

Original Article

Keeping an ear out: size relationship of the tympanic bullae and pinnae in bandicoots and bilbies (Marsupialia: Peramelemorphia)

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Abstract

Bandicoots and bilbies (Order Peramelemorphia) occupy a broad range of habitats across Australia and New Guinea, from open, arid deserts to dense forests. This once diverse group has been particularly vulnerable to habitat loss and introduced eutherian predators, and numerous species extinctions and range retractions have occurred. Understanding reasons for this loss requires greater understanding of their biology. Morphology of the pinnae and tympanic bullae varies markedly among species. As hearing is important for both predator avoidance and prey location, the variability in ear morphology could reflect specialization and adaptation to specific environments, and therefore be of conservation relevance. We measured 798 museum specimens representing 29 species of Peramelemorphia. Controlling for phylogenetic relatedness and head length, pinna surface area was weakly negatively correlated with average precipitation (rainfall being our surrogate measure of vegetation productivity/complexity), and there were no environmental correlates with effective diameter (pinna width). Controlling for phylogenetic relatedness and skull length, tympanic bulla volume was negatively correlated with precipitation. Species that inhabited drier habitats, which would be open and allow sound to carry further with less obstruction, had relatively larger pinnae and tympanic bullae. In contrast, species from higher rainfall habitats, where sounds would be attenuated and diffused by dense vegetation, had the smallest pinnae and bullae, suggesting that low-frequency hearing is not as important in these habitats. Associations with temperature did not reach statistical significance. These findings highlight linkages between hearing traits and habitat that can inform conservation and management strategies for threatened species.

Key words: external ear, hearing ecology, marsupial, middle ear, sound perception.

Hearing is used in several aspects of day-to-day life, including predator detection, foraging, and communication, and is therefore critically important for survival and fitness in many species (Vaughan et al. 2015). Sounds are emitted from various sources in the environment, biotic and abiotic, resulting in a complex auditory environment of

varying relevance to survival. These sounds are captured by the external ear (pinna) and directed into the external ear canal (Figure 1). In the air-filled middle ear, they are augmented by the auditory ossicles (malleus, incus, and stapes) to match the impedance of the fluid-filled inner ear (Khanna and Tonndorf 1969; Tucker 2017). In many

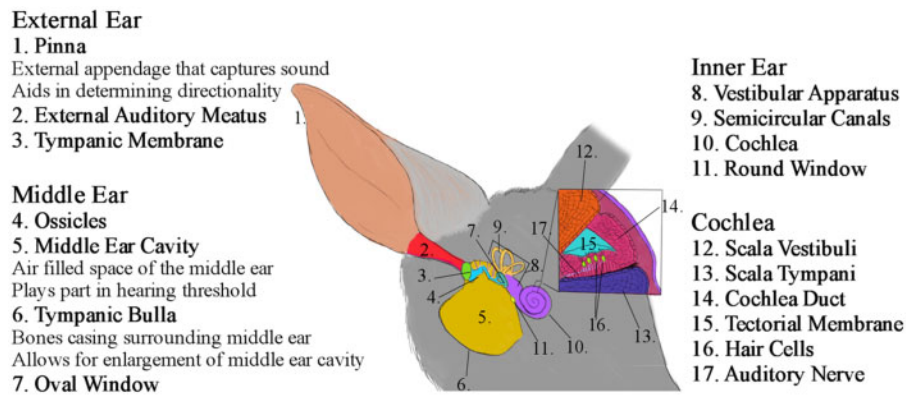


Figure 1. Diagram of the ear structure of the bilby, separated by section with summary of function for relevant structures. Image source: M. Taylor.

mammals, the bony cavity that encloses the middle ear (tympanic bulla) has become enlarged into a visible protrusion at the base of the skull.

Ear morphology is adapted to detect certain frequencies at a range of distances relevant to each species' environment. Pinnae can serve multiple purposes, from sound localization using different cues, to altering the hearing range of a species. Pinnae can facilitate sound localization by creating different level (interaural level difference [ILD] cues) and time (interaural timing difference [ITD] cues) between each ear (Kuhn 1987). ILD cues can be caused by an "acoustic shadow" created by the head and pinnae size, where sound is less intense for the pinnae further away from the sound source (King et al. 2001). These cues are most useful at higher frequencies (Heffner et al. 1996; King et al. 2001). ITD cues are created in timing differences between each pinnae detecting the sound and are most pronounced in lower frequencies (Wightman and Kistler 1992; King et al. 2001). Localization may be aided in some animals with large mobile pinnae that can be turned toward the sound source (Webster 1966). In smaller mammals, it has been suggested that relatively large pinnae may also facilitate the detection of lower frequency sounds (Heffner and Heffner 2008, Jones et al. 2011). In contrast, relatively small pinnae are more targeted to the detection of high-frequency sounds and have limited capacity to detect directionality of sound (Heffner et al. 1996). Pinnae size and shape can therefore impact the way a species perceives the auditory landscape of its environment.

The volume of the middle ear cavity influences hearing frequency range, with larger middle ears allowing greater sensitivity to lower frequencies (Lay 1972; Ravicz and Rosowski 1997). The size of the tympanic bulla (the bone covering around the middle ear) can therefore provide insight into the range of frequencies that animals can detect. For example, the tympanic bulla is often particularly large in small insectivorous mammals (Keen and Grobbelaar 1940), whose small skull size would otherwise restrict their hearing range to higher frequencies.

The environment influences attenuation of sound, with different conditions impacting the distance sounds can travel. In arid conditions, higher frequency soundwaves attenuate more severely than in other open environments (Knudsen 1931; Lay 1972; Huang et al. 2002). This would make low-frequency sound detection more useful in arid conditions or where sound carries (i.e., for open conditions rather than closed environments). As a result, arid-adapted species tend to have larger, better-developed bullae compared with species from more mesic environments (Keen and Grobbelaar 1940; Lay

1972; Hunt 1974; Basso et al. 2020). Conversely, wetter environments, often typified by dense vegetation, pose a different kind of auditory environment: acoustic signals degrade rapidly as a result of obstacles blocking, refracting, and possibly altering the frequency of the signals (Blumenrath and Dabelsteen 2004; Boncoraglio and Saino 2007). Dense vegetation will consequently result in a complex acoustic environment with a large variety of sound sources. Habitats with varying levels of aridity and vegetation complexity consequently have different soundscapes and will result in selection for differences in the hearing range requirements of species.

Some selective pressures may act on both pinnae and bullae, but there is also evidence suggesting that these 2 structures can be selected for independently. Pinnae and bullae sizes are negatively correlated in some desert-specialized rodents (Pavlinov and Rogovin 2000). In contrast, both pinnae and tympanic bullae increase in size with increasing temperature and aridity in the Indian gerbil *Tatera indica* (Khajeh et al. 2019). Similarly, some leporid lagomorph species (*Bunolagus* spp.) have both enlarged pinnae and bullae (Kraatz et al. 2015). Notably, many of these studies do not account for relatedness between species. Studies on desert rodents that do account for phylogenetic relationships have similarly found a correlation between tympanic bullae and temperature (Alhajeri et al. 2015; Alhajeri and Steppan 2018), whereas correction for phylogenetic relatedness eliminated any significant relationship between pinnae and either temperature or precipitation for gerbils (Gerbillinae) (Alhajeri 2016). Accounting for phylogeny helps to identify the strength of factors selecting for both larger and smaller ear structures in different environments.

Bandicoots and bilbies (Order Peramelemorphia) inhabit a range of habitats across Australia and New Guinea, including rainforests, woodlands, heath, and arid areas (Driessen and Rose 2015; Hall et al. 2016; Warburton and Travouillon 2016). They are generally crepuscular or nocturnal, and most species are omnivorous, taking a variety of invertebrates, fungi, and plant material in their diet (Hall et al. 2016; Warburton and Travouillon 2016). Many species are known to scratch-dig for subterranean food items, whereas the greater bilby *Macrotis lagotis* also burrows for shelter (Van Dyck and Strahan 2008). Australian mammal species in the "critical weight range" (body mass of 35 g to 5.5 kg), especially those occupying low-rainfall areas, have suffered disproportionate extinction losses since European settlement (McKenzie et al. 2007; Woinarski et al. 2014, Johnson and Isaac 2009) with predation by introduced predators being one of the most important threats for mammal extinction on the continent (Woinarski et al. 2015). All bandicoot and bilby species lie within this

weight range (Woinarski et al. 2015). Eight out of the 18 recognized modern Australian species within Peramelemorphia are now extinct and a further 5 species are classified as Critically Endangered or Threatened (Warburton and Travouillon 2016). Conservation of these animals requires greater understanding of their biology and ecology, yet basic biological information for many species, particularly those from New Guinea, is still lacking.

