# Environmental Influences on Neuromorphology in the Non-Native Starling *Sturnus vulgaris*

Adam P.A. Cardilini[a, b]    Sarah Micallef[a, b]    Valerie R. Bishop[c]
Craig D.H. Sherman[a, b]    Simone L. Meddle[c]    Katherine L. Buchanan[a, b]

[a]Deakin University, Geelong, VIC, Australia; [b]School of Life and Environmental Sciences, Centre for Integrative Ecology (Waurn Ponds Campus), Waurn Ponds, VIC, Australia; [c]The Roslin Institute, The Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush Campus, Midlothian, UK

**Abstract**

Cognitive traits are predicted to be under intense selection in animals moving into new environments and may determine the success, or otherwise, of dispersal and invasions. In particular, spatial information related to resource distribution is an important determinant of neural development. Spatial information is predicted to vary for invasive species encountering novel environments. However, few studies have tested how cognition or neural development varies intraspecifically within an invasive species. In Australia, the non-native common starling *Sturnus vulgaris* inhabits a range of habitats that vary in seasonal resource availability and distribution. We aimed to identify variations in the brain mass and hippocampus volume of starlings in Australia related to environmental variation across two substantially different habitat types. Specifically, we predicted variation in brain mass and hippocampal volume in relation to environmental conditions, latitude, and climatic variables. To test this, brain mass and volumes of the hippocampus and two control brain regions (telencephalon and tractus septomes-encephalicus) were quantified from starling brains gathered from across the species' range in south eastern Australia. When comparing across an environmental gradient, there was a significant interaction between sex and environment for overall brain mass, with greater sexual dimorphism in brain mass in inland populations compared to those at the coast. There was no significant difference in hippocampal volume in relation to environmental measures (hippocampus volume, $n = 17$) for either sex. While these data provide no evidence for intraspecific environmental drivers for changes in hippocampus volume in European starlings in Australia, they do suggest that environmental factors contribute to sex differences in brain mass. This study identifies associations between the brain volume of a non-native species and the environment; further work in this area is required to elucidate the mechanisms driving this relationship.

© 2018 The Author(s)
Published by S. Karger AG, Basel

Adam P.A. Cardilini
Deakin University, Faculty of SEBE
75 Pigdons Rd
Waurn Ponds, VIC 3216 (Australia)
E-Mail a.cardilini@gmail.com

## Introduction

To succeed in new, challenging environments, animals must utilize complex spatial information, as well as learn and retain the location of key resources which are essential for their survival and reproduction [Sol et al., 2005]. A range of factors dictates such cognitive abilities, including the development of the brain, along with the associated internal structures, which are associated with particular tasks [Lefebvre et al., 2004]. At the species level brain size is commonly, though contentiously, linked to the ability to process and store complex social and spatial information [Healy and Rowe, 2007]. Comparative studies in birds have documented the potential impact of social groupings, sexual selection, breeding group composition, or developmental mode on brain size [Iwaniuk and Arnold, 2004; Garamszegi et al., 2005; Emery, 2006; Willemet, 2013]. Together, such studies highlight the complexity of the selective forces at work causing these intriguing interspecific differences in brain size. Across species, relative brain size presumably represents the outcome of contrasting selection on cognitive capacity, while the increased associated metabolic demands may [Clarke and Sokoloff, 1999] or may not [Isler and van Schaik, 2006] represent a biologically meaningful constraint on brain size.

Invasive species have particular challenges, as arriving in new environments involves selection on phenotypic characteristics which promote survival, dispersal, and rapid reproduction [Blackburn et al., 2009]. It seems reasonable therefore to suppose that the evolutionary forces acting to select invasive phenotypes also affect neuromorphology. One interspecific study comparing a large number of historic avian introduction events concluded that, at least for birds, invaders that are more successful tend to be species with relatively larger brains [Sol et al., 2005]. Not only this, but analyses suggested that their ability to succeed was linked to their ability to innovate, suggesting that cognitive mechanisms are involved in determining the success of invasions [Sol et al., 2005]. The challenges of invasions are exacerbated in highly variable environmental conditions, because environmental heterogeneity is associated with a need to retain both spatial and temporal information, potentially over large scales. This "cognitive buffer hypothesis" [Sol, 2009] suggests that larger brains allow animals to withstand seasonal or spatial variation in resource availability. Consistent with this interpretation, South American parrot species inhabiting climatically more variable environments tend to have larger brain sizes [Schuck-Paim et al., 2008]. However, there are a number of problems associated with such broad interspecific comparisons [Gonda et al., 2013]. First, different species inhabit different environmental conditions and so the impact of environmental variables on neural development may not be comparable. Second, understanding the nature of the biological impact is difficult when comparing neuromorphology at the gross level of absolute brain mass, which seems unlikely to directly control any single cognitive trait.

