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On the evolution of brain size in relation to migratory behaviour in birds

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Abstract

Migratory birds appear to have relatively smaller brain size compared to sedentary species. It has been hypothesized that initial differences in brain size underlying behavioural flexibility drove the evolution of migratory behaviour; birds with relatively large brains evolved sedentary habits and those with relatively small brains evolved migratory behaviour (migratory precursor hypothesis). Alternative hypotheses suggest that changes in brain size might follow different behavioural strategies and that sedentary species might have evolved larger brains because of differences in selection pressures on brain size in migratory and nonmigratory species. Here we present the first evidence arguing against the migratory precursor hypothesis. We compared relative brain volume of three subspecies of the white-crowned sparrow: sedentary *Zonotrichia leucophrys nuttalli* and migratory *Z. l. gambelii* and *Z. l. oriantha*. Within the five subspecies of the white-crowned sparrow, only *Z. l. nuttalli* is strictly sedentary. The sedentary behaviour of *Z. l. nuttalli* is probably a derived trait, because *Z. l. nuttalli* appears to be the most recent subspecies and because all species ancestral to *Zonotrichia* as well as all older subspecies of *Z. leucophrys* are migratory. Compared to migratory *Z. l. gambelii* and *Z. l. oriantha*, we found that sedentary *Z. l. nuttalli* had a significantly larger relative brain volume, suggesting that the larger brain of *Z. l. nuttalli* evolved after a switch to sedentary behaviour. Thus, in this group, brain size does not appear to be a precursor to the evolution of migratory or sedentary behaviour but rather an evolutionary consequence of a change in migratory strategy.

Keywords

behavioural flexibility; brain size; cognition; migratory strategies; neuoethology; passerine; selection; white-crowned sparrow; *Zonotrichia leucophyrs*

Birds are well known for their migratory behaviour, and the evolution of avian migration has attracted much attention (e.g. Zink 2002; Rappole 2003). Whereas some gradation exists between purely migratory and purely sedentary strategies, many species do follow only one of these strategies by either showing seasonal migration every year or by staying on the same territories year round. Yet, it remains unclear why given similar ecological conditions in seasonal environments, some species regularly migrate from their breeding grounds while others remain sedentary throughout the year (Sol et al. 2005a). Sol et al. (2005a) hypothesized

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that evolution of migratory behaviour is related to behavioural flexibility. According to Sol et al. (2005a), birds that are flexible and capable of behavioural and, more specifically, foraging innovations are able to successfully survive during seasonally changing environments and thus have evolved sedentary habits. Less flexible species, on the other hand, might have evolved migratory behaviour to avoid energetically demanding seasons because they do not have the ability to quickly adjust to changing foraging conditions (Sol et al. 2005a). Sol et al. (2005b) showed that birds capable of flexible behavioural responses had enhanced survival when placed into novel environment, supporting the hypothesis that increased behavioural flexibility might be related to sedentary habits.

Interestingly, at least two studies compared multiple species and reported that compared to nonmigratory species, migratory species have relatively smaller brain size (Winkler et al. 2004; Sol et al. 2005a). In addition, it has been suggested that brain size is a good indicator of behavioural flexibility, and avian species with relatively larger brains are more behaviourally flexible and more capable of behavioural and especially foraging innovations compared to species with smaller brains (Lefebre et al. 1997, 2004; Sol et al. 2005b). Thus, if migratory species have evolved migratory behaviour because they are less behaviourally flexible (at least with regards to foraging behaviour), they should have relatively smaller brain size compared to nonmigratory species, which might provide an explanation for reported differences in brain size between migratory and nonmigratory species (Sol et al. 2005a).