Hearing ability could make bandicoots and bilbies vulnerable to habitat loss and predation. For example, hearing characteristics could have implications for their ability to detect and therefore escape from terrestrial predators, or their ability to locate insect prey. Bandicoots and bilbies have marked species variation in pinna and tympanic bulla sizes (Hall et al. 2016; Travouillon and Phillips 2018), but it is not understood how this variation may be related to their ecology. In this study, we tested the relationships between relative bulla and pinna sizes in 29 peramelemorphian species and subspecies and examined to what extent these correlated with environmental characteristics. This knowledge may be useful for conservation of species, for example, in identifying suitable habitats for endangered species, particularly in relation to translocation and reintroduction efforts.

Materials and Methods

Specimens

Skins preserved in alcohol and dry skulls of representative species were sourced from museums (Table 1). Only adult specimens were used: wet skins were considered adult by their body size and if the pouch or testes appeared fully developed, skulls were considered adult if all permanent teeth had erupted fully. A total of 798 specimens were measured from 29 species and subspecies, with roughly equal numbers of skins ($n=389$) and skulls ($n=409$; Table 1). Wet skins were only used if at least 1 ear was in good condition and able to be flattened out in order to take reliable measures. Only skulls that were in a reasonable condition (intact) to obtain their dimensions were included. One dry skin was used as the only accessible wet skin was for a juvenile (*Perameles myosuroides*, $n=1$), although due to the shrinkage of dry tissues the results for this specimen should be considered an underestimate of actual size.

Skins

The right pinna was used when intact. For those that were damaged or too stiffly bent in such a way that may influence the measurements, the left pinna was used instead. Head length was measured in millimeters (mm) for the wet skins (Figure 2A). The height and width of the pinnae (Figure 2B, C) were measured (mm) using digital calipers (Absolute Cooland Proof IP67, Mitutoyo). Most specimens still contained their skulls ($n=375$), and for those that had the skull removed, they were measured to the same approximate point beyond the ears as those that still contained skulls. Pinna dimensions were used to estimate pinnae surface area (PSA) of the inner surface using the area of an ellipse:

$$PSA = \pi^{1/2} PW^{*1/2} PH \quad (1)$$

where PW = pinna width at widest point, and PH = pinna height from the base to tip.

We also directly measured PSA using a silicon-based mold (Pinkysil[®] putty, Barnes, Sydney, Australia) from which a secondary malleable mold was created (using RubberLatex liquid latex, Jacksons Drawing Supplies, Perth, Australia) that could be flattened

out, scanned (open source painting program Krita; Stitching Krita Foundation, 2018), and then digitized (ImageJ; Rasband, 1997–2018). Not all specimens were available for a mold to be taken (Supplementary Table S1). The 2 methods for calculating PSA were compared using generalized linear mixed model (GLMM) with species as a random factor to account for non-independence of data due to species relatedness (Supplementary Figure S1) using the *glmer* function in the “lme4” package (Bates et al., 2014) in R version 4.0 (R Development Core Team 2010). They were highly correlated ($n=380$; $R^2=0.893$), and the slope of this relationship was tested using an analysis of variance (ANOVA) and was significantly different from $\beta=1$ ($F_{1,358}=178.52$, $P=0.005$). We retained the dimension-derived values for further analyses as we had the least missing data for this measure and also used dimension-derived values for tympanic bulla volume (TBV) (see below).

An additional pinna metric, effective diameter (ED), which is believed to better capture the acoustic impact of pinna size, was calculated as per Jones et al. (2011) (Supplementary Table S2).

$$ED = \sqrt{PW * PH} \quad (2)$$

Skulls

Measurements were made of maximum skull length (Onar 1999; Cooper 2000) (mm) using digital calipers (Figure 3B). Maximum length, width, and height of the right tympanic bulla (Figure 3A, C–E; Basso et al. 2017) were measured if it was intact or had suffered only superficial damage that would not affect these measurements. In cases where the right tympanic bulla was deemed too damaged to be used, the left was measured. The TBV was estimated based on half the volume of an ellipsoid:

$$TBV = 1/2 \left(4/3 \pi^{1/2} TBL * 1/2 TBW * TBH \right) \quad (3)$$

where TBL = maximum tympanic bulla length, TBW = maximum tympanic bulla width, and TBH = tympanic bulla height from the glenoid fossa, where the mandible connects with the zygomatic arch (Figure 3D and E).

We tested a second method for measuring TBV using a paper funnel to fill the bulla with fine sand which was then weighed to calculate volume (from a known density of the sand). Not all specimens were available for sand measurements (Supplementary Table S1) and unreliable volume measures were obtained for the New Guinean species (except *I. m. moresbyensis*) due to the open nature of their tympanic bulla. The dimension-derived and sand methods were compared using GLMM with species as a random factor to account for non-independence of data due to species relatedness (Supplementary Figure S2). The 2 methods provided highly correlated results ($n=388$; $R^2=0.966$) but the relationship was significantly different from slope of linearity ($\beta=1$) (slope comparison ANOVA test: $F_{1,226}=361.91$, $P \leq 0.005$). The challenges to obtaining a volume measure using the sand method for the New Guinean genera, plus incomplete data for this method led us to elect to retain the TBV estimated from bulla dimensions for further analyses (Supplementary Figure S2).

Choice of moderator variables (fixed effects)

Species' distribution maps (Supplementary Figure S3) were drawn in QGIS (QGIS Development Team 2019) using data obtained from the IUCN (2017) terrestrial mammal database, Warburton and Travouillon (2016), modified from Travouillon and Phillips (2018), and the Mammals of New Guinea (Flannery 1995). These maps

Table 1. Summary of data used for these analyses, showing the number of specimens from which measures were collected and the environmental predictor traits used in analysis for each species

