NATURAL AND INDUCED REMANENT MAGNETISM IN BIRDS

Holly H. Edwards,[1] Gary D. Schnell,[1,2] Robert L. DuBois,[3]
and Victor H. Hutchison[1]

[1]Department of Zoology,
[2]Oklahoma Biological Survey, and
[3]Department of Geology and Geophysics, University of Oklahoma,
Norman, Oklahoma 73019, USA

Abstract.—We measured values for natural remanent magnetization (NRM) and isothermal-induced remanent magnetization (IRM) in the head and neck for relatively large samples of eight bird species, and smaller samples of 13 additional species. Significant differences were found in mean NRM values among species; values ranged from 3.090 × 10⁻¹² T (tesla) for the Carolina Wren (*Thryothorus ludovicianus*) to 38.069 × 10⁻¹² T for the Northern Bobwhite (*Colinus virginianus*). Mean IRM values ranged from 337.6 × 10⁻¹² T in Chimney Swifts (*Chaetura pelagica*) to 1,889.1 × 10⁻¹² T in European Starlings (*Sturnus vulgaris*), with intraspecific variation being notably high. For two European Starlings and a Common Grackle (*Quiscalus quiscula*), about three-fourths of the IRM was located in the head and one-fourth in the neck; heads of two Northern Bobwhites contained an even greater proportion of the IRM. In general, the direction of the ferromagnetic material varied substantially among individuals within species. No significant differences were found in mean-vector directions among species. Linear regressions of NRM and IRM values on the logs of mean body mass indicate that the intensity of magnetism is related to species size. Insectivores, which also were the smallest species, had lower NRM and IRM values than found for omnivores sampled. Characteristic demagnetization-remagnetization curves suggest that most of the magnetic materials are interacting single-domain or pseudosingle-domain grains of magnetite. Three species may contain some superparamagnetic material. No differences were found between migratory and nonmigratory species with respect to the amount of remanent magnetism, or the extent of intraspecific variability in orientation direction of NRM. *Received 24 May 1990, accepted 23 September 1991.*

Experimental evidence has documented remarkable navigational capabilities in birds (Keeton 1974, Emlen 1975). The ability of wild birds to return to their home territories after displacement of distances up to several thousand kilometers serves as a illustration of the effectiveness of avian navigation (Griffin 1944, Matthews 1953, Mewaldt 1964, Keeton 1974).

Sensory information from a variety of sources is available to birds and may be used for navigation and orientation (Semm and Beason 1990b). Several types of visual cues are used by birds to aid in their orientation and movements. In an early set of experiments, Kramer (1952) manipulated the perceived direction of the sun and showed that birds were capable of utilizing the sun's position as a source of directional information. Some species determine compass direction by assessing the center of rotation of the starry sky, an indicator of north direction in the Northern Hemisphere. These species then learn the star pattern to determine compass direction (Emlen 1975). In addition, recognition of familiar landmarks, perception of ultraviolet light

(Wright 1972, Kreithen and Eisner 1978, Goldsmith 1980, Parrish et al. 1981), perception of linearly polarized light (Kreithen and Keeton 1974, Delius et al. 1976, Able 1982, 1989, Moore 1986), and use of olfaction (Wallraff et al. 1986, Wiltschko et al. 1987) may serve as navigational aids.

The geomagnetic field also may provide birds with navigational information. The orientation of caged birds in migratory condition is in the seasonally appropriate migratory direction, even in the absence of visual compass cues. Such orientation, however, may be deflected by alteration of the magnetic field surrounding bird test cages (Wiltschko et al. 1971, Wiltschko and Wiltschko 1972). Young birds without extensive experience seem particularly dependent on magnetic cues (Southern 1969, 1972, 1975, Keeton 1971).

Sensitivity to natural and artificial magnetic fields has been suggested for many nonavian organisms. These include bacteria (Blakemore 1975), insects (Towne and Gould 1985, MacFadden and Jones 1985), amphibians (Phillips

1987), reptiles (Rodda 1984), fish (Quinn et al. 1981, Kalmijn 1988), and mammals (Zoeger et al. 1981) including humans (Baker 1985). Although no magnetoreceptive organ in animals has been identified, several receptor types have been suggested as possibilities. Most involve a magnetic iron oxide—magnetite. The manner in which single-domain and pseudosingle-domain magnetite particles align with the ambient magnetic field of the earth renders them suitable for magnetic field perception (Beason and Brennan 1986). The detection of a magnetic compass direction would require only a few hundred to perhaps a thousand crystals of magnetite (Kirschvink and Gould 1981). This type of magnetic sensitivity has been documented clearly only for magnetotactic bacteria in which chains of single-domain magnetic particles align in both natural and artificial magnetic fields (Blakemore 1975).

Behavioral and physiological studies suggest that birds may be sensitive to magnetic fields. Deposits of magnetite occur inside the skull of homing pigeons (Columba livia; Walcott et al. 1979), as well as in the head and neck of feral pigeons, White-crowned Sparrows (Zonotrichia leucophrys), and other birds (Presti and Pettigrew 1980). These findings indicate that birds have the potential to use permanent magnets as magnetic-field detectors. An ability to perceive magnetic fields could provide birds with both a map and a compass sense. Because intensity and inclination of the geomagnetic field vary as a function of position on the earth's surface, use of them by navigating birds seems plausible (Presti 1985). Gould et al. (1978) outlined three possibilities for how animals might detect the earth's magnetic field. They suggested that animals may possess: (1) a device that measures the charge separation induced when it moves through the earth's field (probable method of sharks); (2) permanent magnets that act like compass needles and produce a measurable torque as they align in the earth's field (probable method of bacteria); (3) superparamagnetic material that, in the presence of an external field, produces additional magnetism parallel to the external field (probable method of honeybees). Remanence (i.e. the permanent magnetism residing in ferromagnetic materials that is independent of existing external magnetic fields) found in birds may be related to their ability to sense external fields. More knowledge about the intensity of mag-

netism occurring naturally in birds (i.e. their natural remanent magnetization, NRM) and the potential of birds to become magnetic (i.e. their isothermal-induced remanent magnetization, IRM) will assist in determining whether birds possess magnetic materials for detection of a geomagnetic field.

