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## The genesis of giants: behavioural ontogeny of male northern elephant seals

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1 **The genesis of giants: Behavioural ontogeny of male northern elephant seals**

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17

18 Dominance hierarchies structure the adult social networks of many mammals. To identify the  
19 conditions that support the establishment of stable hierarchical relationships within groups of  
20 familiar rivals, we explored the ontogeny of spatial, social, and communicative behaviour among  
21 male northern elephant seals (*Mirounga angustirostris*). We demonstrate that as male seals reach  
22 sexual maturity, they increase their residency time ashore and restrict their fine-scale movement  
23 patterns within the breeding colony. These movement patterns create a predictable social  
24 environment in which repeated interactions promote greater social connectivity between older  
25 individuals. Moreover, as males become physically and behaviourally mature, their ritualized vocal  
26 displays transition from highly variable calls to stable and unique individual acoustic signatures,  
27 supporting recognition between familiar competitors. The developmental onset of reliable signature  
28 calls—along with concurrent changes in space occupancy—coincide with the formation of stable,  
29 structured dominance relationships among top-level competitors. These findings advance our  
30 understanding of the ontogeny of social behaviour under conditions of extreme competition.

31

32 **Keywords:** animal communication; acoustic communication; behavioural ontogeny; dominance  
33 hierarchies; individual recognition; vocal signature; learning; male-male competition; social  
34 network

35 Dominance hierarchies are common among social animals from insects to mammals when  
36 individuals compete for access to limited resources (1, 2). As hierarchical status influences  
37 reproductive success, physiology, and health (3, 4), understanding the development and structure  
38 of dominance relationships has broad implications for the ecology and evolution of populations  
39 and species (5). While an individual's position within a hierarchy is often linked to size, strength,  
40 or fighting ability (*e.g.* 3), factors related to social knowledge—including long-term memory of  
41 competitors, transitive inference of fighting ability, and winner/loser effects—may be equally  
42 important determinants of dominance (*e.g.* 4).

43  
44 In systems where individuals occupy predictable breeding environments and frequently interact  
45 with familiar competitors, dominance hierarchies may be maintained through individual  
46 recognition rather than direct assessment (8). Rivals rely on memory of prior experiences to limit  
47 costly aggressive encounters with opponents with whom they have previously fought (9).  
48 Recognition of competitors is enabled by cues that are reliable and unique that receivers can  
49 perceive and decode (8, 10). Consequently, individuals must have the opportunity to not only  
50 learn the characteristics of their familiar competitors, but also to have sufficient experience with  
51 these individuals for their associated cues to become meaningful. Thus, we define “familiarity” as  
52 the acquisition of social knowledge (*e.g.* relative rank and/or fighting ability) associated with  
53 competitors learned through previous experience with that individual.

54  
55 When familiarity is necessary to the formation of dominance relationships among adults, the  
56 behaviour of individuals during maturation should provide ample experience to fine tune  
57 recognition abilities. Juveniles may gain social knowledge by assessing one another during low-  
58 stakes interactions while at the same time acquiring unique characteristics that others may learn  
59 and remember. The developmental process by which individuals provide and obtain information

60 within their social environment should become imperative to their long-term reproductive success  
61 (6). Here, we explore behavioural development among males in one of the most competitive  
62 breeding systems known among mammals, the northern elephant seal *Mirounga angustirostris*.

63  
64 Northern elephant seals are an ideal model to evaluate the ontogeny of agonistic social behavior  
65 owing to tremendous selection pressures for rival assessment (11). Adult males compete fiercely  
66 to establish structured dominance hierarchies while ashore during the annual breeding season,  
67 which may span more than 100 days without access to food or water (12, 13). During this time  
68 males are nearly continuously active, and do not appear to exhibit a significant difference in  
69 interaction rate between day and night (14). The exception to this activity level is found during  
70 extremely warm periods, reflecting the tendency for males to avoid vigorous exertion in during  
71 higher temperatures (14). Compared to females, males live shorter and more dangerous lives (15):  
72 only 5% of males survive to sexual maturity (16) with less than 1% ever gaining reproductive  
73 access to females (15).

74  
75 Once established, dominance relationships among competing males remain stable throughout the  
76 breeding season, with most contests resolved through the exchange of ritualized multi-modal  
77 threat displays that include stereotyped posturing, seismic cues, and extremely loud, pulsatile  
78 vocalizations (17, 18). The vocal component of these threat displays is usually sufficient to elicit a  
79 directional response from familiar competitors: either attack if the caller is subordinate or retreat  
80 if the caller is dominant (19). Each adult male in the breeding colony produces a unique acoustic  
81 signature (20) and vocal differences between males support individual recognition through  
82 associative learning (21). Both the timbre and rhythm of these calls are of particular importance,  
83 as males remember subtle differences in call structure, which allow the seals to distinguish  
84 between familiar competitors (22).

85

86 While the behaviour of adult males has been extensively described, less is known about the lives  
87 of young seals. Their fine-scale movement patterns and social relationships have not been  
88 characterized, and the structure and function of their acoustic displays remains unresolved.

89 Subadult males emit threat calls during intrasexual interactions that are more variable than those  
90 of adults, particularly with respect to call structure and pulse rate (23). This suggests that males  
91 undergo a transitional period during development prior to which their calls lack the individually  
92 reliable characteristic exhibited by adult males (23). If the social structure of adults relies on  
93 accurate assessment of competitors, the behavioural development of young individuals should  
94 facilitate their ability to learn how to provide and acquire information in this highly competitive  
95 social system.

96

97 To evaluate developmental changes in space-use, social interactions, and vocal signaling among  
98 different age classes of male elephant seals, we combine fine-scale temporal and movement  
99 patterns of individual males with social network analyses to determine how occupancy of the  
100 breeding colony influences male-male competition during reproductive development.

101 Additionally, through cross-sectional age comparisons, we describe the ontogeny of vocal  
102 signatures and identify the timing during maturation that these calls become individually distinct  
103 and recognizable to others. Finally, we assess how responsiveness to acoustic displays of  
104 unfamiliar competitors changes as a function of age through the use of field-playback  
105 experiments. Our integrated approach captures the genesis of extreme intrasexual competition in a  
106 social system based on individual recognition of familiar rivals.

