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Author(s): Sue Healy and Tim Guilford

Source: *Evolution*, Vol. 44, No. 2 (Mar., 1990), pp. 339-346

Published by: [Society for the Study of Evolution](#)

Stable URL: <http://www.jstor.org/stable/2409412>

Accessed: 20/05/2013 10:26

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OLFACTORY-BULB SIZE AND NOCTURNALITY IN BIRDS

SUE HEALY AND TIM GUILFORD

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

Abstract.—Recent evidence shows that, despite earlier beliefs, many birds have a functional sense of smell. There is also considerable variation in olfactory-bulb size among bird species, yet the evolutionary significance of this variation has remained elusive. We argue that birds living under low-light conditions, where vision is less efficient, should have evolved or maintained an increased olfactory ability and, hence, larger olfactory bulbs. Using a family-level comparative analysis to control at least partially for taxonomic artifacts, we show that none of a series of ecological variables (diet, nest type, development, nest dispersion, and migratory behavior) accounts for variation in olfactory-bulb size once the effects of body size and brain size (measured by cerebral-hemisphere length) have been controlled. Activity timing, however, accounts for significant variation even after the removal of these other variables. We discovered 13 independent cases in which nocturnal or crepuscular lineages have evolved a diurnal habit, or vice versa, and compared relative olfactory-bulb sizes between each branch pair. In all but one case, nocturnal or crepuscular birds have larger olfactory bulbs than their diurnal counterparts. We therefore demonstrate a widespread relationship between ecology and the evolutionary development of a part of the brain.

Received January 26, 1989. Accepted October 17, 1989

Despite earlier beliefs to the contrary, recent behavioral and neurophysiological evidence leaves little doubt that many birds can smell (reviewed in Bang and Wenzel [1985]). The ability to locate food by smell has now been demonstrated in the kiwi, *Apteryx australis*, (Wenzel, 1971), turkey vulture, *Cathartes aura*, (Stager, 1964), and a number of petrels (Grubb, 1972; Hutchinson et al., 1984; Jouventin and Robin, 1984). Pigeons can use olfactory cues in orientation and homing (e.g., Grubb, 1974; Schmidt-Koenig, 1979; Baker, 1984; Papi, 1986; Waldvogel, 1989) and can be conditioned to odors (e.g., Henton, 1969; Stattleman et al., 1975). Domestic chicks (*Gallus gallus*) prefer the smell of their own bedding material (Jones and Faure, 1982; Jones and Gentle, 1984) and are capable of odor-aversion learning (Guilford et al., 1987). Clark and Mason (1987) have shown that starlings (*Sturnus vulgaris*) can discriminate between plant species using olfactory cues alone. Wenzel (1971, 1982) has demonstrated both heart-rate changes and electrical activity in the olfactory bulb of the chicken in response to odor presentation and has shown graded activity in the olfactory-nerve fiber bundles in response to odor concentration similar to that of the rat.

However, the evolutionary significance of the striking variation in the development of olfactory apparatus across bird taxa has re-

mained unclear. In particular, anatomical studies reveal considerable variation between species in the size of the olfactory bulb. In the common crow (*Corvus brachyrhynchos*), for example, the longest diameter of the olfactory bulb is only 5% as long as the cerebral-hemisphere length, whereas in the snow petrel (*Pagodroma nivea*) olfactory-bulb length is 37% of cerebral-hemisphere length (Bang, 1971). Here, we investigate the evolution of olfaction in birds using an interspecific comparative analysis of olfactory-bulb size in relation to ecological variables. We hypothesize that olfaction is most likely to be selected for in birds, which are primarily visual animals, under low-light conditions in which the effectiveness of vision is reduced. Because experimental evidence suggests that bird olfaction may operate in association with a variety of activities, many of which are likely to be affected by reduced visual efficiency, the evolution of enhanced olfactory ability (e.g., in discrimination) may be a generalized response to reduced-light conditions. Olfaction may be a poor substitute in some activities for which vision is important, such as locating and capturing fast moving prey, in which case we may expect to see either the enhancement of other capacities (such as echolocation in nocturnal bats or hearing in owls [e.g., Knudsen, 1981]) or the further refinement of vision itself (also in owls). But

for activities such as site-recognition, the location of slow moving or stationary food items, or the detection of some predators, olfaction may well be a useful substitute for (or addition to) vision under no-light (or low-light) conditions. Nocturnal or crepuscular birds may therefore have evolved or retained a greater olfactory capacity than diurnal birds. We have chosen the size of the olfactory bulb as a measure of olfactory capacity because the olfactory bulb is involved in olfaction (Wenzel, 1971, 1982), because good quantitative data already exist for a wide range of species (Cobb, 1960; Bang, 1971), and because it is reasonable to hypothesize that the size of a brain component may be related to its capacity (a suggestion supported by recent studies; e.g., Nottebohm et al., 1981; Krebs et al., 1989).