The IRM in Bobolinks (Dolichonyx oryzivorus), a long-distant migrant, was thought sufficient to allow a sensitivity to slight changes in the geomagnetic field (Beason and Brennan 1986). Also, Presti and Pettigrew (1980) measured the IRM for pigeons and White-crowned Sparrows, while Ueda et al. (1982) obtained NRM and IRM values for two migratory species (Rustic Bunting, Emberiza rustica; Reed Bunting, E. schoeniclus) and two that are nonmigratory (Siberian Meadow Bunting, E. cioides; Eurasian Tree Sparrow, Passer montanus). No other detailed magnetometry studies to date provide sufficient data for evaluating statistically intra- and interspecific differences in birds.

A number of factors, including migratory habits, diet, and mass of the bird, may influence avian magnetic characteristics. We evaluated properties of magnetic remanence in a variety of birds to assess the potential relationship, if any, of magnetic remanence to these factors. The characterization of naturally occurring magnetic material and differences within and among species is one of the initial steps that may provide insight concerning avian orientation via magnetic-field detection.

METHODS

Specimens.—We sampled 92 birds of 21 species collected in the vicinity of Norman, Oklahoma from January to September 1989. Samples included: 10 Northern Bobwhites (Colinus virginianus), 10 Chimney Swifts (Chaetura pelagica), 2 Downy Woodpeckers (Picoides pubescens), 2 Eastern Phoebes (Sayoris phoebe), 10 Cliff Swallows (Hirundo pyrrhonota), 2 Blue Jays (Cyanocitta cristata), 2 Carolina Chickadees (Parus carolinensis), 6 Carolina Wrens (Thryothorus ludovicianus), 1 Northern Mockingbird (Mimus polyglottus), 1 Brown Thrasher (Toxostoma rufum), 1 American Robin (Turdus migratorius), 10 European Starlings (Sturnus vulgaris), 6 Red-winged Blackbirds (Agelaius phoeniceus), 1 Northern Oriole (Icterus galbula), 2 Common Grackles (Quiscalus quiscula), 10 Brown-headed Cowbirds (Molothrus ater), 2 Northern Cardinals (Cardinalis cardinalis), 1 Indigo Bunting (Passerina cyanea), 2 Dark-eyed Juncos (Junco hyemalis), 1 Harris' Sparrow (Zonotrichia querula), and 10 House Sparrows (Passer domesticus). All were captured as wild birds, except for the North-

ern Bobwhites, which were obtained from the Darlington Game Farm, El Reno, Oklahoma. We removed the head and neck of each bird with a glass-cutting tool, and washed each section thoroughly with a nonmagnetic detergent and deionized water to remove any possible contaminants. The mouth and nasal areas were flushed with a small pipette.

Magnetometry.—We used a SQUID magnetometer (SCT Superconducting Rock Magnetometer, Model A100, United Scientific Corporation, San Diego, California) to measure the NRM within the head and neck of each specimen, and Helmholtz sensing coils to measure the specimen's magnetism in three orthogonal directions (referred to as X, Y, and Z; see Fig. 1). An acrylic-plastic holding tube was used to insert and hold each specimen in the magnetometer's core (measuring area was at 0°C). The magnetometer was calibrated with the plastic holding tube inserted. The tube was then retracted and the specimen oriented on the holding platform of the tube with the beak of the bird pointing toward 0°. Upon reinsertion, we recorded a magnetic reading for the specimen. The tube was emptied and inserted a third time to check the accuracy of the zero calibration. Specimens were retested if marked deviations from zero occurred.

All heads and necks were magnetically induced with a variable-intensity magnet (six-inch Electromagnetic system, Model V-3700 with a Mark II Fieldial Magnetic Field Regulator, Varion, Inc., Palo Alto, California). Each specimen was placed horizontally in the magnet with the left eye facing toward the north pole, then the magnet was activated for 10 s with the intensity of the magnetic field set at 1,500 × 10^{-4} T (tesla; 1 tesla = 10^4 gauss = 10^4 electromagnetic units [e.m.u.]). The specimen was removed from the magnet and tested in the magnetometer to obtain a value for the isothermal-induced remanent magnetization (IRM).

Twenty-eight specimens were remagnetized progressively with the field intensity set at 50, 75, 100, 150, 300, 600, 800, 1,000, 1,500 × 10^{-4} T for 10 s. Recorded values were used to construct a remagnetization curve. After each change in intensity, a new IRM value was obtained. Stronger fields up to 3,000 × 10^{-4} T were used during initial stages of this study. Typically, saturation of the ferromagnetic material occurred at and above 1,500 × 10^{-4} T, producing little increase in remanent magnetization. Therefore, a maximum field value of 1,500 × 10^{-4} T was used for subsequent tests.

Following the induction of magnetism, specimens were progressively demagnetized in an alternating field created by a specially designed copper coil consisting of a solenoid 22.6 cm long, 38.1 cm in diameter, and wound with about 2,000 turns of copper wire. The coil contained a tumbling mechanism that rotated the specimen at a 9-to-11 ratio simultaneously through vertical and horizontal axes. This mechanism was de-
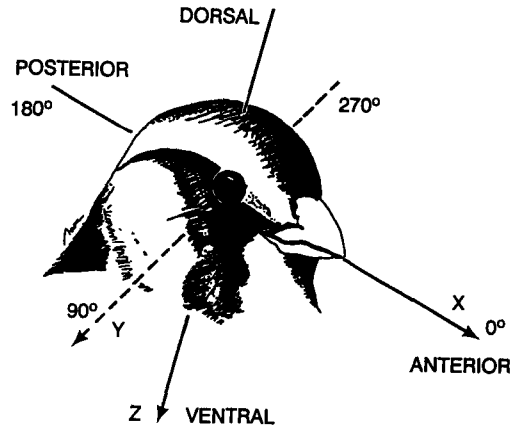

Fig. 1.   Specimen's position in magnetometer relative to magnetic directions X, Y, and Z.

signed to produce a random demagnetizing field within the specimen by minimizing the recurrence of the specimen's orientation within the field. The coil was set at field values of 40, 57, 74, 94, 130, 171, 194, 230, 260, 293, 455, 612, 770, and 1,167 × 10^{-4} T. Resultant values of remaining magnetization were measured by the magnetometer and used to construct a demagnetization curve.

The head and neck were separated in five of the specimens (2 Northern Bobwhites, 2 European Starlings, and 1 Common Grackle). We placed the subsamples in the magnetometer to obtain more precise information on the location of magnetic materials.

