



Allometric brain reduction in an insular, dwarfed population of black-tailed deer

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Abstract

Insular populations of mammals have been shown to undergo drastic morphological changes relative to mainland counterparts, and these adaptations can provide insight into the evolutionary effects of predation and competition. Selection has been shown to favor more energetically efficient body plans in insular mammals, even when this entails the reduction of anti-predator defenses, but few studies have focused on morphological effects within the same species. Previous research has established that insular large mammals tend to reduce in body size, and that size reduction may not scale isometrically across all body parts. The brain has been a particular subject of interest due to its high energy requirements. Here, we report that an extant, dwarfed island population of black-tailed deer (*Odocoileus hemionus columbianus*) exhibits significantly reduced brain mass relative to body mass in comparison to their mainland conspecifics, with brain mass 4.9% smaller in the island population for a given body mass. Further, in the dwarfed population, orbital area was 4.1% smaller for a given body mass, but this reduction was not significant. Foramina magna reduced isometrically. In resource-limited insular environments, negative allometry of the brain is consistent with predictions of reduced investment in energetically costly organs. This study is, to our knowledge, the first to examine the morphological effects of insularity on brain size in two conspecific populations, and these findings suggest that selection toward reduced brain size may act relatively quickly after isolation.

Keywords Brain size · Dwarfism · Energy allocation · Intraspecific competition · Island rule · Predation

Introduction

Insular populations of mammals have been observed to undergo various morphological changes in comparison with their mainland counterparts. Body size changes are particularly common and have been linked to resource availability and predation, a phenomenon described by Foster's Rule (the island rule) (Foster 1964). Further, changes in body size of insular populations may relate to evolution in life-history patterns (Raia et al. 2003; Long et al. 2019). According to Foster's Rule, small animals will experience an increase in body size to increase metabolic efficiency, while large animals will decrease in size due to lack of food resources available (Meiri et al. 2008). For example, endemic palaeo-oloxodontine elephants (*Palaeoloxodon falconeri* and *P. mnaidriensis*) found in Pleistocene deposits on the island

of Sicily underwent a drastic reduction in size in comparison to their mainland ancestors (Palombo 2007; Lyras 2018; Hennekam et al. 2020). On the other hand, endemic rats (*Canariomys bravoii* and *C. tamarani*) in the Canary Islands greatly increased in size following their isolation (Renom et al. 2021). While the overall generalization of the island rule to various clades has been questioned, Artiodactyla demonstrate a general tendency toward dwarfism (Lomolino 1985; Meiri et al. 2004, 2008; but see Raia and Meiri 2006).

While island dwarfism has been observed in a variety of species, insular populations may experience differing patterns of dwarfism. Many insular populations dwarf allometrically, with a disproportionately large reduction of certain body parts (Palombo 2001; Köhler and Moyà-Solà 2004; Rozzi and Palombo 2014; Lyras 2018; Young 2020). For instance, when comparing endemic insular species with closely related mainland lineages, Köhler and Moyà-Solà (2004) and Palombo (2007) found that brains of dwarfed island endemics tended to shrink more than overall body size, a trend which has been suggested to relate to limited resource availability. However, when insular dwarfism is

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extreme, positive allometry of brain volume relative to body size may occur to preserve minimal functional brain volume (Larramendi and Palombo 2015; Lyras 2018).

Islands are relatively simple ecosystems, which may allow for a reduction in cognitive function; research has also associated a decrease in brain size in insular populations of extinct artiodactyls with release of the population from predation pressure (Palombo et al. 2008; Martinez et al. 2016; Pan et al. 2016). *Myotragus* spp., members of an extinct genus of insular caprine from the islands of Majorca and Menorca in the Mediterranean, had brain masses smaller than expected for their body mass, indicating that their brain mass did not scale isometrically with their body mass as the caprines dwarfed (Köhler and Moyà-Solà 2004; Palombo et al. 2008). However, recent comparison of 426 taxa did not find an effect of insularity on brain size, when phylogenetic effects were accounted (Castiglione et al. 2021).