The first of these problems can be tackled through intraspecific studies assessing how neuromorphology is selected across environmental gradients. For example, examining variation in the morphology of chickadee populations across a gradient of climate predictability, Kozlovsky et al. [2014] showed that populations living in hasher environmental conditions have larger brains. Interestingly, they also found that, across populations, there was a strong negative relationship between brain mass and the mass of the digestive tract. They interpret these data in line with the "expensive tissue hypothesis" which suggests an energetic trade-off between the development and maintenance of brain and digestive tract investment. However, looking across bird species, there appears to be only weak support for this hypothesis [Isler and van Schaik, 2006].

As a way of addressing the second of these problems, researchers have tried to look at key areas in the brain associated with known cognitive tasks. The role of the hippocampus has been extensively studied in food-caching birds [Sherry et al., 1992; Healy et al., 1994; Lee et al., 1998]. Despite some interesting inconsistencies [Garamszegi and Lucas, 2005], it seems that, both within [Pravosudov et al., 2006] and between species [Sherry et al., 1992], a greater use of spatial memory is associated with a more developed hippocampus [Biegler et al., 2001]. Hippocampal development seems to be driven by evolutionary pressures related to the value of spatial information in relation to resource availability, whether it is food, reproductive opportunity, or some other limiting resource [Mayer et al., 2013]. Associations between a relatively larger hippocampus volume and/or a better performance of spatial tasks [Healy et al., 2005] have been criticized for making the assumption that size relates to better functional outcomes [Roth et al., 2010]. However, recent studies have sought to relate functional outcomes to measures of neuron generation and synapse formation with promising results [Barnea and Pravosudov, 2011]. It has been proposed that interpopulation comparisons within species, where populations differ in clearly defined ecological variables, represent a powerful way to test the ecological processes driving hippocampus evolution [Pravosudov and Clayton, 2002; Pravosudov and Roth, 2013].

Cardilini/Micallef/Bishop/Sherman/
Meddle/Buchanan

In this study we sought to address the evolutionary pressures leading to changes in brain size and hippocampal development across the range of an invasive species. The common starling *Sturnus vulgaris* was introduced into Australia at several locations in the mid to late 1800s [Long, 1981] and has since spread to encompass a range of environments across Australia's east coast. At the landscape scale this distribution covers areas which differ in habitat suitability and also in environmental predictability. On the eastern coastline of New South Wales, Australia, starlings inhabit landscapes characterized by highly productive pastures, while those living inland at the range edge encounter arid landscapes with a much reduced degree of agricultural development and patchily placed, unpredictable resources [Higgins et al., 2006]. Significant variation in morphological parameters has been identified in contemporary populations across environmental clines [Cardilini et al., 2016]. Potentially, multiple processes may influence neuromorphology in starlings over habitats with significant environmental variation, driven by differences in resource distribution and predictability between habitats [Schuck-Paim et al., 2008; Kozlovsky et al., 2014]. Coastal populations have higher densities of starlings and are characterized by wetter conditions with the suggestion that foraging resources may be more widely distributed. In comparison, populations along the edge of the inland range are sparser, subject to drier conditions and they are likely to encounter more patchily distributed food resources. To the best of our knowledge no study has ever tested the impact of environmental variables on the evolution of brain morphology within an invasive species. Consequently, the aim of this study was to determine whether the brain size and hippocampus volume of starlings in south eastern Australia is significantly related to environmental variations in climatic variables.

