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Canine morphometrics as a tool for distinguishing species, sex, and age class in Southern Ocean fur seals

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Abstract

Carcasses resulting from natural mortalities are invaluable for use in scientific studies, provided species, sex, and age class are known. When such data are unavailable, identifying skeletal remains is necessary if one is to use the information contained within samples. Teeth are amongst the best preserved skeletal remains owing to the durability of enamel and dentine. Here, we tested whether external measurements of canines could be used to distinguish two partially sympatric species of Southern Ocean fur seals, the Antarctic *Arctocephalus gazella* and Sub-Antarctic *A. tropicalis* fur seals. We also investigated whether the external measurements of canines could be used to determine the age, sex, as well as island of origin of the animals. Eight morphological variables (crown length, root length, crown width, root width, crown thickness, root thickness, total canine length, and count of external surface annular ridges) were recorded from canines of 340 individuals of known species, sex, and island of origin. The count of external annular ridges provided a good estimate of age, which was confirmed by counting the growth layer groups of sectioned teeth, especially for older animals (> 9 years old). External canine measurements proved useful in distinguishing species, as well as sex within and between species, particularly in adult animals. Species were more difficult to distinguish in females than in males. The islands of origin could only be inferred in male Antarctic fur seals. This study indicates that fur seal teeth of unknown provenance, found either in breeding colonies or as vagrants, provide evidence on species, sex, and age of the animal, which increases the value of associated samples. It further highlights the importance of external measurements of skeletal remains such as canine teeth in separating closely related species.

KEYWORDS
age, Antarctic fur seal, sexual dimorphism, Sub-Antarctic fur seal, tooth

1 | INTRODUCTION

Scientific information gleaned from dead specimens is invaluable. For the carcasses to be useful to science, a minimum of information is required; typically the species, age class, and sex. Usually, this information can reliably be obtained from the carcass when the animal has died recently. It can be difficult to obtain this information when a carcass is in an advanced state of decomposition, when no (or little) sexual dimorphism exists within a species, or when only parts of a skeleton are available for investigation (Molina-Schiller & Pinedo, 2004b). In such cases, morphological characteristics of skeletal remains can prove useful in providing missing life history information (e.g., Cassini, 2013; Tarquini et al., 2020). This could provide a platform from which it is possible to use preserved remains as a retrospective archive of information, mitigating the lack of information.

Among skeletal remains, teeth are generally the best-preserved elements (Bergqvist, 2003) owing to the hardness of enamel and dentine (Giannini, Soares & de Carvalho, 2004; Gwinnett, 1992). Mammalian tooth morphology is diverse and has been used successfully to determine species (e.g., Balasse & Ambrose, 2005), sex (e.g., Vodanović et al., 2007), age (e.g., Chevallier et al., 2017; Richardson et al., 1995; White et al., 2016), body size (e.g., Gingerich et al., 1982; Read et al., 2018), and diet (e.g., Chemisquy et al., 2021; Tarquini et al., 2020; Uchida, 1998a). Marine mammals are no exception, with tooth morphology having been used to inform on age (e.g., Jeglinski et al., 2010; Oosthuizen & Bester, 1997; Read et al., 2018), sex (e.g., Ramos et al., 2000), and diet (e.g., Ford et al., 2011; Purnell et al., 2017) of various species. Further, many marine mammals, particularly cetaceans and pinnipeds, are born with permanent dentition which represents the full postnatal record of that animal (Kubota et al., 2000; Read et al., 2018). Teeth of pinnipeds grow continuously throughout life, with new layers of dentine being deposited on the inside of the pulp cavity until it closes in older adults (e.g., Boyd & Roberts, 1993; Hohn & Fernandez, 1999; Lowry & Folk, 1990; Read et al., 2018). Each one of these growth layers can be seen externally as ridges on the root of the tooth (EARs: external annular ridges) and internally as growth layer groups (GLGs) on longitudinally sectioned teeth (Boyd & Roberts, 1993; Lowry & Folk, 1990; Oosthuizen & Bester, 1997). These annual accumulations represent a year in the life of the animal with dentinal age being close to true age (Hohn et al., 1989; Oosthuizen & Bester, 1997).

In addition, tooth size is a good predictor of skull and body size in several pinniped species; tooth morphometrics should thus be useful in distinguishing between animals of different groups (e.g., age classes, sexes). Indeed, in sexually dimorphic species such as California sea lions Zalophus californianus (Lowry & Folk, 1990), Galapagos sea lions Zalophus wollebaeki (Jeglinski et al., 2010), Antarctic fur seals Arctocephalus gazella (Boyd & Roberts, 1993; Hoffman et al., 2010), and South American fur seals Arctocephalus australis (Molina-Schiller & Pinedo, 2004b), canine length is longer in males than in females from an early age.

Two species of fur seals inhabit the Southern Ocean: the Antarctic and the Sub-Antarctic Arctocephalus tropicalis fur seals.

They are largely spatially segregated with Antarctic fur seals breeding mainly south of the Antarctic Polar Front and the Sub-Antarctic fur seal to the north (Hofmeyr, 2015, 2016). However, they breed in sympatry at three island groups: Macquarie Island, Crozet Archipelago, and the Prince Edward islands (Kingston & Gwilliam, 2007; Lancaster et al., 2006; Wege et al., 2016). After Antarctic fur seals were exploited to extinction and Sub-Antarctic fur seals, close to extinction, at the Prince Edward islands (Hofmeyr et al., 1997), the populations of both species re-established and increased until 2004 (Hofmeyr et al., 2006). Antarctic fur seals are still increasing in abundance while the Sub-Antarctic fur seals population may have reached carrying capacity (Wege et al., 2016). Understanding the drivers of these and future demographic changes is crucial to defining the impacts of these species on the marine ecosystem. For this, opportunistic sampling of carcasses is key, since both species are protected (Hofmeyr, 2015, 2016). While distinct cranial morphological characteristics distinguish the two species (Brunner et al., 2004; Condy, 1978), this is only helpful when an entire intact skull is available for identification.

Therefore, the aim of the present study was to evaluate whether the upper canine morphology can be used to distinguish between the Antarctic and Sub-Antarctic fur seals, as well as to reliably determine age, sex, and island of origin within each species. Upper canines were chosen instead of lower canines as they have proved more useful in age determination in a closely related species, the Cape fur seal A. pusillus pusillus (Oosthuizen & Bester, 1997). Upper canines are less curved than lower canines (pers. obs), making it easier to count EARs, and to longitudinally section teeth for the counting of internal GLGs (Oosthuizen & Bester, 1997; Oosthuizen, 1997). Firstly, we hypothesized that upper canine measurements can be used to accurately age animals from both species. We predicted that both left and right canines can be used with confidence when aging an animal, and that EARs on the roots of the canine closely correlate to the age determined from the counting of dentinal GLGs. The second hypothesis was related to determining sex within species. Both species are sexually dimorphic, with males being considerably bigger than females when adults (Bonner, 1968; Laws, 1993). Because sexual dimorphism allows for different tooth dimensions and growth rates, we hypothesized that, in at least adult animals, upper canine measurements can be used to distinguish between male and female fur seals within each species. Our third hypothesis dealt with species. As tooth size is related to body size at least in Antarctic fur seals (Boyd & Roberts, 1993; Hoffman et al., 2010) and Antarctic fur seals are larger in body size than Sub-Antarctic fur seals on average, especially in males (Condy, 1978), we hypothesized that the males of both species can be distinguished using measurements of the upper canines. We predicted that on average Antarctic fur seal male canines will be larger than Sub-Antarctic fur seal male canines. In females, however, although Antarctic fur seals are significantly heavier than Sub-Antarctic fur seals, and have longer flippers, the average difference in weight is only approximately 2.2 kg (Luque et al., 2007). Further, they do not differ significantly in body length and axillary girth (Luque et al., 2007). We thus hypothesized that it is not

possible to distinguish between females from the two species using canine measurements. The final hypothesis was related to the island of origin. Adult body size also differs between different islands (Bester & Jaarsveld, 1994; Brunner et al., 2002; Dabin et al., 2004). We therefore hypothesized that tooth measurements can be used to determine the island of origin for both species of fur seals. It has been suggested that animals from low-latitudinal islands, such as Amsterdam Island, are larger than their counterparts at higher-latitudinal islands, such as Marion Island (Bester & Jaarsveld, 1994; Brunner et al., 2002; Dabin et al., 2004; but see Authier et al., 2011; Kerley et al., 2000). We thus predicted that within species animals from lower latitudinal islands will have bigger teeth than those from higher latitudes.