In addition to demonstrating reduced brain size relative to body size, *Myotragus* also exhibited disproportionately small orbits. Allometric orbit reduction in *Myotragus* was associated with a reduction of the visual cortex, which was attributed to the lack of predation experienced by the caprids (Köhler and Moyà-Solà 2004). *Myotragus*, however, demonstrated other unique adaptations associated with vision (e.g., binocular vision), and it remains unclear whether allometric orbit reduction is commonly associated with insular dwarfism. Although visual cortex size may or may not change in conjunction with orbital area, insular populations of herbivores are often released from predation pressure and develop more diurnal activity patterns (Loe et al. 2007; Long et al. 2013). Nocturnality has been associated with increased orbit size in various lineages (Kay and Kirk 2000; Smith et al. 2018); therefore, reductions in nocturnality associated with predator release may lead to allometric reduction of orbit size.

Most studies on island dwarfism compare endemic island species to a mainland population of a different species, and relatively little research has compared vicariant, extant populations of the same species (but see Goltsman et al. 2005; Islam et al. 2018; Diniz-Filho et al. 2021). However, to our knowledge, no prior studies have observed allometric brain reduction of an insular population in comparison to extant mainland populations of the same species.

Here, we studied a specific insular population of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) found on Blakely Island, a mid-sized, predator-free island in Washington State, USA. There is little gene flow between the Blakely deer and mainland black-tailed deer populations, and deer density on Blakely Island exceeds mainland densities, resulting in increased intraspecific competition for limited resources (Wilson et al. 2009; Long et al. 2013, 2019).

Like many other populations of insular artiodactyls, the Blakely deer have dwarfed in size relative to their mainland

conspecifics (Long et al. 2019). This population has experienced an increase in intraspecific competition, lacks predation pressure, and demonstrates increased diurnal activity relative to mainland deer (Long et al. 2013, 2019). Therefore, we predict that the brains of the Blakely deer will demonstrate allometric reduction relative to reductions in body size. We also predict that, due to decreased nocturnality, the orbits of the Blakely deer will exhibit allometric reduction.

Materials and methods

Study area

Blakely Island (48.56° N, 122.80° W; 17.3 km²) is part of the San Juan Archipelago, a collection of islands in the Salish Sea. Located 8 km from mainland Washington State (USA), Blakely Island experiences a mild climate year-round, with cool, wet winters and warm, dry summers. Temperatures range from 0.4 °C (mean winter minimum) to 22.4 °C (mean summer maximum). With Blakely Island's temperate climate, snowfall occurs infrequently, and maximum elevation is 318 m, resulting in minimal climatic variation. The island is forested by Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*), with an undergrowth composed predominantly of sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*). The resident deer were isolated from their mainland conspecifics 12,000–10,000 years BP, which also released the deer from predation pressure, as the largest mammals on Blakely Island other than the deer are raccoons (*Procyon lotor*) (Wilson et al. 2007; Long et al. 2019). As on other predator-free islands in the San Juan Archipelago, deer density on Blakely Island (~30/km²) greatly exceeds mainland deer density (Bender et al. 2004; Martin et al. 2011; Long et al. 2013).

Morphological measurement

To test the prediction that black-tailed deer on Blakely Island exhibit disproportionate brain and orbit reduction relative to body size, we collected cranial measurements on 127 black-tailed deer specimens, (Blakely Island, n = 100; mainland, n = 27). Skulls from Blakely Island were collected opportunistically in the field, and mainland specimens were on loan from the Burke Museum (University of Washington, Seattle, Washington, USA) and Beaty Biodiversity Museum (University of British Columbia, Vancouver, BC). All mainland specimens were from locations in Washington and Oregon west of the Cascade Mountain Range to minimize environmental differences between mainland and island deer. Some partial crania precluded measurement of all morphological features; thus, sample sizes do not always sum to 127.

To relate brain mass to body mass, we measured cranial capacity and occipital condyle width. Even within individuals, body mass may vary substantially for a given skeletal size; for example, adult deer have been shown to increase body mass 40–50% from spring minima to fall maxima (DelGiudice et al. 1992). Despite this variation, width of the occipital condyle has been shown to scale reliably with body mass in a variety of taxa (Marino et al. 2004; Palombo et al. 2008; Jukar et al. 2018; Engelman 2022). We tested the relationship between occipital condyle width (OCW) and body mass in adult *Odocoileus* (black-tailed deer, $n=12$; white-tailed deer [*O. virginianus*], $n=8$). To investigate potential additional allometric changes in skull morphology, we also measured orbital area and foramen magnum area. We restricted analysis to adult deer, which we defined based on dental eruption patterns such that the 3rd molar was erupted (Wemmer and Wilson 1987). Occipital condyle width, foramen magnum height and width, and orbit height and width measurements were obtained with digital calipers to 0.01 mm (Fig. 1).