## Materials and Methods

### Sample Collection

Adult starlings (30 females and 38 males) were collected from 8 localities from across eastern Australia (minimum and maximum distance between sites: 210 and 990 km) between April 28 and June 2, 2012 (Fig. 1; Table 1). Birds were shot with a shotgun loaded with birdshot. Global positioning system (GPS) coordinates were taken at the collection site of each individual. Collections were made at eight sites in New South Wales in wet productive landscapes at the center of the starling range, and "inland" at three sites on the edge of the starlings range in semiarid landscapes of low productivity. Immediately after collection the birds were decapitated and their heads were placed in individual plastic containers of formaldehyde solution (36.5–38% in $H_2O$; Sigma-Aldrich®); care was taken to
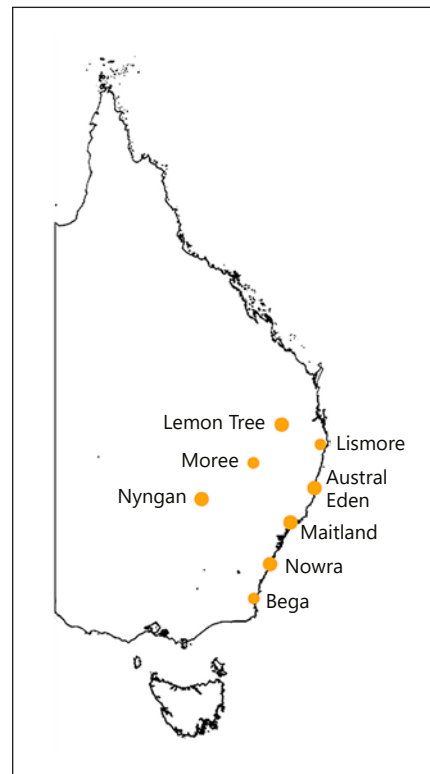


**Fig. 1.** Map of eastern Australia where the circles represent collection localities and the size of the circles represents the number of samples collected. The number of samples ranged from 8 to 10.

ensure that the entire head was submerged in excess formaldehyde. The heads were left to fix for a minimum of 1 month at 4°C. Each brain was then extracted from the skull and placed in a new container of formaldehyde and stored at 4°C.

### Morphological and Environmental Data

Body mass (±0.1 g) was recorded upon collection (before removing the head) and used as a proxy for size. The scaled mass index, a proxy for body condition, was calculated following Peig and Green [2009], referred to below as "body condition." The scaled mass index relates individual mass and tarsus length with population values and has been shown to be a good proximate measure of body condition [Peig and Green, 2010]. Sex was determined anatomically. For samples where anatomical information was not available, genetic sexing was used [Fridolfsson and Ellegren, 1999]; see online supplementary File 1 for specific details (for all online suppl. material, see www.karger.com/doi/10.1159/000491672). The wet brain mass following fixation was measured using analytical scales (±0.001 g). Environmental variables included latitude (°S), which was derived from GPS coordinates. For each sample, location climatic variables were extracted from Bioclim data sets (bio01–19) [Hijmans et al., 2005] and aridity data was extracted from the CGIAR-CSI Global-Aridity and Global-PET Geospatial Database [Zomer et al., 2007, 2008]. The "raster" package in R was used to extract the climate and aridity data [Hijmans, 2015].

**Table 1.** Collection locality co-ordinates and the number of samples from each locality, by sex

| Collection locality | Latitude | Longitude | Transect | Brains (female, male), n | Sectioned brains (female, male), n |
|---|---|---|---|---|---|
| Bega | 36.618 | 149.871 | Coastal | 1, 2 | 1, – |
| Nowra | 34.875 | 150.691 | Coastal | 4, 6 | –, 3 |
| Maitland | 32.761 | 151.720 | Coastal | 6, 4 | 1, 3 |
| Austral Eden | 31.014 | 152.938 | Coastal | 6, 4 | 2, 1 |
| Lismore | 28.799 | 153.238 | Coastal | 5, 3 | 2, 3 |
| Nyngan | 31.572 | 147.230 | Inland | 3, 6 | –, 6 |
| Moree | 29.736 | 149.846 | Inland | 2, 6 | 1, 4 |
| Lemon Tree | 27.790 | 151.281 | Inland | 3, 7 | –, 1 |
| Total | | | | 30, 38 | 7, 21 |