2 | MATERIALS AND METHODS

2.1 | Study areas and sample collection

Upper canines were obtained from the Graham Ross Marine Mammal Collection of the Port Elizabeth Museum, South Africa, which houses an extensive collection of Antarctic fur seals, *Arctocephalus gazella* Peters, 1875, and Sub-Antarctic fur seals, *Arctocephalus tropicalis* Gray, 1872, (Supporting Information: Table S1). Specimens were collected between 1974 and 2015 and originated from six islands: Amsterdam (37°49′33″ S, 77°33′17″ E), Bouvet (54°25′08″ S, 03°22′08″ E), Gough (40°19′0″ S, 9°56′0″ W), Heard (53°02′20″ S, 72°36′04″ E), Marion (46° 53′19″ S, 37° 44′08″ E), and South Georgia (54°42′96″ S, 36°58′79″ W). The Antarctic fur seal samples originated from Bouvet, Heard, Marion, and South Georgia islands, and the Sub-Antarctic fur seal samples originated from Amsterdam, Gough, and Marion islands (Figure 1). Antarctic fur seal samples were

FIGURE 1 Geographical origins of canines measured in this study; breeding populations of Antarctic (▲) and Sub-Antarctic (■) fur seals, sites with both species (●) breeding in sympatry. The positions of the subtropical front (STF), sub-Antarctic front (SAF), and Antarctic polar front (APF) were adapted from Bost et al. (2009).

thus collected over of latitudinal range of over 870 km and the Sub-Antarctic fur seal samples over 1000 km. A total of 340 individuals were selected for this study, all with intact skulls and at least one upper canine present: 137 male and 27 female Antarctic fur seals, and 125 male and 51 female Sub-Antarctic fur seals. The distribution of Antarctic fur seals per island was 124 specimens (105 males, 19 females) from Bouvet, 31 (23 males, 8 females) from Marion, 6 (all males) from Heard, and 3 (all males) from South Georgia. Sub-Antarctic fur seals came from 3 islands: 93 from Marion (71 males, 22 females), 75 from Gough (51 males, 24 females), and 8 from Amsterdam (3 males, 5 females) (Supporting Information: Table S1). Both upper canines from 19 individuals were collected to compare the dimensions of left and right canines per individual. Apart from these, left canines were preferentially selected (*n* = 242; 71.2% of samples) for consistency. Canines were gently pulled out of the tooth socket. The species and sex were known for all the selected specimens. When a relatively intact carcass was found in the field, the species, sex, and estimated age class were noted before starting sample collection. Where only the skull and teeth were available (in the field or in the Museum collection), species and sex were determined through physical examination of the skull features as described by Condy (1978) and Brunner et al. (2004).

The skulls of the two species differ in morphology. Antarctic fur seals have larger skulls with a broader rostral area and palate and their post-canine teeth are unicuspid and small (Brunner et al., 2004; fig. 9a in Condy, 1978). The Sub-Antarctic fur seal skulls are smaller with a narrower rostral area, a longer and deeper palate and the post-canines are larger and in a straighter line (Brunner et al., 2004; fig. 9b in Condy, 1978). While sexual dimorphism is less evident in the morphology of the Sub-Antarctic fur seal skulls than in Antarctic fur seal skulls (Brunner et al., 2004), sexes were still easily distinguishable in adult Sub-Antarctic fur seals with the skulls of adult males being more robust and larger than the skulls of adult females.
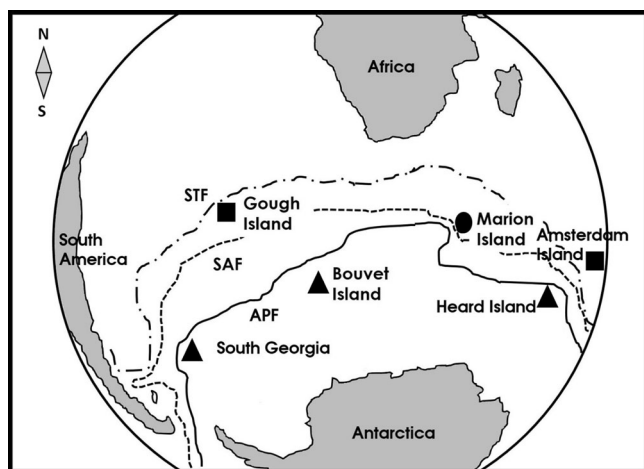
2.2 | Canine measurements

Morphometric measurements of the canines were taken along six axes with a vernier caliper (±0.01 mm). The measurements, crown length, root length, crown width, and root width were taken on the lateral aspect (mesial-distal axis) of the teeth, while crown thickness, root thickness, and total canine length were taken on the anterior aspect (buccal-lingual axis; Figure 2; Lowry & Folk, 1990; Molina-Schiller & Pinedo, 2004b).

2.3 | Canine age determination: External annular ridge counts and dentinal growth layer group counts from sectioned teeth

Because all samples came from remote islands and mostly unmarked populations, the true age of the specimens was unknown. All specimens were aged by counting the EARs with the naked eye under a bright light
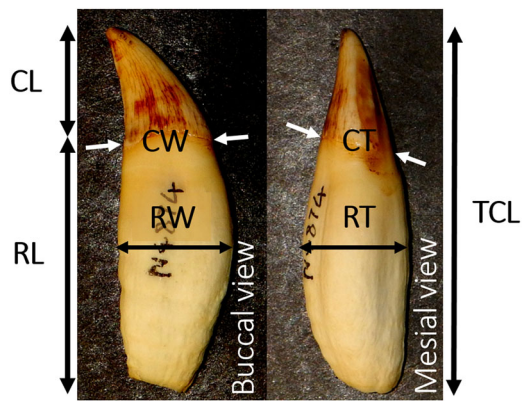
FIGURE 2 Measurement axes taken of Antarctic and Sub-Antarctic fur seal teeth: (CL) crown length, (RL) root length, (CW) maximum crown width, (RW) maximum root width, (CT) maximum crown thickness, (RT) maximum root thickness and (TCL) total canine length

(Oosthuizen & Bester, 1997). In the few cases where teeth had closed pulp cavities in older individuals, the age was then recorded by counting to the last visible ring. The age of a subset of 63 individuals was then estimated using a second method: the counting of dentinal individual GLGs in longitudinally sectioned teeth, as adapted from Oosthuizen and Bester (1997). Each GLG comprises of a thick opaque layer and a thin translucent layer (Molina-Schiller & Pinedo, 2004a). To expose the dentinal GLGs for age estimation, each canine was coated with an epoxy resin (2:1 parts Translux D150 resin to catalyst). The resin-mounted teeth were then sectioned longitudinally using an IsoMet diamond-wire saw as close to the midline as possible. The cut surfaces of the teeth were polished and thereafter glued to a transparent glass slide. Each canine was then cut again to leave a 1.5–2 mm slice of tooth attached to the slide. The exposed tooth surface was once again polished using sanding papers of increasing grit numbers to expose the midline before being thoroughly rinsed with distilled water. GLGs were defined as the repetitive pattern of parallel incremental growth layers and were then counted starting from the neonatal line under a dissecting microscope or directly from the slide when the GLGs were obvious.

2.4 | Data analysis

All analyses were performed in the R environment version 4.0.2 (R Core Team, 2021). Significance level was set at p-value < 0.05.

To determine whether there was a significant difference between the measurements of left and right upper canines, a sub-sample of 19 animals was selected where both upper canines were available for measurement. As differences between paired measurements were normally distributed (Shapiro–Wilks test, p values > .05), paired samples t-tests (package *rstatix*; Kassambara, 2021) were used to compare measurements from the right and left upper canines.

For the subset of 63 teeth, counts of the EARs and dentinal GLGs of each canine were conducted three times independently by the

same person. GLG were counted by MC, who trained for EAR and GLG readings using a reference collection of known aged Cape fur seals, a closely related species. EAR were counted by LP, with a subset checked by MC. If one of the values differed, the age obtained twice was kept. When partial growth of the last deposited EAR or GLG was noted, a half a year was added to the final age estimate. Residuals were then calculated as the difference between the age obtained using dentinal GLG counts minus the one obtained using EAR counts. Due to their right-skewed distribution, residuals were first log-transformed. To test for differences in residuals between species and between sexes, a linear model was then fitted to the data once outliers (two Sub-Antarctic fur seal females, one Antarctic fur seal female) were removed; outliers were identified by the Cook distance (Cook, 1977). In addition, the two methods of age estimation were compared between two age groups: younger or equal to 9 years old, and older ages. The limit of 9 years old was chosen as this was the age from which pulp cavities were observed filled in some teeth. The non-parametric Mann-Whitney test was used for the comparison as the residual data failed normality (Shapiro–Wilks test, $p < 0.05$).

To test whether canine tooth measurements were useful in distinguishing island of origin, tooth measurements were compared between Gough and Marion islands for Sub-Antarctic fur seals, and Marion and Bouvet islands for Antarctic fur seals. Further, comparisons were restricted to males between 5.5 and 11.5 years of age for both species due to the low number of teeth outside these age limits. Similarly, no island comparison could be conducted on female teeth due to low sample size per age category. Spatial comparisons were conducted independently on Sub-Antarctic and Antarctic fur seals and on each measurement separately. Generalized linear models were run with the response variable being the canine measurement and the fixed factors being "island" and "EAR" with the family Gamma (link Identity) (package *nlme*; Pinheiro et al., 2021). Outliers were identified using the Cook's distance (Cook, 1977) (Supporting Information: Table S2). The left-skewed distribution of the crown length data required the use of transformation via $y' = \log(\text{constant} - y)$. Normalities of residuals were checked graphically using a Q–Q plot.

A total of 330 canine teeth were available to test whether canine measurements could be used to infer the species, sex, and age of fur seals. Each of the seven measurements was first analyzed individually. As above, generalized linear models with a Gamma family (link identity) were fitted to examine the influence of species, sex, age, and their interactions on all canine measurements except root and crown length. For these two measurements, a linear model was found to best fit the data as shown by a lower Akaike's Information Criterion (AIC). For crown length, the data further required a log transformation as above. Outliers were identified using the Cook's distance and removed from the models (Supporting Information: Table S2). A suite of possible models were fitted and these were then ranked using the AIC corrected for small sample size (AICc). The selection of the best model explaining the data was based on the lowest AICc or the most parsimonious model when several models exhibited ΔAIC < 2 (Burnham et al., 2011).

Finally, all seven measurements were analyzed together for a predictive classification of canine teeth to species, sex, and sex within species. Measurements were first normalized individually so all comprised between 0 and 1 (Breiman, 2001). The classifications were then conducted using a random forest algorithm (Breiman, 2001) run using the package *randomForest* (Liaw & Wiener, 2002). For all three models, 70% of the data were used to train the model while the remaining 30% were used to test the model performances. The number of trees to be grown from bootstrap samples was set at 1001 to ensure convergence of the results (Supporting Information: Figure S1). The number of randomly selected variables at each node was the default value for classification (i.e., square root of the total number of variables, three in our case). The accuracy of the models was then approached using the out-of-bag error estimates calculated with the train data set as a proportion of correct classification.

