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

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Migratory birds appear to have relatively smaller brain sizes 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 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; neuroethology; 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 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 a 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 a relatively smaller brain

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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 regard to foraging behaviour), they should have a 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 they 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 a 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 leucophrys 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* spp., *Pipilo* spp., *Melospiza* spp., *Passerella* spp.; 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