107

## 108 **Materials and Methods**

### 109 *General*

110 Research occurred at Año Nuevo State Reserve in San Mateo County, California, USA which  
111 includes mainland and island coastal sandy beach haul-outs where northern elephant seals  
112 congregate each winter to breed. Approximately 2000 seals are distributed over the 2.7 km span  
113 of mainland beaches. Roughly 430 of these are males, and of that 12% (~52) are considered to be  
114 reproductive adults (based on the presence of secondary sexual characteristics). The mainland site  
115 includes at least 20 harems annually, each with an average of 100 adult females and their  
116 dependent pups (range: 50-150 females). As part of a long-term population monitoring effort, 300  
117 weaned pups are tagged annually each season with two serially numbered tags placed in the  
118 interdigital webbing of their hind-flippers (Jumbo@ Rototags, Dalton Supplies Ltd, Henley-on-  
119 Thames, UK). Consequently, approximately 35% of the males included in this study had known  
120 birth years. Additionally, some males are flipper-tagged as subadults or adults without a known  
121 birth record. Tag numbers are observed on animals at the beginning of the season through the use  
122 of binoculars, and animals are subsequently marked with these numbers to enable easy  
123 identification.

124

125 Between 2010 and 2018, we identified subadult and adult males upon their annual return to the  
126 site for the breeding season (December-March) by placing unique dye marks on their dorsal  
127 flanks (as in 13). These marks were referenced to flipper tags and associated metadata when  
128 available. Once marked, all males were photographed to document their size and physical  
129 features. Between 81 and 350 males were identified in this manner each season.

130

131 Once male elephant seals have survived adolescence (ages 1-3), they accelerate through rapid  
132 physical maturation over a five year period (ages 4-8), during which time they more than triple in  
133 body size (24). Coincident with this physical maturation are dramatic transformations in both in  
134 social and acoustic behavior. To fully capture the developmental procession of these physical and

135 behavioral changes, we categorized male elephant seals into one of five age categories based on  
136 several physical features including overall body size, the development of the proboscis, and  
137 scarring of the chest shield (as in 25). Due to the importance of identifying developmental stages  
138 in this work, we used photographs of known-age males that were tagged at weaning to further  
139 define the physical criteria used to determine age classes. Males categorized as sub-adult 1 (SA1)  
140 were four years old. These individuals were approximately the size of adult females, with a wide  
141 nose that is not elongated and without a mid-nose indentation; these males have no scarring on the  
142 chest (Figure 1. SA1). Males categorized as sub-adult 2 (SA2) were five years old. These  
143 individuals had a proboscis that extends down to the mouth when the seal rests flat on the ground;  
144 they had no mid-nose indentation. Wrinkles are present along the chest-shield but there is no  
145 scarring (Figure 1. SA2). Males categorized as sub-adult 3 (SA3) were six years old. Their  
146 proboscis extends down past the mouth while resting on the ground, and a mild mid-nose  
147 indentation is evident. Scarring of the chest-shield is noticeable, with thickened skin and some  
148 wrinkles but no pink tissue (Figure 2. SA3). Males categorized as sub-adult 4 (SA4) were  
149 approximately seven years old. These seals have a proboscis that folds onto the ground while  
150 resting, a significant mid-nose indentation, and scarring along the chest that has some pink  
151 coloration. The chest shield can extend proximally towards the eye while observed resting on the  
152 ground (Figure 1. SA4). Fully mature males were categorized as adults (8+ years old). Adults had  
153 a wide proboscis with a pronounced mid-nose indentation; while at rest, the nose extends to the  
154 ground and folds back under the mouth. Adults typically display a noticeable, calloused pink  
155 chest shield that extends proximally past the eyes and up along the dorsal side of the head (Figure  
156 1 Adult). At the end of each breeding season, three experienced observers (blind to the identity of  
157 the male) reviewed photographs of each male to confirm his age designation.

158

159 *Space utilization and residency patterns*



160

161 To characterize within-colony movement patterns and describe how male home range changes  
162 with maturation, exhaustive re-sight data were collected during four breeding seasons concluding  
163 in 2013, 2014, 2017, and 2018. Observations began each season in November coincident to the  
164 arrival of males and extended through the end of the breeding season and male departure (mid-  
165 March). During each season, an average of 55 daily surveys of animal distribution were  
166 conducted (range 34-71) by experienced observers that monitored the colony and recorded  
167 whether marked and/or tagged individuals were present. The GPS position of each identified male  
168 was recorded once per survey day with a Bad Elf Pro+ GPS (site accuracy of +/- 1.5 m); these  
169 measurements were obtained within 3 body lengths of target individuals (< 12 m). Sampling  
170 effort was directed towards adult males in the 2013 and 2014 seasons, and expanded to include  
171 younger males during the 2017 and 2018 seasons.

172

173 To evaluate the amount of time male elephant seals spend ashore and whether their tenure varies  
174 with age, we tracked a subset of tagged individuals from each age class (n=10). We compared  
175 male tenure (number of days from the first sighting to the last sighting) across all age classes  
176 using a one-way ANOVA, with a Tukey-Kramer HSD *post-hoc* test to evaluate differences  
177 between age-classes.

178

179 Location data were used to estimate home range size for each male observed at the colony for 10  
180 or more days during the 2012, 2014, 2016-18 seasons. These data were compiled for 208  
181 individuals (SA1 = 9, SA2 = 27, SA3 = 40, SA4 = 56, AD = 76). The occurrence probability  
182 distribution—or home range—for each male was calculated using the kernel density tool in the  
183 geospatial modeling environment module of ArcGIS (version 10.6.1) and QGIS (version 3.2.2). A  
184 polygon was created with a grid cell size of 1m<sup>2</sup> to encompass sighting locations within 95% and

185 50% home range boundaries. We applied a boundary layer of available space which did not  
186 include water below mean high tide and inland areas (unsuitable habitat). We used the 95% kernel  
187 density estimate (KDE) to quantify each male's overall distribution, and the 50% KDE to  
188 represent the core area of his space use, as this measure is typically considered an accurate  
189 representation of home range as it removes outliers (26). Home range data were calculated for  
190 each individual and averaged by age class (Mean and range number of locations used for KDE  
191 analysis provided in Table 1). We compared the mean 50% and 95% home range sizes between  
192 age classes using one-way ANOVAs, with a Tukey-Kramer HSD *post-hoc* test to evaluate  
193 differences between age classes.