Magnetometry data were used to calculate standard magnetic measures (Fisher 1953, Cox and Doell 1960): magnetic intensity (J) for an individual; declination (angle of magnetic moment along horizontal component of the field); inclination (angle between horizontal component and total field); and precision parameter k (dispersion of vectors about the mean) for a species. The value of J is calculated as the square root of the sum of squares of the magnetism values for the three axes (X, Y, Z). The value of

$$k = (N - 1)/(N - R),$$

where N is the number of specimens and R is the total vector length in the direction of the mean field (with the maximum of $R = N$, when all individual unit-length vectors have the same direction). The k-value of a uniformly dispersed group of vectors is less than one and independent of N (when N is relatively large); high values of k indicate a tight grouping about the mean (Fisher 1953, Cox and Doell 1960).

Direction-cosine values for X, Y, and Z were used to determine the mean vector for each species. Non-overlapping 95% confidence intervals around the mean vectors (Fisher 1953, Cox and Doell 1960) for two species were used to indicate statistically significant directional differences between species. The angular

TABLE 1. Mean intensity of natural and isothermal-induced remanent magnetism (NRM and IRM), as well as mean mass, for eight species represented by relatively large samples. Magnetic values given as 10^{-12} tesla and based on data in Appendix, while bird mass given in grams.

Species	NRM	IRM	Mass
Northern Bobwhite	38.069	1,354.4	199.8
Chimney Swift	4.562	337.6	20.8
Cliff Swallow	6.435	377.0	19.4
Carolina Wren	3.090	476.7	19.7
European Starling	30.088	1,889.1	80.4
Red-winged Blackbird	10.092	891.3	64.5
Brown-headed Cowbird	10.018	845.2	48.8
House Sparrow	8.854	586.6	27.9

difference (θ) between two vectors was calculated as the

$$\arccos(\cos I_1 \cos I_2 \cos[D_1 - D_2] + \sin I_1 \sin I_2),$$

where I is the inclination and D the declination. If the angular difference between two vectors is less than the sum of the radii of their confidence intervals, the vectors are not considered to be significantly different.

We used a t-test for paired comparisons to evaluate differences between NRM and IRM within a species (NRM and IRM values for individuals were paired). We compared average intensity values among species by a single-classification ANOVA and the Tukey-Kramer procedure for comparisons among all pairs of means. Linear regression was used to analyze the relationship between bird mass and average intensity of the magnetic material within a species. The statistical methods outlined above are described by Sokal and Rohlf (1981).

RESULTS

The NRM and IRM values were derived from data on individual birds given in the Appendix, which includes values for X, Y, Z, intensity, declination, and inclination. In each of the eight species with relatively large samples (Table 1), the intensity prior to magnetic induction (NRM) was significantly less than after induction (IRM; paired t-test for individual birds within a species, $P < 0.05$ for all eight analyses). Three species (Chimney Swifts, Cliff Swallows, Carolina Wrens) had NRM values (Table 1) indistinguishable from the overall background readings of the magnetometer (i.e. $< 7 \times 10^{-12}$ T). The NRM values were significantly different among species (single-classification ANOVA, $F = 3.25$, df = 7 and 64, $P < 0.01$). In comparisons

of pairs of NRM means for the eight species, Cliff Swallows and Chimney Swifts were significantly lower than Northern Bobwhites, and all other comparisons were not statistically different (Tukey-Kramer method, $P < 0.05$). The NRM average for the Carolina Wren is the lowest of the eight species (Table 1). However, with a sample of six, the wren is not statistically different from the Northern Bobwhite. For IRM mean intensities, there was a significant difference among species (single-classification ANOVA, $F = 2.21$, $P < 0.05$). However, there was considerable variation within species. When the more conservative Tukey-Kramer procedure was used to make all pairwise comparisons, no significant differences were found ($P > 0.05$).

By separating the head from the neck of a European Starling, we were able to localize 76% of the IRM in the head and 24% in the neck region. In a second specimen, the values were 73% and 27%. For a Common Grackle, the head and neck values were 78% and 22%, respectively. In two Northern Bobwhites we found an even greater percentage of the IRM localized in the head region. One contained 98% in the head and 2% in the neck, while the other had 89% and 11%, respectively.

We found considerable variation among the eight species in orientation of the NRM (Fig. 2). Also, its orientation appears not to be directed precisely within species, as indicated by the variability found and the resulting low values of the precision parameter k (see Fig. 2). Overlapping confidence intervals indicate that there are no significant statistical differences in mean vector direction among these eight species ($P > 0.05$). Figure 3 includes representative normalized plots of the alternating-field demagnetization and remagnetization curves for individuals of the eight species.

For the eight species, mean NRM and the log of mean mass exhibit a strong association (R^2 of 0.835; see Fig. 4A). The linear regression is highly significant ($F = 30.29$, $P < 0.01$), with

$$Y = -0.3984 \times 10^{-10} + 0.3286 \times 10^{-10} \log X,$$

where Y is the average NRM in tesla and X the mean bird mass in grams. The value for the European Starling (no. 5 in Fig. 4A) is substantially above the regression line, while those for the Brown-headed Cowbird (no. 7) and Red-winged Blackbird (no. 6) fall below the line.

The mean IRM and log of mean mass are closely associated (R^2 of 0.968; Fig. 4B). The lin-

ear regression is very highly significant ($F = 182.88$, $P < 0.001$), with

$$Y = -8.8399 \times 10^{-10} + 9.9569 \times 10^{-10}\log X,$$

where Y is the average IRM in tesla and X the mean bird mass in grams. Again, the European Starling (no. 5 in Fig. 4B) is considerably above the line, while the Northern Bobwhite (no. 1) has the greatest deviation below.

DISCUSSION

The alternating-field demagnetization and remagnetization curves (Fig. 3) provide helpful information that can be used to infer the particle type, domain state, and particle interaction of magnetic material present. Characteristics of the demagnetization-remagnetization curves are consistent with those of magnetite as opposed to hematite (the theoretical maximum coercivity for magnetite is $3,000 \times 10^{-4}$ T; other ferromagnetic material continues to gain magnetism in stronger fields; Evans and McElhinny 1969, Cisowski 1981), suggesting that the material in birds is magnetite.