Cranial capacity can be used as a reliable estimator of brain mass (Ebinger 1974; Röhrs and Ebinger 2001 [in Palombo et al. 2008]; Köhler and Moyà-Solà 2004). To determine cranial capacity, we first plugged the auditory foramina (i.e., retroarticular foramen and external auditory meatus) with soft, compressible foam earplugs. The spaces between the tympanic bullae and basioccipital likewise were plugged with soft foam earplugs to occlude the foramen lacerum. The skulls' ventral foramina (foramen ovale, orbital fissure, and optic canal), as well as any cranial fenestrae surrounded by thin bone, were covered with masking tape. Four-millimeter glass beads were poured into the crania through the foramen magnum until the beads were flush with the foramen magnum (Wemmer and Wilson 1987), and the volume of the beads was then measured in a graduated cylinder. Following Köhler and Moyà-Solà (2004), cranial capacity was converted to brain volume using the following equation:

$$\log_{10} BrV = \frac{\log_{10} CC + 0.0015}{1.0222}$$

where BrV is brain volume (cm^3) and CC is cranial capacity (cm^3). Brain mass (BrM, in g) was then calculated by

multiplying brain volume by the specific weight of brain matter (1.036 g/cm^3) (Ebinger 1974 [in Köhler and Moyà-Solà 2004]):

$$BrM = BrV \times 1.036 \text{ g/cm}^3$$

Again, following Köhler and Moyà-Solà (2004), we estimated body mass from the occipital condyle width:

$$\log_{10} BM = \log_{10} OCW \times 2.975 - 3.364$$

where BM is body mass (in kg) and OCW is width of occipital condyle (in mm) (Fig. 1). For the relationship between occipital condyle width and known body mass, recorded body mass values were sourced from both museums' online databases.

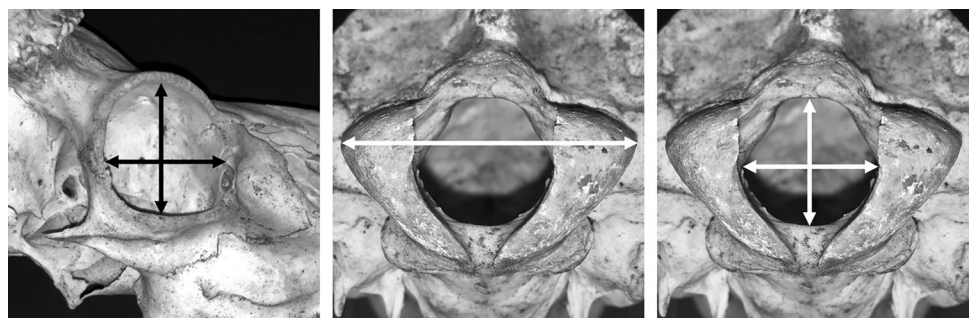
To investigate potential changes in orbital surface area, we measured orbit width as the diameter of the orbit parallel to the palate, starting from the lacrimal process at the anterior of the orbit and measuring to the orbit's posterior, and orbit height was measured as the diameter of the orbit perpendicular to the palate (Fig. 1). If both orbits were intact, the orbit dimensions were averaged for each skull to obtain a single width and height for each skull. Orbital surface area was estimated as the product of the height and width (Köhler and Moyà-Solà 2004).

Finally, we measured surface area of the foramen magnum, which is associated with basal brain function (Acer et al. 2006). Because basal brain function should remain relatively unchanged as the deer dwarf, we predicted that the foramen magnum would not shrink allometrically with body mass. With this information, we measured height of the foramen magnum as the dorsoventral diameter and width as the mediolateral diameter (Fig. 1). The surface area of the foramen magnum (FM) was estimated as the product of the height and width (Köhler and Moyà-Solà 2004).