194

### 195 ***Assessment of social relationships***

196

197 To determine how social relationships between males change during development, we scored  
198 dyadic interactions involving identified male elephant seals during the 2018 breeding season (29  
199 November through 8 March) using the methods described by Casey *et al.* (2015). All occurrence  
200 sampling of competitive interactions was conducted by 1-2 experienced observers who were  
201 stationed at different areas of the breeding colony and in communication with one another via  
202 radios to prevent repeated sampling between 0700-1700h each day. During this time observers  
203 had full visual coverage of the sampling area, and all aggressive interactions were recorded,  
204 irrespective of age-class. We defined a dyadic competitive interaction between two individuals  
205 when we observed the agonistic behavior of one individual (visual posturing, vocalizing, or  
206 forward movement) directed towards or affecting the behavior of another male. The victor in each  
207 pairwise interaction was defined by his displacement of another male, evidenced by the loser  
208 moving away with either a slight change in body position (*e.g.* head turn away from dominant

209 animal) or an obvious change in phonotaxis (negative = retreat). For each interaction, we  
210 recorded the identity of the apparent winner and loser.

211

212 We used social network analysis to determine the number of social partners and strength of  
213 association between male seals from different age classes. We constructed directed weighted  
214 social networks based on the competitive interactions scored in the field using the ‘igraph’  
215 package in R (version 3.3.0) (27). To investigate differences among age classes with respect to  
216 social relationships, we compared degree centrality (number of social partners) and average nodal  
217 strength (number of pairwise interactions) between males of different ages. We evaluated the  
218 significance of these relationships using one-way ANOVAs for each parameter, with a Tukey-  
219 Kramer HSD *post-hoc* test to evaluate differences between age classes.

220

### 221 *Acoustic displays*

222

223 To evaluate how the spectral and temporal patterns of vocal displays change during maturation,  
224 we opportunistically recorded the vocal displays produced by males of all age classes during six  
225 breeding seasons (2011, 2012, 2013, 2014, 2017, and 2018). Calls were recorded with a Neumann  
226 KMR 82I Condenser Shotgun Microphone linked to a Fostex FR-2 Field Memory Recorder (24-  
227 bit/48 kHz) or a Brüel and Kjær 4189 condenser microphone (with UA-1650 windscreen)  
228 connected to a Brüel and Kjær 2250 sound-level meter (24-bit/48 kHz). During recording,  
229 microphones were at 1-10 m distance and between 0° and 90° orientation. Recordings were  
230 obtained without disruption of normal behavior by remaining below the seals’ response threshold  
231 to human presence, as in Casey et al. (2015).

232

233 We selected acoustic displays from males of each age class from high quality recordings (*i.e.* low  
234 background noise, no overlap with other vocalizations) where all acoustic parameters could be  
235 readily identified. Because adult males show reliable substructure within the repeating units  
236 comprising the rhythmic portion of their acoustic display (21, 22), we examined the temporal  
237 features of each male's vocalization as well as spectral content. Following the methods described  
238 in Casey et al. (2018), we defined a call bout as the entire vocalization, including any introductory  
239 and terminal snorts and rumbles. We identified the rhythmic portion of the vocalization as the  
240 bout component that had a defined pattern, which often consisted of repeating intervals. Each  
241 repeating interval of the bout's rhythmic portion was defined as a unit, measured from the onset  
242 of the first sonic element in the unit to the onset of the following unit. Each unit contained  
243 individual elements, which were defined as perceptually discrete sonic components. Elements  
244 were divided into two types based on duration: those < 200 ms were considered pulses, whereas  
245 those > 200 ms were considered bursts. This duration criterion was selected based on perceptual  
246 differences between the sounds evident to human listeners.

247

248 Calls were analyzed using Raven Pro 1.5 sound analysis software. Eight temporal variables were  
249 manually measured from the waveform: rhythmic portion duration (s), unit duration (s), duration  
250 of the sonic portion of each unit (s), duration of the silent portion of each unit (s), number of  
251 elements in each unit, number of different element types in each unit, unit repetition rate (Hz) –  
252 measured as the mean number of units/second calculated over the rhythmic portion of the bout,  
253 and degree of isochronicity within the call – measured as the standard deviation of the unit  
254 duration, with lower values corresponding to a greater consistency in tempo. Additionally, we  
255 noted whether introductory or terminal snorts and rumbles were associated with each  
256 vocalization. Five spectral characteristics were measured from the average spectrum (sampling  
257 rate 48 kHz; Hamming window; FFT size 2048 with filter bandwidth 7 Hz; overlap 90%): the

258 25%, 50% and 75% frequency quartiles (1st quartile: 'Q25', 2nd quartile: 'Q50' and 3rd quartile:  
259 'Q75', in Hz), peak frequency (Hz), and the 90% frequency bandwidth (Hz). Additionally, we  
260 noted whether each call had a harmonic structure, and if so, we measured the fundamental  
261 frequency,  $f_0$  (Hz).

262

263 We applied a permutational multivariate analysis of variance (PERMANOVA) to these acoustic  
264 measurements to determine whether the calls produced by males vary significantly as a function  
265 of age. Following this PERMANOVA, we evaluated whether specific call variables changed  
266 linearly with age utilizing a linear mixed effects model (LMM). We performed a likelihood ratio  
267 test on these data, which compared the LMM with and without the explanatory variable (age  
268 class). Both models included individual as a random effect, and adjusted the outcomes for  
269 multiple testing using a Bonferroni correction.

270

271 To evaluate whether the stability of specific call features changed as a function of age, the  
272 potential for individual coding (PIC) for each acoustic feature was determined for each age class  
273 following the methods described by Charrier and Harcourt (2006). A PIC value  $> 1.0$  indicates  
274 that a given acoustic feature is more variable among individuals than within individuals and can  
275 potentially function to convey individual identity. This analysis was applied to all call except for  
276 the number of elements in each unit, and the number of different elements in each unit.

277

278 To determine how the consistency of a male's display call changes during development, we  
279 conducted a standard multivariate Discriminant Function Analysis (DFA) using five call features.  
280 We selected the call variables showing the highest PIC values in adult males, excluding any call  
281 variables that were highly correlated (features with an  $R^2$  value  $> 0.5$ ). Within each age class, we  
282 classified calls by individual, with identity as the group identifier and acoustic measures as

283 discriminant variables. Correct classification scores obtained from the DFA provide a metric of  
284 how well the measured variables separated individuals within each age-class in acoustic space. To  
285 determine the effect that age has on the accurate classification of individuals, percent-correct  
286 scores for each age-class were compared with a N-1 Chi-squared test. All statistical tests were  
287 conducted using R (version 3.3.0).