The point of intersection projected on the abscissa of a demagnetization and IRM acquisition curve (for examples, see Fig. 3) approximates the remanent coercive-force field. At the coercive-force field the magnetization realigned by the reversed field (IRM acquired at this steady applied field) should equal the magnetization unaffected by the reversed field (saturation IRM undemagnetized at this alternating field; Cisowski 1981). For non-interacting single-domain particles (i.e. particles within which potential magnetic carriers are aligned in the same direction), the ratio of saturation remanence (demagnetized to the remanent coercive-force value) to undemagnetized saturation remanence should be 0.5. This ratio is equivalent to the point of intersection projected to the ordinate axis. Samples dominated by multidomain particles (i.e. those with potential magnetic carriers in a definite zonal arrangement, with all zones not aligned in the same direction) display nonsymmetric acquisition-vs.-demagnetization curves, yet can be differentiated because of steep IRM acquisition curves at low field values (Cisowski 1981) from strongly interacting single-domain grains.

Although the crossover point of the demagnetization-remagnetization curve can be helpful in estimating domain state, other factors such as grain size and the degree of clumping within the grains can influence the curve and its intersection point. Because little is known about biologically occurring magnetite and the factors that influence it, characteristics of the particles can only be inferred. The crossover point for the European Starling, Red-winged Blackbird, and the Brown-headed Cowbird occurred at approximately 50% (0.5) of the normalized average intensity (Fig. 3), suggesting that the particles in these birds may be noninteracting single domain. While one House Sparrow (Fig. 3H) had a crossover point of 60%, crossovers for the other two House Sparrows evaluated were near 50%. The steep slope of the House Sparrow remagnetization curve may indicate presence of some multidomain particles. All other species gained saturation magnetism below $2,000 \times 10^{-4}$ T and had crossover points well below 50%, suggesting that their magnetic material is interacting single-domain or possibly pseudosingle-domain magnetite (i.e. larger particles with magnetic properties of single-domain particles, but which likely are multidomain; Banerjee and Moskowitz 1985). The rapid decay in the IRM for Carolina Wrens, Cliff Swallows and Chimney Swifts suggests that some superparamagnetic material (i.e. an ensemble of single-domain particles with a net magnetic moment of zero, but with a net alignment of magnetic moments in an applied field; Banerjee and Moskowitz 1985) is present in these species.

In addition to measuring IRM in a number of pigeons and White-crowned Sparrows, Presti and Pettigrew (1980) reported that "approximately 40 other species of birds were tested for inducible magnetic remanence in the head and neck," although they presented only example values for a few of these species. They indicated that results varied widely from species to species, but that "all cases of appreciable remanence were associated with migratory birds." Our comparisons of the NRM and IRM values indicate that, although the amount of magnetic material occurring naturally (NRM) in different species may vary, there is no general difference between migratory and nonmigratory birds with respect to their potential to acquire magnetization (IRM; see Appendix). The highest naturally occurring magnetism was found in nonmigratory species, the Northern Bobwhite and the European Starling (the latter is migratory in some regions). In contrast, the most highly migratory species (i.e. Chimney Swifts and Cliff
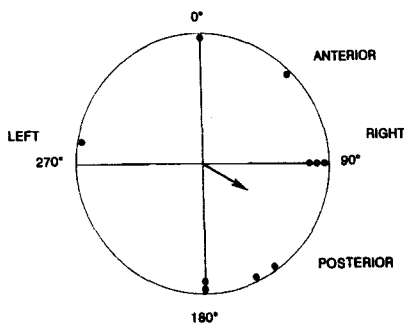
DECLINATION

INCLINATION
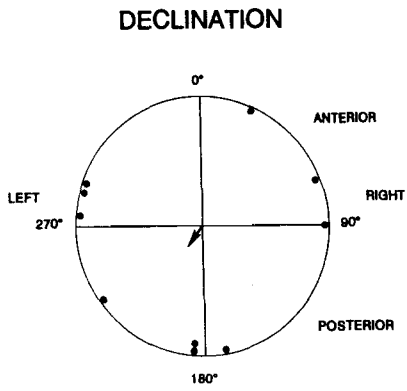
A.

Northern Bobwhite

$R = 1.702$
$k = 1.085$
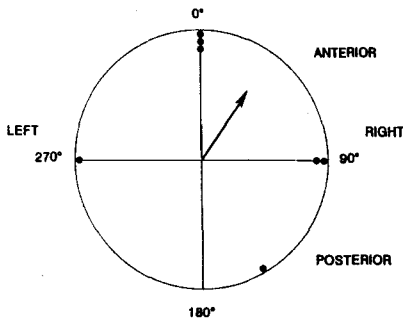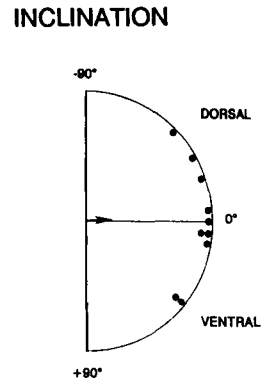
B.

Chimney Swift

$R = 5.393$
$k = 1.953$
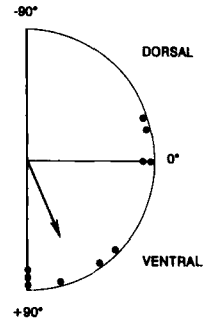
C.

Cliff Swallow

$R = 3.311$
$k = 1.346$
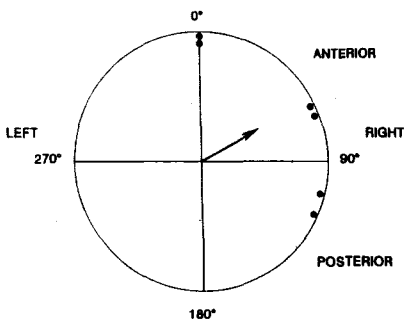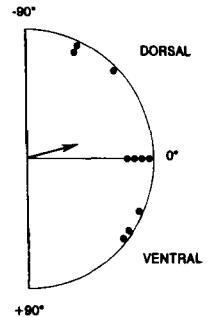
D.