Sol et al. (2005a) hypothesized that some pre-existing differences in behavioural flexibility and brain size preceded the evolution of migratory/sedentary strategies (behavioural flexibility–migratory precursor hypothesis) and suggested that species with larger brains were able to evolve sedentary behaviour, whereas species with smaller brains and associated reduced behavioural flexibility evolved migratory behaviour. At least one alternative hypothesis, however, suggests that changes in brain size might have evolved in response to changes in migratory strategies and that sedentary birds have evolved larger brains because of intense selection pressure for behavioural innovations stemming from the need to survive seasonally changing environment (Winkler et al. 2004). Sol et al. (2005a) argued that this alternative hypothesis is unlikely because differences in brain size between lineages seem to have evolved before the development of recent migratory systems, although there is currently no evidence to support this view. Sol et al. (2005a) also stated that it would be impossible to test whether relative brain size is a precursor or a consequence of migratory strategies because the ancestral states of migratory behaviour are difficult to establish. There are, however, multiple potential alternative hypotheses that might explain why migratory species have smaller brain sizes than nonmigratory species. For example, migratory species might have smaller brain sizes because selection might favour a reduction in brain weight and energy expenditure related to larger brain, which would make long-distance migration more efficient, whereas sedentary species might have evolved larger brains because of no limiting selection on brain size related to migratory behaviour. Alternatively, sedentary species might have evolved a larger brain size because of increased selection pressure for behavioural/foraging innovations, which would increase fitness of birds living in seasonally changing environments, whereas migratory species might have evolved a smaller brain size because they do not require cognitive skills related to behavioural/foraging innovations. There may be more alternative hypotheses, but none of them has been tested so far.

Here, we specifically tested the behavioural flexibility-migratory precursor hypothesis using a model system in which the ancestral migratory state appears to be well established. We compared telencephalon volume (both absolute and relative to body mass) in three subspecies of the white-crowned sparrow, *Zonotrichia l. gambelii* and *Z. l. oriantha*, which show ancestral migratory behaviour, and *Z. l. nuttalli*, which is strictly sedentary. There are five recognized subspecies of the white-crowned sparrow; four of them are migratory and only one, *Z. l.*

nuttalli is nonmigratory. The rufous-collared sparrow, *Zonotrichia capensis*, which has both migratory and nonmigratory populations, is considered the ancestral form for all other *Zonotrichia* species (Zink et al. 1991; Zink & Blackwell 1996). The white-crowned sparrow, *Zonotrichia leucophrys*, on the other hand, appears to be the youngest species together with the migratory golden-crowned sparrow, *Z. atricapilla*. Two *Zonotrichia* species that have also been assumed to be ancestral to *leucophrys* are migratory species: the Harris' sparrow, *Z. querula* and the white-throated sparrow, *Z. albicollis* (Zink et al. 1991; Zink & Blackwell 1996). In addition, all species ancestral to *Zonotrichia* are migratory (*Junco* sp., *Pipilo* sp., *Melospiza* sp., *Passerella* sp.; Sibley & Ahlquist 1990; Zink & Blackwell 1996). Thus, the common ancestor of *Z. leucophrys* was probably migratory (Zink 2002). Within the white-crowned sparrow, *Z. l. nuttalli* and *Z. l. pugetensis* appear to be the most recent subspecies, whereas migratory *Z. l. gambelii* and *Z. l. oriantha* have an earlier origin (Sibley & Ahlquist 1990), which suggests that the ancestors of *Z. l. nuttalli* were also migratory and that the sedentary habits of *Z. l. nuttalli* evolved later. Interestingly, nonmigratory *Z. l. nuttalli* still express migratory restlessness at night during times of regular migration for migratory subspecies (Mewaldt et al. 1968; Smith et al. 1969), which strongly suggests that they still carry migration-related genes inherited from their migratory ancestors (Rappole 2003). Thus, potential differences in brain size between *Z. l. nuttalli* and the two migratory subspecies are likely to be a result of the switch from migratory habits to sedentary habits. Both *Z. l. gambelii* and *Z. l. oriantha* show typical migratory behaviour, migrating hundreds to thousands of kilometres between breeding and wintering grounds every year (Chilton et al. 1995). *Zonotrichia l. nuttalli*, on the other hand, is strictly sedentary and resides permanently within the same areas along the coastline of California, U.S.A. (Chilton et al. 1995). All other features of ecology such as social structure, breeding and foraging ecology appear to be extremely similar between these subspecies, and thus, the only striking difference between them seems to concern migratory tactics (Chilton et al. 1995). Thus these three subspecies present an excellent model to test the behavioural flexibility–migratory precursor hypothesis because their migratory behaviour falls within clear migratory/sedentary strategies and their ancestral state seems to be well known.