Statistical analyses

To confirm the positive relationship between OCW and body mass in *Odocoileus*, we conducted a two-way analysis of covariance (ANCOVA), testing the predictors of sex, species (*O. hemionus* and *O. virginianus*), and body mass on

Fig. 1 Illustrated measurements of orbit height and width (left); occipital condyle width (center); and foramen magnum height and width (right)



OCW. Then, to compare brain and orbit size to body mass in the Blakely Island and mainland populations, we conducted three additional two-way analyses of covariance. In each analysis, sex and location were included as independent variables and body mass was included as a covariate. Brain mass, orbit area, and foramen magnum size were included as dependent variables. To meet statistical assumptions associated with ANCOVA, and following Köhler and Moyà-Solà (2004), we transformed morphometric data (i.e., cube root \log_{10} body mass, square root \log_{10} orbital surface area, and square-root \log_{10} foramen magnum surface area). Following these transformations, normality was confirmed with the Shapiro-Wilk test, and homogeneity of variance was confirmed with Levene's test. In addition to presenting results from models parameterized using estimated body mass, we also provide supplementary results demonstrating the direct relationship between occipital condyle width and cranial measurements.

Results

Using cranial specimens of *Odocoileus* for which body mass was known ($n = 20$), we confirmed that body mass and occipital condyle width are positively related ($F_{1,12} = 9.53$, $p = 0.009$). When controlling for variations in body mass, neither species ($F_{1,12} = 0.19$, $p = 0.67$) nor sex ($F_{1,12} = 1.53$, $p = 0.24$) influenced OCW. Likewise, there were no significant two-way or three-way interactions among these predictor variables ($p \geq 0.25$). Thus, we modeled the

positive relationship between body mass and OCW using simple bivariate Pearson correlation analysis ($R = 0.61$, $p = 0.005$), such that.

$$OCW = 0.27(\pm 0.08)BM + 34.17(\pm 4.30)$$

where OCW is width of occipital condyle (mm), BM is body mass (kg), and values in parentheses are standard errors of coefficient estimates (Fig. 2). From this linear relationship, we converted occipital condyle width to estimated body mass for display of subsequent morphological analyses. In the supplementary material, we provide results of comparable analyses, relating OCW directly to brain mass, orbital surface area, and foramen magnum surface area, thereby reducing error inherently associated with body mass estimation.

Consistent with our prediction, we found that deer on Blakely Island exhibited disproportionately reduced brain mass, relative to their body mass (Fig. 3).

Brain mass correlated positively with body mass for all deer ($F_{1,117} = 40.61$, $p < 0.001$, $n = 118$). After controlling for body mass, we found no significant effect of sex on brain mass ($F_{1,117} = 1.249$, $p = 0.266$, $n_{\text{female}} = 70$, $n_{\text{male}} = 48$), and there was no significant interaction between the predictor variables of sex and location ($F_{1,117} = 0.459$, $p = 0.499$). However, when controlling for body mass, brain mass in deer from Blakely Island was significantly smaller than brain mass of deer on the mainland ($F_{1,117} = 6.126$, $p = 0.015$, $n_{\text{island}} = 100$, $n_{\text{mainland}} = 18$). Back-transformed estimated marginal means suggest

Fig. 2 Occipital condyle width (OCW) versus body mass of *Odocoileus* species. *Odocoileus hemionus* specimens ($n = 12$) are shown with solid symbols, and *O. virginianus* specimens ($n = 8$) are shown with open symbols; females ($n = 9$) are displayed with circles, and males ($n = 11$) are displayed with squares. The relationship between body mass and OCW did not differ between species or sex; thus, a single regression line is shown for all specimens together