Carolina Wren

$R = 4.144$
$k = 2.694$
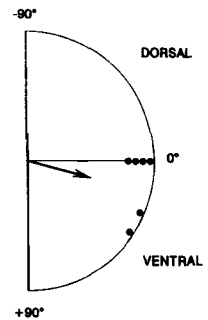
Fig. 2. Circular and semicircular plots showing orientation of natural remanent magnetism (NRM) for individual birds of eight species. Arrow registers mean direction and total vector length in direction of mean field based on unit-length vectors for individuals (radius of circle equivalent to vector length of 8). Vector length (R) in mean direction and precision parameter (k) indicated for each species.
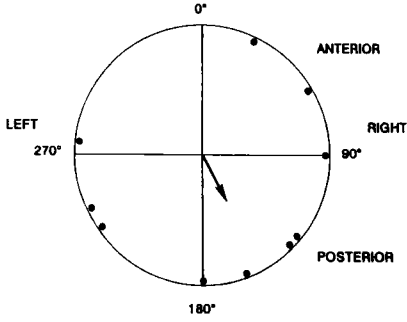
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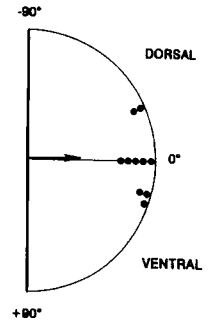
E.
European Starling
$R = 3.194$
$k = 1.322$
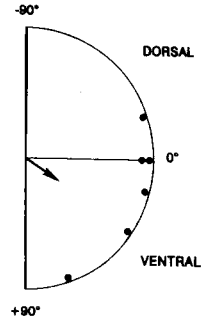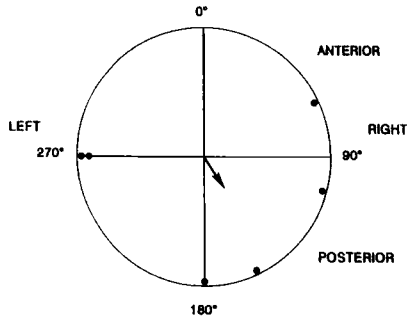
F.
Red-winged Blackbird
$R = 2.488$
$k = 1.424$
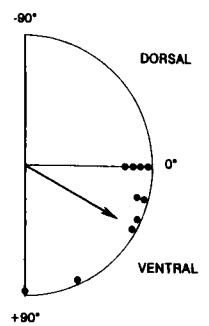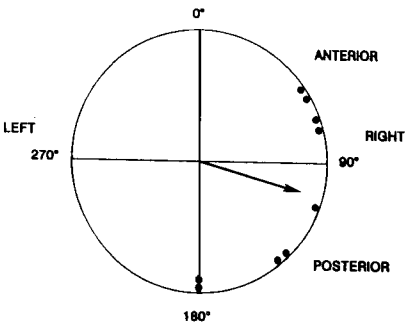
G.
Brown-headed Cowbird
$R = 6.739$
$k = 2.760$
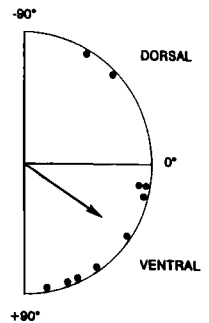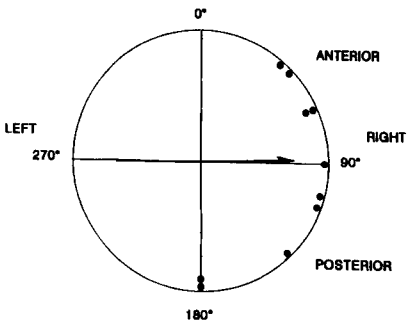
H.
House Sparrow
$R = 5.957$
$k = 2.226$

Fig. 2.   Continued.

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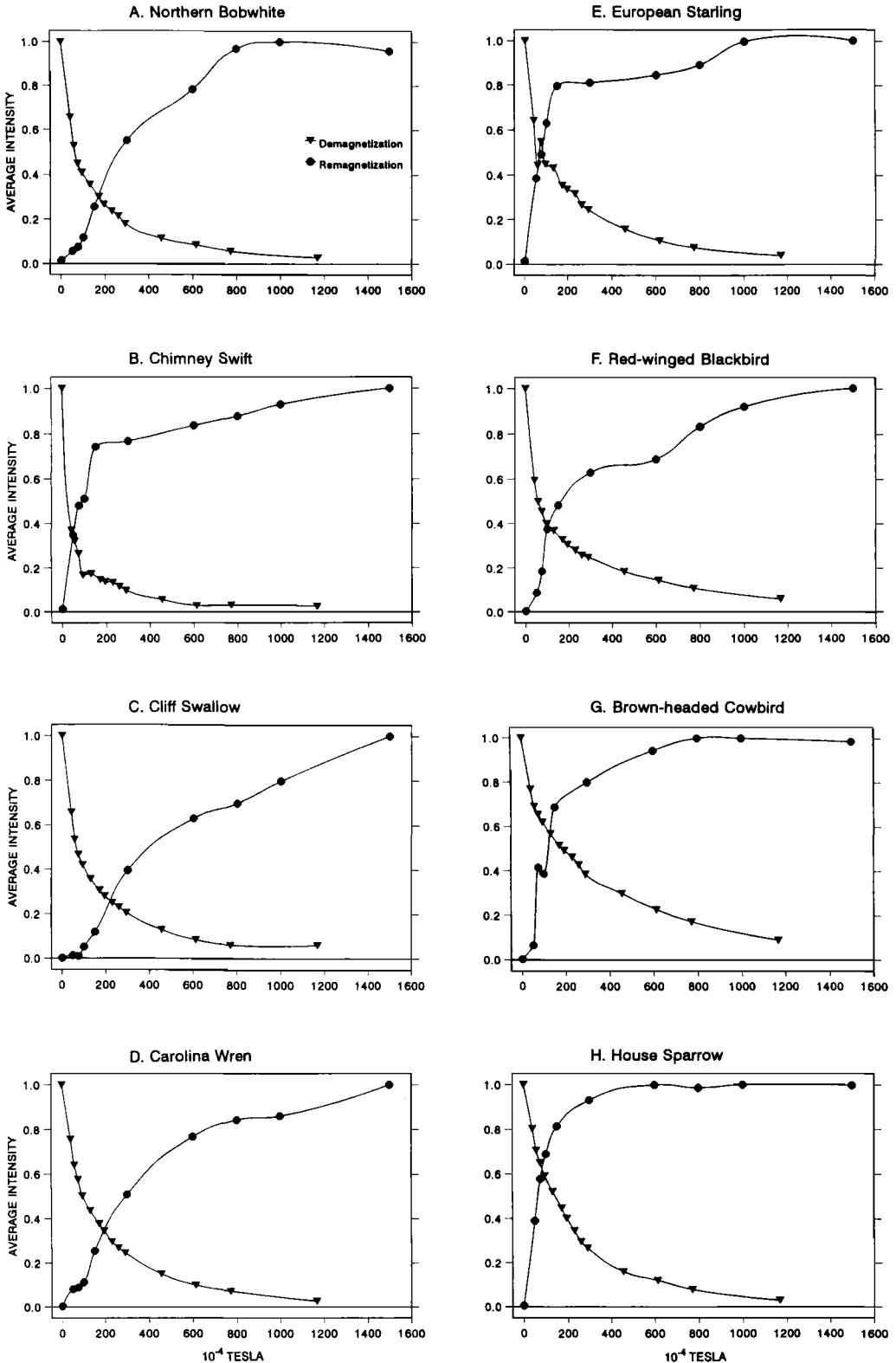
Fig. 3.   Alternating-field demagnetization and remagnetization curves for the head and neck of represen-tative individual birds of eight species. Average intensity values (*J*) are normalized.

