Brain size/body size ratios of insular and mainland foxes: possible implications for *Homo floresiensis*

Angela D. Schauber

Florida State University Department of Anthropology

Abstract

Although the discovery of *Homo floresiensis* has drawn attention to the 'island rule,' it is unknown how insular dwarfing affects relative brain size (RBS). The objective of this study is to compare brain size/body size ratios of insular dwarf foxes and normal-sized mainland foxes to determine whether dwarf foxes' RBS scale in line with allometric expectations compared to their normal-sized relatives. The samples consist of complete crania and femora from male and female adult specimens belonging to 45 island gray foxes (*Urocyon littoralis*) from the California Channel Islands and 43 mainland gray foxes (*Urocyon cinereoargenteus*) from California. Cranial capacity, which was used as a surrogate for brain size, was determined from endocranial volumes. A body size proxy was determined by measuring femoral length and circumference. Statistical analyses were performed and results indicate that, as expected, dwarf island foxes have smaller absolute brain sizes than normal-sized mainland foxes. Contrary to the general principles of brain size/body size allometric scaling, however, dwarf island gray foxes have the same, rather than a larger, mean RBS when compared to their larger relatives. This suggests that, with respect to RBS, insular dwarfs come closer to being proportional miniatures of their mainland counterparts than to being proportioned in line with traditional allometric expectations, i.e., with greater RBS. Research on LB1, the type specimen for *Homo floresiensis*, shows that its RBS is most similar to the great apes and the australopithecines. Although brain size/body size ratios of insular dwarfs and mainland counterparts have hitherto been unknown, the results of this study suggest that the larger-bodied ancestor from whom *Homo floresiensis* is descended would have had a RBS that is similar to LB1's.

Introduction

The cranial capacity of LB1, the type specimen of *Homo floresiensis* from the Indonesian island of Flores (Brown et al., 2004), is estimated at 417 cm³ (Figure 1) (Falk et al., 2005). Body weight for LB1 is estimated between 16 and 36 kg (Brown et al., 2004). The **brain size/body size ratio of LB1 reveals that its relative brain size (RBS) is similar to that of great apes and the australopithecines** (Figure 2) (Falk et al., 2005).

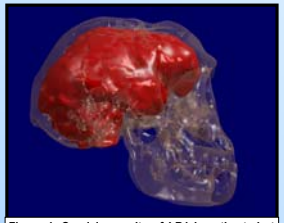

Figure 1. Cranial capacity of LB1 is estimated at 417 cm³ from 3DCT reconstruction of the virtual endocast (from Falk et al., used with permission).

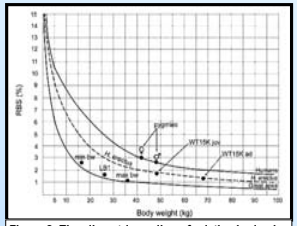

Figure 2. The allometric scaling of relative brain size (RBS) against body weight for humans, human pygmies, *Homo erectus*, LB1, and great apes (from Falk et al., 2005, used with permission).

The 'island rule' states that body sizes in species living on islands may become reduced (insularly-dwarfed) or enlarged (insularly-gigantic) because of constraints on food resources and lack of predators (Foster, 1964; Lomolino, 1985; Van Valen, 1973). ***Homo floresiensis* may be descended from a larger-bodied ancestor (*Homo erectus* or some other early *Homo*) that became dwarfed in an island habitat** (Brown et al., 2004; Falk et al., 2005; Morwood et al., 2005; Morwood et al., 2004). This hypothesis is consistent with the fact that the island of Flores is home to other insular species (Figure 3).

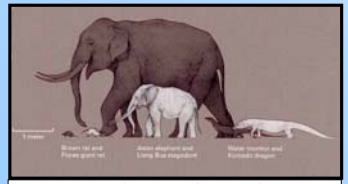

Figure 3. Examples of insular dwarfs or giants from the island of Flores (from National Geographic 207, April 2005).

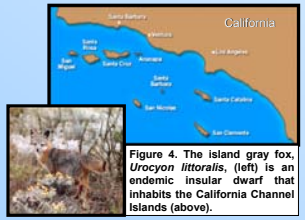

Figure 4. The island gray fox, *Urocyon littoralis*, (left) is an endemic insular dwarf that inhabits the California Channel Islands (above).