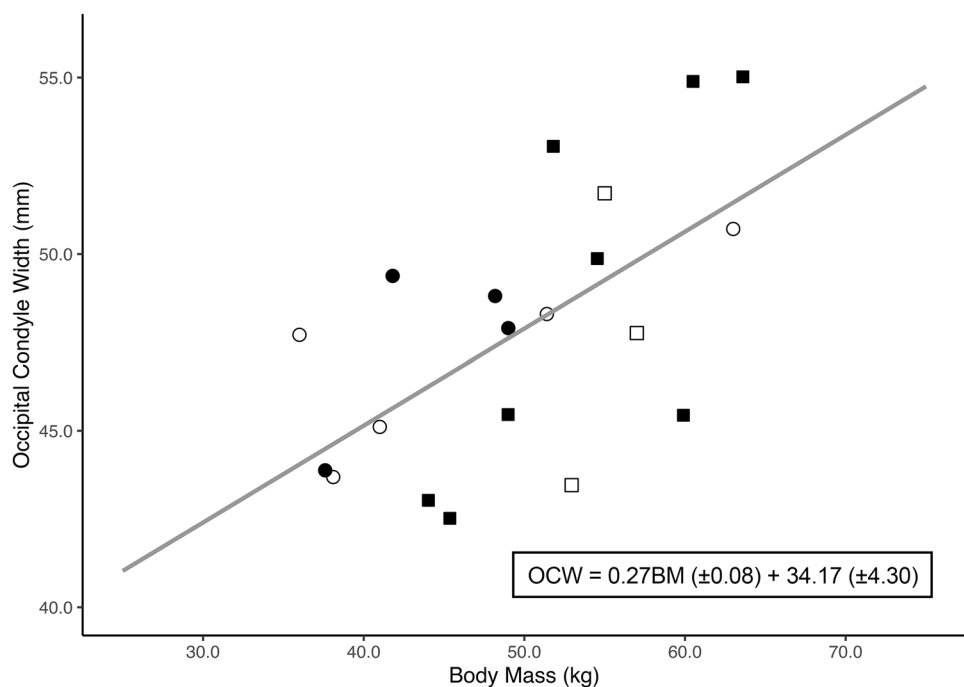
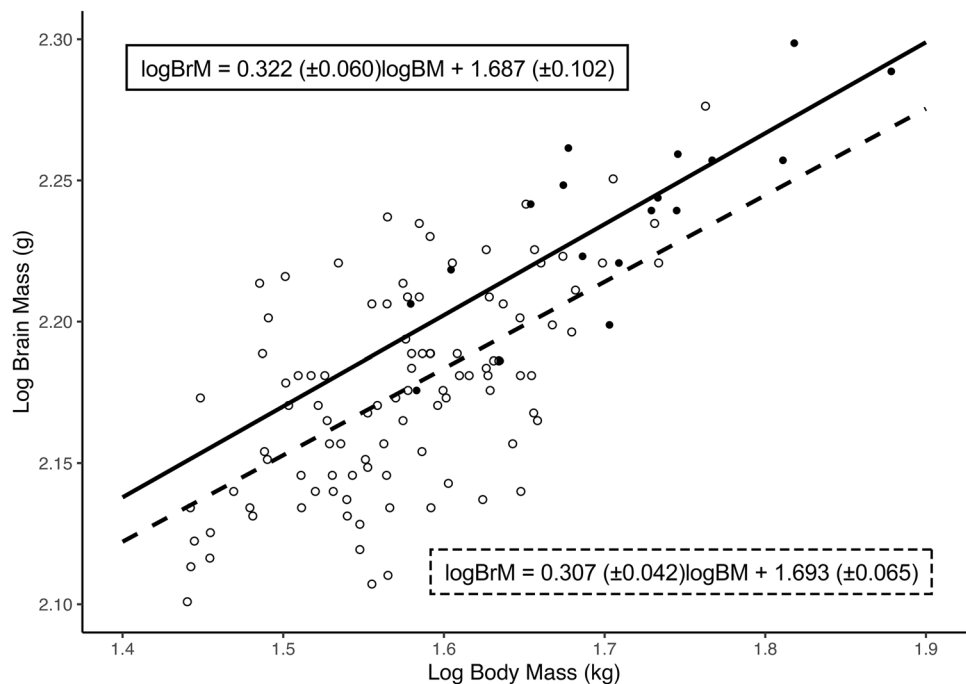


Fig. 3 Brain mass versus body mass of mainland (solid line, solid circles) and Blakely Island (dashed line, open circles) populations of black-tailed deer ($R_{\text{mainland}} = 0.80$, $R_{\text{island}} = 0.60$)



brain mass of deer from Blakely Island averaged 152.1 g (\pm SE = 151.0–153.1); whereas estimated marginal means of brain mass of mainland deer was 159.9 g (157.0–163.0). Thus, for a given body mass, brain mass of deer from Blakely Island tended to be 4.9% smaller than brain mass of deer from the mainland. Direct comparison of OCW to brain mass demonstrated similar patterns (Online Resource 1).