Swallows) had NRM intensities indistinguishable from background readings of the magnetometer. Ueda et al. (1982) compared NRM and IRM values of four species and did not find differences between migratory and nonmigratory species.

Because magnetism has been proposed as a navigational aid used by migrating birds, it is not clear why some nonmigratory birds have more naturally occurring magnetite then highly migratory birds. Possibly, magnetic perception also is helpful for movements more limited than those associated with long-range migration. Magnetic-based orientation and navigation could be used for local movements by birds, such as those associated with foraging and other daily activities. If only very small amounts of magnetic material are needed, higher levels simply may represent an excess. Another possibility is that the magnetic materials found in the heads and necks of birds have no function in orientation or navigation.

Diet also may have some effect. Birds with NRM values at the level of background readings (i.e. Carolina Wrens, Chimney Swifts and Cliff Swallows) are 90% or more insectivorous (Bent 1940, 1942, 1948), while those showing NRM levels higher than background level are omnivorous. Although magnetite is biogenic in some organisms (Kirschvink and Gould 1981), the synthetic pathway is not known. Birds may pick up iron, store it in compound form, and eventually convert it into magnetite. Alternatively, ingested magnetite, occurring naturally in food sources, might contribute to the deposition of magnetite in tissues. Because the insectivores also were the smallest birds studied, it is not possible from our data to discriminate between possible effects due to diet and those related to bird size. It, of course, is possible that neither is particularly important.

For species with the highest IRM values (Northern Bobwhites, European Starlings, Common Grackles), most of the magnetic material occurred in the head rather than in the neck. In four species, higher IRM values were reported for the head than the neck by Ueda et al. (1982), although recorded differences were not as great as we obtained. In contrast to our results, V. H. Hutchison and Robert L. DuBois (pers. comm.) found that equal or greater amounts of magnetic material are in the neck than in the head of homing pigeons. The significance, if any, of this difference is not apparent. Bobolinks have concentrations of in-
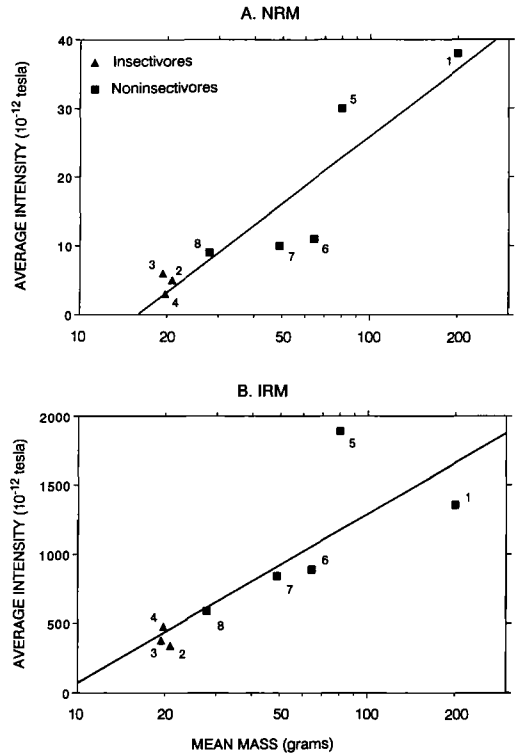
Fig. 4. Relationship of mean mass for eight species to: (A) NRM (natural remanent magnetism); and (B) IRM (isothermal-induced remanent magnetism). Species identified as primarily insectivorous or omnivorous; numbers adjacent to points indicate species as listed in Table 1. R^2 values 0.835 and 0.968, respectively. Linear regression lines shown (see Results for equations).

organic iron around the olfactory nerve and bulb, and in the bristles that project into the nasal cavity (Beason and Nichols 1984).

Beason and Brennan (1986) found NRM orientation of Bobolinks to be similar for all but 1 of 12 birds used in their study. We found dissimilarities in NRM orientations among individuals within a species (Fig. 2), which indicates that the magnetite was not oriented in the same direction in each individual. Reasons for this dichotomy in results are not evident. The NRM orientation of Bobolinks (Beason and Brennan 1986) was similar to that observed in our study after magnetic induction (IRM). Lack of uniform alignment in different birds of the same species does not rule out the possibility that these birds have magnetite that orients appropriately when placed under particular conditions (e.g. a proper magnetic field).

Induction of magnetism in most specimens

usually aligns the IRM in the direction of the applied field (for our study, the field was oriented across specimen at a declination of 270°). In the eight species evaluated in detail and in birds with more limited samples ("other species" in Appendix), the values of the declination are shifted on average +20° from the normal alignment of 270°. Undoubtedly, some variability was due to less than precise specimen placement in the magnetometer or in the magnet. However, if the error could be accounted for fully by placement alone, we would expect the shift of the declination to occur in both positive and negative directions, not just one. This shift may be related to a systematic orientation of physically elongated grains and subsequent magnetization along their long axis. The shift could be associated with preferred orientation of crystals and their direction of easy magnetization.

While we have mentioned several possible reasons for the substantial intraspecific directional differences in magnetic remanence, none convincingly explains it. Other possible explanations exist. Conceivably, different individuals measured within a species might come from populations with differing migratory patterns. If this were the case and the magnetic material present is relevant to a type of internal avian compass, variability in directions of magnetic vectors might be expected (see Kiepenheuer's [1984] discussion of the magnetic compass mechanism of birds and its possible association with migratory direction). While sample birds might be from different populations, this seems unlikely for most of our species samples. Considering the four species with the greatest intraspecific dispersion in magnetic direction, we note that: the Northern Bobwhites were from one "population" (game-farm birds); the European Starlings, while taken on several different dates, all were from the same general vicinity; the Cliff Swallows were collected from the same colony on the same date; and the Redwinged Blackbirds were taken together on the same day. Likewise, Brown-headed Cowbirds, which exhibited the least dispersion in magnetic vectors, were taken on the same day in the same area. The information at hand, while incomplete, does not suggest that patterns of within- or between-population sampling account for the magnetic vector variability. Another possibility—that some birds were in a state of migratory restlessness, while others were

not—is even more speculative and cannot be evaluated critically.

