

the sample allowing for an error of  $p < 0.05$  [14]. Clearly, the (GATA)<sub>4</sub> oligonucleotide will provide a highly powerful tool in the analysis of intracolony demography in feral honeybee populations. It may be highly rewarding to determine whether this probe can also be used for DNA fingerprinting in other social insect systems.

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## Hippocampal Volume and Migration in Passerine Birds

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The avian dorsomedial cortex, or hippocampal region, is known to play a role in processing and/or storing memory [1]. Lesion studies of food-storing black-capped chickadees (*Parus atricapillus*) and homing pigeons [2,3] have suggested that the hippocampal region is especially important in processing spatial information. In this article, we investigate whether or not migratory birds have an evolutionary specialization of the hippocampal region parallel to that found in food-storing birds [4,5]. In a study of 35 species of passerine birds, Krebs et al. [4] found that the relative volume of the hippocampus is larger among food-storing species than among non-storers, when effects of phylogeny are taken into account. It is known that food-storing

birds require an accurate memory to relocate their food stores successfully [6]. This has led to the hypothesis that food-storing birds have evolved an enlarged hippocampal region in association with the requirement for storing spatial information [7]. Given the role of the hippocampus in navigation by pigeons within the familiar area near the loft [8], it is possible that migrant birds have evolved a specialization of the hippocampus parallel to that shown by food-storers, associated with the need to learn two home ranges in the winter and summer areas and perhaps to learn about landmarks on the migration route.

We therefore investigated whether or not the relative size of the avian hippocampus is correlated with migratory be-

havior. We used the same techniques and database as that studied by Krebs, et al. [4]. Fifty-four individuals belonging to 35 passerine species distributed among 9 families were sacrificed with a lethal intraperitoneal dose of sodium pentobarbitone and perfused transcardially with physiological saline followed by formal-saline. The brains were dissected from the skull following perfusion and post-fixed for 3–7 days in 10% formalin before being transferred to 30% sucrose-formalin. The brains were then cut in the coronal plane as 25  $\mu$ m frozen sections and every tenth section was stained with cresyl violet. The sections were enlarged to a magnification of ten times using a photographic enlarger and the areas of the telencephalon and hippocampal region (including hippocampus and parahippocampus) drawn, with the boundaries determined as described in [4]. The areas were digitized on a Summa-graphics tablet and volumes of the hippocampal region and the telencephalon were calculated using the formula for a truncated cone. The data were logarithmically transformed for analysis.

When comparative data are used to test evolutionary correlations, such as the hypothesized relationship between relative hippocampal volume and migratory behavior, the problem of sta-

tistical non-independence is important. Related species may show similar values for traits, not because of independent evolution, but because of shared ancestry. One way of resolving this problem is to use the method of independent comparisons [9]. The essence of this method is to consider only differences among the immediate descendents of a single common ancestor, for example, differences between pairs of species within a genus or between pairs of genera within a sub-family. Differences that have arisen after the divergence of two taxa from a common ancestor must be the result of evolutionary divergence rather than shared ancestry. These differences are expressed as "linear contrasts", a statistical estimate of the deviation from expected values. Different versions of the independent comparisons method, including different assumptions for taking into account multiple branches and evolutionary divergence time, are described in [9,10]. Here we use Pagel's and Harvey's version of the method. In our analysis, the contrast values refer to migratory behavior and to residual hippocampal volume, separating effects of body size and telencephalon volume by multiple regression.