Orbital surface area increased significantly as body mass increased ($F_{1,114} = 16.425$, $p < 0.001$, $n = 115$) and like brain mass, when controlling for differences in body mass, sex did not predict orbit size ($F_{1,114} = 0.282$, $p = 0.596$, $n_{\text{female}} = 68$, $n_{\text{male}} = 47$), although there was an interaction between sex and location ($F_{1,114} = 4.896$, $p = 0.029$). When controlling for body mass, orbit area of deer on Blakely Island tended to be smaller, but this reduction was not significantly different relative to deer from the mainland ($F_{1,114} = 2.938$, $p = 0.089$, $n_{\text{island}} = 95$, $n_{\text{mainland}} = 20$; Fig. 4).

Back-transformed estimated marginal means of orbital area for Blakely Island deer averaged 1419 mm² (\pm SE = 1407–1431); whereas, estimated marginal means of orbital area for mainland deer was 1479 mm² (1448–1511), which, when controlling for differences in body mass, indicates a 4.1% reduction of orbit area in island deer relative to mainland deer. Direct comparison of OCW to orbital surface area demonstrated similar patterns (Online Resource 2).

Similar to brain mass and orbit area, foramen magnum surface area increased significantly with increased body mass ($F_{1,120} = 5.761$, $p = 0.018$, $n = 121$), and after controlling for body mass, sex was not a significant predictor of

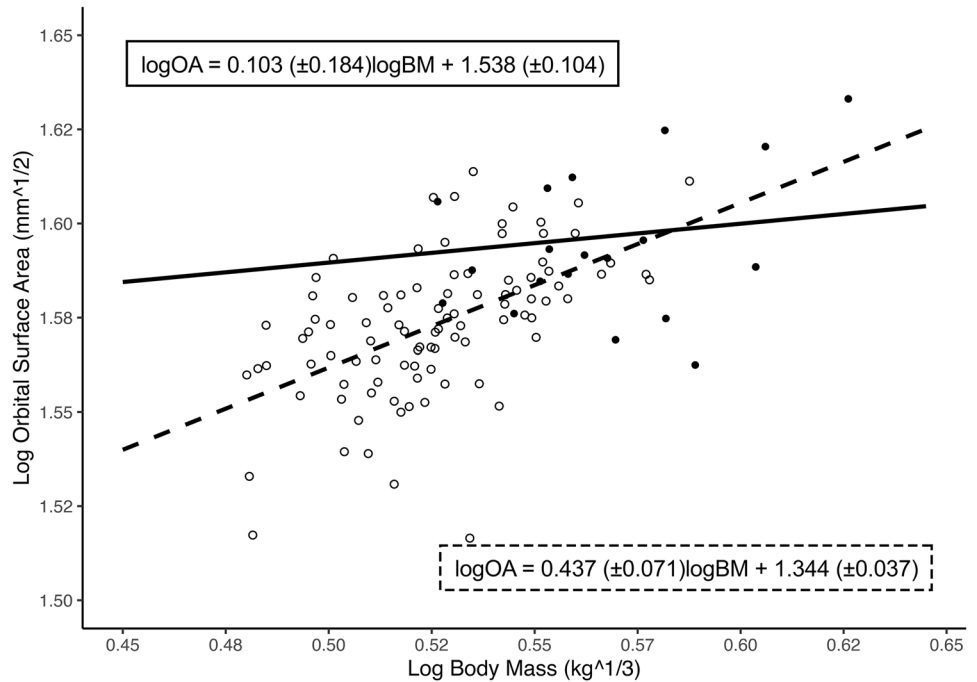
foramen magnum size ($F_{1,120} = 2.386$, $p = 0.125$, $n_{\text{female}} = 73$, $n_{\text{male}} = 48$). There was no evidence of disproportionate changes in foramen magnum on the island relative to the mainland ($F_{1,120} = 0.311$, $p = 0.578$, $n_{\text{island}} = 100$, $n_{\text{mainland}} = 21$; Fig. 5), nor was there any interaction between sex and location ($F_{1,120} = 2.482$, $p = 0.118$). Direct comparison of OCW to foramen magnum surface area demonstrated similar patterns (Online Resource 3).