*Sectioning and Methods*

A subset of 28 brains (7 female and 21 male; Table 1; limited by funding) was cryoprotected in sucrose solution in 0.1 M phosphate buffer (15% followed by 30% sucrose; both for 24 h at 4°C). Brains were then frozen on dry ice and stored at –80°C until sectioning. Brains were coronally sectioned at 60 μm using a freezing microtome. All sections were mounted on gelatinized microscope slides and then stained with hematoxylin and eosin and serially dehydrated through ethanol and coverslipped with DPX mountant (Sigma, St. Louis, MO, USA). Slides were scanned on a Nikon COOLSCAN V ED slide scanner (LS-50ED; resolution = 4,800 dpi true optic resolution, saved to an 8-bit grey scale) and the resulting images were analysed using ImageJ (version 1.49n). There was no magnification at scanning, only during image analysis. Brain region volumes (mm³) were calculated from the sequential areas of each region across the slides ($V = tx_i + tx_{i+1} + ... + t_{xi+n}$; where V is volume and t is section depth [0.06 mm] and x is the measured area of the section). The volumes (mm³) of the left and right hemispheres of each of the following regions were calculated: telencephalon, hippocampus, and tractus septomesencepahlicus (TrSM) [Stokes et al., 1976]. The telencephalon and the TrSM were included as control regions in order to compare with the hippocampus. Where a section of brain was not measured, the measurement of the proceeding section was used in its place. For the hippocampal, TrSM, and telencephalon regions, respectively, an average of 54, 86, and 53% of all sections were measured and used to reconstruct the volume. Hippocampus and telencephalon volumes were calculated from up to 30 sections; the telencephalon volume included the hippocampus volume. To assess the repeatability of the image analysis each brain region was remeasured 3 times in 37 sections. The results showed that this measurement technique was reliable to ±0.02 pixels/mm.

*Statistical Analysis*

A principle component analysis, including all Bioclim variables and aridity, was run to help determine the environmental difference between collection localities. A principle component analysis plot showed clear environmental differences between collection localities (online suppl. Fig. 1). The first principle component (PC1), which explained 68.2% of the environmental variation, was used as a composite environmental measure for testing the effect of environmental variation on brain measurements (online suppl. Table 1). PC1 represented variations in temperature and rainfall seasonality, with negative values indicating colder, wetter environments within collection localities along the coast and positive values indicating drier, hotter environments inland. We use the terms "coast" and "inland" to refer to two environmentally distinct groupings of collection localities. The principle component analysis was run in R using the "prcomp()" function [R Team, 2015].

The effects of sex, PC1, and latitude on individual mass and body conditions were tested using multivariate linear regression models.

A multivariate linear regression model was used to test the influence of PC1 on individual brain mass. Bird mass was also included in the model as an independent covariate. An interaction term of sex and PC1 was included in the model to test differences in response between sexes.

There was no significant difference between the volumes of the right and left hemispheres ($p = 0.540$), so measures were combined to create a total volume which was used as the dependent variable in linear regression models testing the relationship between brain regions and PC1. Where only one side of a region had an estimated volume, the sample was excluded from analysis. PC1 and sex were included in the models as independent variables for the hippocampus and the TrSM. To test for the effect of brain size, telencephalon volume was included along with the other standard independent variables (PC1 and sex) in an alternative model. Models testing telencephalon size were also run and include the same independent variables as those included for hippocampus and TrSM models, except that bird mass was included as an independent variable. We found no relationship when testing the effect of an interaction between sex and PC1 on brain region volume; we chose to exclude the interaction term from brain region models to reduce the number of independent variables being tested with small sample sizes. Results were considered significant if the p value was less than 0.05. Complete brain region section data was not available for all samples, which resulted in different sample sizes for the analysis of each brain region (online suppl. Table 2).

We also tested transect for all response variables and found the same results as PC1. We were unable to separate the effects of location versus environmental variables and chose to focus on environmental variation in the Discussion.

Before running the models all of the variables were normalized around a mean of zero and with an SD of 1 to make parameter estimates comparable. All analyses were conducted in the statistical software R, using base functions, and models were run using the "lm()" function (R Core Team, 2015). Figures were produced using the graphical package "ggplot2" [Wickham, 2009].

## Results

Males were significantly heavier than females in terms of body mass (30 females, mean 75.35 g, range 66.8–83.3 g; 38 males, mean 79.76 g, range 68.8–88 g; estimate = 0.909, SE = 0.227, $t_{64} = 4.012$, $p < 0.001$, $R^2 = 0.176$). Starling body mass was not significantly related to PC1 (esti-