The NRM and IRM values obtained by Beason and Brennan (1986) for Bobolinks were 3.20×10^{-11} and 2.49×10^{-9} T, respectively ($3,000 \times 10^{-4}$ T field). Their results for one Indigo Bunting and one Savannah Sparrow (*Passerculus sandwichensis*) were similar. The magnetic-intensity values we recorded (Appendix) are similar in magnitude to those obtained by Beason and Brennan, suggesting that birds differ relatively little in this magnetic characteristic.

As mentioned earlier, differences in remanent strength were not associated with whether or not the species is migratory. Body mass appears to be a more important factor in determining total magnetic intensity of a bird than does the length of the migratory pathway. Because only minute quantities of magnetite may be needed for magnetoreception, perhaps all birds can detect magnetic fields. The increase of magnetism with an increase in body mass may be only epiphenomenal. Not unexpectedly, how birds perceive and use magnetic field information is not made clear by examination only of the physical characteristics of the magnetic material. Also, researchers have had little success to date in pinpointing a magnetoreceptor in birds (however, see recent work on sensitivity of units in the opthalmic nerve and trigeminal ganglion of Bobolinks to small changes in magnetic field; Semm and Beason 1990a). Further studies of the histology, physiology, and development of magnetite-containing tissues will be necessary to determine the mechanism or mechanisms involved in avian magnetic perception.

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APPENDIX. Natural and isothermal-induced remanent magnestism in 21 species. Values for X, Y, Z and magnetic intensity given as 10^{-12} tesla. Declination and inclination in degrees.

		Natural remanent magnetism					Isothermal-induced remanent magnetism					
	X	Y	Z	Intensity	Declination	Inclination	X	Y	Z	Intensity	Declination	Inclination
						Northern Bobwhite (n = 10)						
	9	4	0	9.85	24.0	0.0	−45	−1,967	132	1,972	268.7	3.8
	11	28	2	30.15	68.6	3.8	305	−1,979	433	2,049	278.8	12.2
	−31	6	5	31.97	169.0	9.0	370	−1,370	231	1,438	285.1	9.2
	6	−15	1	16.19	291.8	3.5	0	−352	111	369	270.0	17.5
	12	−42	−27	51.35	285.9	−31.7	988	−2,714	501	2,931	290.0	9.8
	0	12	10	15.62	90.0	39.8	281	881	−285	968	72.3	−17.1
	−13	−18	18	28.58	234.2	39.0	425	−969	504	1,172	293.7	25.5
	3	−23	−23	32.66	277.4	−44.8	92	−986	−31	991	275.3	−1.8
	−128	−14	−47	137.07	186.2	−20.1	277	−921	142	972	286.7	8.4
	−27	−3	−2	27.24	186.3	−4.2	356	−550	190	682	302.9	16.2
Mean	−16	−6	−6	38.069	216.0	−3.1	305	−1,093	193	1,354.4	286.9	10.5
						Chimney Swift (n = 10)						
	0	1	4	4.12	90.0	76.0	82	−269	98	298	287.0	19.2
	0	0	3	3.00	—	90.0	327	−904	357	1,025	289.9	20.4
	3	0	−1	3.16	360.0	−18.4	19	−284	−7	285	273.8	−1.4
	4	0	4	5.66	360.0	45.0	70	−301	80	319	283.1	14.5
	0	0	4	4.00	—	90.0	81	−506	242	567	279.1	25.3
	0	0	2	2.00	—	90.0	25	−180	82	199	277.9	24.3
	8	0	−2	8.25	360.0	−14.0	14	−294	86	307	272.7	16.3
	0	6	0	6.00	90.0	0.0	26	−133	83	159	281.1	31.5

APPENDIX.   Continued.