The idea that ecology may cause variation in avian olfactory-bulb sizes is not new. Cobb (1960) found a weak association between large olfactory-bulb size and aquatic habits. Bang (1971) examined 151 bird species and found several ecological variables associated with large olfactory bulbs. Those species with larger olfactory bulbs tended to be ground-nesting, water-associated, carnivorous/piscivorous, and colonial breeders. However, de Speroni and Pirlot (1987) found large differences among the olfactory-bulb sizes of three unrelated bird species and suggested that olfaction should be more active in the terrestrial than in the aquatic species they examined.

The conclusions of these analyses must be treated with caution for a number of reasons. Our first point concerns allometric relationships. The size of the brain and its component parts scale allometrically with body size, so it is necessary to remove the potentially confounding effects of body size (see Bennett and Harvey [1985] for methods), especially because body size is correlated with ecological variables (e.g., Clutton-Brock and Harvey, 1983). The method used by both Cobb (1960) and Bang (1971) to compare the size of olfactory bulbs among species was to examine the ratio between the longest diameter of the olfactory bulb and the longest diameter of the ipsilateral cerebral hemisphere. This method fails to account satisfactorily for either the allometric effect of increasing body size or the

possibility that brain size itself has additional effects, independent of body size, on the size of the olfactory bulb (Pagel and Harvey, 1988*a*). In this paper, we remove the confounding effects of body size and brain size.

Our second point concerns taxonomic associations. All hypotheses tested using a comparative analysis face the problem of the nonindependence of species points. The aim of such analyses is to judge whether variation in some feature or ability (e.g., olfaction) can be accounted for by the response of natural selection to a problem set by the environment (indicated by the ecological variable, for example). Each time natural selection converges on the same solution represents an independent test of the adaptive hypothesis. It is important to find many such independent tests, because it is possible that the coincidence between the apparent "problem" and the "solution" is just that: a coincidence, caused in fact by some unrecorded variable or variables. Two species do not always represent two independent tests, because they may come from a lineage that has radiated after solving the problem, so they may have jointly inherited the solution, and most importantly, those unrecorded variables that will make them prone to the same coincidence as well (this danger may of course occur at higher taxonomic levels too, but is particularly acute at the species level). The aim, then, is to identify convergent solutions, at least as far as possible. These issues have been well reviewed by Pagel and Harvey (1988*a*), Felsenstein (1985), Ridley (1983), and Harvey and Mace (1982). Unlike earlier studies (Cobb, 1960; Bang, 1971), whose adaptive inferences may have been confounded by taxonomic associations, we address the problem of nonindependence.

In this paper, we use the solutions of Harvey and Mace (1982) to reduce the confounding effects of taxonomy by making comparisons of olfactory-bulb size with relation to several ecological variables at the family, rather than species, level (Bennett [1986] has already shown that maximum variation in the relative size of the brain and its components occurs at the family level in birds). In addition to ecological variables examined in previous studies, we investi-

gate the effect of another variable, activity timing, on the evolution of olfactory-bulb size variation, hypothesizing that birds active in low-light conditions should have a greater dependence on olfaction and, therefore, be under selection to evolve or maintain larger olfactory bulbs. We also test this hypothesis using a conservative method close to that of Ridley (1983) and Read (1987), in an attempt to identify independent instances of changes in activity timing. Furthermore, we control for the effects of allometry by first removing both body size and brain size from olfactory-bulb size.

MATERIALS AND METHODS

Body masses of 124 bird species (representing 112 genera, 55 families, and 17 orders) were collated from several sources, chiefly Ali and Ripley (1983), Brough (1983), and Dunning (1984). Olfactory-bulb sizes for the same 124 species, together with ipsilateral cerebral-hemisphere diameters, which we used as a measure of brain size, were taken from Bang and Cobb (1968) and Bang (1971) (for both olfactory bulbs and cerebral hemispheres, the longest diameters were used in all cases). Phylogeny follows Sibley et al. (1988) as far as possible, with lower taxonomic distinctions, where unresolved, following Peters (1931 [and subsequent volumes]).