Genus Species	IUCN Status	Number of specimens			Sources	Habitat	Temperature (°C)		Precipitation (mm)	
		Skulls	Skins	Total			T_{\max}	T_{avg}	P_{\max}	P_{avg}
CHAEROPODIDAE										
<i>Chaeropus</i>										
<i>C. yirratji</i>	EX	3	4	7	SAM, NMV	Open	42.4	22.7	513	249
THYLACOMYIDAE										
<i>Macrotis</i>										
<i>Ma. lagotis</i>	VU	38	19	57	AM, WAM	Open	43.3	25.0	909	354
<i>Ma. leucura minor</i>	EX	5	1	6	NMV, AM, NHMUK	Open	42.4	22.6	513	249
PERAMELIDAE										
<i>Perameles</i>										
<i>Pe. bougainville</i>	EN	13	15	28	WAM	Open	35.0	22.0	268	227
<i>Pe. eremiana</i>	EX	2	1	3	AM, MV/NMV	Open	43.3	21.8	626	268
<i>Pe. gunnii</i>	VU	3	8	11	AM, WAM, NMV, QVMAG	Open	25.3	13.4	1,958	880
<i>Pe. gunnii gunnii</i>	VU	5	—	5	AM, WAM	Open	22.9	10.6	2,258	971
<i>Pe. myosuroides</i>	EX	3	1 ^a	4	AM, WAM	Open	33.2	17.2	1,158	404
<i>Pe. nasuta</i>	LC	33	27	60	AM, WAM	Open	35.8	17.1	7,625	1,028
<i>Pe. papillon</i>	EX	5	3	8	WAM	Open	32.8	17.8	391	224
<i>Isoodon</i>										
<i>I. auratus auratus</i>	VU	8	14	22	WAM	Open	38.7	26.4	1,525	1,123
<i>I. auratus barrowensis</i>	VU	9	30	39	WAM	Open	35.8	25.7	309	303
<i>I. fusciventer</i>	LC	85	125	210	AM, WAM	Mixed	31.5	16.0	1,405	712
<i>I. macrourus macrourus</i>	LC	13	46	59	AM, WAM	Mixed	40.4	26.9	1,888	1,134
<i>I. macrourus moresbyensis</i> (NG)	LC	5	1	6	AM	Mixed	34.3	26.2	3,453	1,988
<i>I. macrourus torosus</i>	LC	11	16	27	AM, WAM	Mixed	38.0	21.7	7,625	977
<i>I. obesulus affinis</i>	EN	3	3	6	AM, WAM, QVMAG	Closed	22.6	10.0	2,924	1,354
<i>I. obesulus nauticus</i>	EN	5	2	7	WAM, SAM, NHMUK	Closed	25.0	16.6	308	297
<i>I. obesulus obesulus</i>	EN	4	10	14	AM, WAM	Closed	30.1	13.8	1,958	848
PERORYCTIDAE										
<i>Peroryctes</i>										
<i>Per. raffrayana</i> (NG)	LC	17	4	21	AM, WAM	Mixed	34.1	20.1	7,322	3,046
<i>Echymipera</i>										
<i>E. clara</i> (NG)	LC	13	3	16	AM	Closed	33.2	25.8	4,244	2,798
<i>E. davidi</i> (NG)	EN	4	3	7	AM	Closed	31.3	26.5	3,751	3,518
<i>E. kalubu</i> (NG)	LC	69	27	96	AM, WAM	Closed	34.3	24.0	7,322	3,044
<i>E. rufescens</i> (NG)	LC	14	6	20	AM, WAM, QM	Closed	34.2	24.0	7,322	3,024
<i>E. rufescens australis</i>	LC	6	1	7	AM, QM	Closed	36.2	26.0	2,150	1,559
<i>Microperoryctes</i>										
<i>Mi. longicauda</i> (NG)	LC	1	—	1	AM	Mixed	30.8	19.1	3,357	3,117
<i>Mi. murina</i> (NG)	DD	1	1	2	AM, AMNH	Closed	26.2	10.8	3,442	3,395
<i>Mi. ornata</i> (NG)	LC	26	13	39	AM, WAM	Closed	33.5	19.2	7,322	3,128
<i>Mi. papuensis</i> (NG)	LC	5	5	10	AM, WAM	Closed	32.4	19.0	3,642	2,695
Total		409	389	798						

NG indicates species from New Guinea (all others are from Australia). Ten skulls were removed from the data set for the analysis due to some ambiguity in their taxonomy (*Isoodon* sp. $n = 1$ and *I. obesulus* $n = 1$), their TBV being markedly smaller than the other individuals of that species (*Mi. ornata*, $n = 4$), or due to being outliers when comparing all species (*I. fusciventer*, $n = 3$; *Ma. lagotis*, $n = 1$); totals do not include specimens which were removed for analysis. ^a Denotes the use of a dry skin—a mounted specimen; a piece of tissue paper was folded around the back of the ear and then the shape of the ear was traced onto it. From this, the width and height of the pinna were able to be measured using digital calipers. LC, Least Concern, VU, Vulnerable, EN, Endangered, EX, Extinct; AMNH, American Museum of Natural History; AM, Australian Museum; NHMUK, Natural History Museum UK; NMV, Museum Victoria; SAM, South Australian Museum; QM, Queensland Museum; QVMAG, Queen Victoria Museum & Art Gallery; WAM, Western Australian Museum.

were used to obtain maximum and average values for temperature (T_{\max} and T_{avg} ; as a measure of the level of thermal challenge for each species) and precipitation P_{\max} and P_{avg} (as a proxy for vegetation productivity and therefore habitat complexity; Sala et al. 1988; Huxman et al. 2004) for each species' distribution range using the Worldclim dataset (Global Climate Data: <http://worldclim.org/version2>; Fick and Hijmans 2017), which aggregated monthly climate

data across a spatial resolution of 1 km² between 1970 and 2000. The spatial average was calculated across all pixels in the species' distribution range for 2 variables summarizing annual temperature: band 15 (T_{\max} of the warmest month) and band 19 (annual mean temperature). Both spatial average and maximum values were calculated for precipitation from band 8 (annual precipitation). Habitat type (Open = 0, Mixed = 0.5, Closed = 1; sensu Warburton and

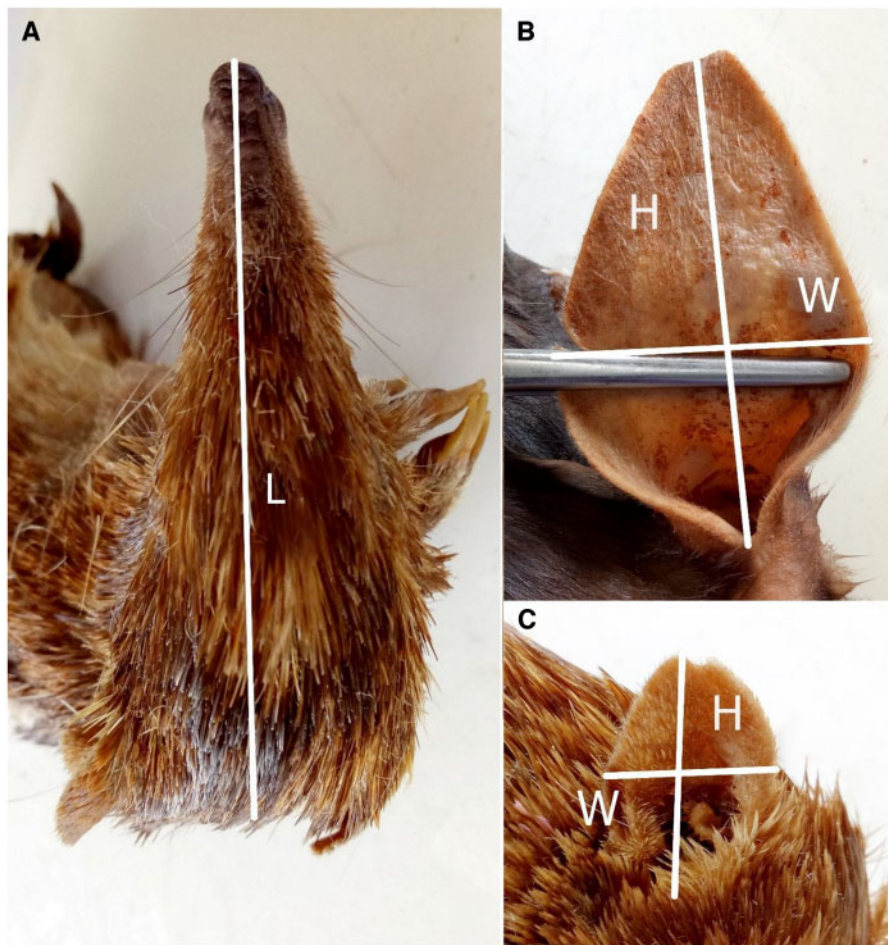


Figure 2. Skin measurements for all specimens. (A) Head length for skins. (B) Pinna height and (C) pinna width.

Travouillon 2016), as a proxy of the type of ground and overhead cover, was also considered in modeling. We tested for collinearity between predictor variables using *vif*. *MCMCglmm* in the package “MCMCglmm” (Hadfield 2010) in R.

Choice of moderator variables (random effects)

To control for the potential non-independence of species’ data due to phylogenetic relatedness between species (Harvey and Pagel 1991; Chamberlain et al. 2012; Nakagawa and Santos 2012), we implemented phylogenetic information as a variance–covariance matrix in analyses. A phylogenetic tree was constructed by combining 2 trees constructed using genetic information (Westerman et al. 2012; Travouillon and Phillips 2018) and creating a tree with branch segments representing approximate million year intervals that was built using *Mesquite* (Figure 4). Four species were not found in either of the existing trees (*P. myosuroides*, *Isodon m. moresbyensis*, *I. o. nauticus*, and *Microperoryctes murina*) and were therefore placed in polytomies with the expected closest relative (Cruz-Neto et al. 2001).

Statistical analysis

For comparative purposes, we calculated species residuals for both pinnae and bullae size against head and skull length, respectively. These residual values were plotted against each other to represent the relative size of both the PSA and TBV for each of the species

(Figure 5). Due to the lack of specimens from which PSA was measured, *Mi. longicauda* had a species residual calculated from the average of all the species residuals of *Microperoryctes* species and *Pe. gunnii* was allocated the same standardized residual as *Pe. gunnii* (of which it is a sub-species). These values were not used for further analysis and are for visual inspection of the data only.