In light of the australopithecine/ape-like relative brain size (RBS) of LB1, understanding the relationship between RBS of insular dwarfs and their normal-sized mainland relatives is an important challenge. **I compare brain size/body size ratios and RBS of gray foxes, *Urocyon cinereoargenteus*, from mainland California to island gray foxes, *Urocyon littoralis*, from the California Channel Islands.** The island gray fox, *Urocyon littoralis*, is an endemic insular dwarf that inhabits six of the eight California Channel Islands (Figure 4) and is significantly smaller (Moore and Collins, 1995) than the mainland gray fox, *Urocyon cinereoargenteus*.

Materials and Methods

The sample consists of **88 crania and femora of adult *Urocyon*** (fox) specimens comprising two separate species, *cinereoargenteus* and *littoralis*, that represent mainland and insular counterparts, respectively (Table 1, Figure 5). Skeletal collections were accessed at the Museum of Vertebrate Zoology (MVZ), the Natural History Museum of Los Angeles County (LACM), and the National Museum of Natural History (USNM).

Table 1. The sample (*n* = 88) of *Urocyon* species and subspecies.

	Subspecies	N
Mainland fox, *Urocyon cinereoargenteus*		**43**
Mainland California	*U. c. californicus*	16
Mainland California	*U. c. scottii*	7
Mainland California	*U. c. townsendi*	20
Island fox, *Urocyon littoralis*		**45**
Santa Catalina Island	*U. l. catalinae*	9
San Clemente Island	*U. l. clementae*	6
Santa Cruz Island	*U. l. santacruzae*	6
San Miguel Island	*U. l. littoralis*	11
San Nicolas Island	*U. l. dickeyi*	5
Santa Rosa Island	*U. l. santarosae*	8

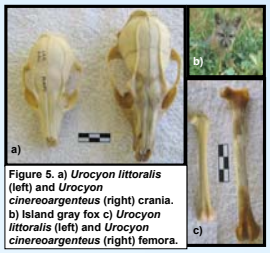

Figure 5. a) *Urocyon littoralis* (left) and *Urocyon cinereoargenteus* (right) crania. b) Island gray fox c) *Urocyon littoralis* (left) and *Urocyon cinereoargenteus* (right) femora.

Brain size and body size data were measured by obtaining cranial capacities and femoral dimensions. Cranial capacity (**CC**) was measured by sealing cranial foramina with polymer clay and filling the cranium with mustard seeds. The greatest length (**FEMGL**) and the smallest mid-shaft circumference (**FEMCD**) of femora were used to derive a proxy for body size, **FEMAREA** (= FEMGL x FEMCD).

Results

Descriptive statistics (total number, mean, standard deviation) are presented in Table 2. Least squares bivariate regressions ($p < 0.05$) of brain size (CC) against body size (FEMAREA) are significant for each species (*cinereoargenteus*: t (42) = 3.32, $p < 0.002$; *littoralis*: t (44) = 4.88, $p < 0.000$) Table 3, Figure 7.

Table 2. Descriptive statistics of the *Urocyon* sample (*n* = 88).

		CC		FEMGL		FEMCD	
	N	M	SD	M	SD	M	SD
Mainland fox							
Urocyon cinereoargenteus	43	39.21	2.28	110.75	5.25	25.74	1.27
Island fox							
Urocyon littoralis	45	28.13	2.08	85.89	4.04	22.89	1.93

Although the slopes of the lines are similar, mainland foxes scale above island foxes as reflected in their different *y*-intercepts. **Dwarf island foxes have smaller absolute brain sizes than their normal-sized mainland counterparts at any given body size**.

The mean relative brain size (RBS = brain size/body size) for both mainland foxes and island foxes is 0.014 (Figure 6, Figure 7); the difference is not significant (t (83) = -1.56, $p < 0.1232$). **Dwarf island foxes have the same RBS as normal-sized mainland foxes**.

Table 3. Least squares bivariate regressions ($p < 0.05$) of brain size (CC) against body size (FEMAREA).

	Intercept	SE	Slope	SE
Mainland fox				
Urocyon cinereoargenteus	27.16	3.64	.004	.001
Island fox				
Urocyon littoralis	17.31	2.23	.005	.001

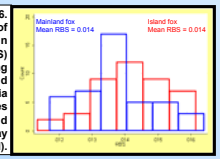

Figure 6. Histogram of relative brain sizes (RBS) among mainland California gray foxes (blue) and island gray foxes (red).