3 | RESULTS

A total of 359 canines from 340 individuals were available for this study: 137 Antarctic fur seal males and 27 females, and 125 Sub-Antarctic fur seal males and 51 females (Supporting Information:

Table S1). For both species, no significant difference was found in tooth measurements between left and right canine teeth taken from the same individual (paired samples *t*-tests, $p > 0.13$ in all cases; Table 1).

3.1 | Comparison of age determination using external annular ridge counts versus dentinal growth layer group counts

The two independent age estimation methods (EARage and GLGage) were compared for 63 canine teeth, separately for both species and sexes (Supporting Information: Table S3). Age estimates ranged from 3.5 to 13 years old in Antarctic fur seals and from 7.5 to 14 years old in Sub-Antarctic. The age range was larger in females than in males, particularly in Antarctic fur seals. Overall, EARage estimated younger ages than GLGage, but the difference was relatively small in most cases being ±1 year in 83% of teeth (Figure 3). Within sexes, 87% and 79% of canines exhibited differences less than 2 years between the two age estimation methods in males and females, respectively. The largest differences were seen in females in both species (4 years in an Antarctic fur seal female and 5 years in a Sub-Antarctic fur seal

Measurement	Species	Right Mean ± SD	Left Mean ± SD	Statistics *t*	*p* Value
Crown length	AFS males	18.56 ± 1.76	18.65 ± 2.01	0.447	0.662
	SAFS males	17.14 ± 0.55	15.82 ± 0.40	−2.450	0.134
	SAFS female	11.47	11.62		
Root length	AFS males	29.25 ± 6.92	29.23 ± 6.71	−0.119	0.907
	SAFS males	26.02 ± 1.04	26.39 ± 1.26	1.940	0.192
	SAFS female	20.38	19.91		
Crown width	AFS males	12.78 ± 1.08	12.75 ± 1.09	−0.407	0.690
	SAFS males	10.45 ± 0.79	10.17 ± 0.46	−0.915	0.457
	SAFS female	6.79	6.88		
Root width	AFS males	15.97 ± 1.37	16.00 ± 1.41	0.345	0.735
	SAFS males	13.19 ± 1.00	13.08 ± 0.86	−1.170	0.363
	SAFS female	8.59	8.72		
Crown thickness	AFS males	10.22 ± 0.75	10.30 ± 0.88	0.913	0.377
	SAFS males	8.88 ± 0.64	8.84 ± 0.52	−0.540	0.643
	SAFS female	5.71	5.70		
Root thickness	AFS males	14.39 ± 1.68	14.29 ± 1.52	−0.974	0.347
	SAFS males	11.01 ± 1.12	10.81 ± 0.95	−1.820	0.211
	SAFS female	7.40	7.30		
Total canine length	AFS males	51.45 ± 6.36	51.75 ± 6.42	1.130	0.276
	SAFS males	44.71 ± 0.35	44.04 ± 0.78	−1.400	0.296
	SAFS female	32.62	32.57		

TABLE 1 Comparison of measurements (mm) of right and left upper canines collected from 19 individuals (Antarctic fur seal [AFS] males: *n* = 15; Sub-Antarctic [SAFS] males: *n* = 3; SAFS female: *n* = 1)
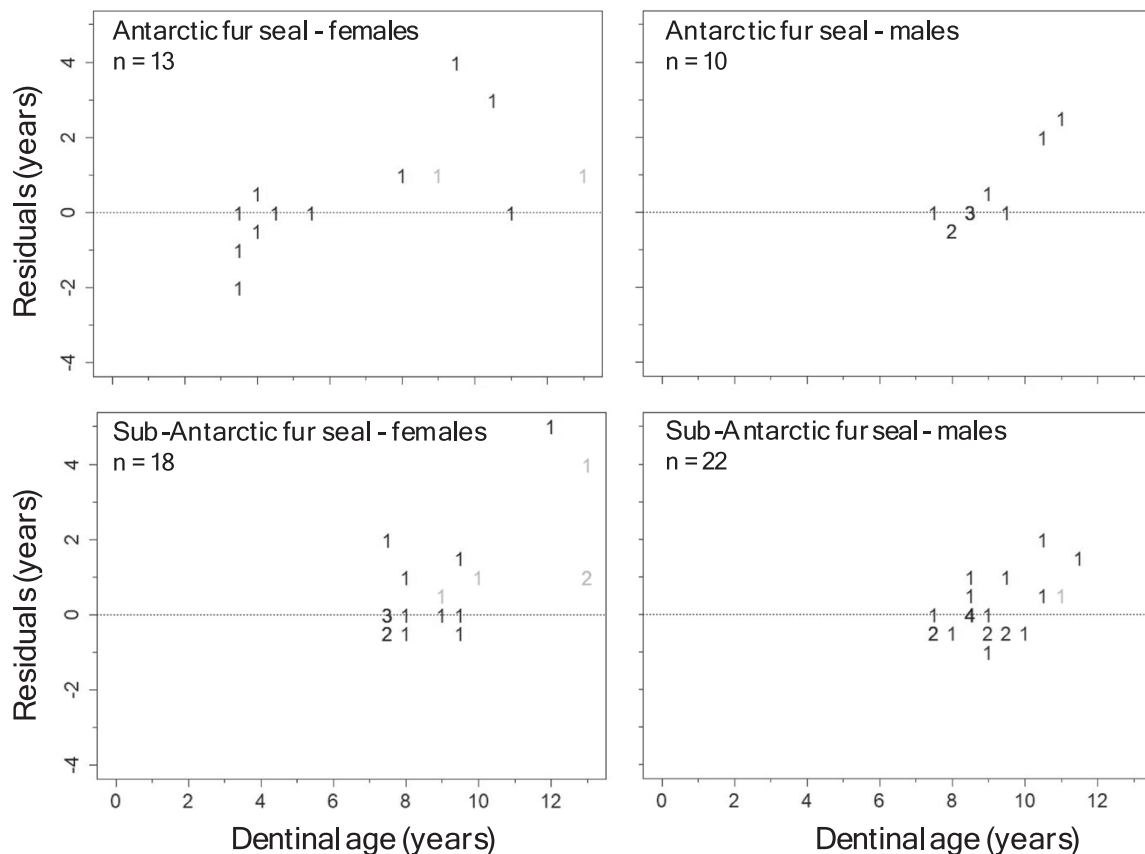
FIGURE 3 Residuals obtained by subtracting age estimated from counting the external ridges to age determined by counting dentinal growth layer groups. *n*: number of upper canine teeth. Numbers in gray correspond to teeth with filled pulp cavities and thus ages estimated by both methods were likely lower than true ages.

female), with differences in males reaching 2.5 years in Antarctic fur seals and 2 years in Sub-Antarctic fur seals. The differences in residuals between sexes (LM, *t* = −0.262, *p* = 0.795), and between species (LM *t* = −0.315, *p* = 0.754) were, however, not significant.

Differences in residuals between the two age determination methods increased with age of the seals. Indeed, residuals were ± 1 year for 95% of teeth aged 9 years or younger and for only 39% for teeth aged older than 9 years. Accordingly, residuals were significantly smaller for the younger seals (≤9 years old) than for the older seals (Mann–Whitney *U* = 200, *p* < 0.001).

3.2 | Spatial comparison of canine tooth measurements

Overall, 110 teeth ranging from 5.5 to 11.5 years were available for male Sub-Antarctic fur seals and 117 for male Antarctic fur seals (EARage). None of the measurements exhibited significant differences between Gough and Marion islands for Sub-Antarctic fur seals (GLM all *p* > 0.153; Supporting Information: Table S5). For Antarctic fur seals, no significant differences existed between canine teeth from Bouvet and Marion islands for crown width (GLM *p* = 0.450), thickness (GLM *p* = 0.282) or length (GLM *p* = 0.153; Supporting

Information: Table S5). However, Antarctic fur seal canine teeth from Bouvet Island were significantly larger than Marion Island canine teeth for the other four measurements linked to the root (thickness, width, length) and the whole canine (total canine length) (GLM all *p* < 0.030); Supporting Information: Table S5).

3.3 | Comparison of tooth measurements for different age class, sex, and species groups

The age distribution (EARage) of the animals ranged from 0.5 to 14.5 years old with 85% of animals falling into the 6–12 years age group. The ages of Sub-Antarctic fur seals ranged between 1.0 and 14.5 years, while the ages of Antarctic fur seals ranged between 0.5 and 11.5 years.