Data on activity-timing were largely drawn from Cramp (1977) and Ali and Ripley (1983), with additional data from Serventy (1939), Bartholomew (1943), Guillion (1953), Kilham (1956), Bang (1965), Nilsson (1965), Meanley (1969), Schifter (1975), Stonehouse (1975), Payne and Price (1979), Fleming (1981), Imber (1983), Rabenold (1983), Goodwin (1986), and Johnsgard (1987). Species were classified as nocturnal/crepuscular if they were known to be active at night or under low-light conditions at any stage of their life history (e.g., nocturnal migrators, nocturnal foragers). The following ecological variables and categories, which have been thought by other authors (Cobb, 1960; Bang, 1971) to be associated with variation in olfactory-bulb size, were also examined: *diet* (1 = fruit; 2 = foliage; 3 = invertebrates; 4 = lower vertebrates [e.g., fish]; 5 = plant material and invertebrates; 6 = animals/carrion [combination of 3, 4,

higher vertebrates, and carrion]); *nest type* (1 = open; 2 = hole); *development* (1 = altricial; 2 = precocial); *nest dispersion* (1 = solitary; 2 = colonial); and *migratory behavior* (1 = resident; 2 = partly migrant; 3 = migrant). Data on these variables were collected from Cramp (1977), Ali and Ripley (1983), and Bennett (1986), and we followed Bennett's (1986) criteria for assigning families into categories.

RESULTS

Species data were transformed logarithmically (Harvey, 1982; Harvey and Martin, 1985). A preliminary analysis to look at the effect of activity timing on the size of the olfactory bulb was performed across all 124 species. Nocturnal or crepuscular species were found to have significantly larger olfactory bulbs than diurnal species ($t = -4.84$, $d.f. = 122$, $P < 0.0001$). This analysis, however, does not take into account the possibility of taxonomic artifact or known allometric effects of body size and brain size. To counter these problems, we first combined the species values into generic means and then combined these into family means (see Pagel and Harvey, 1988a). Families containing both diurnal and nocturnal or crepuscular species were subdivided (following Clutton-Brock and Harvey [1977]). We then examined the effect of body size by subjecting olfactory-bulb size to hierarchical multiple regression, entering body weight followed by activity timing (treated as a dummy variate) as independent variables. This method removes the effect of body size by asking whether, for a given body size, a taxon has a relatively large olfactory bulb.

Body weight explained 48% of the variance in the size of the olfactory bulb ($P < 0.0001$). Having thus controlled for the effect of body weight, adding the effect of activity timing explained a further 15% of the variance ($P < 0.001$). For a given body size, therefore, nocturnal or crepuscular families have larger olfactory bulbs than diurnal families.

Similarly, larger olfactory bulbs of nocturnal or crepuscular bird families could be the result of an allometric effect of their having relatively large brains. After all, nocturnal mammals appear to have relatively large

TABLE 1. Results of one of the hierarchical multiple regressions performed on family means and used to determine the effects of ecological variables on log(olfactory-bulb size). Ecological variables were entered as dummy variates.

| x variable | Cumulative R^2 | Partial correlation | P |
|---------------------------------|------------------|---------------------|---------|
| log(body weight) | 0.633 | — | <0.0001 |
| log(cerebral hemisphere length) | 0.643 | 0.171 | ns |
| Development | 0.655 | 0.181 | ns |
| Nest dispersion | 0.655 | 0.007 | ns |
| Nest type | 0.655 | 0.012 | ns |
| Diet | 0.687 | -0.021 | ns |
| Migration | 0.708 | 0.078 | ns |
| Activity timing | 0.765 | 0.443 | <0.02 |

brains (Mace et al., 1981). Using a hierarchical-multiple-regression analysis similar to that above, we found that brain size, as measured by cerebral-hemisphere length, explained 40% of the variance in olfactory-bulb size. However, brain size has no significant effect once body size has already been added (see Table 1). Brain size does not appear to have an allometric effect on olfactory-bulb size independent of the effect of body size. Activity timing, however, still explains a further (and statistically significant; $P < 0.02$) 15% of the variation in olfactory-bulb size.

The relative size of the olfactory bulb might be influenced by ecological variables other than activity timing, and any effect found in the above analyses could actually be due to one of these other variables. To examine the effect of some of these variables, hierarchical multiple regressions were performed on the family means, entering eight independent variables (ecological variables were entered as dummy variates). In all the analyses, body weight and then cerebral-hemisphere length were always entered first, and activity timing was always entered last. The other five variables were entered in between, but in a series of orders that ensured that each was entered first of the five in at least one analysis. None of the five ever achieved significance, so the results of just one analysis are given in Table 1.