				Natural remanent magnetism						Isothermal-induced remanent magnetism		
	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion
	−5	3	0	5.83	149.0	0.0	15	−137	22	140	276.2	9.1
	0	−2	3	3.614	270.0	56.3	30	−64	31	77	295.1	23.7
Mean	1	1	2	4.562	34.2	66.6	69	−307	107	337.6	281.5	18.4
						Cliff Swallow ($n = 10$)						
	−2	0	0	2.00	180.0	0.0	90	−800	356	880	276.4	23.9
	0	6	5	7.81	90.0	40.0	144	−635	267	704	282.8	22.3
	2	2	0	2.83	45.0	0.0	79	−186	−156	255	293.0	−37.7
	−3	2	−8	8.77	146.3	−65.7	1	−275	50	280	270.2	10.3
	3	−16	12	20.22	280.6	36.4	94	−171	54	202	298.8	15.5
	−6	3	3	7.35	153.4	24.1	105	−303	213	385	289.1	33.6
	0	3	−6	6.71	90.0	−63.4	80	−182	74	212	293.7	20.4
	4	0	−4	5.66	360.0	−45.0	194	−275	145	366	305.2	23.3
	−1	0	0	1.00	180.0	0.0	71	−193	70	217	290.2	18.8
	0	2	0	2.00	90.0	0.0	96	−239	75	268	291.9	16.2
Mean	0	0	0	6.435	120.0	−15.3	95	−326	115	377.0	289.0	15.6
						Carolina Wren ($n = 6$)						
	1	2	0	2.24	63.4	0.0	45	−215	113	247	281.8	27.2
	−1	4	0	4.12	104.0	0.0	−5	−1,152	390	1,216	269.8	18.7
	−1	2	0	2.24	116.6	0.0	−4	−232	92	250	269.0	21.6
	2	0	1	2.24	360.0	26.6	48	−217	80	236	282.5	19.8
	1	0	0	1.00	360.0	0.0	134	−461	−15	480	286.2	−1.8
	2	5	4	6.71	68.2	36.6	90	−365	210	431	283.8	29.2
Mean	1	2	1	3.090	60.9	14.6	51	−440	145	476.7	278.9	19.3
						European Starling ($n = 10$)						
	7	13	0	14.76	61.7	0.0	185	−804	393	914	283.0	25.5
	−4	4	0	5.66	135.0	0.0	190	−719	17	744	284.8	1.3
	−32	38	0	49.68	130.1	0.0	469	−298	813	985	327.6	55.6
	−8	−12	0	14.42	236.3	0.0	693	−1,538	38	1,687	294.3	1.3
	8	−133	−66	148.69	273.4	−26.4	819	−783	464	1,224	316.3	22.3
	4	2	0	4.47	26.6	0.0	343	−831	330	958	292.4	20.2
	−8	3	2	8.77	159.4	13.2	279	−549	−9	616	296.9	−0.8
	−17	0	4	17.46	180.0	13.2	58	−691	10	694	274.8	0.8
	0	6	2	6.32	90.0	18.4	8,065	−4,030	−3,139	9,547	333.4	−19.2
	−13	−25	−12	30.63	242.5	−23.1	235	−1,398	557	1,523	279.5	21.5
Mean	6	−10	−7	30.088	151.0	−1.1	1,134	−1,164	−53	1,889.1	296.6	13.3
						Red-winged Blackbird ($n = 6$)						
	0	−4	3	5.00	270.0	36.9	390	−1,613	54	1,660	283.6	1.9
	−3	0	0	3.00	180.0	0.0	206	−416	14	464	296.3	1.7
	0	−1	3	3.16	270.0	71.6	758	−1,206	157	1,433	302.2	6.3
	−8	26	0	27.20	107.1	0.0	138	−375	32	401	290.2	4.6
	−15	7	−6	17.61	155.0	−19.9	221	−457	−19	508	295.8	−2.1
	2	4	1	4.56	63.4	12.6	443	−728	223	881	301.3	14.7
Mean	−4	5	0	10.092	147.0	35.0	359	−799	77	891.3	294.9	4.5
						Brown-headed Cowbird ($n = 10$)						
	0	0	3	3.00	—	90.0	428	1,161	330	1,281	290.2	14.9
	4	7	2	8.31	60.3	13.9	252	−677	265	769	290.4	20.1
	−1	0	2	2.24	180.0	63.4	361	−2,312	339	2,364	278.9	8.2
	2	5	3	6.16	68.2	29.1	35	−226	8	229	278.8	2.0
	4	6	2	7.48	56.3	15.5	94	−348	−69	367	285.1	−10.8
	−24	0	10	26.00	180.0	22.6	301	−216	230	436	324.3	31.8
	−7	7	0	9.90	135.0	0.0	167	−225	28	306	303.2	5.2
	5	16	0	16.76	72.6	0.0	162	−405	−55	440	291.8	−7.2
	−5	13	0	13.93	111.0	0.0	937	−1,464	−1,009	2,010	302.6	−30.1
	−5	4	0	6.40	141.3	0.0	120	−212	54	250	299.5	12.5
Mean	−3	6	2	10.018	105.5	29.1	286	−728	12	845.2	293.9	4.9
						House Sparrow ($n = 10$)						
	10	9	9	16.19	42.0	33.8	−84	−1,422	−414	1,483	266.6	−16.2
	−2	2	4	4.90	135.0	54.7	367	−862	−122	945	293.1	−7.4
	0	1	3	3.16	90.0	71.6	144	−524	56	546	285.4	5.9

APPENDIX. Continued.

		Natural remanent magnetism					Isothermal-induced remanent magnetism					
	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion
	−2	6	1	6.40	108.4	9.0	101	−323	21	339	287.4	3.6
	4	9	2	10.05	66.0	11.5	218	−389	136	466	299.3	17.0
	−4	0	20	20.40	180.0	78.7	17	−472	5	472	272.1	0.6
	3	6	2	7.00	63.4	16.6	60	−169	5	179	289.5	1.6
	−1	4	−4	5.74	104.0	−44.1	92	−317	−130	355	286.2	−21.5
	−4	0	−7	8.06	180.0	−60.2	194	−438	98	489	293.9	11.6
	2	2	6	6.63	45.0	64.8	158	−561	100	591	285.7	9.7
Mean	1	4	4	8.854	88.2	33.4	127	−548	−25	586.6	285.9	0.5

Other species

Downy Woodpecker (*n* = 2)

	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion	X	Y	Z	Inten-sity	Declina-tion	Inclina-tion
	0	0	7	7.00	—	90.0	−6	−146	183	234	267.6	51.4
	4	0	0	4.00	360.0	0.0	155	−467	16	492	288.4	1.9

Eastern Phoebe (*n* = 2)

	3	0	0	3.00	360.0	0.0	48	−362	164	400	277.6	24.2
	2	0	4	4.47	360.0	63.4	7	−180	7	180	272.2	2.2

Blue Jay (*n* = 2)

	4	−2	3	5.39	333.4	33.9	143	−384	121	427	290.4	16.5
	0	−12	0	12.00	270.0	0.0	108	−397	230	471	285.2	29.2

Carolina Chickadee (*n* = 2)

	2	1	0	2.24	26.6	0.0	224	−440	70	499	297.0	8.1
	0	5	0	5.00	90.0	0.0	127	−1,151	438	1,238	276.3	20.7

Northern Mockingbird (*n* = 1)

	8	20	7	22.65	68.2	18.0	608	−1,061	764	1,442	299.8	32.0

Brown Thrasher (*n* = 1)

	0	2	−3	3.61	90.0	−56.3	205	−1,055	−82	1,078	281.0	−4.4

American Robin (*n* = 1)

	−13	4	5	14.49	162.9	20.2	37	−360	85	372	275.9	13.2

Northern Oriole (*n* = 1)

	0	2	0	2.00	90.0	0.0	123	−345	138	391	289.6	20.6

Common Grackle (*n* = 2)

	10	−7	23	26.04	325.0	62.0	741	−1,578	377	1,784	295.2	12.2
	1	−6	−8	10.05	279.5	−52.8	72	−632	232	677	276.5	20.0

Northern Cardinal (*n* = 2)

	0	0	2	2.00	—	90.0	137	−412	63	439	288.4	8.3
	−4	−2	1	4.58	206.6	12.6	519	−1,218	380	1,377	293.1	16.0

Indigo Bunting (*n* = 1)

	0	0	1	1.00	—	90.0	29	−190	50	199	278.7	14.6

Dark-eyed Junco (*n* = 2)

	0	4	6	7.21	90.0	56.3	208	−409	56	462	297.0	66.9
	−1	2	3	3.74	116.6	53.3	71	−248	64	266	286.0	13.9

Harris' Sparrow (*n* = 1)

	4	8	−1	9.00	63.4	−6.4	130	−314	109	357	292	17.8