METHODS

We used brains of 13 migratory *Z. l. gambelii* captured in October 2004 near Davis, California, 13 nonmigratory *Z. l. nuttalli* captured in October 2004 in Sonoma county, northern California, and 20 migratory *Z. l. oriantha* captured in August 2004 in northern California. All birds were weighed upon capture and subspecies were identified using plumage and bill coloration in addition to trapping locations (Chilton et al. 1995). All birds were sacrificed within a few days after capture for the brain analyses. There are no data on seasonal variation in brain size in white-crowned sparrows, but work on song sparrows, *Melospiza melodia*, found no seasonal variation in telencephalon volume (Lee et al. 2001). Two subspecies in our study were collected at the same time, but the third subspecies was collected almost 2 months earlier. While we cannot rule out seasonal differences in brain size between these three subspecies, such differences seem unlikely. These sparrows were trapped as part of different projects investigating spatial memory and the hippocampus (Pravosudov et al. 2006; K. Sanford, T. P. Hahn & V. V. Pravosudov, unpublished), but these data also allowed us to test the behavioural flexibility–migratory precursor hypothesis for the evolution of overall brain size. Brain preparation procedures were identical for all three subspecies (Pravosudov et al. 2006). Sparrows were anaesthetized with nembutal-sodium solution and perfused transcardially with 4% paraformaldehyde in phosphate buffer. After perfusion, birds were decapitated and their brain was removed from the skull and placed in 4% paraformaldehyde for 1 week. The brains were cryoprotected in a 30% sucrose solution, frozen on dry ice and kept at −70°C until processing. We cut coronal sections at 40 μm on a sliding, freezing microtome. All details of perfusions and brain preparations have been described previously (Pravosudov et al. 2002, 2006; Pravosudov & Clayton 2002; Pravosudov & Omanska 2005a, b). All brain sections were processed using identical standard procedures to insure consistency of our comparisons.

We used StereoInvestigator software (version 3.15a, Microbrightfield, Colchester, VT) for all stereological measurements. We used the Cavalieri principle (Gunderson & Jensen 1987) to measure the volume of the hippocampus and the rest of the telencephalon on Nissl-stained sections (Pravosudov et al. 2006). The Cavalieri method is an unbiased stereological technique used to measure the volume of various structures, and it provides an alternative to older structure-tracing methods (Gunderson & Jensen 1987). This method has proven to be very reliable in estimating brain volumes in small passerines with extremely low measurements errors (Pravosudov et al. 2002, 2006; Pravosudov & Clayton 2002; Pravosudov & Omanska 2005a, b). To estimate hippocampal volume, we used grid size of a 200 μm and we measured every 12th section; sections were 480 μm apart. For telencephalon measurements, we used a 1142.86-μm grid for *Z. l. nuttalli* and *Z. l. gambelii* and a 1200-μm grid for *Z. l. oriantha*. For *Z. l. nuttalli* and *Z. l. gambelii*, we measured every 12th section, and sections were 480 μm apart, whereas for *Z. l. oriantha*, we measured every 16th section, and sections were 640 μm apart.

To calculate the total volume of the telencephalon, we combined our volume measurements for the hippocampus and the rest of the telencephalon, because these data were initially collected separately to investigate whether migratory behaviour was related to enhanced spatial memory and an enlarged hippocampus (Pravosudov et al. 2006; Sanford et al., unpublished data). We used an ANOVA to test for significant differences between migratory and nonmigratory subspecies in total telencephalon volume. To compare relative telencephalon volume, we used a general linear model (GLM) with subspecies as a fixed factor and body mass as a covariate in all analyses. All assumptions for these statistical tests were met.