We carried out GLMMs comparing log-transformed PSA, ED, or TBV as dependent variables in separate analyses. For fixed factors, we included \log_{10} -head length or \log_{10} -skull length (PSA and ED, or TBV, respectively) to account for larger individuals having larger pinnae or bullae. For the analysis of PSA and ED, we also included TBV, and we included PSA for the analysis of TBV; because we rarely had PSA and TBV for the same specimens, \log_{10} -transformed species-average PSA or TBV values were calculated and included. Finally, we included T_{avg} and T_{max} and average (P_{avg}) and maximum precipitation (P_{max}) values as fixed factors. Continuous variables were mean-standardized.

The effect of precipitation and temperature on log-transformed PSA and TBV were isolated using the *ggpredict* function in “ggeffects” package (Lüdtcke 2019) in R on lmer models (keeping other predictor variables constant). These did not account for phylogeny but included species as a random factor.

Sensitivity analyses were carried out to evaluate the effect of statistical assumption of phylogenetic covariance on conclusions (Koricheva and Gurevitch 2014; Noble et al. 2017) by comparing statistical models with and without phylogenetic correction. We ran multilevel/hierarchical analyses comparing (i) linear mixed-effect

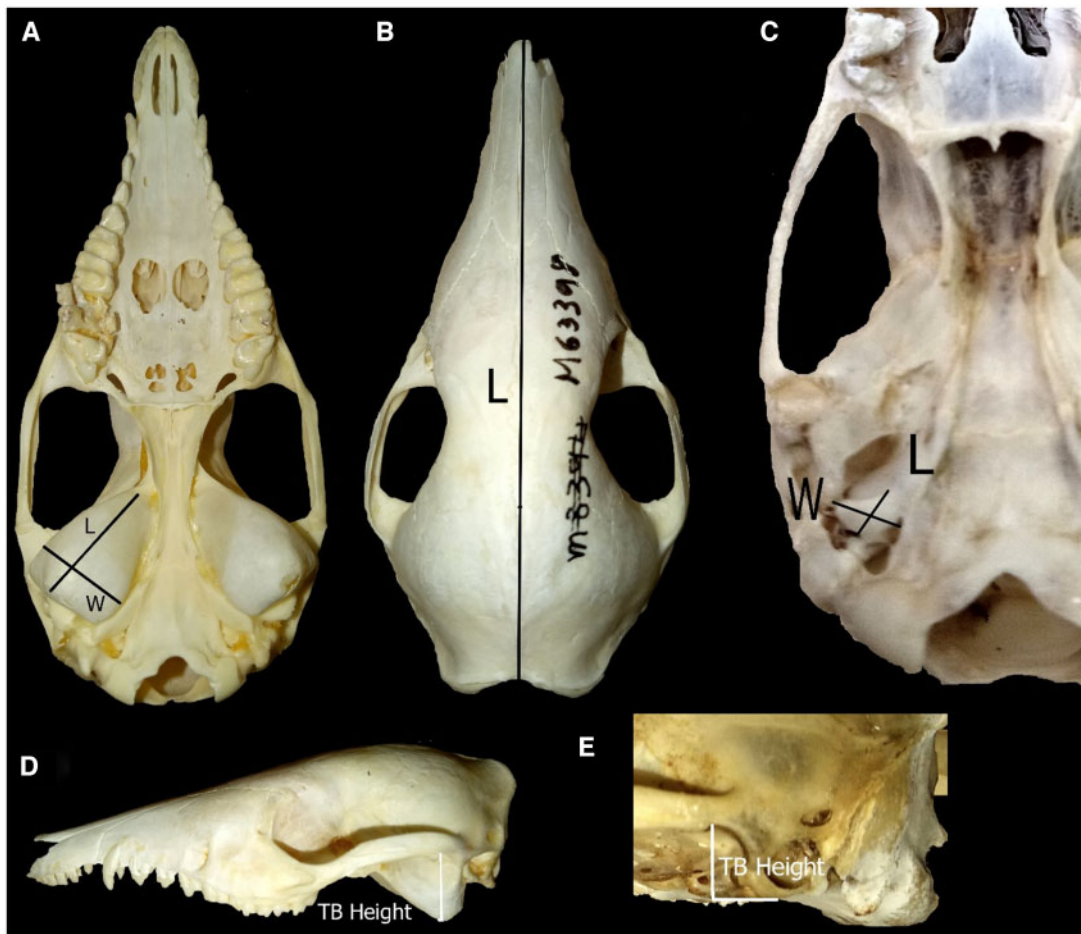


Figure 3. Skull measurements for an Australian (*Isoodon fusciventer*; A, B, and D) and New Guinean (*Echymipera kalubu*; C and E) bandicoot species. (A, C) Length and width of tympanic bulla; (B) Skull length for both species groups; (D and E) tympanic bulla height.

models with species as a random factor using *lmer*, (ii) models with species as a random factor using *MCMCglmm* (Markov chain Monte-Carlo GLMMs) function in the “MCMCglmm” package (Hadfield 2010) in R, and (iii) models with species and phylogeny (a phylogenetic distance matrix) as random factors using *MCMCglmm*. For *MCMCglmm* analyses, we used a burn-in of 1,000 iterations, a thinning rate of 500, and 50,000 iterations for each test with a non-informative prior. There were strong associations between precipitation and temperature with habitat type categories. P_{avg} and P_{max} were positively correlated ($R_s = 0.818$, $P < 0.001$), and T_{avg} and T_{max} were positively correlated ($R_s = 0.682$, $P < 0.001$). Habitat category (Open = 0, Mixed = 0.5, Closed = 1) was negatively correlated with T_{max} ($R_s = -0.434$, $P < 0.05$), and positively correlated with P_{avg} ($R_s = 0.688$, $P < 0.001$) and P_{max} ($R_s = 0.523$, $P < 0.01$). To minimise collinearity for these global models, habitat category and P_{max} for TBV; habitat category and T_{max} for PSA; or PSA, habitat, and T_{max} for ED ensured that all variance inflation factors were < 5 .

We used the models with the greatest weight of support (Model ii for PSA, and Model iii for ED and TBV) for further analysis using the *dredge* function in the “MuMIn” package (Barton and Barton 2020) in R. We dealt with collinearity between environmental variables by ensuring that combinations of strongly correlated environmental variables (T_{avg} and T_{max} ; P_{avg} and P_{max}) were not included in the same models as part of the *dredge* function. Models were ranked by deviance information criterion (DIC) and we averaged

beta estimates across the top models that were within 2 DIC units of the best model using *model.avg* in the “MuMIn” package. For each predictor variable, we calculated their relative variable importance as the sum of model weights (w_i) for all models containing the variable. We present summary statistics (estimates and their credible intervals) for the global Model iii.

Results

A total of 798 museum specimens were measured; 389 skins for pinna measurements (average 14.9 ± 25.2 individuals per species, range 1–125) and 409 skulls for tympanic bulla measurements (average 13.9 ± 19.3 individuals per species, range 1–82; Table 1). Two types of pinnae were noted: smaller, rounded pinnae (*Isoodon* spp., *Echymipera* spp., *Microperoryctes* spp., and *Peroryctes raffrayana*), and larger, more elongated pinnae (*Perameles* spp., *Chaeropus yirratji*, and *Macrotis* spp.). Three types of bullae were noted: incomplete (*Echymipera* spp., *Microperoryctes* spp., and *Per. raffrayana*), spherical (*Perameles* spp. and *C. yirratji*), and oblong (*Isoodon* spp. and *Macrotis* spp.).