288

### 289 *Acoustic playback experiments*

290

291 We conducted playback experiments in order to assess whether males perceive maturational  
292 differences in the vocal characteristics of competitors. We challenged SA2, SA3, and SA4 males  
293 with played back calls from unfamiliar males of their own age class or those from unfamiliar  
294 adults. We aimed to test 30 individuals of each age class with 15 individuals receiving playbacks  
295 from same-aged unfamiliar males and 15 different individuals receiving calls from unfamiliar  
296 adult males. In some instances, we were unable to find 15 unique individuals for each treatment  
297 within each age class and thus tested a subset of males with both treatments (6 out of 30 tested  
298 SA3s, 6 out of 30 tested SA4s and 4 out of 30 tested SA2s). In these cases, playbacks were  
299 conducted at least two days apart to avoid habituation. Calls from 15 different individuals were  
300 used for each treatment to avoid pseudo-replication. These calls were recorded at a distant colony  
301 (Piedras Blancas, San Simeon State Park, CA, USA), located 560 km south of Año Nuevo in the  
302 2012 season.

303

304 Field playback experiments were completed over a two-week period in 2017 during the interval  
305 of female estrous at the colony, when males were most responsive. Playback signals were  
306 broadcasted from a wireless, self-powered amplified Ecoxgear EcoBoulder speaker (7"x 10"x  
307 13", 100-watt power amplifier; frequency range 80-120kHz) which was capable of replicating

308 both the amplitude and frequency characteristics of natural calls (peak frequency = 460 Hz, range  
309 = 232-725 Hz, from Casey et al. 2015). The speaker was positioned  $7 \pm 1$  m from and on axis  
310 with the focal male. The speaker was positioned by personnel who retreated to a location out of  
311 view of the focal animal to videotape the playback trial. The playback began after an interval of at  
312 least 2 minutes without the focal male attending to the speaker or interacting with other males,  
313 and when no other males were within 7 m of the speaker. Each trial included two repetitions of a  
314 single call separated by 3 seconds of silence. The calls were broadcast at a peak level of  $116 \pm 1.5$   
315 dB at 1 m, just below the range reported for adult males of this species (18).

316

317 Behavioural responses that occurred in the 90 second interval from the onset of the playback were  
318 assigned to one of four behavioural categories: no response - the male did not move or change  
319 behaviour during the playback, retreat – the male moved away from the speaker, attack – the male  
320 moved towards the speaker, undecided – the male looks towards the speaker, orients, raises his  
321 head or rears up, but does not move towards or away from the speaker. We used Fisher's exact  
322 tests to determine whether males within each age class respond differently to the calls of  
323 unfamiliar same age and adult males.

324

### 325 *Ethical Note*

326

327 All research was conducted under authorization of the United States National Marine Fisheries  
328 Service marine mammal research permits 14636 and 19108 with oversight from the Institutional  
329 Animal Care and Use Committee of the University of California Santa Cruz (Reicc1911-1).  
330 Permission to work at the field site was provided by Año Nuevo State Park and the UC Natural  
331 Reserve System.

332

333

334 In our playback experiments we were sensitive to the response of the target individuals eliciting  
335 aggression from nearby animals. Given the animal's sensitivity to directional cues and the high  
336 state of arousal of males during this time period (29), we made special effort to position the  
337 speaker so that a directional response from the target animal would not draw him towards another  
338 more dominant individual or into female harems where he was likely to get attacked. This  
339 resulted in our playback being conducted outside of the harems and away from other individuals  
340 in the majority of cases. Of the 90 playbacks conducted, there was one instance in which the  
341 behavior of the target individual elicited an aggressive (approach) response from a nearby  
342 dominant animal, which resulted in a vocal exchanged between the two individuals but no  
343 physical contact.

344

## 345 **Results**

### 346 *Ontogeny of space utilization*

347

348 Space use and movement patterns of male northern elephant seals change with successive  
349 maturational stages (Table 1, A1). As individuals get older, their home ranges within the  
350 terrestrial breeding colony decrease in size while their time spent ashore increases (Figure 1, A1,  
351 2). Four-year old subadult males (class SA1) are the first to arrive and depart the breeding colony,  
352 coming ashore in late November and departing in early January (days ashore =  $37 \pm 11$ ), prior to  
353 the arrival of most females. Five-year-old subadult males (class SA2) and 6-year-old subadult  
354 males (class SA3) arrive nearly a month later and stay ashore much longer ( $49 \text{ days} \pm 12$  and  $64$   
355  $\text{days} \pm 7$ , respectively). Seven-year-old males (class SA4) and mature adults (8+ years old) spend  
356 the longest time ashore, arriving in mid-December and departing at the end of February ( $71 \text{ days}$   
357  $\pm 4$  and  $68 \text{ days} \pm 10$ , respectively). Thus, we find that although time spent ashore varies



358 significantly among age classes (ANOVA:  $F(4, 45) = 12.93$ ,  $p < 0.0001$ ; 50 seals; A1, 2), males  
359 over 5 years old have the opportunity to interact with one another on the breeding colony.

Re-sights used for residency analysis				Presence of males on the colony						
age class	individuals	mean re-sight	range	mean arrival date	SD (days)	mean departure date	SD (days)	mean presence (days)	SD (days)	year
SA1	10	15	10-23	11/27/17	10	1/3/18	11	37	10	2018
SA2	10	16	12-22	12/23/17	13	2/9/18	12	49	8	2018
SA3	10	18	11-24	12/27/17	7	3/1/18	7	64	7	2018
SA4	10	26	12-36	12/17/17	11	2/26/18	4	71	13	2018
AD	10	30	11-47	12/19/17	21	2/26/18	10	68	21	2018
Home range size kernel density estimates (KDE areas, km <sup>2</sup> )										
age class	number of seals	mean re-sight	range	95% area	range	SD	50% area	range	SD	year
SA1	9	15	10-24	0.054	0.0002 - 0.16	0.06	0.01	0.00002 - 0.03	0.01	2018
SA2	27	16	10-32	0.18	0.02 - 0.17	0.1	0.07	0.006 - 0.17	0.05	2012, 2014, 2016, 2017, 2018
SA3	40	18	10-39	0.14	0.02 - 0.28	0.07	0.04	0.042 - 0.1	0.03	2012, 2014, 2016, 2017, 2018
SA4	56	20	10-52	0.13	0.005 - 0.35	0.09	0.04	0.002 - 0.14	0.04	2012, 2014, 2016, 2017, 2018
AD	76	27	11-60	0.08	0.008 - 0.35	0.08	0.02	0.0007 - 0.1	0.02	2012, 2014, 2016, 2017, 2018