RESULTS

Body mass differed significantly between the three subspecies of white-crowned sparrow ($F_{2,43} = 7.9$, $P < 0.01$). Planned comparisons analyses showed that mean ± SD body mass of migratory *Z. l. oriantha* (28.6 ± 3.11 g) was significantly greater than that of the other two subspecies ($P < 0.05$), but there were no significant differences in body mass between migratory *Z. l. gambelii* (24.58 ± 2.89 g) and nonmigratory *Z. l. nuttalli* (25.92 ± 2.81 g) ($P = 0.26$). Telencephalon volume relative to body mass also differed significantly between the three subspecies ($F_{2,\ 42} = 9.7$, $P < 0.001$; Table 1). Planned comparisons analyses showed that compared to both migratory *Z. l. gambelii* and *Z. l. oriantha*, nonmigratory *Z. l. nuttalli* had significantly larger relative telencephalon volume ($P < 0.01$), whereas relative telencephalon volumes of migratory *Z. l. gambelii* and *Z. l. oriantha* were statistically indistinguishable ($P = 0.5$; Table 1). Body mass was not a significant predictor of the telencephalon volume ($F_{1,\ 42} = 0.01$, $P = 0.92$), and results of analyses of absolute telencephalon volume were similar to those of relative telencephalon volume: nonmigratory *Z. l. nuttalli* had significantly larger absolute telencephalon volume compared to migratory *Z. l. gambelii* and *Z. l. oriantha* ($P < 0.01$), whereas there were no significant difference in absolute telencephalon volume between the two migratory subspecies ($P = 0.41$; Table 1).

DISCUSSION

Our results showed that the sedentary behaviour of *Z. l. nuttalli* derived from migratory ancestors was associated with enlarged brain size, suggesting that brain enlargement might have occurred in a subspecies with migratory ancestry. These results contradict the behavioural flexibility (and enlarged brain)–migratory precursor hypothesis (Sol et al. 2005a) and suggest that brain size might have evolved as a consequence of evolutionary changes in behavioural strategies in these birds. Irrespective of whether sedentary habits of *Z. l. nuttalli* are simply a result of migratory suppression caused by ecological conditions (e.g. Rappole 2003) or have indeed evolved from a migratory ancestor, the relatively larger brain size of these nonmigratory birds suggests that selection pressures associated with a specific migratory or nonmigratory strategy have influenced the evolution of brain size in white-crowned sparrows. The presence of nocturnal migratory restlessness in *Z. l. nuttalli*, which is strictly sedentary, only strengthens our conclusion that brain size is affected by current behavioural strategies and that large brain size was not a precursor for the development of a sedentary strategy.

Previously, Pravosudov et al. (2006) reported that compared to nonmigratory *Z. l. gambelii*, migratory *Z. l. nuttalli* have larger hippocampal volume relative to the remainder of the telencephalon and more hippocampal neurons, suggesting that migratory behaviour might provide high selection pressure on spatial memory and the hippocampus. Such results, combined with the findings of the current study, suggest that migratory strategies might provide opposite selection pressures on different parts of the brain responsible for different functions (Pravosudov et al. 2006). While migratory species might benefit from enhanced spatial memory associated with an enlarged hippocampus, the costs of maintaining larger hippocampus might outweigh such benefits in nonmigratory species. Selection pressures on total brain size, however, show the opposite pattern and appear to favour reduced brain size in migratory species and/or increased brain size in nonmigratory species.

Our comparison concerns only three subspecies, and therefore, it is quite limited in scope. However, even one example should be sufficient to falsify a general hypothesis such as the behavioural flexibility–migratory precursor hypothesis. This hypothesis clearly states that brain size was a precursor to the evolution of migratory/sedentary strategies (Sol et al. 2005a). In contrast, our results demonstrate that larger brain size appears to have evolved in a formerly migratory subspecies, suggesting that brain size was not a precursor to the evolution of sedentary behaviour in *Z. l. nuttalli*. Thus, the strength of our comparison mainly concerns falsifying the behavioural flexibility-migratory precursor hypothesis rather than establishing a specific alternative hypothesis.

