (test was nonrandom at the .05 level, 26) and two (tests 4 and 13) were nonrandom at the .01 level. Furthermore, in all three nonrandom releases the bearings were clustered in the homeward half of the circle. In most cases, Matthews compared the results of his overcast releases with those of sun releases made in different years or at different localities, or both, an unsatisfactory procedure in view of the many variables with which orientation studies must contend under even the best of circumstances. However, if we examine, as an example, his comparison of overcast test 13 (conducted in 1950) with sun test 3 (1949), we find the bearings under overcast considerably more scattered but with the mean differing from that under sun by only approximately 17°. In short, Matthews' data do not conflict with our finding that pigeons can orient without using the sun.

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- 18. According to Matthews, the birds would determine, by measuring the highest point on the sun's arc and comparing that remembered value for the home with the location. that they were not appreciably north or south of home. The releases were conducted conducted in the afternoon, and, according to Matthews, the birds could detect that fact by observing the sun's position in arc; but the shifted birds' internal clocks would erroneously tell them that it was morning at home, hence they would determine the release site to be would determine the release site to be thousands of miles east of the loft, and they should therefore fly toward the west. contrast, according to Kramer, the birds' ternal clocks would say it was morning, when the sun should be in the southeast, hence west should be more than  $90^{\circ}$  and less than  $180^{\circ}$ clockwise from the sun (the exact angle varying with time); but since it was actually afternoon, and the sun was in the southwest, the birds' choice of such a large angle clock-
- the birds' choice of such a large angle clock-wise from the sun sent them north.
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- 25. wind speeds in this paper are as follows: wind speeds in this paper are as follows: very light, 3 miles/hour or less; light, 4 to 5 miles/hour; moderate, 6 to 10 miles/hour; strong, 11 to 16 miles/hour; very strong, more than 16 miles/hour.
- Andre Gobert, Lorraine Pakkala, Irene Brown, and Donald Windsor helped carry out 26 the releases reported here, and I am very grateful to them. Thanks are also due to grateful to them. Thanks are also due to Stephen T. Emlen and Thomas Eisner for critically reading the manuscript 26 May 1969

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