EAR was not included in the most parsimonious model for crown thickness and width, but was included in the models for the other five measurements (Table 2). Thus, age did not influence crown thickness or width measurements (Figure 4). The model Species * Sex + EAR was the best-fitted model for crown length, root thickness, and root width while the three factors and their interactions were revealed as the best model for root length and total canine length (Table 2). Although the crown length and total canine length could not

TABLE 2 Model selection of factors influencing the canine tooth features in Sub-Antarctic and Antarctic fur seals

Models	Fixed effects	df	Length			Thickness			Width		
			Deviance	ΔAICc	w	Deviance	ΔAICc	w	Deviance	ΔAICc	w
A) CROWN											
1	Null	2	6.24	346.90	0.00	16.87	791.58	0.00	17.74	780.37	0.00
2	Sex	3	3.64	172.20	0.00	4.06	322.60	0.00	5.29	382.59	0.00
3	Species	3	4.46	238.97	0.00	12.68	699.01	0.00	12.10	655.61	0.00
4	EAR	3	6.22	347.82	0.00	16.05	777.16	0.00	17.17	771.61	0.00
5	Sex + Species	4	2.39	36.78	0.00	2.25	130.33	0.00	2.28	106.61	0.00
6	Sex + EAR	4	3.38	149.56	0.00	3.98	318.01	0.00	5.06	369.70	0.00
7	Species + EAR	4	4.27	226.47	0.00	11.01	654.26	0.00	10.73	617.93	0.00
8	Sex * Species	5	2.18	8.50	0.01	**1.50**	**0.00**	**0.66**	1.64	**0.60**	**0.36**
9	Sex * EAR	5	3.33	146.87	0.00	3.89	313.07	0.00	4.98	366.40	0.00
10	Species * EAR	5	4.23	225.47	0.00	10.87	652.03	0.00	10.51	613.05	0.00
11	Sex + Species + EAR	5	2.36	33.58	0.00	2.22	128.35	0.00	2.27	107.76	0.00
12	Sex * Species + EAR	6	**2.11**	**0.00**	**0.89**	1.50	1.78	0.27	1.64	2.16	0.16
13	Sex + Species * EAR	6	2.32	31.08	0.00	1.99	94.29	0.00	2.01	69.97	0.00
14	Species + Sex * EAR	6	2.26	21.40	0.00	2.06	106.12	0.00	2.08	80.93	0.00
15	Sex * Species * EAR	9	2.10	4.45	0.10	1.49	4.69	0.06	**1.60**	**0.00**	**0.48**
B) ROOT											
1	Null	2	14397.61	537.70	0.00	24.99	772.02	0.00	21.53	760.36	0.00
2	Sex	3	8532.55	368.14	0.00	7.47	375.21	0.00	5.21	293.03	0.00
3	Species	3	12881.53	503.24	0.00	18.22	669.29	0.00	16.82	679.13	0.00
4	EAR	3	7928.47	344.05	0.00	21.86	729.56	0.00	19.22	723.24	0.00
5	Sex + Species	4	7747.40	338.52	0.00	4.77	229.34	0.00	3.12	126.10	0.00
6	Sex + EAR	4	5301.97	214.12	0.00	7.29	369.13	0.00	5.19	293.73	0.00
7	Species + EAR	4	4573.74	165.66	0.00	13.23	565.60	0.00	12.89	593.20	0.00
8	Sex * Species	5	7195.13	316.33	0.00	3.05	84.49	0.00	2.42	44.20	0.00
9	Sex * EAR	5	5270.17	214.21	0.00	7.27	370.38	0.00	5.19	295.55	0.00
10	Species * EAR	5	4247.35	143.44	0.00	12.84	557.56	0.00	12.69	590.12	0.00
11	Sex + Species + EAR	5	3117.66	42.02	0.00	3.72	150.23	0.00	2.65	74.52	0.00
12	Sex * Species + EAR	6	2910.09	21.49	0.00	**2.34**	**0.00**	**0.69**	**2.10**	**0.00**	**0.90**
13	Sex + Species * EAR	6	2791.39	7.83	0.02	3.14	95.86	0.00	2.42	46.38	0.00
14	Species + Sex * EAR	6	3117.55	44.08	0.00	3.66	146.34	0.00	2.61	72.15	0.00
15	Sex * Species * EAR	9	**2673.62**	**0.00**	**0.98**	2.31	1.60	0.31	2.09	4.47	0.10
C) TOTAL CANINE											
1	Null	2	13.62	693.36	0.00						
2	Sex	3	5.37	389.80	0.00						
3	Species	3	10.47	608.87	0.00						
4	EAR	3	10.16	599.09	0.00						
5	Sex + Species	4	3.99	294.07	0.00						
6	Sex + EAR	4	4.56	337.90	0.00						

TABLE 2 (Continued)

Models	Fixed effects	df	Length Deviance	ΔAICc	w	Thickness Deviance	ΔAICc	w	Width Deviance	ΔAICc	w
7	Species + EAR	4	5.66	409.31	0.00						
8	Sex * Species	5	3.15	219.50	0.00						
9	Sex * EAR	5	4.55	339.83	0.00						
10	Species * EAR	5	5.33	391.49	0.00						
11	Sex + Species + EAR	5	2.18	98.63	0.00						
12	Sex * Species + EAR	6	1.66	12.14	0.00						
13	Sex + Species * EAR	6	1.82	41.36	0.00						
14	Species + Sex * EAR	6	2.16	97.97	0.00						
15	Sex * Species * EAR	9	**1.57**	**0.00**	**1.00**						

Note: df: number of parameters; Deviance: residual deviance; AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference between the current model and the model with the lowest AICc; w- relative support for a model given the data and the other models tested. The best-supported model (lowest AICc) for each canine measurement is in bold (most parsimonious in the case of crown width).

distinguish the two fur seal species (GLM $p = 0.900$ and $p = 0.173$, respectively; Supporting Information: Table S6), this was not the case for the other five measurements. Indeed, Antarctic fur seals exhibited bigger crown and root thickness and width as well as longer root than Sub-Antarctic fur seals. Differences were more readily apparent for males, with male Antarctic fur seal canines always being larger and longer than those of male Sub-Antarctic fur seals (Tukey's post hocs all $p < 0.001$; Supporting Information: Table S6), while the teeth of females were more similar in size. Females could only be discriminated using the width of crown and root (Tukey's post hocs $p < 0.001$ and $p = 0.007$, respectively; Supporting Information: Table S6). Males exhibited crowns that were always thicker than 7.3 mm, while females had crowns that were always slimmer than 6.6 mm (Figure 4). In addition, the canines of males were always larger than those of females within and across species whether accounting for age (root thickness, width and length, crown length, and total canine length) or not (crown width and thickness) (GLM all $p < 0.001$; Tukey's post hocs all $p < 0.001$; Supporting Information: Table S6). A positive influence of age was particularly obvious in total canine length and root length (Figure 4, Supporting Information: Table S6), while a negative but still significant influence was observed for crown length (Figure 4, Supporting Information: Table S6).

3.4 | Classification of canine teeth using morphometrics

The separation of groups (i.e., species, sex, and sex within species) using canine measurements varied depending on the groupings (Figure 4). The most obvious measurement to be used for separating males from females was crown thickness, with no overlap between the sexes (see above, Figure 4e). However, distinguishing between species, or sex within species, could not be achieved using one measurement alone due to overlap in measurements (Figure 4). When using all measurements together, the global accuracy of prediction of sex, species, and sex within species, using the random forest algorithm was above 86% (Table 3). As suggested by the overlap in canine measurements (Figure 4), it was most difficult to distinguish between the females of the two species (Table 3).

4 | DISCUSSION

Using a data set of 359 canine teeth of two partially sympatric species of fur seals, we showed that upper canines can be used to identify basic life history information. We highlighted that the EARs on the canine roots can be used as a first approximation of the age of animals in Antarctic and Sub-Antarctic fur seals as it approached the age determined by GLG; a method shown to relate well with true age in a closely related species, the Cape fur seal (Oosthuizen, 1997; Oosthuizen & Bester, 1997). Furthermore, we used seven standard measurements to show that species and sex could be assigned in Antarctic and Sub-Antarctic fur seals, as well as populations in Antarctic fur seals.

4.1 | Determining age from dental morphology

The ability to age an animal is an important aspect of population studies since different age classes often experience different rates of mortality, behave differently, and may have different diets (Hohn et al., 1989; Kienle & Berta, 2016). Estimation of age through the examination of the external features as well as internal tooth structure are well-used methods not only in fur seals, but also in other marine mammals (Evans et al., 2007) when true age is unknown.
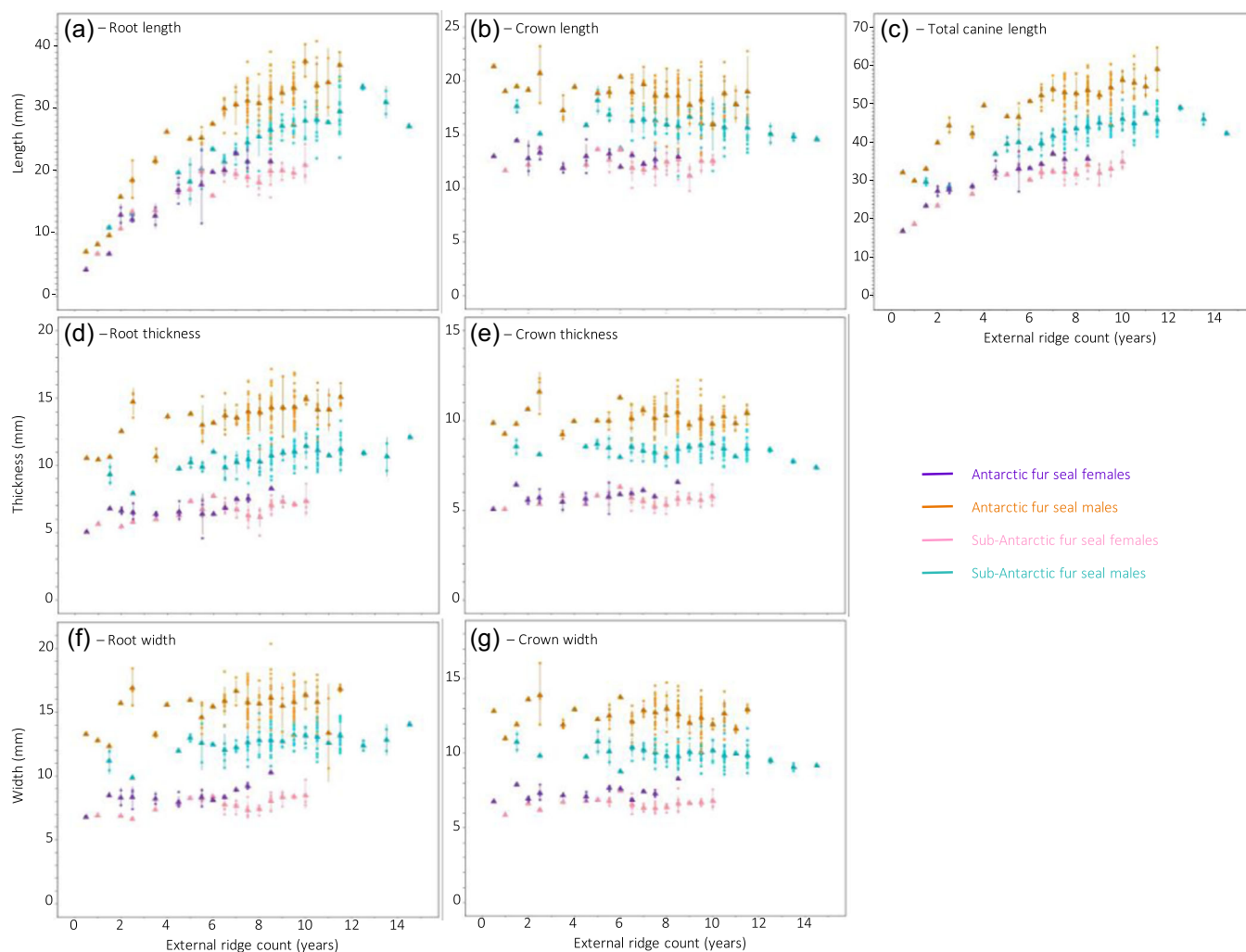
FIGURE 4 Individual (●) and mean (± standard deviation; ▲) measurements of (a) root length, (b) crown length, (c) total canine length, (d) root thickness, (e) crown thickness, (f) root width, and (g) crown width according to age estimated through external annual ridge count. Antarctic fur seal males are represented in orange, Antarctic fur seal females in purple, Sub-Antarctic fur seal males in blue, and Sub-Antarctic fur seal females in pink.