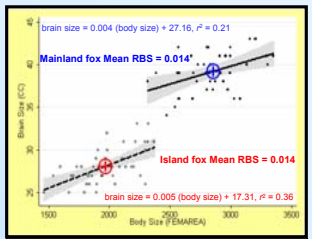

Figure 7. Brain size (CC) against body size (FEMAREA) among mainland California gray foxes (solid circles, solid line-top) and island gray foxes (open circles, dashed line-bottom). The mean RBS (⊕) for both mainland and island gray foxes is 0.014.

Discussion

Island gray foxes have smaller absolute brain sizes but identical mean relative brain sizes (RBS) compared to mainland gray foxes. This pattern fails to conform to the general allometric expectation that smaller-bodied individuals of closely related species will have larger mean RBS.

'Dwarf' species are expected to retain paedomorphic features that result in larger relative brain size (RBS) than is the case for larger related species, in accordance with the ontogenetically-constrained allometric scaling that occurs within species (Weidenreich, 1941). For instance, Weidenreich noted that **smaller breeds of domesticated dogs have larger RBS than larger breeds** (Figure 8). Weidenreich applied this phenomenon as a general principle for providing expectations regarding RBS for a wide range of species at all body sizes. Moreover, he saw the relationship as strong enough to provide support for using increased RBS as a criterion for determining if something is a 'dwarf' type of a given species (Weidenreich, 1941).

Interestingly, Weidenreich obtained contradictory results when he studied 'dwarf' and large versions of wild dogs and found that "the disproportion between the size of the body or skull and the size of the brain is less pronounced in wild dogs than in domesticated animals" (1941, p. 351) and that "dwarf wild dogs, in contrast to the domesticated dog, are diminutive forms of the large types" (1941, p. 352). Although **Weidenreich observed that smaller wild dogs did not conform to the allometric expectation** of increased RBS but instead were proportioned similarly to their larger-sized wild relatives, he continued to generalize the hypothesis that RBS in 'dwarfs' of closely-related species scales according to traditional allometric expectations.

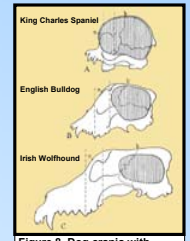

Figure 8. Dog crania with cranial capacities (shaded-area) depicting increasing relative brain size (RBS) among smaller breeds (modified from Weidenreich, 1941).

However, the fact that **smaller wild dogs and island foxes both appear to be nearly proportional miniatures of their larger-bodied relatives (i.e., with respect to RBS) suggests that one rule does *not* govern all 'dwarf' types.** If so, similar proportional scaling may also apply to RBS in other insularly-dwarfed mammals.

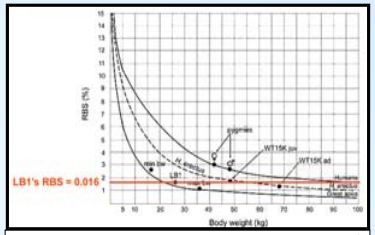

Figure 9. LB1 and WT15000 have similar relative brain size (RBS) (modified from Falk et al., 2005, used with permission). The red line is drawn through the RBS of LB1, 0.016. The RBS of WT15000 is 0.013.

Falk et al., (2005) argued that *Homo floresiensis* may not be an insularly-dwarfed descendant of *Homo erectus* because LB1's relative brain size (RBS) does not fall on the projected ontogenetic curve for RBS in *Homo erectus* (Figure 2). This would be a realistic assumption if insular dwarfs scaled allometrically as human pygmies do. However, comparison of RBS in *Homo erectus* and *Homo floresiensis* reveals that RBS does not differ greatly in the two species. The adult brain size (909 cm³) and body weight (68,000 g) of WT15000 and the adult brain size (417 cm³) and mean body weight (26,000 g) of LB1 were used to calculate the RBS of each. **The RBS of WT15000 is 0.013 and the RBS of LB1 is 0.016** (Figure 9). Thus, LB1's RBS is slightly larger than *Homo erectus*.

Conclusion

- **Insularly-dwarfed species need not have increased relative brain size (RBS) as expected based on conventional allometric scaling when compared to their normal-sized counterparts.**
- **Island gray foxes (*Urocyon littoralis*) and mainland gray foxes (*Urocyon cinereoargenteus*) have identical RBS.**
- **LB1 (*Homo floresiensis*) has a similar RBS to WT15000 (*Homo erectus*).**
- **Results of this study suggest the hypothesis that LB1 may be an endemically-dwarfed descendant of a species of early *Homo* that had a similar RBS.**

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