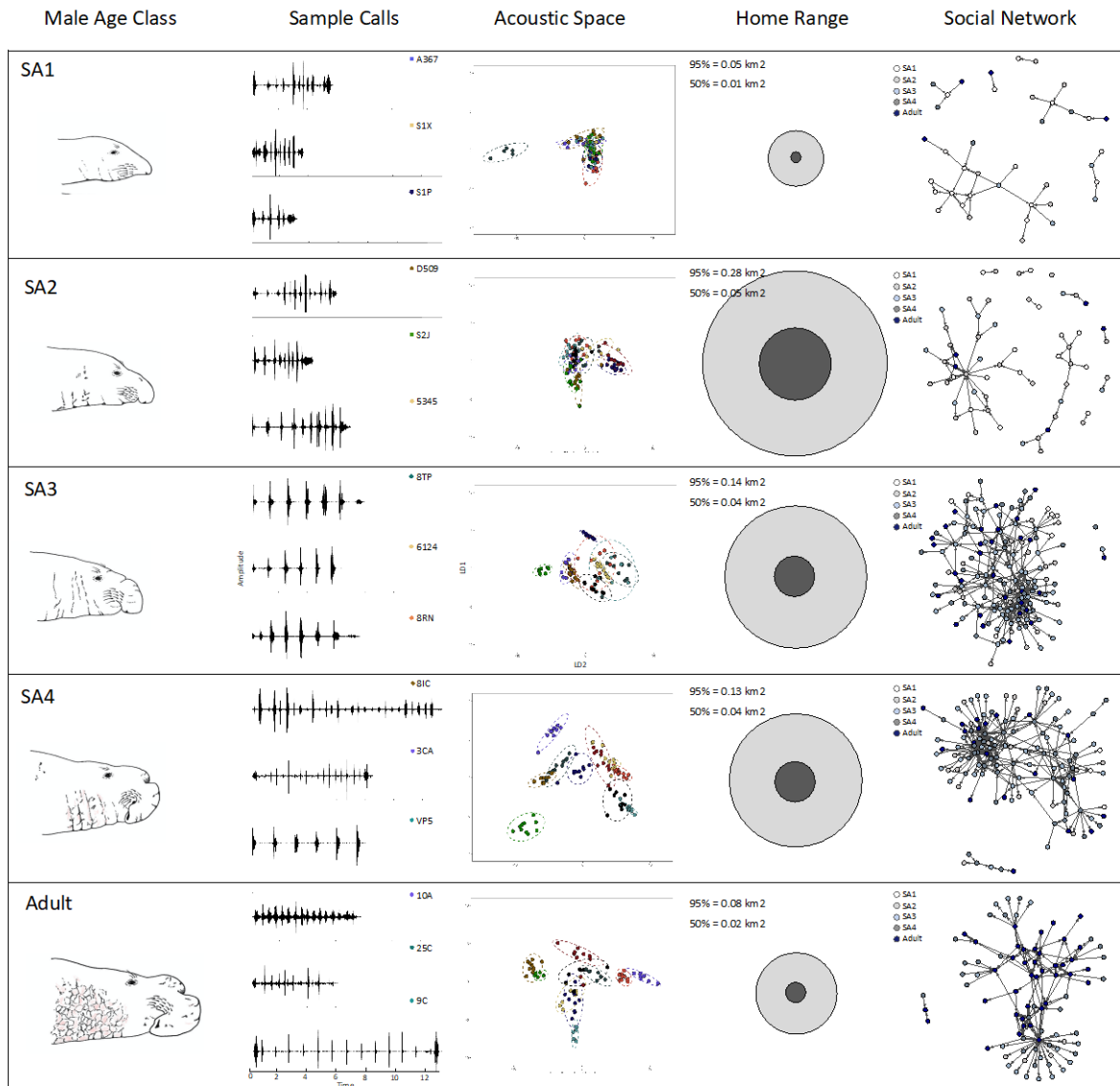
361 **Table 1. Male tenure and home range size at the Año Nuevo breeding colony.** The upper panel provides a  
362 summary of attendance patterns exhibited by male seals (n=10 seals per age class) during the 2018 breeding season,  
363 including the number of days spent ashore for each age class (mean and SD, standard deviation). Male tenure  
364 increased with age class. The lower panel provides a summary of spatial patterns exhibited by 208 male seals  
365 sampled during five annual breeding seasons (n=9-76 seals per age class). Home ranges for each age class are  
366 expressed as both 95% and 50% mean kernel density estimate (KDE) areas (km<sup>2</sup>). With the exception of the youngest  
367 age class, male home range decreased with increasing age.

368  
369 Fine-scale space utilization within the breeding colony also changes with developmental stage.  
370 The home ranges of males, measured as kernel density estimates (KDE), vary considerably  
371 between age classes (ANOVA:  $F(4, 201) = 14.21, p < 0.0001$ ; 208 seals; Figure 1, Table 1, A1,  
372 2). With the exception of the youngest subadult males (class SA1) who show little movement  
373 within the colony (50% KDE = 0.01 km<sup>2</sup>), home ranges decrease as individuals mature. The SA2  
374 class has the largest home ranges (50% KDE = 0.07 km<sup>2</sup>), while adults occupy the smallest areas  
375 within the colony (50% KDE = 0.02 km<sup>2</sup>). This pattern of restriction in home ranges throughout  
376 development likely has a significant influence on the social associations of males as they mature.

### 377 378 *Development of social relationships*

379  
380 We observed males over 71 days of sampling effort (~ 215 h of behavioural recording containing  
381 1,352 interactions between 207 identified individuals: 40 adults, 46 SA4s, 66 SA3s, 38 SA2s, 17  
382 SA1s). We find that social relationships between competing rivals change as males age: young  
383 individuals have fewer social partners with whom they are less familiar, whereas older males  
384 compete with a greater number of rivals, and associations between competing rivals is much  
385 stronger throughout the breeding season (Figure 1, A3, 4).