Discussion

Populations of mammals have been observed to undergo various morphologic changes when isolated for long periods (Köhler and Moyà-Solà 2004; Palombo et al. 2008; McFadden and Meiri 2012; Lyras 2018). These morphologic changes have been linked to resource availability which requires large animals to reduce energy expenditure, often through a reduction in body size (McNab 2002, 2010). Artiodactyls, in particular, generally show trends of body size reduction (Köhler and Moyà-Solà 2004; Palombo et al. 2008). Furthermore, brain size in artiodactyls is thought to evolve relatively quickly on evolutionary timescales; in *Myotragus*, body size reduction was accompanied by disproportionate brain mass reduction (Köhler and Moyà-Solà 2004; Kopperud 2017). Consistent with these findings, the deer on Blakely Island exhibited disproportionate brain mass reduction.

The high density of deer on Blakely Island results in a shortage of food resources, which increases the pressure

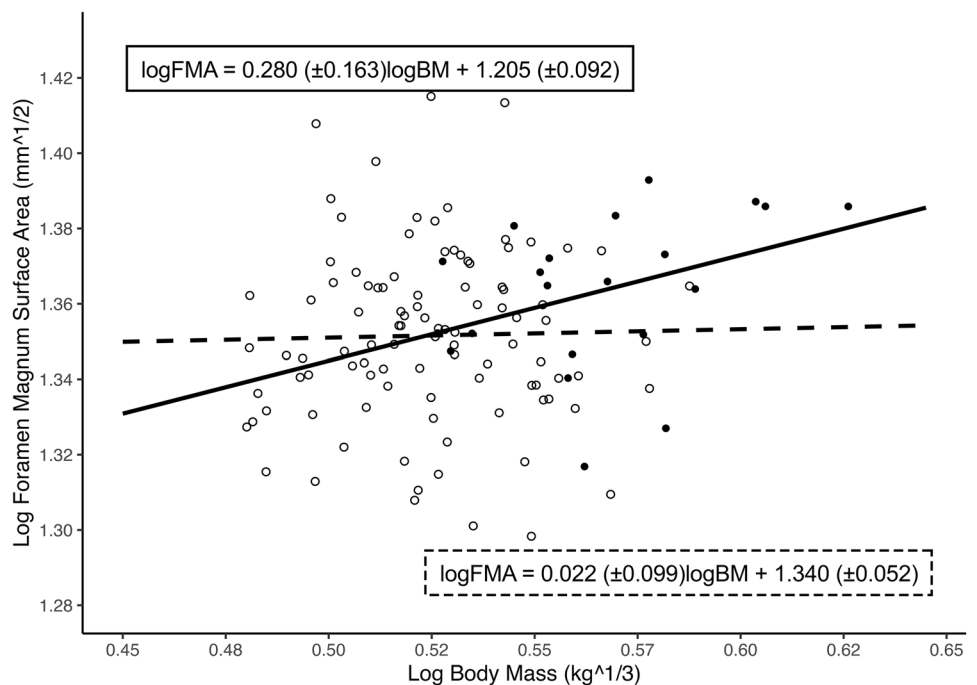
Fig. 4 Orbital surface area versus body mass of mainland (solid line, solid circles) and Blakely Island (dashed line, open circles) populations of black-tailed deer ($R_{\text{mainland}} = 0.13$, $R_{\text{island}} = 0.54$)



of intraspecific competition, and the body size reduction observed in the deer on Blakely Island has previously been related to low food availability (Long et al. 2019). Because the brain is disproportionately energetically costly, individuals with relatively small brains (and thus lower energetic needs) may have higher fitness than individuals with relatively large brains when resources are limited (McNab 2002; Isler and Van Schaik 2006; Weston and Lister 2009). Although tradeoffs associated with brain reduction are

not well understood, brain reduction may be associated with decreased sensory perception or cognition. However, because islands are often simplified ecosystems and devoid of predators, costs associated with reduced brain function on islands may be minor relative to energy-saving advantages where there is increased intraspecific competition for limited food resources. In this way, selective pressures that favor small body sizes on islands may similarly favor allometric