No significant differences in the external measurements of left and right canines in the same individuals were highlighted in our study, allowing either canine to be used with confidence when aging an animal. For pinnipeds, both canines and post-canines are generally used for aging (e.g., Evans et al., 2007; Scheffer & Myrick, 1980). Similar to other studies that compared different aging methods in Antarctic fur seals (Boyd & Roberts, 1993) and California sea lions (Molina-Schiller & Pinedo, 2004a), EARs were more clearly visible on the outer root surface of the upper canine teeth in both species used in this study when compared to the lower canine teeth.

EARs are most visible during the younger years because the tooth grows fastest (Payne, 1978), while, in older animals, it becomes increasingly difficult to estimate age using EARage since the EARs are laid down closer together and the deposition of cementum conceals the ridges (Boyd & Roberts, 1993; Molina-Schiller & Pinedo, 2004a; Oosthuizen & Bester, 1997; Oosthuizen, 1997; Payne, 1978), making visual counting more difficult. Although EARage estimated a younger

age than GLGage in our study, the difference was small. The Sub-Antarctic female where the biggest difference occurred (5 years), was 12 years old (through GLG counts) and therefore close to the upper age limit (14 years) of animals examined in this study. The longevity of free-living male and female Sub-Antarctic fur seals at Gough Island have been recorded as approximately 18 and 23 years, respectively (Bester, 1987; D.E.H., 2004), but most live until 16–17 years old (Authier et al., 2011). The longevity of Antarctic fur seal males is more uncertain, but ages ranging from 10 to 14 years have been recorded (Payne, 1979; McCann & Doidge, 1987). Female Antarctic fur seals live more than 20 years, with an observed maximum of 24 years (Lunn et al., 1994; Forcada & Staniland, 2018). Several studies showed different upper age limits at which age determination by external ridge counts becomes inaccurate. Payne (1978) used EAR counts to accurately aged 95% of Antarctic fur seal females less than 7 years old. Payne (1978) also obtained matched age estimates in 60% of animals less than 11 years when comparing EAR and GLG

TABLE 3 Confusion matrices and accuracy for the three prediction models using a random forest algorithm for species, sex, and sex within species. Train data sets and test data sets corresponded to 70% and 30% of the data, respectively.

a) Species

Train data set				Test data set			
OOB = 6.38%	AFS (observed)	SAFS (observed)	Total	Accuracy = 86.3%	AFS (observed)	SAFS (observed)	Total
AFS (predicted)	107	9	116	AFS (predicted)	39	7	46
SAFS (predicted)	6	113	119	SAFS (predicted)	6	43	49
Total	113	122		Total	45	50	

b) Sex

Train data set				Test data set			
OOB = 0.85%	Female (observed)	Male (observed)	Total	Accuracy = 100%	Female (observed)	Male (observed)	Total
Female (predicted)	47	1	48	Female (predicted)	21	0	21
Male (predicted)	1	186	187	Male (predicted)	0	74	74
Total	48	187		Total	21	74	

c) Sex within species

Train data set						Test data set					
OOB = 5.96%	AFS_Female (observed)	AFS_Male (observed)	SAFS_Female (observed)	SAFS_Male (observed)	Total	Accuracy = 88.4%	AFS_Female (observed)	AFS_Male (observed)	SAFS_Female (observed)	SAFS_Male (observed)	Total
AFS_Female (predicted)	12	0	4	1	17	AFS_Female (predicted)	5	0	4	0	9
AFS_Male (predicted)	0	96	0	3	99	AFS_Male (predicted)	0	35	0	2	37
SAFS_Female (predicted)	2	0	29	0	31	SAFS_Female (predicted)	2	0	10	0	12
SAFS_Male (predicted)	1	3	0	84	88	SAFS_Male (predicted)	0	3	0	34	37
Total	15	99	33	88		Total	7	38	14	36	

Abbreviations: AFS, Antarctic fur seal; OOB, out-of-bag measure; SAFS, Sub-Antarctic fur seal.

count, with the remaining 40% differing by no more than 1 year. Oosthuizen and Bester (1997) compared EAR counts to GLG counts in Cape fur seal teeth and obtained accurate matched estimates for ages up to approximately 10 years old in both sexes. For female Cape fur seals, EAR counts on upper canines tended to overestimate age in animals less than 5 years old and underestimated ages in animals 6 years and older (Oosthuizen & Bester, 1997). When comparing GLG counts to the true age of known-age females (tagged at 6 weeks of age), age estimates from the GLG counts appeared to underestimate age, likely due to poor sample preparations (Oosthuizen, 1997). For male Cape fur seals, accuracy of upper canine EAR counts was within 2 years of the true age in animals less than 7 years old, while underestimating age in animals from 9 years and older by up to 4 years (Oosthuizen & Bester, 1997). Comparing GLG counts to the true age of known-age males (tagged at 6 weeks of age), the error in estimated age was always within 1 year of age (Oosthuizen, 1997). Oosthuizen (1997) also stated that accurate age estimation in Cape fur seals is not possible in animals where the pulp cavities have closed (from approximately 13 years of age in that species). Only eight teeth (two Antarctic fur seal females, five females, and one male Sub-Antarctic fur seals) with closed pulp cavities were included in the present study. The ages of these animals ranged between 8 and 14 years and EARage differed from GLGage by >1 year only in one of the eight animals. The sample size, however, is small and not representative of the various groups, and precluded making statistical inferences. In other pinniped species, the upper limit of accuracy was approximately 7 years in California sea lions (Molina-Schiller & Pinedo, 2004a), whereas Boyd and Roberts (1993) found that counting EARs became inaccurate in Antarctic fur seals over the age of 10 years. Similarly to the canines examined in the present study, EARs were more pronounced (and thus easier to count with the naked eye) in adult males compared to adult females (Boyd & Roberts, 1993). In our study, EAR counts generally appeared to estimate younger ages when compared to GLG counts, with the biggest differences in females of both species (Antarctic fur seal males: 3 years, females: 4 years; Sub-Antarctic fur seal males: 2 years, females: 5 years). Aging by counting the EARs can thus be used where a quick, preliminary estimate of age is required (Oosthuizen & Bester, 1997), but may need to be confirmed by counting the internal GLGs under a microscope for older animals or whenever EARs are not easily distinguishable, even though it is more expensive, labor intensive, requires specialized equipment and causes irreparable damage to the teeth.

4.2 | Identification of sex and species from dental morphology

Tooth size and morphology can be useful in determining sex and species in various marine mammal species, for example, California sea lions (Lowry & Folk, 1990), South American fur seals (Molina-Schiller & Pinedo, 2004b; Zeder & Pilaar, 2010), dolphins (Santos et al., 2003) and killer whales *Orcinus orca* (Newsome et al., 2009). Antarctic and Sub-Antarctic fur seals are phenotypically distinct (Kerley & Robinson, 1987) and exhibit extreme sexual dimorphism (Bonner, 1968; Laws, 1993; Weise et al., 2010). Females reach both sexual and social maturity at approximately 3–6 years of age (Bester, 1995; Dabin et al., 2004); Lunn et al., 1994; McCann & Doidge, 1987). However, while males reach sexual maturity between 3 and 4 years of age (Bester, 1990; McCann & Doidge, 1987), they only reach social maturity (and thus start breeding) much later, at approximately 8 years of age when they have attained a physical maturity to defend territories in harems (Bester, 1990; Bester & Jaarsveld, 1994; Kerley et al., 2000; McCann & Doidge, 1987; Payne, 1979; Stewardson et al., 2010). Sexual dimorphism is also observed in the skull morphology (Brunner et al., 2004; Condy, 1978). It is thus not surprising that the sexes could be distinguished from upper canines in both species (particularly in adults), with all male canine measurements being significantly larger than in females when accounting for age (Figure 4). The measurement most important for distinguishing sex across or within species with no overlap in canine measurements between males and females was crown thickness (Figure 4e). Sexual differences were also observed with all the other measurements but some slight overlaps were detected depending on age and species (Figure 4). In sub-adult animals where sexual dimorphism is not as clearly pronounced, it might prove difficult to distinguish between the sexes (Bester & Jaarsveld, 1994; Condy, 1978; Molina-Schiller & Pinedo, 2004b) or even species (Condy, 1978) on initial appraisal. Male Antarctic fur seals are larger in body size than male Sub-Antarctic fur seals (Condy, 1978; Laws, 1993; Hofmeyr, 2015, 2016) and this study showed that this distinction between species was also represented in all tooth measurements, with Antarctic fur seal males exhibiting longer, wider and thicker upper canines across age (Figure 4, Supporting Information: Table S6). Females from both species are, however, more similar in size (Condy, 1978; Luque et al., 2007) and only measurements related to root and crown width proved useful in distinguishing between the species, with Antarctic fur seal females exhibiting slightly wider canines when accounting for age (Supporting Information: Table S6). Due to the similarity in tooth size in females, it might prove more difficult to make the distinction especially in field situations.