This analysis reveals two points. First, the supposed relationships found by previous authors (Cobb, 1960; Bang, 1971) between ecological variables (such as diet or nest dis-

persion) and olfactory-bulb size should be reconsidered. When the confounding effects both of body size and brain size are removed and when the nonindependence of species units is at least partially controlled for, none of the ecological variables we explored (which to a large extent coincide with those of Cobb [1960] and Bang [1971]) can explain olfactory-bulb size variation. Second, even after the effects of all these variables have been removed, activity timing still has a highly significant influence on relative olfactory-bulb size.

However, although the use of family comparisons greatly reduces the potential for taxonomic artifact, only the identification of separate evolutionary incidents can provide independent units in a comparative test (Ridley, 1983). We located 13 independent cases in which the phylogeny split dichotomously into nocturnal/crepuscular-versus-diurnal pairs. Each pair of sister taxa must be the result of an independent incident of the evolution of the nocturnal (or crepuscular) habit from the diurnal habit (or vice versa), so each can provide an independent test of the effect of activity timing on olfactory-bulb evolution (note that we do not need to distinguish between those dichotomies in which diurnality is ancestral and those in which it is derived, because we are equally interested in both directions of evolutionary change). Values of olfactory-bulb size, cerebral-hemisphere length, and body mass, were averaged over those species on either side of the nocturnal/crepuscular-versus-diurnal dichotomy. No species contributed to more than one comparison.

We plotted the mean olfactory-bulb size against the mean body size separately for the nocturnal/crepuscular group and the diurnal group within each taxonomic pair and calculated the vertical deviations of each group from the averaged least-squares regression line for all species (see Pagel and Harvey [1988a, 1988b] for method), thus controlling for body size. We then controlled for brain size in the same way, by calculating the residuals of these values (i.e., residuals of olfactory-bulb size regressed against body size) from the regression line with cerebral-hemisphere length. Two-tailed paired t tests were then used to test whether the residuals from this line were greater for

nocturnal/crepuscular taxa than for their diurnal relatives (i.e., whether within a taxonomic group nocturnal/crepuscular members had relatively larger olfactory bulbs than their diurnal counterparts). Although most nocturnal/crepuscular-versus-diurnal dichotomies occur between families, some splits occurred only at higher taxonomic levels. In these cases, data points consisted of the combined means of those families below and to each side of the dichotomy. In 12 of the 13 evolutionarily independent paired comparisons, nocturnal or crepuscular birds had larger olfactory bulbs than their diurnal counterparts (two-tailed *t* test, *d.f.* = 12, *P* = 0.02), and these results are shown graphically in Figure 1. The results of our earlier, family-level comparison therefore remain robust even after phylogenetic effects have been more carefully controlled (see also Huey and Bennett [1987]).

DISCUSSION

Our analysis shows that nocturnal or crepuscular birds have larger olfactory bulbs than diurnal birds. Furthermore, despite the results of previous studies suggesting relationships between olfactory-bulb size and other ecological variables (for example, diet or nest dispersion), we find that with the effect of body size removed and with taxonomy at least partially controlled for, no other variable tested accounts for a significant amount of variation in olfactory-bulb size. Why, then, are olfactory bulbs relatively larger in birds that are active under low-light conditions?

Given that olfaction in birds may have a variety of functions (e.g., food finding, orientation and homing, recognition of odor cues associated with self), the most likely possibility is that olfactory ability is generally increased to compensate for the reduced effectiveness of vision under reduced light, whatever olfaction's specific function in the group in question. We assume that increases in sensory requirements or ability will be reflected in increases in the sizes of relevant brain components (further tests of this assumption might be especially fruitful using species from the sister-group pairs identified in our analysis). Differences in both behavior and ecology have been shown