The arid-dwelling bilbies (*Macrotis* spp.) are extreme in their combination of pinnae and tympanic bullae that were both relatively much larger than expected for their skull and head size (upper right quadrant of Figure 5 showing relative PSA against relative TBV). *Macrotis lagotis* had the largest relative pinna size and the second

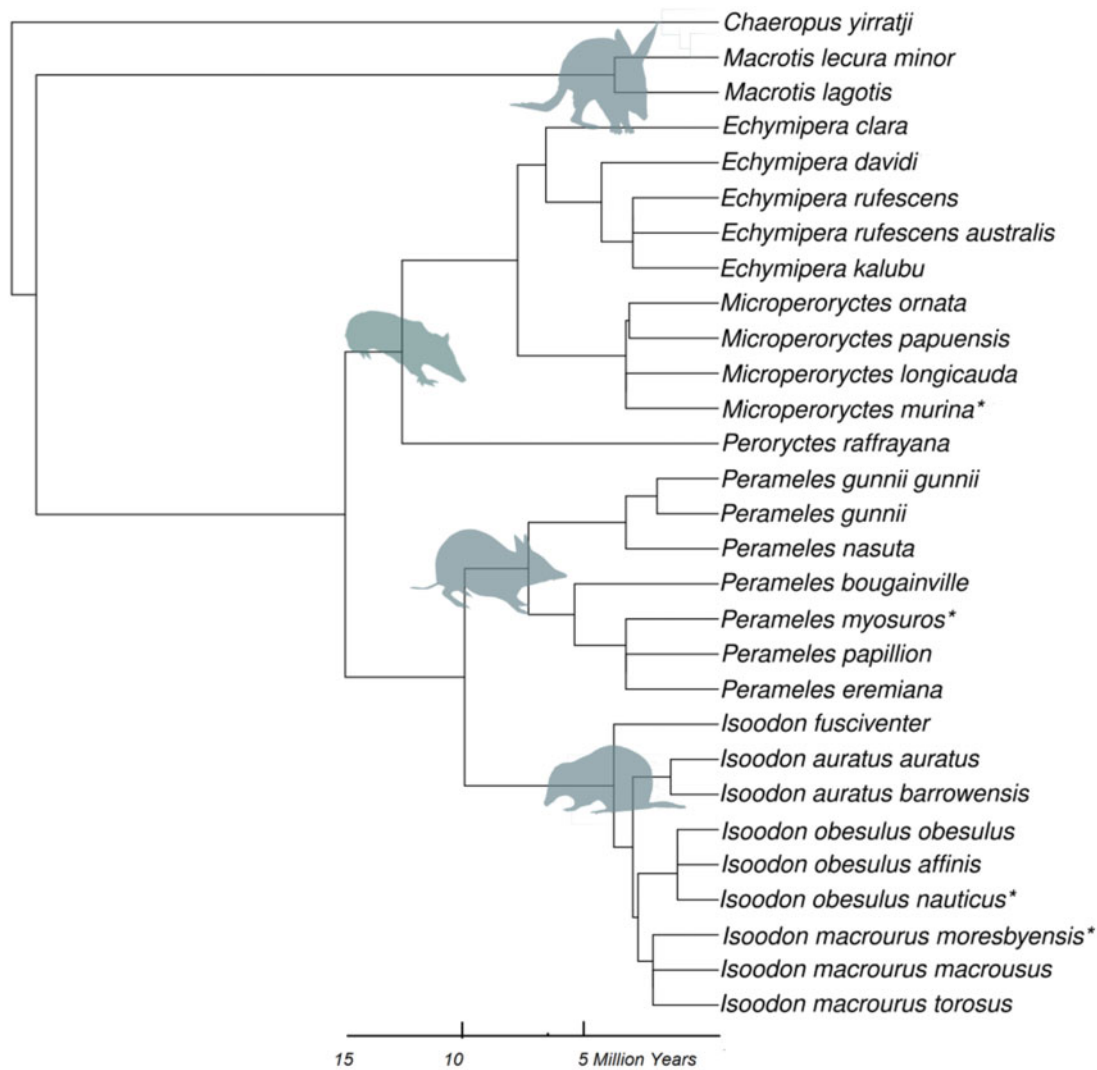


Figure 4. Phylogenetic tree showing relative relatedness of all 29 species and subspecies in the analysis. Asterisks denotes species not present on existing trees.

largest relative bulla size overall (after *Ma. leucura minor*). *Chaeropus yirratji* had average-sized tympanic bulla, but the fourth largest relative pinna size.

Short-nosed bandicoots (*Isoodon* spp.) generally had tympanic bullae that were larger than expected but pinnae that were smaller than expected (lower right quadrant of Figure 5). The exception was the New Guinean *I. macrourus moresbyensis*, which had noticeably smaller relative bullae size than the rest of its genus.

All long-nosed bandicoots (*Perameles* spp.) had larger than expected pinnae (upper quadrants of Figure 5), although there are species with both larger and smaller than expected bullae. *Perameles nasuta* stood out from other *Perameles* spp., with the third largest pinnae overall and the smallest bullae of Australian genera.

The New Guinean bandicoot species (*Echymipera* spp., *Microperoryctes* spp., and *Per. raffrayana*) shared similar ear morphology, having both smaller pinnae and smaller bullae than expected for their size (lower left quadrant of Figure 5). The 1 species found on the Australian mainland, *E. r. australis*, has the largest bullae of these 3 genera.

For the global model for PSA (i.e., including all environmental variables simultaneously except for those that caused a high VIF

value), Model ii had marginally more support than Model iii ($\Delta AIC = 1.66$), indicating that phylogenetic correction did not markedly improve model-fit (Table 2). For thoroughness, we have included the results for both Model ii and Model iii for PSA. For ED and TBV, Model iii was the best fit for the global model.

PSA was strongly correlated with head length, which was retained in all the top models (i.e. $\Delta AIC < 2$) describing PSA. For the un-corrected analyses (Model ii), species-average TBV was included in 1 of 3 top models that included *Pe. myosuuros* (Table 3a), and 1 of 2 top models describing the dataset that excluded the single *Pe. myosuuros* specimen (Table 3b). Average temperature was included in 1 of 3 top models that included *Pe. myosuuros*, while none of the best models describing the dataset that excluded *Pe. myosuuros* included any environmental predictor variables. For the models that included phylogeny (Model iii), the dataset that included *Pe. myosuuros* was best described by a single model that also included only head length (Table 3c). When the single *Pe. myosuuros* specimen was excluded, species-average TBV, P_{max} and T_{avg} were each included in 1 of 4 top models (Table 3d). For the global Model iii -Pm, the strongest environmental factor was a negative correlation with P_{avg} which had a nonsignificant effect (estimate = -

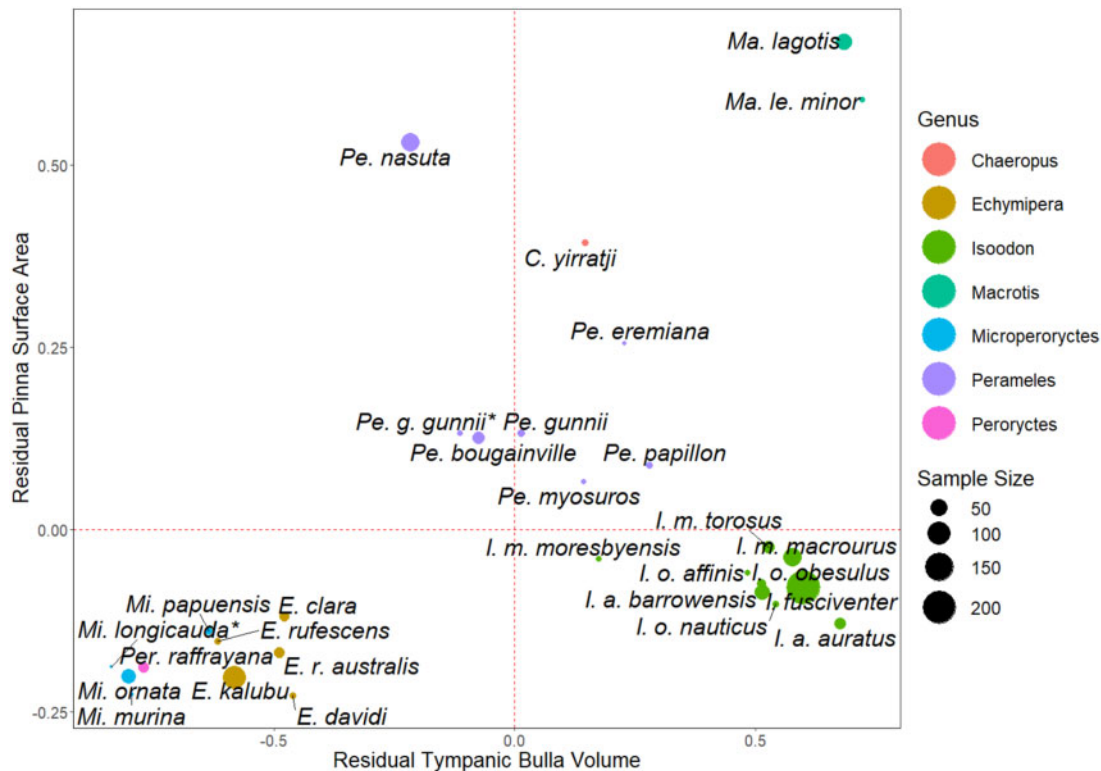


Figure 5. Comparison of standardized residuals for each species and sub-species. Dotted red line represents the average expected value across all species for both pinna surface area (PSA) and tympanic bulla volume (TBV) when accounting for skull and head length. Asterisks denotes species where only TBV values were available: *Microperoryctes longicauda* had a species residual calculated from the average of all the species residuals of *Microperoryctes* species and *Perameles g. gunnii* was allocated the same standardized residual as *Perameles gunnii* as it is a sub-species of it.