**Table 2.** Output of the linear regression model testing the relationship between environmental variables and starling relative and absolute brain mass

| Response variable | Predictor variable | Estimate | SE | T value | p value |
|---|---|---|---|---|---|
| Relative brain mass | Intercept | −0.662 | 0.177 | −3.733 | <0.001 |
| n = 68 samples | **Sex × PC1** | **0.713** | **0.218** | **3.276** | **0.002** |
| $R^2$ = 0.315 | **Sex** | **1.040** | **0.243** | **4.285** | **<0.001** |
| df = 64 | **PC1** | **−0.407** | **0.174** | **−2.337** | **0.023** |
| | Mass | 0.025 | 0.120 | 0.211 | 0.833 |
| Absolute brain mass | Intercept | −0.677 | 0.161 | −4.205 | <0.001 |
| n = 68 samples | **Sex × PC1** | **0.719** | **0.214** | **3.356** | **<0.001** |
| $R^2$ = 0.325 | **Sex** | **1.063** | **0.214** | **4.975** | **<0.001** |
| df = 64 | **PC1** | **−0.415** | **0.169** | **−2.466** | **0.016** |

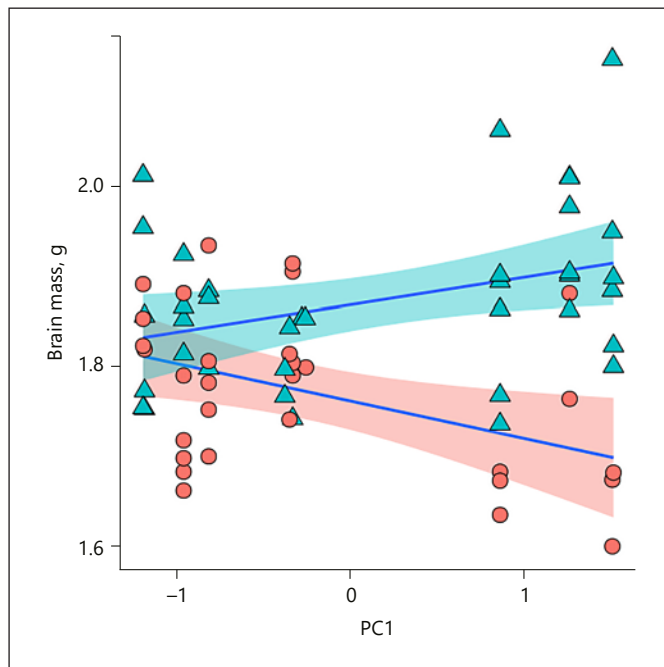Variables in bold indicate those with a p value below 0.05.



**Fig. 2.** Lines represent the predicted values from a multivariate linear regression model testing the relationship between brain mass as the dependent variable, sex × PC1 as an interaction term, and bird mass as an independent variable. Circles represent females and triangles represent males. The points represent the real brain mass values.

$t_{60}$ = −0.128, $p$ = 0.898, $R^2$ < 0.001), environment (estimate = −0.158, SE = 0.137, $t_{60}$ = −1.154, $p$ = 0.253), or latitude (estimate = −0.236, SE = 0.146, $t_{60}$ = −1.624, $p$ = 0.110).

The variation in relative and absolute brain mass was explained by a significant interaction between sex and PC1, with males having heavier brains than female starlings. This sexual dimorphism in brain mass was more pronounced in inland populations. Inland males had heavier brains than coastal males, whereas inland females had lighter brains than coastal females (Table 2; Fig. 2; brain mass by PC1 within each sex; females, $p$ = 0.017, $R^2$ = 0.159; males, $p$ = 0.031, $R^2$ = 0.098). There was no relationship between brain mass and body size or latitude (Table 2). Brain mass did not show a relationship with body condition (estimate = −0.067, SE = 0.116, $t_{59}$ = −0.581, $p$ = 0.564, $R^2$ = 0.301) when controlling for an interaction of sex and PC1.

Hippocampus volume did not show a significant relationship with PC1 or sex (Table 3). There was a trend for TrSM to be larger with higher values of PC1 and it was significantly larger in brains with greater telencephalon volume, but there was no relationship with sex (Table 3). Telencephalon showed no indication of a relationship with PC1 (Table 3).