386



387  
 388 **Figure 1. Development of male elephant seals.** Several aspects of ontogeny are shown left to right pertaining to  
 389 age class, call structure, call differentiation, home range, and social network. **Column 1** depicts the secondary sexual  
 390 characteristics associated with each age class. Males categorized as sub-adult 1 (SA1) were four years old, sub-adult  
 391 2 (SA2) were five years, sub-adult 3 (SA3) were six years old, sub-adult 4 (SA4) were seven years old, and fully  
 392 mature males were categorized as adults (8+ years old). **Column 2** provides representative waveforms for different  
 393 males of each age class. **Column 3** illustrates results of the DFA analysis for each class represented on identical x-y  
 394 axes. Colored points represent different males within each age class. The x and y-axes represent the maximum  
 395 difference between groups based on a combination of predictor variables. The dotted ellipses illustrate a 95%  
 396 confidence level for the data. **Column 4** shows the average 95% (lighter shaded area) and 50% (darker shaded area)

397 Kernel Density Area as represented as relative circles for each age class. Apart from SA1 males that constrain their  
398 space-utilization, as males increase in age their home range decreases in size. **Column 5 (see Figure A3 for an**  
399 **enlarged version)** demonstrates the social networks of successive age classes from one breeding season (2018) -  
400 SA1s (n = 17), SA2s (n = 38), SA3s (n = 66), SA4s (n = 46), and adults (n = 40). Circles are males and directed lines  
401 are dyadic competitive interactions, with the thickness of each line corresponding to the number of interactions  
402 observed between two individuals. Age classes are separated by color. SA1 males interacted with an average of 2.8  
403 different individuals within their social network (SD = 2.2, range = 1-7) and encountered each individual an average  
404 of 1.2 times (SD = 0.3, range = 1-2). SA2 males interacted with an average of 3.8 unique individuals (SD = 4.1, range  
405 = 1-20), with an average of 1.2 interactions with each individual (SD = 0.45, range = 1-3.2). SA3 males interacted  
406 with an average of 6.0 different individuals (SD = 5.4, range = 1-32), with an average of 1.3 interactions with each  
407 animal (SD = 0.45, range = 1-3.4). SA4s interacted with an average of 10.3 unique individuals (SD = 7.5, range = 1-  
408 32), with an average of 1.7 interactions with each individual (SD = 0.6, range = 1.32). Adult males interact with an  
409 average of 12 individuals over the breeding season (SD = 9.1, range = 2-34), and averaged 1.9 interactions with each  
410 individual (SD = 0.7, range = 1-4.2). Young males (SA1 and SA2) interact with only a few individuals, and avoid  
411 older males. As males mature, they exhibit greater connectivity to competitors within the network.

412  
413 An analysis of male interaction networks across age classes demonstrates that the number of  
414 social partners (degree centrality) and the number of pairwise encounters (average nodal strength)  
415 change as a function of increasing age (ANOVA:  $F_{4, 190} = 10.31$ ,  $p < 0.0001$  and  $F_{F4, 190} = 14.28$ ,  
416  $p < 0.0001$  respectively; Figure 1, A3). Young males (4-5 years old) participate in aggressive  
417 interactions with fewer individuals within their same-age or adjacent cohort throughout the  
418 season. SA1 males are frequently observed interacting in low stakes encounters with other SA1s  
419 (58% of total interactions). SA2 males interact most frequently with SA3s (30% of all  
420 interactions), and the vast majority of their interactions with older males results in retreat (98%).  
421 SA3s interact with males of all age classes, however 85% of these interactions occur with males  
422 that are the same age or older. Adult and SA4 males display a significantly higher degree  
423 centrality and a stronger nodal strength than other age classes, indicating that they have more  
424 social partners (Figure 1, A3) and develop stronger associations with these familiar competitors

425 (ANOVA, Tukey-Kramer HSD post-hoc test  $p < 0.001$ ). SA4 and adult males preferentially  
 426 interact with other SA4 or adult males (67% and 73% for each age class, respectively). Thus, it  
 427 appears that all SA4 and adult males that survive to social maturity are operating within a  
 428 relatively large—yet familiar—social network.

429  
 430 ***Description of vocal behaviour***

431  
 432 We recorded a total of 443 calls from 47 individual seals. Within each age class, we recorded 7-  
 433 10 males, and obtained 5-10 calls per individual. We found that the calls produced by males vary  
 434 significantly between individuals (PERMANOVA:  $F_{\text{model}} = 23.2$ ,  $R^2 = 0.5$ ,  $p < 0.001$ ), and across  
 435 age classes (PERMANOVA:  $F_{\text{model}} = 153.9$ ,  $R^2 = 0.3$ ,  $p < 0.001$ , Figure 1). The results of the  
 436 LMM demonstrated that 7 of the 11 call parameters measured did not change lineally as a  
 437 function of increasing age (Table 2, A4).

438

	Quartile 1 frequency (Hz)	Center frequency (Hz)	Quartile 3 frequency	90% frequency bandwidth (Hz)	Peak frequency (Hz)	Call duration (s)	Unit duration (s)	Duration of sonic portion in each unit (s)	Duration of silent portion of each unit (s)	Unit repetition rate (Hz)	Degree of isochronicity
Null model (AIC)	5740.9	5797.7	5853.6	6118.1	6170.1	2198.5	772.1	-505.81	-564.13	379.1	-1019.4
Alternative model (AIC)	5724.5	5779.6	5833.6	6079.2	6157.6	2175.5	-796.66	-510.55	-567.16	369	-1021.9
	$P > 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.01$	$P < 0.001$	$P = 0.237$	$P = 0.286$	$P = 0.366$	$P < 0.05$	$P = 0.366$

439  
 440 **Table 2.** Results from linear mixed effects models to compare the relationship between individual acoustic  
 441 parameters and the explanatory variable age class (alliterative model) versus a model without age class as an  
 442 explanatory variable (null model). AIC values and Bonferroni corrected values P values for each variable are  
 443 presented.

444  
 445

446 Younger individuals (SA1 and SA2 males) produce calls that are relatively brief in duration and  
447 contain repeating units that are shorter than those of older males (A4, 5, Supplementary Audio 1,  
448 2). Within one recording session, SA1 and SA2 males often oscillate between simplified versions  
449 of the adult male vocal display and calls that more closely resemble female threat vocalizations.  
450 These vocalizations are emitted during low-stakes social exchanges away from female harems.

451  
452 SA3 males exhibit stronger consistency in call structure (Figure 1, A5, Supplementary Audio 3).  
453 Despite the increase in stability of call features within individuals, it is difficult to ascribe a  
454 particular call to an individual given the similarity in the calls of different SA3 males (Figure 1).  
455 Across the SA1 to SA3 age classes, several frequency features (*i.e.* 90% frequency bandwidth,  
456 peak frequency, and Q1) of the vocalizations appear to change with maturation (A4, 5). This  
457 supports the notion that call parameters are constrained by vocal tract length and resonators  
458 among these age classes, and thus can provide honest information about body size to listeners.

459  
460 Consistent differences between individual males emerge at approximately 7 years of age (SA4),  
461 aligning with the timing at which males develop more stable associations with others in the  
462 dominance hierarchy (Figure 1, Supplementary Audio 4). It is within this age class that sub-  
463 structural call components begin to emerge, with individuals reliably emitting one or more  
464 elements and different element types within each repeating unit of their vocalization (A5). Unlike  
465 the calls emitted by younger males, the vocal displays produced by both SA4 and adults are  
466 produced from a stereotyped body posture. Once these vocalizations become fixed among SA4s  
467 and adults, their structure is consistent across years and social contexts (13).

