

Are Navigational Errors by Homing Pigeons Near Jersey Hill/Cornell, New York, Due to Misleading Olfactory Information?

The hypothesis that homing pigeons, *Columba livia*, derive positional (map) information from olfactory cues has received more support from European than North American research (e.g. Papi et al. 1978; Waldvogel 1989). In most cases, olfactory deprivation has had only minor effects upon homing by pigeons raised at the Cornell University loft in Ithaca, New York, suggesting that olfaction is not essential to their navigation (e.g. Keeton et al. 1977; Madden, unpublished data). But, it is possible that olfaction is important under special circumstances.

Our experiments explore the possibility that misleading olfactory information might underlie the serious navigational difficulties faced by Cornell pigeons when they are released in or near Jersey Hill State Park, 109 km west of their home loft (see Keeton 1974). When first released in this Jersey Hill region, pigeons from the Cornell loft tend to orient randomly or in the opposite direction from home (Keeton 1971; Moore, unpublished data), and many fail to return to the loft.

Our first experiment used a false release site design in which pigeons initially are transported to one site (the false release site), then deprived of further olfactory input and transported to a second site (the true release site) for testing. European researchers report that pigeons treated in this way orient as if at the false site, their most recent source of olfactory information (e.g. Benvenuti & Wallraff 1985; Kiepenheuer 1985). To the best of our knowledge, this design has not been used in North American research. But if misleading olfactory cues underlie the navigational difficulties at Jersey Hill, then exposure to a false release site in that region should disrupt subsequent orientation from another (true) release site.

In 1986–1988, 193 young pigeons (6–12 months of age) from the Cornell loft were trained to return from 32 km north, south, east and west of the loft, then tested once each. In the experiment, birds were transported in open canvas baskets in two similar trucks to a staging point midway between two false release sites. One truck then continued westward to Jersey Hill while the other went eastward to Newfield, 18 km west-southwest of the loft. Birds were exposed to local air at these false release sites for 2 h, then placed in chambers ventilated with odourless (bottled, manufactured) air for transport to the true release site near Campbell, New York, from which the home loft was 70 km east-northeast (71.6°). Half of the birds from each false release site were made temporarily anosmic 5–20 min

before release by spraying their internal nares with 1% aqueous tetracaine. The remaining birds were untreated and remained in the bottled air chambers until release. All assignments to treatments were random. The birds were released individually and watched through 10×40 binoculars until they vanished. All tests were conducted under sunny skies.

Although Cornell pigeons released for the first time at Newfield and Jersey Hill typically give very different mean vanishing bearings (long northeast vectors for Newfield, short southwest vectors for Jersey Hill; Moore, unpublished data), no analogous difference between birds exposed to Newfield and Jersey Hill as false sites was apparent in our data. There also was no apparent effect of tetracaine; instead all groups showed significant homeward orientation (*V*-tests, $P < 0.0001$; see Table I). Mean homing speeds were also similar across groups, but homing success did show an effect of false site: the incidence of homing failure (not home by day 3) was over twice as high for birds exposed to Jersey Hill as for those exposed to Newfield ($\chi^2 = 10.24$, $df = 1$, $P < 0.01$).

This experiment provided only partial support for the hypothesis that Cornell pigeons are misled by olfactory cues in the Jersey Hill region. Although initial orientation was not disrupted by exposure to Jersey Hill, pigeons were less successful in returning home from Campbell after exposure to Jersey Hill than after exposure to Newfield.

If misleading olfactory information from the Jersey Hill region produced this difference in homing success, perhaps elimination of olfactory input would allow pigeons to navigate successfully from that region. Our second experiment tested this hypothesis.

Thirty-nine young pigeons (6–12 months of age) and 25 yearlings from the Cornell loft were trained to return from 32 km north, south, east and west of home, and then randomly assigned to olfactory-deprived or untreated groups. Two to seven days before release, a solution of zinc sulphate and local anaesthetic (4% ZnSO₄, 1% tetracaine) was sprayed into the internal nares of birds in olfactory-deprived groups. This procedure eliminates the conditioned cardiac responses of pigeons to *n*-amyl acetate at about 0.5% air saturation for at least 10 days (Madden, unpublished data), and thus ensured olfactory deprivation during the outward journey, and for several days after release.

Test releases were conducted at Arkport, 101 km west of the loft (home = 90°). Arkport is 8 km east of Jersey Hill, which could not be used because the fire tower needed for observation had been dismantled. Arkport is well within the region in which Ithaca pigeons have navigational problems.