### Discussion

mate = −0.163, SE = 0.123, $t_{64}$ = −1.328, $p$ = 0.189) and there was no relationship between body mass and latitude (estimate = 0.052, SE = 0.135, $t_{64}$ = 0.388, $p$ = 0.699). Body condition did not vary significantly between sexes (29 female and 35 male birds; estimate = −0.032, SE = 0.2505,

Species that can invade successfully require the ability to innovate [Diquelou et al., 2015] and, as such, need a range of motor and cognitive skills to be able to thrive in challenging, novel environments [Sih et al., 2011; Griffin et al., 2014]. The ability to respond to new environmental

**Table 3.** Output of linear regression models testing the relationship between environmental variables and the volume of starling brain regions

| Response variable | Predictor variable | Estimate | SE | *t* value | *p* value |
|---|---|---|---|---|---|
| Hippocampus volume[a] | Intercept | −0.015 | 0.211 | −0.073 | 0.943 |
| *n* = 17 samples | **Telencephalon volume** | **0.653** | **0.239** | **2.732** | **0.017** |
| $R^2$ = 0.242 | PC1 | −0.327 | 0.235 | −1.394 | 0.187 |
| df = 13 | Sex | −0.113 | 0.234 | −0.484 | 0.636 |
| Hippocampus volume[b] | Intercept | <−0.001 | 0.245 | −0.003 | 0.998 |
| *n* = 18 samples | PC1 | −0.136 | 0.266 | −0.512 | 0.616 |
| $R^2$ = −0.074 | Sex | 0.216 | 0.256 | 0.845 | 0.411 |
| df = 15 | | | | | |
| TrSM volume[a] | **Intercept** | **0.689** | **0.180** | **3.825** | **0.003** |
| *n* = 14 samples | **Telencephalon volume** | **0.424** | **0.184** | **2.304** | **0.044** |
| $R^2$ = 0.310 | PC1 | −0.457 | 0.213 | −2.139 | 0.058 |
| df = 10 | Sex | 0.3114 | 0.210 | 0.544 | 0.598 |
| TrSM volume[b] | Intercept | −0.039 | 0.206 | −0.188 | 0.852 |
| *n* = 25 samples | PC1 | −0.134 | −0.238 | −0.564 | 0.579 |
| $R^2$ = −0.027 | Sex | −0.149 | 0.240 | −0.618 | 0.543 |
| df = 22 | | | | | |
| Telencephalon volume[a] | Intercept | −0.012 | 0.199 | −0.159 | 0.954 |
| *n* = 17 samples | **Brain mass** | **0.707** | **0.259** | **2.728** | **0.017** |
| $R^2$ = 0.422 | PC1 | −0.032 | 0.240 | −0.133 | 0.896 |
| df = 13 | Sex | 0.054 | 0.233 | 0.233 | 0.819 |
| Telencephalon volume[b] | Intercept | <0.001 | 0.231 | 0.000 | 1.000 |
| *n* = 17 samples | Mass | −0.018 | 0.411 | −0.045 | 0.965 |
| $R^2$ = 0.092 | PC1 | 0.286 | 0.306 | 0.936 | 0.366 |
| df = 13 | Sex | 0.385 | 0.344 | 1.120 | 0.283 |

Models with and without volumetric controls are included. [a] With volumetric control. [b] Without volumetric control. Variables in bold indicate those with a *p* value below 0.05.

challenges with innovative behaviors is likely to influence survival and the chance of successful reproduction in the new range. Interspecific comparisons suggest that this ability is thought to be in part determined by overall brain size [Sol et al., 2005], but no study to date has tested this within the range of an invasive species. In this study, we set out to test first if there was a relationship between overall brain mass and environmental conditions for the invasive European starling in Australia. Our data show that environmental conditions have an effect on sexual dimorphism in overall brain mass in this species. Second, we predicted that hippocampal volume would vary significantly in relation to environmental variation across the starling's habitat range, but our data provide no evidence for any such pattern. This may be because selection on hippocampal volume does not occur across this spatial scale, or because there is no difference in the benefit of spatial memory between these sites. This latter possibility

seems unlikely given the differences in starling distribution across the range [West, 2008], which suggests a greater resource density in coastal populations. Finally, it may be that the sample size of the individuals measured for this study was not sufficient to be able to demonstrate any population level differences in hippocampal investment. We would argue that this is unlikely, as previous work utilizing similar sample sizes has been able to demonstrate interpopulation differences [Pravosudov et al., 2006].