Unfortunately, there are no data on differences in behavioural flexibility between the compared subspecies and so our comparison rests only with brain size data. However, because our study involved different subspecies of the same species, differences in behaviours between these subspecies (other than migratory behaviour) appear to be minimal (Chilton et al. 1995). In particular, social and mating tactics, which might also affect the evolution of brain size, appear to be extremely similar in all three subspecies (Chilton et al. 1995). While it is impossible to rule out all differences between these well-studied subspecies, difference in migratory tactics appears to be the major one (Chilton et al. 1995).

Evidence from another species, dark-eyed junco, *Junco hyemalis*, which has migratory and nonmigratory populations, also seem to support our conclusions. Absolute brain measurements presented in Cristol et al. (2003) suggest that nonmigratory *J. h. carolinensis* have significantly larger telencephalon volumes than do migratory *J. h. hyemalis*. Furthermore, nonmigratory *J. h. carolinensis* that are truly sedentary have significantly larger telencephalon volumes than do *J. h. carolinensis* that move short distances during winter (Cristol et al. 2003). Phylogeny data suggest that ancestors of dark-eyed juncos were migratory, because species that diverged basal to dark-eyed juncos (*Melospiza* spp., *Pipilo* spp., *Passerella* spp.) are all migratory (Sibley & Ahlquist 1990; Zink & Blackwell 1996). Thus, dark-eyed juncos might present another example in which secondarily derived sedentary behaviour appear to correlate with larger brain size, suggesting that larger brains might have evolved to support sedentary habits rather than brain size being a precursor to evolution of migratory behaviour.

Thus, our results suggest that the evolution of sedentary behaviour in Nuttall's white-crowned sparrows was likely shaped by ecological factors independent of pre-existing brain size. Different behavioural strategies, on the other hand, might have provided different selection pressure on behavioural flexibility and brain size, resulting in their gradual evolution following the divergence in such strategies.

Maintaining a large brain appears to be energetically expensive (Armstrong & Bergeron 1985), so selection might favour a decrease in brain size when the cognitive skills associated with large brain size do not increase fitness. Alternatively, the lower energetic costs associated with reductions in overall brain size or relative brain size to body mass may have been favoured by natural selection in migratory species (Winkler et al. 2004). Consequently, migrants may have gradually lost their behavioural innovation capabilities as a result of a gradual decrease in brain size. A sedentary strategy, on the other hand, appears to favour behavioural and foraging innovations, and thus, selection pressure for these traits might result in a gradual increase in brain size in nonmigrants. While our results are consistent with this hypothesis, they do not allow us to rule out other alternative hypotheses. For example, migratory species may maintain a relatively smaller brain size because of the high selection pressure associated with migratory behaviour, but once such pressure has been removed (e.g. as a result of a switch to sedentary life style), these species might evolve larger brains. Thus, many potential alternative hypotheses remain viable, and our results do not allow us to differentiate between them. Irrespective of the causes for the differences in brain size and migratory strategy of migratory and nonmigratory subspecies, our results suggest that the changes in brain size occurred following the changes in behaviour. Our results contradict the behavioural flexibility-migratory precursor hypothesis, which states that the evolution of behaviour followed differences in brain size.

Our results also argue against the hypothesis that main differences in brain size between the lineages have evolved early in evolutionary history, which preceded formation of current migratory systems (Sol et al. 2005a). In our study, a sedentary subspecies appears to have evolved a larger brain size fairly recently compared to the evolution of migratory behaviour in its ancestral species/subspecies which suggests that the evolution of brain size might potentially occur at any time under prevailing selection pressures. More comparisons of species and subspecies with known migratory ancestry are necessary to elucidate general mechanisms of the evolution of brain size in birds.

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Table 1

Telencephalone volume (absolute and relative to body mass) in three subspecies of the white-crowned sparrow. Results presented as least square means from General Linear Models with standard errors.

Subspecies	**Absolute volume, mm^3**	**Volume relative to body mass, mm^3**	**n**
Z. l. gambelii	513.4 ± 18.0	512.7 ± 19.6	13
Z. l. oriantha	494.0 ± 14.5	494.7 ± 16.0	20
Z. l. nuttalli	598.1 ± 18.0	597.8 ± 18.4	13