Table I. Results of false release site experiment

False site*	Treatment*	Birds released (bearings)	Mean bearings	Mean vector (r) length	Mean homeward component	Mean homing speed (km/h)†‡	Returns by day 3‡	Later or lost‡
1986 releases								
J	T	16 (15)	21.5	0.537	0.344	24.2	11	5
	U	14 (13)	45.0	0.857	0.766	31.8	9	4
N	T	15 (13)	41.7	0.874	0.758	30.0	13	1
	U	13 (13)	25.8	0.745	0.519	24.0	12	1
1987 releases								
J	T	19 (16)	57.2	0.664	0.643	42.9	13	4
	U	19 (13)	33.6	0.875	0.690	39.3	14	4
N	T	19 (16)	28.3	0.946	0.689	30.4	16	3
	U	19 (14)	40.5	0.910	0.779	37.2	17	1
1988 releases								
J	T	15 (10)	51.0	0.646	0.605	22.0	8	7
	U	15 (11)	61.9	0.620	0.611	24.0	6	9
N	T	15 (12)	71.9	0.851	0.851	19.3	10	5
	U	15 (9)	34.3	0.668	0.531	21.9	12	3
3 years combined								
J	T	50 (41)	44.3	0.590	0.524	28.6	32	16
	U	48 (37)	44.3	0.778	0.691	32.1	29	17
N	T	49 (41)	44.7	0.856	0.763	27.1	39	9
	U	47 (36)	34.2	0.785	0.624	27.5	41	5
Pooled across treatments								
J		98 (78)	44.3	0.679	0.603	30.2	61	33
N		96 (77)	40.0	0.819	0.698	27.2	80	14
	T	99 (82)	44.5	0.723	0.644	27.8	71	25
	U	95 (73)	39.3	0.778	0.658	29.2	70	22

*J: Jersey Hill; N: Newfield; T: tetracaine; U: untreated.

†Includes only birds that returned home on day of release.

‡Excludes birds that arrived home together.

Releases were conducted on clear days in 1988 and 1989.

Olfactory deprivation failed to improve orientation in either the young birds (untreated birds: mean vanishing bearing = 211° , $r = 0.432$, $N = 8$; olfactory-deprived birds: mean vanishing bearing = 186° , $r = 0.377$, $N = 11$), or the yearlings (untreated birds: mean vanishing bearing = 34° , $r = 0.385$, $N = 12$; olfactory deprived birds: mean vanishing bearing = 319° , $r = 0.196$, $N = 12$). None of these groups displayed significantly non-random orientation according to the Rayleigh test ($P_s > 0.1$), as is common in the Jersey Hill region.

Olfactory deprivation also did not affect homing success (return by day 3) of young birds (11 out of

20 untreated birds, 6 out of 19 olfactory-deprived birds) or yearlings (2 out of 13 untreated birds, 2 out of 12 olfactory-deprived birds). Poor homing success is typical of Cornell-loft pigeons released in the Jersey Hill region.

Together, the results of these experiments provide scant support for the hypothesis that misleading olfactory information underlies the navigational difficulties displayed by Cornell pigeons when released near Jersey Hill. Although the significant effect of false release site upon homing success in our first experiment suggested that some navigational information was derived at or en route to Jersey Hill and/or Newfield, the specific hypothesis that olfactory cues near Jersey Hill are misleading

was not supported by the results of the second experiment. Thus, we may need to look to other sensory systems for the primary source of pigeons' navigational difficulties in this region.

The procedures used in these experiments were approved by the Institutional Animal Care and Use Committee. We thank Charles Walcott and Irene Brown for use of the Cornell facilities and for their helpful comments. This research was supported by NSERC grants (M.L.S. OGP0038861; B.R.M. OGP0008345) and by NSF grants to Cornell University (BNS 85-13839; C. Walcott, principal investigator).

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The Effect of Wing Orientation on Aposematic Signalling in the Pipevine Swallowtail Butterfly, *Battus philenor*

Recently, there has been renewed discussion on the evolution of aposematism (e.g. Guilford 1988). In the classic view, flamboyant coloration of unpalatable prey reinforces predator learning (Darwin 1874). Harvey et al. (1982) presented a model for the evolution of aposematic individuals from cryptic stock that assumes reduced learning time with the conspicuous morph relative to the ancestral form. Specifically, the number of conspicuous prey attacked (V_a) should be fewer than the cryptic prey taken (V_c); i.e. $V_a/V_c < 1$. Previous tests of the 'learning reinforcement' hypothesis have generally compared predator reactions to prey items with different coloration (e.g. Gittleman et al. 1980). In this study, we report differential predator response to intra-individual signal variation in an unpalatable prey species.

Many butterflies and moths exhibit a striking dissimilarity in dorsal and ventral wing surface coloration (see plates in Opler & Krizek 1984 for examples). If conspicuous coloration enhances learning, then visually orienting predators should require relatively fewer trials with distasteful butterflies whose most conspicuous wing surface is exposed. The *Aristolochia*-feeding pipevine swallowtail butterfly, *Battus philenor*, is highly unpalatable to birds (Brower 1958b; Codella & Lederhouse 1989). The darkly hued adults bear a bold orange and blue pattern on the ventral hindwings; in contrast, the dorsal hindwings possess a uniform blue-green iridescence (plates in Opler & Krizek 1984). Avian predators learn to avoid *B. philenor*, which is the model for an extensive Batesian mimicry complex (Brower 1958b; Codella & Lederhouse 1989) and references therein).

Previously frozen, thawed *B. philenor* and yellow-morph *Papilio glaucus*, a palatable control, were presented to isolated predators (six blue jays, *Cyanocitta cristata*) that had been deprived of food overnight. All jays underwent a conditioning period prior to experimentation and readily attacked butterfly prey (see Codella & Lederhouse 1989 for details of outdoor aviary design and of jay history and care). The order of presentation followed Brower's (1958a) format: for each experimental-control pair, butterflies were offered individually and in random sequence. Jay responses within a 2-min period were scored as (1) attack or (2) reject. Subsequent to the first rejected *B. philenor*, a final control specimen was presented. Thereafter, in contrast to Brower's (1958a) design, we offered a sequence of *B. philenor* specimens only and concluded testing when two additional, con-