468  
469 ***Ontogeny of male responsiveness to competitors' calls***

470

471 Field playback experiments revealed that males perceive maturational differences in the vocal  
 472 characteristics of competitors.  
 473

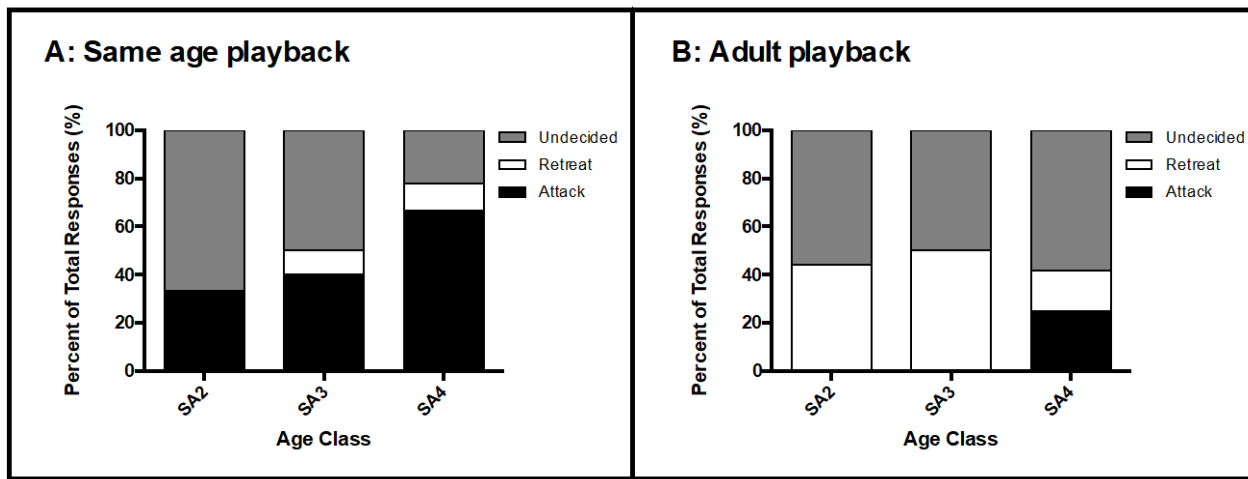
Age Class	Total Males Tested	Playback Treatment	Target Male Response			
			No Response Detected	Undecided	Retreat	Attack
SA2	15	SA2	6	6	0	3
SA2	15	AD*	6	5	4	0
SA3	15	SA3	5	5	1	4
SA3	15	AD*	7	4	4	0
SA4	15	SA4	5	2	1	6
SA4	15	AD	3	7	2	3

\* Fisher's exact test,  $p < 0.05$

474  
 475 **Table 3. Summary of behavioral responses to playbacks of calls from unfamiliar same-age males and**  
 476 **unfamiliar adult males.** Behavioural responses were assigned to one of four behavioural categories: no response -  
 477 the male did not move or change behaviour during the playback, undecided – the male looks towards the speaker,  
 478 orients, raises his head or rears up, but does not move towards or away from the speaker, retreat – the male moved  
 479 away from the speaker, and attack – the male moved towards the speaker. A Fisher's exact test was used to compare  
 480 the responses of males in each age class to the calls of unfamiliar same age and adult males.

481  
 482 SA2 males are more likely to attack when they are exposed to calls of a similar age class, and  
 483 retreat when they hear the calls of adult males (Table 3, Figure 2, Fisher's exact test,  $p < 0.05$ ).  
 484 SA3 males are also more likely to attack the speaker when they hear similar-aged males, and  
 485 retreat when they hear the calls of unfamiliar adults (Table 3, Figure 2, Fisher's exact test,  
 486  $p < 0.05$ ). Conversely, SA4 males are more inclined to challenge the calls of both same-aged and  
 487 adult males (Table 3, Figure 2, Fisher's exact test,  $p > 0.05$ ).  
 488





489

490

491 **Figure 2. Of the males that responded to the playback, proportion of attack, retreat, and undecided responses**  
 492 **of subadult males (SA2, SA3, SA4) exposed to calls from (A) unfamiliar same-age males and (B) unfamiliar**  
 493 **adult males.** Each column includes the percent of total responses scored from playback trials with 15 individuals.  
 494 Subadult males were more likely to attack unknown callers of the same or similar age, suggesting the ability to  
 495 extract some age/size-related information from the calls of rivals.

496

497 In the absence of other cues, subadult males appear able to extract some age/size-related  
 498 information from the vocal signals of unfamiliar individuals and respond differentially to  
 499 playback treatments based on the relative age of callers.

500

501 ***The emergence of individual vocal signatures***

502

503 Individual stereotypy of male vocal displays increases as individuals get older (Supplementary  
 504 Audio 1-5). The calls of SA1 males were correctly assigned to individuals with an average  
 505 classification rate of 39% (chance classification = 5.2-14.3%). SA2 calls were correctly assigned  
 506 to the correct individual with a classification rate of 48% (chance = 5.3-10.5%), SA3 calls  
 507 exhibited a 54% correct classification rate (chance = 5.4-10.8%), while SA4s and adults produce  
 508 calls that could accurately be assigned to the correct male with an average classification rate of

509 83% (chance = 6.0-12.0%) and 84% (chance = 14.3%), respectively. While the correct  
510 classification rates did not differ between SA1s and SA2s, the accuracy of call classification did  
511 increase significantly for SA3s relative to SA1s (N-1 Chi-squared  $X^2(1) = 28.2$ ,  $p < 0.05$ ), and for  
512 SA4-Adults relative to SA3s (N-1 Chi-squared  $X^2(1) = 40.8, 41.39$ ,  $p < 0.0001$  for both  
513 comparisons). Thus, the reliability of individual vocal signatures increases from 4 to 6 years old  
514 and begins to stabilize once males reach 7 years of age (Figure 1), just prior to achieving physical  
515 maturity.