0.278 [confidence interval [CI] -0.611 to 0.001], $P = 0.061$) whereas T_{avg} had minimal effect (estimate = 0.020 [CI -0.123 to 0.172], $P = 0.714$) (Figures 6d and 7a,b).

The ED was strongly positively correlated with head length, which was retained in both top models. Species-average TBV was retained in 1 of the 2 top models but neither this value nor any of the environmental predictors significantly improved model fit (Figure 6E).

TBV was strongly positively correlated with skull length, which was retained in all 7 of the top phylogenetically-corrected models (Model iii) (Table 3f). Species-average PSA was retained in 1 of the 7 top models (Table 3f). P_{avg} was retained in 2 of the 7 top models (Table 3f) and had a significant effect on the global Model iii (estimate = -0.99 [CI -1.359 to -0.634], $P \leq 0.01$). P_{max} and T_{avg} were both retained in 2 models; P_{max} was not included in the global Model iii due to collinearity, while T_{avg} had a nonsignificant effect on the global Model iii (estimate = 0.308 [CI -0.256 to 0.682], $P = 0.184$). T_{max} was retained in 3 of the 7 top models; although it had the second highest sum of model weights (0.458 for model selection; Table 3f), it had a nonsignificant effect on the global Model iii (estimate = -0.181 [CI -0.585 to 0.249], $P = 0.388$). The model excluding these 3 factors was not strongly ranked ($\Delta DIC = 2.006$). The strongest factor was a negative correlation with P_{avg} which resulted in a significant effect for the lmer global model ($P < 0.01$) (Figures 6F and 7C,D).

There was only a weak relationship between PSA (residual of \log_{10} -PSA relative to \log_{10} -head length) and TBV (residual of \log_{10} -

TBV relative to \log_{10} -skull length; Figure 5). Although species-average TBV was retained in the models for PSA, it was not a significant predictor variable; similarly, species-average PSA was retained in the models for TBV but it was not a significant predictor variable (Table 3). Instead, the distribution of data for both (PSA and TBV) measures strongly reflected environmental patterns.

Discussion

Hearing anatomy for bandicoots and bilbies (Peramelemorphia) is influenced by a species' environment. TBV, which is typically associated with auditory wavelength sensitivity or hearing range (Mason 2016), was strongly correlated with environmental factors. PSA showed a weaker relationship with precipitation, which could reflect other selective pressures in addition to sound localization acting on pinnae, including thermoregulation and physical obstruction (Webster 1966; Heffner et al. 1996). The relationship between TBV and PSA in bandicoots and bilbies was weak. For example, whereas PSA and TBV were generally positively correlated, short-nosed bandicoots (*Isoodon* spp.) had relatively small pinnae but large bullae. This finding suggests that there are independent selective pressures acting on PSA and TBV, with different relationships with precipitation and temperature observed.

Bulla volume had a negative relationship with precipitation and (to a lesser degree) a positive relationship with temperature, both of which are factors reflecting environmental aridity. The largest bullae were seen in the arid-dwelling bilbies (*Macrotis* spp.) and the more

Table 2. Results of multilevel/hierarchical analyses comparing (i) linear mixed-effect models with species as a random factor using *Imer*, (ii) models with species as a random factor using *MCMCglmm*, and (iii) models with species and phylogeny as random factors using *MCMCglmm*. Data for PSA are shown with and without the single specimen for *Perameles myosuuros*.

Random factors		Pinna surface area (PSA)							
		(a) with <i>Pe. myosuuros</i>		(b) without <i>Pe. myosuuros</i>		(c) Effective Diameter (ED)		(d) Tympanic bulla volume (TBV)	
		df	BIC	df	BIC	df	BIC	df	BIC
Model i Imer	species	8	-273.36	8	-274.30	8	-753.05	8	-753.05
Model ii glmm	species	8	-399.09	8	-397.42	8	-918.11	8	-918.11
Model iii glmm_pc	Species + phylogeny	8	-397.43	8	-398.09	8	-918.43	8	-918.43

Bold indicates the model with the strongest weight of support; for PSA (a), Model ii had the strongest support but Model iii also had strong support ($\Delta AIC = 1.66$); therefore we present the results for both models. For PSA, we also re-ran the analysis with and without the single *Pe. myosuuros* specimen, as there was shrinkage evident for this specimen.

Table 3. Summary of top models ($\Delta DIC < 2$) for (a–d) PSA Models ii and iii, (e) ED Model iii and (f) TBV Model iii for 29 species of bandicoots and bilbies (*Peramelemorphia*). Italics indicate the model-averaged beta coefficients for each predictor variable, and the relative importance of variable (*sw*: the sum of model weights for those models that variable was included in).

	(Intercept)	Head length	sp.-avg TBV	Hab	<i>P</i> _{avg}	<i>P</i> _{max}	<i>T</i> _{avg}	<i>T</i> _{max}	df	logLik	DIC	delta	<i>w</i> _i
(a) Pinna Surface area (PSA)—Model ii + <i>Pe. myosuuros</i>													
Model1	6.256	0.183	—	—	—	—	—	—	4	223.67	-439.24	0	0.273
Model2	6.406	0.182	0.266	—	—	—	—	—	5	224.00	-437.83	1.40	0.135
Model3	6.242	0.185	—	—	—	-0.022	—	—	5	223.88	-437.6	1.64	0.120
Average	6.301	0.183	0.266	—	—	-0.022	—	—	—	—	—	—	—
<i>sw</i>	—	1	0.201	—	—	0.279	—	—	—	—	—	—	—
(b) Pinna surface area (PSA)—Model ii - <i>Pe. myosuuros</i>													
Model1	6.265	0.185	—	—	—	—	—	—	4	223.48	-438.85	0	0.220
Model2	6.412	0.182	0.264	—	—	—	—	—	5	224.44	-438.72	0.13	0.206
Average	6.338	0.183	0.264	—	—	—	—	—	—	—	—	—	—
<i>sw</i>	—	1	0.408	—	—	—	—	—	—	—	—	—	—
(c) Pinna surface area (PSA)—Model iii + <i>Pe. myosuuros</i>													
Model1	6.249	0.182	—	—	—	—	—	—	4	224.01	-439.92	0	0.391
Average	6.249	0.182	—	—	—	—	—	—	—	—	—	—	—
<i>sw</i>	—	1	—	—	—	—	—	—	—	—	—	—	—
(d) Pinna surface area (PSA)—Model iii - <i>Pe. myosuuros</i>													
Model1	6.417	0.182	0.271	—	—	—	—	—	5	223.49	-436.83	0	0.191
Model2	6.246	0.184	—	—	—	—	—	—	4	222.18	-436.26	0.57	0.144
Model3	6.282	0.183	—	—	—	-0.027	—	—	5	222.64	-435.12	1.70	0.082
Model4	6.261	0.184	—	—	—	-0.245	—	—	5	222.59	-435.02	1.81	0.077
Average	6.301	0.183	0.271	—	—	-0.245	-0.027	—	—	—	—	—	—
<i>sw</i>	—	1	0.225	—	—	0.18	0.105	—	—	—	—	—	—
(e) Pinna effective diameter (ED)—Model iii													
Model1	3.253	0.089	—	—	—	—	—	—	4	483.12	-958.14	0	0.299
Model2	3.328	0.089	0.138	—	—	—	—	—	5	483.37	-956.59	1.55	0.138
Average	3.29	0.089	0.138	—	—	—	—	—	—	—	—	—	—
<i>sw</i>	—	1	0.304	—	—	—	—	—	—	—	—	—	—
(f) Tympanic bulla volume (TBV)—Model iii													
Model1	5.068	0.208	—	—	-0.903	—	—	—	5	58.28	-106.42	0	0.139
Model2	4.882	0.209	—	—	—	-0.903	—	—	5	57.97	-105.8	0.62	0.102
Model3	5.037	0.206	—	—	—	—	—	0.331	5	57.89	-105.65	0.77	0.094
Model4	4.994	0.21	—	—	—	—	0.237	—	5	57.79	-105.44	0.97	0.085
Model5	4.885	0.214	—	—	—	-0.772	—	0.219	6	58.41	-104.61	1.81	0.056
Model6	5.046	0.206	0.623	—	—	—	—	0.164	6	58.36	-104.5	1.92	0.053
Model7	5.066	0.211	—	—	-0.909	—	0.145	—	6	58.34	-104.46	1.95	0.052
Average	4.997	0.209	0.623	—	-0.906	-0.837	0.191	0.238	—	—	—	—	—
<i>sw</i>	—	1	0.035	—	0.274	0.246	0.222	0.458	—	—	—	—	—