Our data show (Fig. 2) that sexual dimorphism in overall brain mass increases when moving from the coast to inland starling populations. Such sexual dimorphism in brain mass has been previously reported [Casto and Ball, 1996], but our study is the first to report the influence of environmental conditions. Interpreting these differences is challenging without accompanying behavioral or dispersal data [Healy and Rowe, 2007], but there are a

Cardilini/Micallef/Bishop/Sherman/
Meddle/Buchanan

number of possible interpretations. Functionally, these sex differences in brain mass suggest that environmental conditions across the range in south eastern Australia have sex-specific effects on life history traits associated with brain structure, traits such as female natal dispersal or male song production [Bernard et al., 1993; Ball et al., 1994]. While several studies have shown that brain mass can vary between environments, it is important to note that such variation is difficult to interpret, because brain mass is a composite measure of many brain regions that may respond independently to different conditions [Healy and Rowe, 2007]. Mechanistically, it seems possible that a single unmeasured brain region contributed to the overall brain mass differences. In this population of Australian starling body mass varies with maximum temperature in accordance with Bergmann's rule [Cardilini et al., 2016], where birds are smaller in areas with hotter climatic conditions. A similar pattern (nonsignificant) was detected in this dataset and may in part underlie the increased sexual dimorphism in brain size at inland sites, where the residual brain mass is greater in males than in females.

While we were able to demonstrate sex differences in the relationship between environmental conditions and brain mass, this study found no difference in avian hippocampus volume between populations of an invasive species that inhabit environments that differ substantially in resource distribution and predictability [Morton et al., 2011]. Further work is required first to test the physiological impact of environmental stress on hippocampal development across populations of an invasive species [Pravosudov and Clayton, 2002]. Second, an integrated understanding of the costs and benefits of spatial memory is needed in order to predict the likely selection pressures working on hippocampal development in an invasive bird, but it seems possible that population differences could be used to infer the benefit of spatial information. Future research needs to be conducted to investigate potential differences in the inland habitats that might drive differences in neuromorphology and cognition.

## Disclosure Statement

All authors declare no conflict of interests in the submission of this work.

## References

Ball GF, Casto JM, Bernard DJ (1994): Sex differences in the volume of avian song control nuclei: comparative studies and the issue of brain nucleus delineation. Psychoneuroendocrinology 19:485–504.

Barnea A, Pravosudov V (2011): Birds as a model to study adult neurogenesis: Bridging evolutionary, comparative and neuroethological approaches. Eur J Neurosci 34:884–907.

Bernard DJ, Casto JM, Ball GF (1993): Sexual dimorphism in the volume of song control nuclei in European starlings: assessment by a Nissl stain and autoradiography for muscarinic cholinergic receptors. J Comp Neurol 334:559–570.

Biegler R, McGregor A, Krebs JR, Healy SD (2001): A larger hippocampus is associated with longer-lasting spatial memory. Proc Natl Acad Sci USA 98:10–13.

Blackburn TM, Lockwood JL, Cassey P (2009): Avian Invasions: The Ecology and Evolution of Exotic Birds. Oxford, Oxford University Press.

Cardilini APA, Buchanan KL, Sherman CDH, Cassey P, Symonds MRE (2016): Tests of ecogeographical relationships in a non-native species: what rules avian morphology? Oecologia 181:783–793.

Casto JM, Ball GF (1996): Early administration of 17beta-estradiol partially masculinizes song control regions and alpha2-adrenergic receptor distribution in European starlings (*Sturnus vulgaris*). Horm Behav 30:387–406.

Clarke DD, Sokoloff L (1999): Circulation and energy metabolism of the brain; in Siegel GJ, Agranoff BW, Albers RW, Fisher SK, Uhler MD (eds): Basic Neurochemistry: Molecular, Cellular, and Medical Aspects, ed 6. Philadelphia, Lippincott Williams & Wilkins.

Diquelou MC, Griffin AS, Sol D (2015): The role of motor diversity in foraging innovations: a cross-species comparison in urban birds. Behav Ecol 27:584–591.

Emery NJ (2006): Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc Lond B Biol Sci 361:23–43.

Fridolfsson AK, Ellegren H (1999): A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121.

Garamszegi LZ, Eens M, Erritzoe J, Moller AP (2005): Sperm competition and sexually size dimorphic brains in birds. Proc Biol Sci 272:159–166.

Garamszegi LZ, Lucas JR (2005): Continental variation in relative hippocampal volume in birds: the phylogenetic extent of the effect and the potential role of winter temperatures. Biol Lett 1:330–333.

Gonda A, Herczeg G, Juha M (2013): Evolutionary ecology of intraspecific brain size variation: a review. Ecol Evol 3:2751–2764.

Griffin AS, Diquelou M, Perea M (2014): Innovative problem solving in birds: a key role of motor diversity. Anim Behav 92:221–227

Healy SD, Clayton NS, Krebs JR (1994): Development of hippocampal specialisation in two species of tit (*Parus* spp.). Behav Brain Res 61:23–28.