The method of independent comparisons requires an accurate phylogeny of the group under study. We used the phylogeny based on DNA-DNA hybridization [11]. Nomenclature follows that in [12]. Data on migratory behavior were obtained from [13], supplemented by information from C.M. Perrins (pers. commun.). We divided the species into four categories according

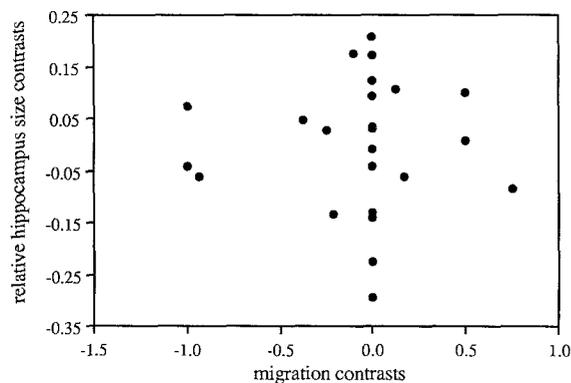


Fig. 1. The linear contrasts produced from the method of independent comparisons, demonstrating that variation in relative hippocampus volume is not positively associated with variation in migration distance. Body weight and telencephalon have been removed from the hippocampus contrasts by multiple regression

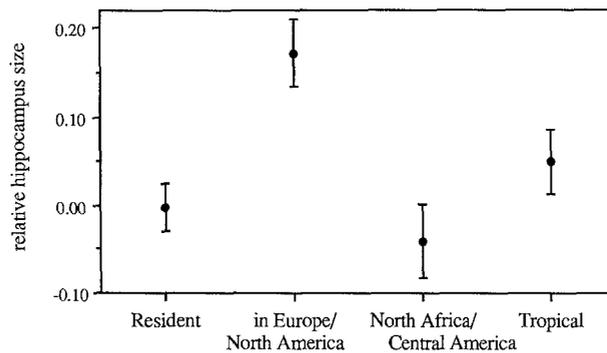


Fig. 2. Means and standard errors for each category of migration distance; see text for details. Resident species (with number of individuals): jay, *Garrulus glandarius* (2); red-billed magpie, *Cissa erythrorhyncha* (1); magpie, *Pica pica* (1); alpine chough, *Pyrrhonorax graculus* (1); jackdaw, *Corvus monedula* (2); rook, *Corvus frugilegus* (1); African stonechat, *Saxicola torquata axillaris* (2); nuthatch, *Sitta europaea* (1); treecreeper, *Certhia familiaris* (1); great tit, *Parus major newtoni* (2); blue tit, *Parus caeruleus* (2); coal tit, *Parus ater* (2); marsh tit, *Parus palustris* (2); willow tit, *Parus montanus* (2); starling, *Sturnus vulgaris* (2); wren, *Troglodytes troglodytes* (2); dunnoek, *Prunella modularis* (1); greenfinch, *Carduelis chloris* (2); English robin, *Erithacus rubecula melophilus* (2); zebra finch, *Poephila guttata* (1); bengalese finch, *Lonchura striata* (1); paradise whydah, *Vidua paradisaea* (2). All the Europeans birds except *Pyrrhonorax graculus* are from British populations. Migrant species: within Europe: blackbird, *Turdus merula* (2); song thrush, *Turdus philomelos* (1); chaffinch, *Fringilla coelebs* (2); reed bunting, *Emberiza schoeniclus* (2); within North America: black-capped chickadee, *Parus atricapillus* (1); European birds to North Africa: European stonechat, *Saxicola torquata rubicola* (2); German robin, *Erithacus rubecula rubecula* (2); blackcap, *Sylvia atricapilla* (1); chiffchaff, *Phylloscopus collybita* (1); North American birds to Central America: redwinged blackbird, *Agelaius phoeniceus* (1); European birds to tropical Africa: garden warbler, *Sylvia borin* (2); willow warbler, *Phylloscopus trochilus* (2); collared flycatcher, *Ficedula albicollis* (1)

to migration distance. (1) *Residents*: birds with a winter range identical to the breeding range. (2) *Within Europe/North America migrants*: including those species in which many individuals leave the northern part of the range in winter. (3) *European birds migrating to North Africa or North American birds migrating to Central America*. (4) *European birds migrating to Tropical Africa*.