4.3 | Differences in dental morphology between islands of origin

Bergmann's rule suggests that within a broadly distributed taxon, populations and species of larger size will be found in colder environments (higher latitudes), while populations and species of smaller size are found in warmer regions (lower latitudes) (Bergmann, 1847 cited in Meiri, 2011). In our study, the rule was verified for Antarctic fur seal males but not Sub-Antarctic fur seal males. Previous studies on fur seals, which covered a similar latitudinal range as our study, suggested a latitudinal graded difference in the body size in Sub-Antarctic fur seal females, with the biggest females at low-latitude Amsterdam Island and the smallest at high-latitude Marion

Island (Bester & Jaarsveld, 1994; Dabin et al., 2004). Unfortunately, we could not test the spatial difference in the morphology of female Sub-Antarctic fur seal teeth due to low sample size but, similar to findings by Kerley et al. (2000), spatial differences were not found in Sub-Antarctic fur seal male canine teeth measurements.

Population differences in dental morphology have been found in a number of species. This is especially so for primates, with clear differences recorded for humans *Homo sapiens* (Hanihara, 2008; Scott & Turner, 1988), gorillas *Gorilla gorilla* (Uchida, 1998a), and orangutans *Pongo pygmaeus* (Uchida, 1998b). Population differences in other taxa have also been noted, both in terrestrial species such as horses *Equus caballus* (Seetah et al., 2014) and caribou *Rangifer tarandus* (Rivals & Solounias, 2007), and in marine species such as spinner dolphins *Stenella longirostris* (Akin, 1988). These differences may be due to differences in the genotypes of populations (Akin, 1988; Hanihara, 2008; Uchida, 1998a, 1998b) or due to differences in wear, associated with differing diets (Ford et al., 2011; Rivals & Solounias, 2007).

Neither genetics nor diet is likely to result in population differences in dental morphology of Antarctic fur seals. The species was reduced to low levels of abundance by uncontrolled harvesting before the 20th Century (Hofmeyr et al., 2005). Current populations are descended from a few survivors and show relatively little genetic diversity (Wynen et al., 2000). Antarctic fur seal populations have a varied diet (Hofmeyr, 2016; Jones et al., 2020; Walters et al., 2020), with those from Bouvet Island feeding primarily on krill (Kirkman et al., 2000), and those from Marion Island being generalists (including myctophids, cephalopods, and even penguins; Hofmeyr & Bester, 1993; Makhado et al., 2008; Reisinger et al., 2018). While greater tooth wear (and thus shorter crown length) would be expected for species or populations that feed on sharks for example (Allen & Huveneers, 2005; Byron & Morgan, 2016; Condit & Le Boeuf, 1984; Fallows et al., 2015) due to the abrasive nature of shark skin, neither of the tested Antarctic fur seal populations have been recorded to consume sharks and it's unlikely that the observed differences in diet between the two islands would result in change in tooth wear. The observations of larger Antarctic fur seal males at Bouvet Island which translate in bigger, longer, and thicker roots compared to Marion Island specimens as seen in our study, may be the result of ecological or behavioral drivers. Bigger animals may be selected at the more southerly island due to the higher competition for breeding space (Lindenfors et al., 2002).

5 | CONCLUSION

We determined that both upper canines (left and right) can be used with confidence when aging Antarctic or Sub-Antarctic fur seals. Although counting EARs provides a quick estimate of age, it is more accurate to confirm age by counting internal GLGs, especially in older animals or unusual canine teeth. Adults of both species can be sexed by examination of upper canines, with adult males exhibiting bigger measurements overall than females within species. The seven canine

parameters can be used to distinguish between species in adult males, with Antarctic fur seals exhibiting larger measurements than Sub-Antarctic fur seals. The canines of adult females are more similar in size between the species and therefore it is more difficult to distinguish the species. Canine measurements could discriminate between the different islands of origin for Antarctic fur seal males only. Additional canines would be necessary to test whether this spatial difference holds in female Antarctic fur seals, and whether an absence of differences holds for female Sub-Antarctic fur seals.

We present a method that uses canine teeth to determine age, sex, and species for specimens of unknown provenance, whether picked up loose or from decayed or damaged remains. This result will be of particular relevance at islands where the two species occur in sympatry such as Prince Edward, Crozet, and Macquarie islands (Kingston & Gwilliam, 2007; Lancaster et al., 2006; Robinson et al., 2002; Wege et al., 2016), but also for locations where vagrant fur seals are recorded (Acevedo et al., 2011; Bester & Reisinger, 2010; Ferreira et al., 2008; Hofmeyr & Amir, 2010; Jouventin et al., 1982; Zanre & Bester, 2011). More generally, our study further highlights the value of external measurements of skeletal remains such as canine teeth in separating closely related species.

AUTHOR CONTRIBUTIONS

Liezl E. Pretorius: Formal analysis (equal); investigation (equal); writing – original draft (lead). **Marthán N. Bester**: Conceptualization (equal); investigation (supporting); supervision (lead); writing – review and editing (equal). **Maëlle Connan**: Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (lead); supervision (equal); writing – review and editing (equal). **G. J. Greg Hofmeyr**: Conceptualization (equal); funding acquisition (lead); investigation (equal); project administration (lead); supervision (equal); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available in article supplementary material.

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REFERENCES

Acevedo, J., Matus, R., Droguett, D., Vila, A., Aguayo-Lobo, A., & Torres, D. (2011). Vagrant Antarctic fur seals, *Arctocephalus gazella*, in Southern Chile. *Polar Biology*, *34*, 939–943. https://doi.org/10.1007/s00300-010-0951-4

Akin, P. A. (1988). Geographic variation in tooth morphology and dentinal patterns in the spinner dolphin, *Stenella longirostris*. *Marine Mammal Science*, *4*, 132–140. https://doi.org/10.1111/j.1748-7692.1988.tb00193.x

Allen, S., & Huveneers, C. (2005). First record of an Australian fur seal (*Arctocephalus pusillus doriferus*) feeding on a wobbegong shark (*Orectolobus ornatus*). *Proceedings of the Linnean Society of New South Wales*, *126*, 95–97.

Authier, M., Cam, E., & Guinet, C. (2011). Selection for increased body length in SubAntarctic fur seals on Amsterdam Island. *Journal of Evolutionary Biology*, *24*, 607–616. https://doi.org/10.1111/j.1420-9101.2010.02193.x

Balasse, M., & Ambrose, S. H. (2005). Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C4 grassland environments. *Journal of Archaeological Science*, *32*, 691–702. https://doi.org/10.1016/j.jas.2004.11.013

Bergmann, C. (1847). Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. *Gottinger studien*, *3*, 595–708.

Bergqvist, L. P. (2003). The role of teeth in mammal history. *Brazilian Journal of Oral Sciences*, *2*, 249–257. https://doi.org/10.20396/bjos.v2i6.8641693

Bester, M. N. (1987). Subantarctic fur seal *Arctocephalus tropicalis* at Gough Island (Tristan da Cunha group). In J. P. Croxall & R. L. Gentry (Eds.), *NOAA Technical Report NMFS 51. Status, biology, and ecology of fur seals* (pp. 57–60).

Bester, M. N. (1990). Reproduction in the male sub-Antarctic fur seal *Arctocephalus tropicalis*. *Journal of Zoology*, *222*, 177–185.

Bester, M. N. (1995). Reproduction in the female subantarctic fur seal, *Arctocephalus tropicalis*. *Marine Mammals Science*, *11*, 362–375.

Bester, M. N., & Jaarsveld, A. S. V. (1994). Sex-specific and latitudinal variance in postnatal growth of the Subantarctic fur seal (*Arctocephalus tropicalis*). *Canadian Journal of Zoology*, *72*, 1126–1133. https://doi.org/10.1139/z94-150

Bester, M. N., & Reisinger, R. R. (2010). Vagrant Antarctic fur seals at Gough Island in 2009. *Polar Biology*, *33*, 709–711. https://doi.org/10.1007/s00300-009-0749-4

Bonner, W. N. (1968). The fur seal of South Georgia. *Scientific Report of the British Antarctic Survey*, *56*, 1–88.

Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., Ainley, D. G., & Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, *78*, 363–376. https://doi.org/10.1016/j.jmarsys.2008.11.022

Boyd, I. L., & Roberts, J. P. (1993). Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: An indicator of long-term growth history. *Journal of Zoology*, *229*, 177–190. https://doi.org/10.1111/j.1469-7998.1993.tb02630.x

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32.