Healy SD, De Kort SR, Clayton NS (2005): The hippocampus, spatial memory and food hoarding: a puzzle revisited. Trends Ecol Evol 20:17–22.

Healy SD, Rowe C (2007): A critique of comparative studies of brain size. Proc Biol Sci 274: 453–464.

Higgins P, Peter J, Cowling S (2006): Handbook of Australian, New Zealand and Antarctic Birds: Boatbill to Starlings. Part B: Dunnock to Starlings. Melbourne, Oxford University Press, vol 7.

Hijmans RJ (2015): raster: geographic data analysis and modeling. 2017. http://www.rspatial.org/.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005): Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978.

Isler K, van Schaik C (2006): Cost of encephalization: the energy trade-off hypothesis on birds. J Hum Evol 51:228–243.

Iwaniuk AN, Arnold KE (2004): Is cooperative breeding associated with bigger brains? A comparative test in the corvida (Passeriformes). Ethology 110:203–220.

Kozlovsky DY, Brown SL, Branch CL, Roth II TC, Pravosudov VV (2014): Chickadees with bigger brains have smaller digestive tracts: a multipopulation comparison. Brain Behav Evol 84:172–180.

Lee DW, Miyasato LE, Clayton NS (1998): Neurobiological bases of spatial learning in the natural environment: neurogenesis and growth in the avian and mammalian hippocampus. Neuroreport 9:15–27.

Lefebvre L, Reader SM, Sol D (2004): Brains, innovations and evolution in birds and primates. Brain Behav Evol 64:233–246.

Long JL (1981): Introduced Birds of the World. New York, Universe Books.

Mayer U, Watanabe S, Bischof HJ (2013): Spatial memory and the avian hippocampus: research in zebra finches. J Physiol Paris 107: 2–12.

Morton SR, Stafford Smith DM, Dickman CR, et al. (2011): A fresh framework for the ecology of arid Australia. J Arid Environ 75:313–329.

Peig J, Green AJ (2009): New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Peig J, Green AJ (2010): The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Funct Ecol 24:1323–1332.

Pravosudov VV, Clayton NS (2002): A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). Behav Neurosci 116:515–22.

Pravosudov VV, Kitaysky AS, Omanska A (2006): The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison. Proc Biol Sci 273:2641–2649.

Pravosudov VV, Roth TC (2013): Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. Ann Rev Ecol Evol Syst 44:173–193.

R Team (2015): R: A Language and Environment for Statistical Computing. Vienna, R Foundation for Statistical Computing.

Roth TC, Brodin A, Smulders TV, LaDage LD, Pravosudov VV (2010): Is bigger always better? A critical appraisal of the use of volumetric analysis in the study of the hippocampus. Philos Trans R Soc Lond B Biol Sci 365:915–931.

Schuck-Paim C, Alonso WJ, Ottoni EB (2008): Cognition in an ever-changing world: climatic variability is associated with brain size in neotropical parrots. Brain Behav Evol 71: 200–215.

Sherry DF, Jacobs LF, Gaulin SJ (1992): Spatial memory and adaptive specialization of the hippocampus. Trends Neurosci 15:64–66.

Sih A, Ferrari MCO, Harris DJ (2011): Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4:367–387.

Sol D (2009): Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biol Lett 5:130–133.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005): Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci USA 102:5460–5465.

Stokes TM, Leonard CM, Nottebohm F (1976): The telencephalon, diencephalon, and mesencephalon of the canary, *Serinus canaria*, in stereotaxic coordinates. J Comp Neurol 156: 337–374.

West P (2008): Distribution and abundance of significant invasive vertebrate pests; in Assessing Invasive Animals in Australia. Bruce, Invasive Animals Cooperative Research Centre, pp 21–56.

Wickham H (2009): ggplot2: Elegant Graphics for Data Analysis. New York, Springer.

Willemet R (2013): Reconsidering the evolution of brain, cognition, and behavior in birds and mammals. Front Psychol 4:1–26.

Zomer RJ, Bossio DA, Trabucco A, Yuanjie L, Gupta DC, Singh VP (2007): Trees and Water: Smallholder Agroforestry on Irrigated Lands in Northern India. Colombo, International Water Management Institute, pp 45.

Zomer RJ, Trabucco A, Bossio DA, van Straaten O, Verchot LV (2008): Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agric Ecosyst Environ 126:67–80.