Figure 1 shows the linear contrasts in residual hippocampal volume plotted against the contrasts for migration. After partialling out the effects of telencephalon volume, which explained 78 % of the variation in hippocampal volume,  $P < 0.005$ ,  $df = 1,22$ , and body weight which explained 0.5 % of the variation,  $P > 0.50$ ,  $df = 2,21$ , migration has a non-significant effect in explaining residual variation in hippocampal volume,  $P > 0.75$ ,  $df = 3,20$ . Figure 2 displays the data in a slightly different way by showing the relative hippocampal volume for the four different categories of migration behavior. The results of this analysis show no relationship between the evolution of migratory behavior and the evolution of relative hippocampal size. This concurs with the preliminary findings of Sherry et al. [5], who reported that migratory distance was not related to the relative volume of the hippocampus in eight species of passerine. In view of the role that the hippocampal region is thought to play in spatial memory it is somewhat surprising that migratory birds do not show an enlargement of hippocampal volume parallel to that

shown by food-storing birds. Our results do not rule out the possibility of a more subtle relationship between migratory behavior and development of the hippocampus. It would be worth examining, for example, the relative hippocampal volume of juvenile and adult migrants to test whether or not an enlargement of the hippocampus is associated with learning about the migration route and winter range for the first time.

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## Pigeon Orientation: Daily Variations Between Morning and Noon Occur in Some Years, But Not in Others

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There are many indications that the magnetic field of the earth is one of the components in the navigational system of homing pigeons [1]. The evidence suggesting such a role includes disorientation at strong magnetic anomalies [2], correlations with natural fluctuations of the geomagnetic field [3,4], and the effects of magnets and treatments with various magnetic fields [5]. At the same time, however, attempts to obtain a more quantitative estimate of the contribution of magnetic information in the navigational process often produce inconclusive results [6]. One of the reasons may be that magnetic effects often proved to vary between different sites and regions. Kowalski et al. [4] found a correlation between the K-indices and the vanishing bearings at only one of two sites. In the experiments of Benvenuti and Ioalè [7], pigeons of Italian origin reacted to a treatment with alternating magnetic

fields, whereas pigeons of German origin that had been raised with them, did not. Here, we report the results of two test series which indicate that there is also temporal variability in magnetic effects.

In 1981 [4], we performed an experimental series at our Frankfurt loft which consisted of repeated releases of two groups of pigeons from the same site, one being released at 6 h in the morning, the other group at noon. The mean vanishing bearings for the noon group lay about 10° clockwise of those of the morning group [4]. These experiments were continued in 1983 and in 1984 at different sites, using only one group of birds that was released twice (or three times, with a third release at 18 h). In all these series, we found a shift in the mean bearings from morning to noon that varied between 8° and 16° clockwise, depending on release site.

The data obtained in 1984 at Ober-Mörlen, 29.5 km north of our Frankfurt loft (50°08'N 8°40'E) may serve as an example. The same 33 pigeons were released on 16 days, and their vanishing bearings were measured with a compass to the nearest 1°. These data are plotted in Fig. 1 (left). The upper diagram gives the means for the morning and noon phase on each of the 16 days. The difference between the two times of days is obvious, with the mean at noon lying clockwise of the morning mean in 15 of 16 cases, the median being 16°. This is highly significant ( $p < 0.001$ , Wilcoxon test). The lower diagram gives the respective data for each of the 33 birds. A more or less pronounced trend was found in all but one pigeon, which is highly significant ( $p < 0.001$ , Wilcoxon test) with a median of 15°. The difference in vanishing bearings disappeared when the pigeons were released with magnets, and we thus concluded that the differences were caused by magnetic effects. We suggested that it might be associated with the normal daily course of the geomagnetic field [8]. This is caused by the solar wind hitting the sun-facing side of the earth, which, at our latitude, results in a certain decrease in intensity from sunrise to a minimum at noon, followed by a corresponding increase until sunset. In the years 1985, 1986, and 1989, similar tests were performed, with some of the same individual pigeons used