Fig. 5 Foramen magnum surface area versus body mass of mainland (solid line, solid circles) and Blakely Island (dashed line, open circles) populations of black-tailed deer ($R_{\text{mainland}} = 0.37$, $R_{\text{island}} = 0.02$)



reduction of disproportionately expensive organs, such as the brain.

Unlike the pattern documented for *Myotragus* (Köhler and Moyà-Solà 2004), we did not detect significant reduction in orbits relative to body size. One possible explanation for this observed pattern is that, due to relatively high energetic costs of brains versus eyes, brain reduction occurs more quickly than eye reduction. The Blakely Island population has only been isolated for 10,000–12,000 years, unlike *Myotragus*, which was isolated for millions of years (Köhler and Moyà-Solà 2004). Additionally, the Blakely deer are at a higher latitude than *Myotragus* (Blakely Island is at 49° N, Majorca and Menorca are at 40° N) and receive less sunlight throughout the year. This lack of light may also contribute to the smaller relative reduction of orbit size observed in the island deer (Pearce and Dunbar 2012).

The foramen magnum size retention of the deer on Blakely Island was also consistent with that of *Myotragus*. Because the foramen magnum is associated with basal brain function (rather than visual or higher-level cognitive functions for predator evasion), the area of the foramen magnum would not be expected to change with differences in predation and competition.

The negative allometric dwarfing of brain size relative to body size observed in the Blakely Island deer contrasts with positive allometry observed in Sicilian elephants (Larramendi and Palombo 2015; Lyras 2018). Similar to our study group, the Sicilian elephants (*Palaeoloxodon falconeri*) showed a dramatic body size reduction, shrinking to just 2% the size of their mainland relatives. But instead of being disproportionately small, the brains of the elephants were unusually large for their body size. A similar trend was observed in three species of extinct insular dwarf hippopotamuses (Lyras 2018), although it should be noted that there was substantial uncertainty associated with estimating body size for these hippopotamuses. Lyras (2018) attributes this phenomenon to paedomorphosis, and considering the extreme degree of dwarfism experienced by the elephants and hippopotamuses, it is plausible that their brains simply could not shrink any further without loss of function (Palombo 2001; Benoit 2015; Lyras 2018). An alternative explanation from Weston and Lister (2009), who studied the same dwarf hippopotamuses as Lyras (2018) and applied their findings to dwarfed hominids (*Homo floresiensis*), suggests that the selective pressures driving brain reduction may be altogether different than those on body reduction, meaning that brain reduction occurs independently from body reduction.

In this study, we demonstrated that the Blakely Island population of black-tailed deer showed allometric body-part reduction, with a significant, disproportionate decrease in brain mass relative to body mass. Similarly, though to a lesser degree, orbits demonstrated a trend toward negative

allometry relative to body mass. These allometric anatomical reductions likely curb energy expenditure, increasing fitness in a resource-limited, predator-free environment. Similar patterns of allometric reduction have been seen in other dwarfed mammals (Köhler and Moyà-Solà 2004; Palombo et al. 2008; Weston and Lister 2009). However, to our knowledge, this study is the first to report disproportionate brain mass reduction within a single species and suggests that the evolutionary pattern of brain reduction can occur relatively quickly following isolation.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s10914-023-09672-6>.

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Author contributions ESL conceptualized the project. COG designed the methodology and performed data collection and visualization. ESL and COG conducted the statistical analysis and co-wrote the manuscript.

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Data availability The datasets created and analyzed in this study are publicly available in the Dryad repository: <https://doi.org/10.5061/dryad.gqnk98stm>.

Declarations

Ethics approval No live animals were used in this study. Collection of deer skulls on Blakely Island was done in accordance with the guidelines of Seattle Pacific University's Institutional Animal Care and Use Committee (IACUC #1112-15R).

Conflicts of interest The authors of this manuscript declare no conflicts of interest.

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