Brunner, S., Bryden, M. M., & Shaughnessy, P. D. (2004). Cranial ontogeny of otariid seals. *Systematics and Biodiversity*, *2*, 83–110. https://doi.org/10.1017/S1477200004001367

Brunner, S., Shaughnessy, P. D., & Bryden, M. M. (2002). Geographic variation in skull characters of fur seals and sea lions (family Otariidae). *Australian Journal of Zoology*, *50*, 415–438. https://doi.org/10.1071/ZO01056

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Byron, C., & Morgan, A. (2016). Potential role of spiny dogfish in gray and harbor seal diets in the Gulf of Maine. *Marine Ecology Progress Series*, *550*, 249–270.

Cassini, G. H. (2013). Skull geometric morphometrics and paleoecology of Santacrucian (late early Miocene; Patagonia) native ungulates (Astrapotheria, Litopterna, and Notoungulata). *Ameghiniana*, *50*, 193–216.

Chemisquy, M. A., Tarquini, S. D., Romano Muñoz, C. O., & Prevosti, F. J. (2021). Form, function and evolution of the skull of didelphid marsupials (Didelphimorphia: Didelphidae). *Journal of Mammalian Evolution*, *28*, 23–33.

Chevallier, C., Gauthier, G., & Berteaux, D. (2017). Age estimation of live Arctic foxes *Vulpes lagopus* based on teeth condition. *Wildlife Biology*, *2017*(1), wlb.00304.

Condit, R., & Le Boeuf, B. J. (1984). Feeding habits and feeding grounds of the Northern elephant seal. *Journal of Mammalogy*, *65*, 281–290.

Condy, P. R. (1978). Distribution, abundance, and annual cycle of fur seals (*Arctocephalus* spp.) on the Prince Edward Islands. *South African Journal of Wildlife Research*, *8*, 159–168.

Cook, R. D. (1977). Detection of influential observation in linear regression. *Technometrics*, *19*, 15–18.

D.E.H. (2004). Biology, threats and conservation status of the Sub-Antarctic fur seal and Southern Elephant seal in Australian waters. *Report for the Department of the Environment and Heritage, Australian Government*, 65 p.

Dabin, W., Beauplet, G., Crespo, E. A., & Guinet, C. (2004). Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*. *Canadian Journal of Zoology*, *82*, 1043–1050. https://doi.org/10.1139/z04-079

Evans, K., Kemper, C., McKenzie, J., & McIntosh, R. (2007). *Age determination of marine mammals using tooth structure*. Retrieved from Adelaïde: In C.D.o.E.a.W. (Ed.), South Australian Museum, p. 70.

Fallows, C., Benoît, H., & Hammerschlag, N. (2015). Intraguild predation and partial consumption of blue sharks *Prionace glauca* by Cape fur seals *Arctocephalus pusillus pusillus*. *African Journal of Marine Science*, *37*, 125–128.

Ferreira, J. M., De Oliveira, L. R., Wynen, L., Bester, M. N., Guinet, C., Moraes-Barros, N., Martins, F. M., Muelbert, M. M. C., Moreno, I. B., Siciliano, S., Ott, P. H., & Morgante, J. S. (2008). Multiple origins of vagrant Subantarctic fur seals: A long journey to the Brazilian coast detected by molecular markers. *Polar Biology*, *31*, 303–308. https://doi.org/10/1007/s00300-007-0358-z

Forcada, J., & Staniland, I. J. (2018). Antarctic fur seal *Arctocephalus gazella*. In B. Wursig, J. G. M. Thewissen & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., p. 1157). Academic Press.

Ford, J., Ellis, G., Matkin, C., Wetklo, M., Barrett-Lennard, L., & Withler, R. (2011). Shark predation and tooth wear in a population of northeastern Pacific killer whales. *Aquatic Biology*, *11*, 213–224. https://doi.org/10.3354/ab00307

Giannini, M. (2004). Ultimate tensile strength of tooth structures. *Dental Materials*, *20*, 322–329. https://doi.org/10.1016/S0109-5641(03)00110-6

Gingerich, P. D., Smith, B. H., & Rosenberg, K. (1982). Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology*, *58*, 81–100. https://doi.org/10.1002/ajpa.1330580110

Gwinnett, A. J. (1992). Structure and composition of enamel. *Operative dentistry*, 5, 10–17.

Hanihara, T. (2008). Morphological variation of major human populations based on nonmetric dental traits. *American Journal of Physical Anthropology*, 136, 169–182. https://doi.org/10.1002/ajpa.20792

Hoffman, J. I., Hanson, N., Forcada, J., Trathan, P. N., & Amos, W. (2010). Getting long in the tooth: A strong positive correlation between canine size and heterozygosity in Antarctic fur seals *Arctocephalus gazella*. *Journal of Heredity*, 101, 527–538. https://doi.org/10.1093/jhered/esq045

Hofmeyr, G. J. G. (2015). *Arctocephalus tropicalis tropicalis*. The IUCN Red List of Threatened Species e.T2062A45224547. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T2062A45224547.en

Hofmeyr, G. J. G. (2016). *Arctocephalus gazella*. The IUCN Red List of Threatened Species e.T2058A66993062. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T2058A66993062.en

Hofmeyr, G. J. G., & Amir, O. A. (2010). Vagrant Subantarctic fur seal on the coast of Tanzania. *African Zoology*, 45, 144–146. https://doi.org/10.1080/15627020.2010.11657265

Hofmeyr, G. J. G., & Bester, M. N. (1993). Predation on king penguins by Antarctic fur seals. *South African Journal of Antarctic Research*, 23, 71–74.

Hofmeyr, G. J. G., Bester, M. N., & Jonker, F. C. (1997). Changes in population sizes and distribution of fur seals at Marion Island. *Polar Biology*, 17, 150–158.

Hofmeyr, G. J. G., Bester, M. N., Makhado, A. B., & Pistorius, P. A. (2006). Population changes in Subantarctic and Antarctic fur seals at Marion Island. *South African Journal of Wildlife Research*, 36, 55–68.

Hofmeyr, G. J. G., Krafft, B. A., Kirkman, S. P., Bester, M. N., Lydersen, C., & Kovacs, K. M. (2005). Population changes of Antarctic fur seals at Nyrøysa, Bouvetøya. *Polar Biology*, 28, 725–731. https://doi.org/10.1007/s00300-005-0732-7

Hohn, A. A., & Fernandez, S. (1999). Biases in dolphin age structure due to age estimation technique. *Marine Mammal Science*, 15, 1124–1132.

Hohn, A. A., Scott, M. D., Wells, R. S., Sweeney, J. C., & Irvine, A. B. (1989). Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science*, 5, 315–342. https://doi.org/10.1111/j.1748-7692.1989.tb00346.x

Jeglinski, J. W. E., Mueller, B., Pörschmann, U., & Trillmich, F. (2010). Field-based age estimation of juvenile Galapagos Sea Lions (*Zalophus wollebaeki*) using morphometric measurements. *Aquatic Mammals*, 36, 262–269. https://doi.org/10.1578/AM.36.3.2010.262

Jones, K. A., Ratcliffe, N., Votier, S. C., Newton, J., Forcada, J., Dickens, J., Stowasser, G., & Staniland, I. J. (2020). Intra-specific niche partitioning in Antarctic fur seals, *Arctocephalus gazella*. *Scientific Reports*, 10, 3238. https://doi.org/10.1038/s41598-020-59992-3

Jouventin, P., Stahl, J. C., & Weimerskirch, H. (1982). La recolonisation des Îles Crozet par les otaries (*Arctocephalus tropicalis* et *A. gazella*). *Mammalia*, 46, 505–514. https://doi.org/10.1515/mamm.1982.46.4.505

Kassambara, A. (2021). *Rstatix: pipe-friendly framework for basic statistical tests. V 0.7.0.*

Kerley, G. I. H., & Robinson, T. J. (1987). Skull morphometrics of male Antarctic and Subantarctic fur seals, *Arctocephalus gazella* and *A. tropicalis*, and their interspecific hybrids. In J. P. Croxall & R. L. Gentry (Eds.), *NOAA Technical Report NMFS 51. Status, biology, and ecology of fur seals* (pp. 121–131).

Kerley, G. I. H., Allen, B. R., & Bester, M. N. (2000). Skull morphometrics of male Subantarctic fur seals (*Arctocephalus tropicalis*) from Marion and Gough Islands. *African Zoology*, 35, 165–171. https://doi.org/10.1080/15627020.2000.11657087

Kienle, S. S., & Berta, A. (2016). The better to eat you with: the comparative feeding morphology of phocid seals (Pinnipedia, Phocidae). *Journal of Anatomy*, 228, 396–413. https://doi.org/10.1111/joa.12410

Kingston, J. J., & Gwilliam, J. (2007). Hybridization between two sympatrically breeding species of fur seal at Iles Crozet revealed by genetic analysis. *Conservation Genetics*, 8, 1133–1145. https://doi.org/10.1007/s10592-006-9269-8

Kirkman, S. P., Wilson, W., Klages, N. T. W., Bester, M. N., & Isaksen, K. (2000). Diet and estimated food consumption of Antarctic fur seals at Bouvetøya during summer. *Polar Biology*, 23, 745–752. https://doi.org/10.1007/s003000000145

Kubota, K., Shibanai, S., Kubota, J., & Togawa, S. (2000). Developmental transition to monophyodonty in adaptation to marine life by the northern fur seal, *Callorhinus ursinus* (Otariidae). *Historical Biology*, 14, 91–95. https://doi.org/10.1080/10292380009380557

Lancaster, M. L., Gemmell, N. J., Negro, S., Goldsworthy, S., & Sunnucks, P. (2006). Ménage à trois on Macquarie Island: Hybridization among three species of fur seal (*Arctocephalus* spp.) following historical population extinction. *Molecular Ecology*, 15, 3681–3692. https://doi.org/10.1111/j.1365-294X.2006.03041.x

Laws, R. M. (1993). Identification of species. In R. M. Laws (Ed.), *Antarctic seals: research methods and techniques* (pp. 1–28). Cambridge University Press.