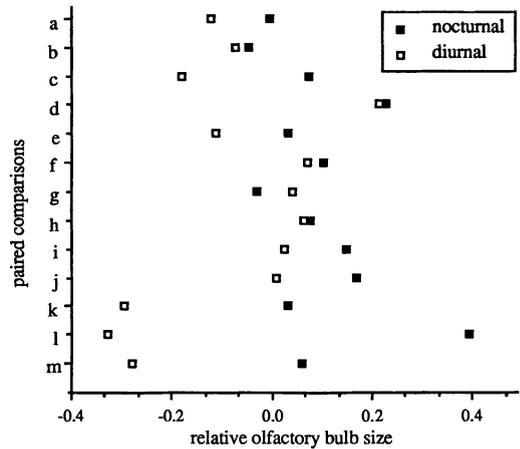


FIG. 1. The relative size of the olfactory bulb in nocturnal/crepuscular (n/c) and diurnal (d) birds. The paired points represent family means or means of higher taxonomic groups for the 13 independent cases where the phylogeny branches dichotomously into a nocturnal/crepuscular and diurnal pair. The horizontal axis represents the residual variation in the size of the olfactory bulb after the effects of body size and brain size have been removed by multiple regression. The letters on the vertical axis represent each paired comparison. Solid symbols represent nocturnal/crepuscular groups; open symbols represent diurnal groups. a) Charadrii: Charadriidae (n/c), Laridae (d), and Alcidae (d); b) Fringillidae (n/c and d); c) Corvidae (n/c and d); d) Procellariidae (n/c and d); e) Ciconiidae: Archeidae (n/c), Phoenicopteridae (n/c), Pelecanidae (d), Ciconiidae (d), Fregatidae (d), Spheniscidae (d), and Gaviidae (d); f) Podicipedidae (n/c and d); g) Scolopacidae: Scolopacidae (n/c) and Jacanidae (d); h) Rallidae (n/c and d); i) Strigidae (n/c), Steatornithidae (n/c), Caprimulgidae (n/c), Apodidae (d), and Chaeturidae (d); j) Cuculida: Cuculidae (n/c) and Centropidae (d); k) Bucerotimorphae: Bucerotidae (n/c) and Upupidae (d); l) Casuarii: Apterygidae (n/c) and Casuariidae (d); m) Anatidae (n/c and d).

to be correlated with variation in total brain size (corrected for body size) among mammalian species, and it has been argued that these differences relate to environmental complexity: the more complex the environment, the greater the required abilities for sensory perception and for information processing, storage, and retrieval. Environmental complexity may therefore select for increased brain size, perhaps through its effects on the size of component parts of the brain (Mace et al., 1980). Hence, in environments where a particular sensory capacity is important, increases solely in those parts of the brain associated with that capacity might lead to an overall increase in brain size. Some

nocturnal mammals, though not all, have relatively larger brains than their diurnal counterparts (Mace et al., 1981; Bauchot and Stephan, 1966, 1969; but see Clutton-Brock and Harvey [1980], Harvey et al. [1980], and Gittleman [1986]), but the cause of this relationship is uncertain, because the importance of size changes in parts of the brain has not been investigated. Certainly it would be interesting to know whether the relationship we have found in birds also occurs in mammals and other taxa.

The generality of the idea that environmental complexity brings about changes in brain size was tested by Bennett and Harvey (1985) who examined the ecological correlates of variation in the size of the brain and its components across 139 bird species. They did not find a significant correlation between relative brain size and activity timing like that found in mammals, nor could they find support for the sensory-complexity hypothesis. In particular, they found no significant correlation between the size of the optic lobes and activity timing. Although some birds may have compensated for the reduced effectiveness of vision under low light by greatly increasing their visual ability, Bennett and Harvey's result suggests that this is not the general rule. We suggest that the evolution of increased olfactory ability, as indicated by increased olfactory-bulb size, is a more widespread response to the visual limitations of life under low light (although this does not exclude the possibility that other nocturnal specializations that do not require larger optic lobes, such as shifts in light-receptor sensitivity, might also be important).

Whatever the precise uses of the increased olfactory capacity of nocturnal or crepuscular birds, it is now clear that low-light activity or some associated factor provides selective forces in favor of olfaction. If this explanation is correct, then further investigation of the functional use of olfaction in birds might best be carried out on nocturnal or crepuscular species. We might also predict that other senses, such as hearing, will follow the same widespread trend as olfaction, though this has not yet been investigated.

Much detailed neurophysiological work has related elements of brain structure to

ecology and behavior in a variety of taxa (e.g., Roth, 1986 [amphibians]; Pollak and Casseday, 1989 [bats]; Northcutt, 1985 [fishes]). In birds, a relationship between hippocampus size and food-storing behavior has been demonstrated among passerines (Krebs et al., 1989), but otherwise the evidence for ecological effects on the evolution of components of the brain in birds is scarce (e.g., Bennett and Harvey, 1985). We believe that the different approach we have used, of making taxonomically widespread comparisons, is complementary to the neurophysiological studies because it can be used to investigate the generality of relationships between ecology and brain structure. In this study, we have used this approach to test a specific hypothesis and to demonstrate a general relationship between the evolutionary development of a part of the brain (the olfactory bulb) and ecology (activity timing) in birds.

ACKNOWLEDGMENTS

We thank M. Dawkins, A. Grafen, P. Harvey, R. Huey, J. Krebs, M. Pagel, C. Perrins, A. Read, and two anonymous referees for comments on earlier drafts of this manuscript and for their critical discussions. S. H. is supported by a SERC research assistantship, and a Raymond Bursary at St. Hilda's College, Oxford, and T.G. is supported by a Junior Research Fellowship at St. John's College, Oxford.

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Corresponding Editor: R. B. Huey