Model ii included species as random factor; Model iii included species and phylogeny as random factors.

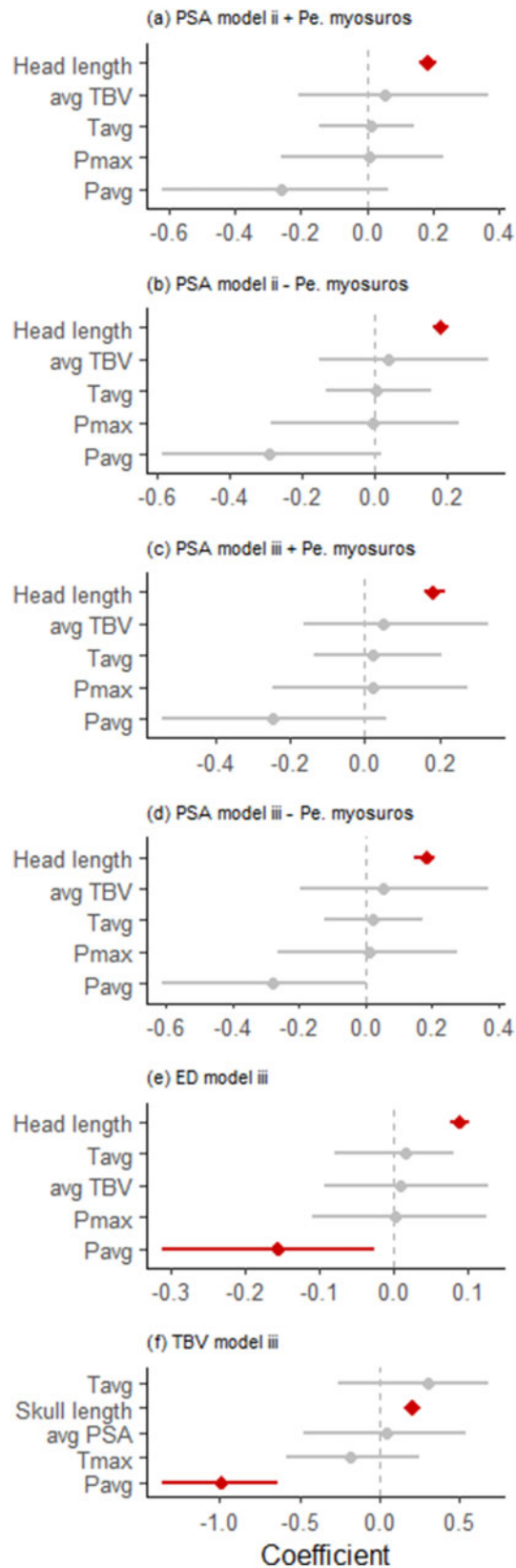


Figure 6. Beta estimates \pm 95% credible intervals for predictor variables included in the global models describing (A–D) pinna surface area (PSA) (A. Model ii with and B. without *Perameles myosuros*; C. Model iii with and d. without *Pe. myosuros*), (E) Pinna effective diameter (E, D), and (F) tympanic bulla volume (TBV) for 29 species of bandicoots and bilbies (*Peramelemorphia*). Variables with 95% CI that do not overlap with zero are considered influential; those with significant P-values are indicated with bold lines. Note that this figure is derived from the global Model iii, and therefore excludes strongly correlated predictor variables.

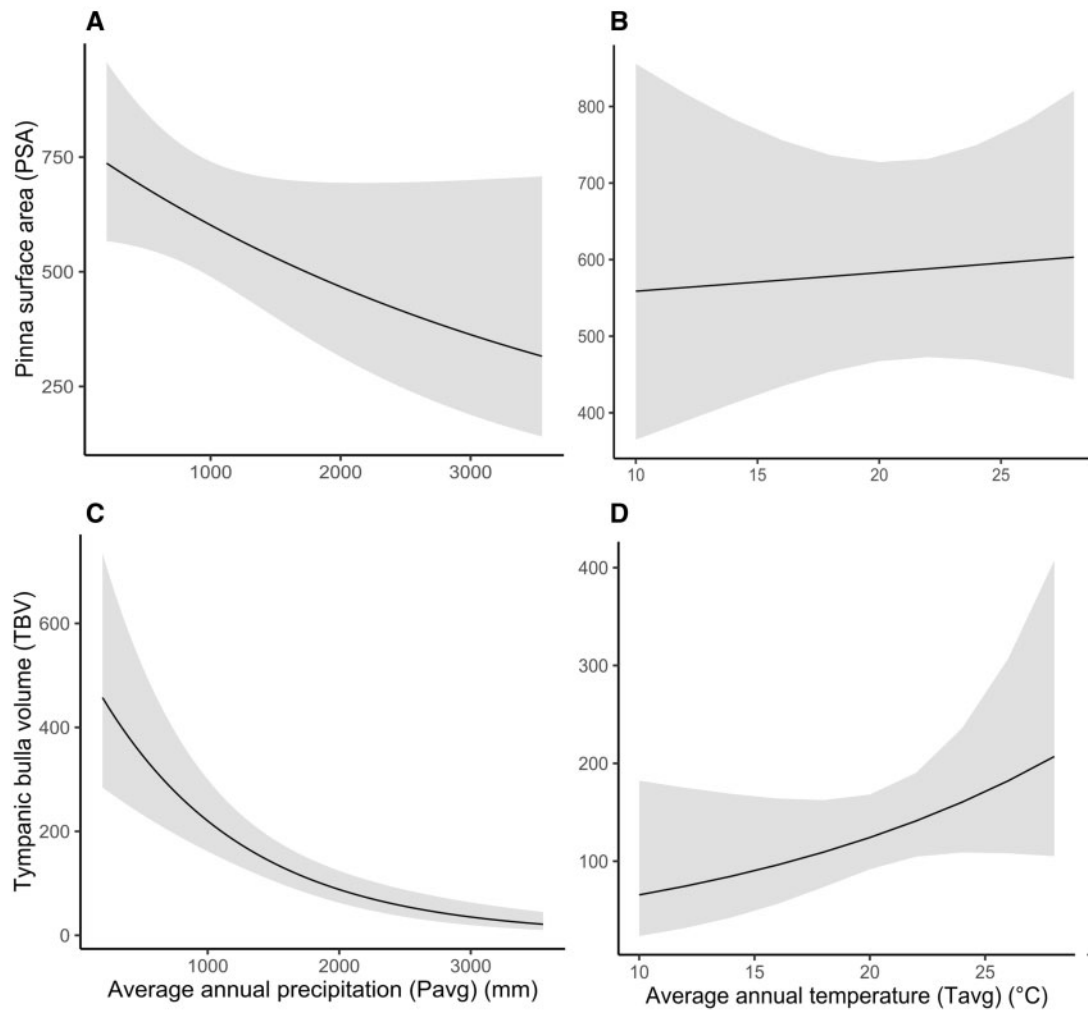


Figure 7. Predicted means (lines) and 95% CIs (shaded areas) for the effects of average precipitation (P_{avg}) and average temperature (T_{avg}) on pinna surface area (PSA) and tympanic bulla volume (TBV), where all other factors in the global model are held constant at their mean values. Note that this figure is derived from the lmer models, which are not corrected for phylogenetic relationships.