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 2, 18–22.

Lindenfors, P., Tullberg, B., & Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology*, 52, 188–193. https://doi.org/10.1007/s00265-002-0507-x

Lowry, M. S., & Folk, R. L. (1990). Sex determination of the California sea lion (*Zalophus californianus californianus*) from canine teeth. *Marine Mammal Science*, 6, 25–31. https://doi.org/10.1111/j.1748-7692.1990.tb00223.x

Lunn, N. J., Boyd, I. L., & Croxall, J. P. (1994). Reproductive performance of female Antarctic fur seals: The influence of age, breeding experience, environmental variation and individual quality. *The Journal of Animal Ecology*, 63, 827–840.

Luque, S. P., Miller, E. H., Arnould, J. P. Y., Chambellant, M., & Guinet, C. (2007). Ontogeny of body size and shape of Antarctic and Subantarctic fur seals. *Canadian Journal of Zoology*, 85, 1275–1285. https://doi.org/10.1139/Z07-092

Makhado, A. B., Bester, M. N., Kirkman, S. P., Pistorius, P. A., Ferguson, J. W. H., & Klages, N. T. W. (2008). Prey of the Antarctic fur seal *Arctocephalus gazella* at Marion Island. *Polar Biology*, 31, 575–581. https://doi.org/10.1007/s00300-007-0391-y

McCann, T. S., & Doidge, D. W. (1987). Antarctic fur seal, *Arctocephalus gazella*. In: J. P. Croxall & R. L. Gentry (Eds.), *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Workshop*, Cambridge, England, 23–27 April 1984, pp. 5–8.

Meiri, S. (2011). Bergmann's rule – What's in a name?: Correspondence. *Global Ecology and Biogeography*, 20, 203–207. https://doi.org/10.1111/j.1466-8238.2010.00577.x

Molina-Schiller, D., & Pinedo, M. C. (2004a). Growth layer patterns in *Arctocephalus australis* canine teeth: Evaluation of techniques for age determination. *Latin American Journal of Aquatic Mammals*, 3, 107–118. https://doi.org/10.5597/lajam00056

Molina-Schiller, D., & Pinedo, M. C. (2004b). Using canine teeth for sex determination of the South American fur seal, *Arctocephalus australis*. *Latin American Journal of Aquatic Mammals*, 3, 19–24. https://doi.org/10.5597/lajam00045

Newsome, S., Etnier, M., Monson, D., & Fogel, M. (2009). Retrospective characterization of ontogenetic shifts in killer whale diets via δ13C and δ15N analysis of teeth. *Marine Ecology Progress Series*, 374, 229–242.

Oosthuizen, W. H. (1997). Evaluation of an effective method to estimate age of Cape fur seals using ground tooth sections. *Marine Mammal Science*, 13, 683–693. https://doi.org/10.1111/j.1748-7692.1997.tb00091.x

Oosthuizen, W. H., & Bester, M. N. (1997). Comparison of age determination techniques for known-age Cape fur seals. *South African Journal of Zoology*, 32, 106–111. https://doi.org/10.1080/02541858.1997.11448440

Payne, M. R. (1978). Population size and age determination in the Antarctic fur seal *Arctocephalus gazella*. *Mammal Review*, 8, 67–73. https://doi.org/10.1111/j.1365-2907.1978.tb00218.x

Payne, M. R. (1979). Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology*, 187, 1–20. https://doi.org/10.1111/j.1469-7998.1979.tb07709.x

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Core Team, R. (2021). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-152, https://svn.r-project.org/R-packages/trunk/nlme/

Purnell, M. A., Goodall, R. H., Thomson, S., & Matthews, C. J. D. (2017). Tooth microwear texture in odontocete whales: Variation with tooth characteristics and implications. *Biosurface and Biotribology*, 3, 184–195. https://doi.org/10.1016/j.bsbt.2017.11.004

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramos, R. M. A., Di Beneditto, A. P. M., & Lima, N. R. W. (2000). Relationship between dental morphology, sex, body length and age in *Pontoporia blainvillei* and *Sotalia fluviatilis* (Cetacea) in northern Rio de Janeiro, Brazil. *Revista Brasileira de Biologia*, 60, 283–290. https://doi.org/10.1590/S0034-71082000000200012

Read, F. L., Hohn, A. A., & Lockyer, C. H. (2018). A review of age estimation methods in marine mammals with special reference to monodontids. *NAMMCO Scientific Publications*, 10, 1–67.

Reisinger, R. R., Landman, M., Mgibantaka, N., Smale, M. J., Bester, M. N., De Bruyn, P. J. N., & Pistorius, P. A. (2018). Overlap and temporal variation in the diets of sympatric Antarctic and Subantarctic fur seals (*arctocephalus* spp.) at Marion Island, Prince Edward Islands. *Polar Research*, 37, 1451142. https://doi.org/10.1080/17518369.2018.1451142

Richardson, J., Cripps, P., & Lane, J. (1995). An evaluation of the accuracy of ageing horses by their dentition: changes of dental morphology with age. *Veterinary Record*, 137, 117–121.

Rivals, F., & Solounias, N. (2007). Differences in tooth microwear of populations of caribou (*Rangifer tarandus*, Ruminantia, Mammalia) and implications to ecology, migration, glaciations and dental evolution. *Journal of Mammalian Evolution*, 14, 182–192. https://doi.org/10.1007/s10914-007-9044-8

Robinson, S. A., Goldsworthy, S. G., Hoff, J., & Hindell, M. A. (2002). The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research*, 53, 1071–1082.

Santos, M. C. d. O., Rosso, S., & Ramos, R. M. A. (2003). Age estimation of marine tucuxi dolphins (*Sotalia fluviatilis*) in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 83, 233–236.

Scheffer, V. B., & Myrick, A. C. (1980). A review of studies to 1970 of growth layers in the teeth of marine mammals. *Report of the International Whaling Commission* (Special Issue 3), pp. 51–63.

Scott, G. R., & Turner, C. G. (1988). Dental anthropology. *Annual Review of Anthropology*, 17, 99–126.

Seetah, K., Cucchi, T., Dobney, K., & Barker, G. (2014). A geometric morphometric re-evaluation of the use of dental form to explore differences in horse (*Equus caballus*) populations and its potential zooarchaeological application. *Journal of Archaeological Science*, 41, 904–910. https://doi.org/10.1016/j.jas.2013.10.022

Stewardson, C. L., Prvan, T., Meÿer, M. A., & Ritchie, R. J. (2010). Sexual dimorphism in the adult South African (Cape) fur seal *Arctocephalus*

pusillus pusillus (Pinnipedia: Otariidae): Standard body length and skull morphology. *Proceedings of the Linnean Society of New South Wales*, 131, 119–140.

Tarquini, S. D., Chemisquy, M. A., & Prevosti, F. J. (2020). Evolution of the carnassial in living mammalian carnivores (Carnivora, Didelphimorphia, Dasyuromorphia): Diet, phylogeny, and allometry. *Journal of Mammalian Evolution*, 27, 95–109.

Uchida, A. (1998a). Variation in tooth morphology of *Gorilla gorilla*. *Journal of Human Evolution*, 34, 55–70. https://doi.org/10.1006/jhev.1997.0186

Uchida, A. (1998b). Variation in tooth morphology of *Pongo pygmaeus*. *Journal of Human Evolution*, 34, 71–79. https://doi.org/10.1006/jhev.1997.0187

Vodanović, M., Demo, Ž., Njemirovskij, V., Keros, J., & Brkić, H. (2007). Odontometrics: A useful method for sex determination in an archaeological skeletal population. *Journal of Archaeological Science*, 34, 905–913. https://doi.org/10.1016/j.jas.2006.09.004

Walters, A., Hindell, M., Goebel, M. E., Bester, M. N., Trathan, P. N., Oosthuizen, W. C., & Lea, M. A. (2020). Southern Ocean isoscapes derived from a wide-ranging circumpolar marine predator, the Antarctic fur seal. *Ecological Indicators*, 118, 106694. https://doi.org/10.1016/j.ecolind.2020.106694

Wege, M., Etienne, M. P., Chris Oosthuizen, W., Reisinger, R. R., Bester, M. N., & de Bruyn, P. J. N. (2016). Trend changes in sympatric Subantarctic and Antarctic fur seal pup populations at Marion Island, Southern Ocean. *Marine Mammal Science*, 32, 960–982. https://doi.org/10.1111/mms.12306

Weise, M. J., Harvey, J. T., & Costa, D. P. (2010). The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, 91, 1004–1015. https://doi.org/10.1890/08-1554.1

White, P. A., Ikanda, D., Ferrante, L., Chardonnet, P., Mesochina, P., & Cameriere, R. (2016). Age estimation of African lions *Panthera leo* by ratio of tooth areas. *PLoS One*, 11, e0153648.

Wynen, L. P., Goldsworthy, S. D., Guinet, C., Bester, M. N., Boyd, I. L., Gjertz, I., Hofmeyr, G. J. G., White, R. W. G., & Slade, R. (2000). Postsealing genetic variation and population structure of two species of fur seal (*Arctocephalus gazella* and *A. tropicalis*). *Molecular Ecology*, 9, 299–314. https://doi.org/10.1046/j.1365-294x.2000.00856.x

Zanre, R., & Bester, M. N. (2011). Vagrant subantarctic fur seal in the Mayumba National Park, Gabon. *African Zoology*, 46, 185–187. https://doi.org/10.1080/15627020.2011.11407492

Zeder, M. A., & Pilaar, S. E. (2010). Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, *Ovis*, and goats, *Capra*. *Journal of Archaeological Science*, 37, 225–242. https://doi.org/10.1016/j.jas.2009.10.002

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