arid-adapted *Perameles* spp. (*P. eremiana*, *P. myosuroides*, and *P. papilion*). Larger bullae have been similarly noted in a number of species residing in low precipitation environments, such as rodents (Alhajeri et al. 2015; Alhajeri 2016; Khajeh et al. 2019), armadillos (Cingulata; Basso et al. 2020), and some leporid lagomorphs (Kraatz et al. 2015). Habitat aridity and complexity impact the distance different sound frequencies travel and therefore which frequencies carry the most useful information for sound localization. Arid conditions result in higher-frequency sounds attenuating at a more rapid rate than in more humid conditions, and therefore lower-frequency sounds carry more information over greater distances than high frequencies (Knudsen 1931; Huang et al. 2002), providing forewarning of potential predation threats. Selection for low-frequency hearing has contributed to relatively larger bullae in small animals that would otherwise have limited capacity to detect low-frequency sounds that would be of use for accurate sound localization (Lay 1972; Ravicz and Rosowski 1997).

In contrast, bandicoot species that live in high rainfall environments (which we would expect would also have dense, closed habitat) had small tympanic bullae. This relationship was exemplified by the New Guinean species: *Echymipera* spp., *Microperoryctes* spp., and *Peroryctes raffrayana*. Small bullae reflect reduced reliance on low

frequencies that would have limited value in dense vegetation, where sound can be reflected and distorted by obstructions and quickly attenuates (Michelsen and Larsen 1983; Blumenrath and Dabelsteen 2004). In fact, being able to hear lower frequency sounds in dense vegetation may cause confusion and obscure high-frequency cues (Michelsen and Larsen 1983; Blumenrath and Dabelsteen 2004). Supporting this interpretation, *I. m. moresbyensis*, a completely different genus of animals inhabiting the same environments in New Guinea, also had markedly smaller bullae than the Australian *Isoodon* species, representing a case of convergent evolution that strongly suggests selection against large bullae (low frequency hearing) in closed habitats.

PSA showed a negative relationship with precipitation. Bandicoot and bilby species residing in arid environments (e.g., *C. yirratji* and *Macrotis* spp.) had relatively large pinnae for their size. A negative relationship between pinna size and precipitation has also been noted in rodents (Rodentia) (Khajeh et al. 2019; Alhajeri et al. 2020). Pinnae can alter the timing (ITD) and sound level (ILD) of auditory cues to each middle ear (Kuhn 1987) independently of head size (Tollin and Koka 2009). Open, arid environments would select for larger pinnae that are more attuned to low frequencies (Wightman and Kistler 1992, Jones et al. 2011) and

better sound localization through ILD cues (Jones et al. 2011) and ITD cues (Wightman and Kistler 1992; King et al. 2001). For our study, the ED of pinnae, a specific measure of ILD cues (Jones et al. 2011) was correlated with head length only, and showed no association with the environmental factors tested.

The weak positive relationship between pinna size and temperature could also reflect thermoregulatory function of pinnae such as seen in bilbies (*Macrotis* spp.) and northern pig-footed bandicoot *C. yirratji* (Figure 5; Supplementary Figure S3). Whereas we have no data on the thermal biology of the extinct northern pig-footed bandicoot, bilbies are known to have low heat tolerance (Gibson and Hume 2000) and escape the extreme heat of the day by residing in subterranean burrows (Johnson and Johnson 1983; Abbott 2001). Their large pinnae may therefore play a thermoregulatory role through shedding heat, as pinna size and vasculature have been linked with thermoregulation in many species (Webster 1966; Maloij et al. 1982), for instance, African elephants (*Loxodonta* spp.; Young 1957; Phillips and Heath 1992) and jackrabbits (*Lepus* spp.; Hill and Veghte 1976). Conversely, animals in cold environments tend to have smaller pinnae to reduce heat loss (Allen 1877).

In contrast, bandicoot species from high rainfall environments, such as the New Guinean bandicoots (*Echymipera* spp., *Microperoryctes* spp., and *Peroryctes raffrayana*) and short-nosed bandicoots (*Isoodon* spp.), had relatively small pinnae for their size. In dense vegetation, high-frequency ILD cues would be of greatest value to sound localization (Heffner et al. 1996; King et al. 2001). In contrast, ITD cues afforded by low-frequency sounds would be distorted by reverberations, making it difficult to locate the source of the sound (Giguère and Abel 1993); this would select against large pinnae (Jones et al. 2011) (or select for small pinnae) as lower frequency hearing would be of limited use to species in these environments. Nonauditory factors can also influence pinna size which may have obscured the direct relationships with environmental factors. Hypothetically, large pinnae could also be a disadvantage in closed habitats where they may cause increased obstruction, or could be damaged during antagonistic behaviors that have been noted in these animals (Johnson and Johnson 1983; Hall et al. 2016; Travouillon and Phillips 2018), but currently, there are no available data around these possible mechanisms.

We recognize a number of limitations of this study. First, we had only a single specimen for *Pe. myosoros* and demonstrated that the results of our statistical analyses were sensitive to inclusion of this specimen. As there was some evidence of shrinkage for the specimen, this limits the interpretation of pinna size in this species. For extinct species, this limitation on data availability is inevitable. Second, the peroryctids (*Echymipera* spp., *Microperoryctes* spp., and *Per. raffrayana*) have an incomplete, “open” bulla compared with the fully enclosed bony bulla present in the Australian taxa. We considered that our TBV values for these species may be underestimates due to this. Future work to investigate the structure of the middle ear in these species is warranted, but requires fresh tissue, not the osteological collections that we had available to us. Understanding the selective pressures acting on this part of the skull may be informative regarding how these animals interact with their environment. Third, the predictor variables used in the analyses were broad and derived from geographic distribution maps that necessarily used a mix of historic and current ranges to obtain environmental data. Many peramelemorphian species have recently experienced large range reductions due to human

expansion, as well as the impacts of introduced eutherian predators, and are likely facing different environmental selective pressures. Greater range of environmental measures would add value to studies such as this one, but the basic biology of many of the species included in these analyses is not well known. Improving our understanding of these data-deficient species would be beneficial. Finally, taxonomy of the Peramelemorphia is also a moving feast (Westerman et al. 2012; Travouillon and Phillips 2018; Travouillon et al. 2019), which could add complexity to the patterns observed. We applied current taxonomic divisions to this Order but acknowledge that description and definition of new species within this Order are ongoing and could cast further light on the ecology of this group in the future.

In conclusion, there are implications of this study that could influence how we manage conservation of threatened species. A number of translocations of bilbies and bandicoot species have been undertaken (Moseby and O'Donnell 2003; Richards and Short 2003; Moseby et al. 2011; Robinson et al. 2018). For these to be successful, it is important to match species with appropriate release sites, which probably include the auditory landscape. A mismatch between predators and hearing has been observed to severely reduce evasion success in kangaroo rats *Dipodomys merriami* after bulla size was reduced (Webster 1962). This suggests that translocating species into more arid areas than their hearing is adapted to may increase predation risk. For example, *Pe. bougainville* has been translocated to arid, predator-proof fenced sanctuaries (e.g., Arid Recovery, South Australia; Moseby et al. 2011), but has relatively smaller pinna and tympanic bulla and is therefore less adapted for hearing in arid environments than *Pe. eremiana*, the species that previously occurred in the area (see Travouillon and Phillips 2018). Such differences may influence their survival and persistence outside the predator-proof sanctuary.

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Conflict of Interest

The authors have no conflict of interest to declare.

Authors' Contributions

P.F. and N.W. conceived the ideas; M.T., K.T., P.F., and N.W. designed the methodology; M.T., K.T., and M.A. collected the data; M.T. and P.F. analyzed the data; M.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary Material

“Supplementary material can be found at <https://academic.oup.com/cz>”.

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