516

## 517 **Discussion**

518 The emergence of dominance hierarchies within the system of extreme intra-sexual competition  
519 scrutinized here is facilitated by individuals transitioning from high variability towards increased  
520 stability with respect to behavioural development. Across several primary measures of behaviour  
521 (space utilization, social relationships, and vocalizations), the period around 6-7 years of age  
522 appears to be a pivotal time for social ontogeny of male northern elephant seals. Younger males  
523 occupy larger areas within the breeding colony for less time and thus maintain fewer stable social  
524 relationships. This is likely due to their smaller size and lower energetic reserves which prevent  
525 them from remaining on the colony for extended periods (24). During this abbreviated time  
526 ashore, young male (4-5 years old) have the opportunity to gather information about individual  
527 competitors while also avoiding conflicts with older, larger and more aggressive males. As males  
528 mature, individuals shift towards smaller home-ranges that they occupy for longer periods during  
529 the breeding season. This reduction of fine-scale movement patterns creates a more stable social  
530 environment in which repeated interactions between competitive rivals occurs, and the  
531 simultaneous onset of a reliable vocal individual signature facilitates the stability of male  
532 hierarchical relationships.

533

534 Few studies have examined the role of ontogeny in dominance hierarchies because social  
535 development is difficult to monitor among long-lived, gregarious mammals. Most information  
536 comes from the extremes of the social spectrum: either small aggregations of adults interacting  
537 over short time periods in experimental settings (7) or complex social groups (*e.g.*, primate  
538 societies, hyena clans) where social cohesion is stabilized by the combination of aggressive  
539 interactions and affiliative social bonds (30, 31). Moreover, little is known about the  
540 developmental mechanisms that promote and sustain dominance hierarchies in the absence of  
541 affiliative relationships. Our work demonstrates that in the case of dominance hierarchies  
542 maintained by agonistic exchanges, individuals preferentially interact with same-aged  
543 conspecifics throughout social development during annual breeding seasons, splitting hierarchies  
544 into age-specific groups. Young males have fewer social partners with whom they are less  
545 familiar, and generally avoid interacting with older individuals that are likely to defeat or injure  
546 them. These young males return to the colony prior to peak breeding activity, during which time  
547 they participate in social exchanges that include mock fighting, chasing, and exchange of calls  
548 with other young individuals. While it is tempting to interpret the behaviour of juveniles as a less-  
549 developed form of the adult repertoire, young animals must solve a suite of social problems that  
550 are very different than those experienced by older animals, including avoiding harm on a breeding  
551 rookery dominated by large adult males.

552

553 Once male elephant seals reach 6-7 years old, they remain in stable locations within the colony  
554 during the breeding season and interact within a structured dominance hierarchy with dozens of  
555 familiar same-aged and adult male seals all jockeying for a prime position relative to females.  
556 Older animals interact with up to 50 competitors within this network and have greater familiarity  
557 with these individuals in comparison to younger animals. Given that only a few males ever attain  
558 female-controlling positions, why do most subordinate SA4 and adult males exhibit fine-scale site

559 fidelity as opposed to shifting their positions to explore different harems around the colony? In  
560 this competitive and high-risk social system, a male's breeding opportunities may depend on  
561 managing knowledge of his relative dominance status compared to others within the hierarchy. In  
562 other species, social knowledge and early connectivity have been shown to predict male success  
563 (4). Although the majority of non-alpha elephant seals rarely mate with females (11), these males  
564 may be "climbing the social ladder" and gaining important information about their contemporary  
565 and future rivals. While this hypothesis has not yet been explicitly explored, studies of red deer  
566 (2) and meerkats (32) have demonstrated clear fitness benefits to individuals exhibiting greater  
567 sociality (defined by the number and types of social bonds) early in life. Long-term studies  
568 tracking the social encounters of individual seals as they progress through developmental stages  
569 would elucidate whether early social patterns and relationships influence later reproductive  
570 success in this species.

571

572 The stable social network of adult competitors is maintained by the use of ritualized and  
573 individually distinct acoustic displays that males learn to recognize throughout the breeding  
574 season (21). Young males appear to have a plastic calling phase, characterized by the production  
575 of various element types used in different combinations. While young male seals lack strong  
576 individual vocal signatures, certain spectral characteristics of the call do appear to change with  
577 age. Given the relationship between vocal tract length and body size in mammals (33), the  
578 spectral content of vocalizations has the potential to provide honest information about the  
579 phenotype of callers (34). The results of our playback experiments demonstrate that young males  
580 can extract such age-related acoustic cues during rival assessment and respond differentially  
581 based on the perceived size of unfamiliar rivals. As young individuals incur a high cost for  
582 misidentifying older and larger competitors, these males that do not exhibit pronounced individual

583 vocal signatures or stable social relationships must rely on size-related information obtained from  
584 vocalizations during rival assessment.

585

586 To facilitate individual recognition among older and socially mature contenders, the vocal display  
587 of males become ritualized, repeatable, and acoustically differentiated once they reach age seven.

588 Timing of call stabilization coincides with a restriction in space-use patterns and increase in

589 tenure, and thus the stabilization of social relationships between dozens of individuals. Small

590 differences in call structure enable older males to associate the outcomes of social interactions

591 with reliable acoustic properties, which they learn to recognize throughout the breeding season

592 (21). The ability to accurately identify and respond to familiar rivals appears to confer great

593 energy savings during periods of extreme and extended fasting in this species. Given the strong

594 association between males within and across seasons due to fidelity to specific breeding sites,

595 multi-year recognition of rivals warrants further investigation in this species.

596

## 597 **Conclusions**

598

599 Growing up in conditions of extreme competition, male northern elephant seals transition from

600 high variability to increased specificity with respect to space utilization, social relationships and

601 vocal behaviour. These changes confer long-term benefits by enabling individuals to learn about

602 their physical and social environments prior to attempting to reproduce within this high-risk,

603 high-stakes system of extreme intrasexual competition. The present research enriches our

604 perspective of the important role that behavioural ontogeny plays in males that compete fiercely

605 for reproductive opportunities, and more specifically, clarifies the developmental process by

606 which individuals provide and acquire information within a social environment that is supported

607 by individual recognition of one's competitors. Overall, our findings advance the understanding  
608 of social systems where individuals exclusively exhibit agonistic exchanges.

609

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611

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625

## 626 **Data availability**

627

628 All data—including digital sound files—are archived at the University of California Santa Cruz,  
629 and are available by contacting the corresponding author.

631 **References**

- 632 1. Kolmer K, Heinze J (2000) Rank orders and division of labour among unrelated  
633 cofounding ant queens. *Proc R Soc B Biol Sci* 267(1454):1729–1734.
- 634 2. Freeman LC, Freeman SC, Romney AK (1992) The implications of social structure for  
635 dominance hierarchies in red deer, *Cervus elaphus*. *Anim Behav* 44(1):239–245.
- 636 3. Sapolsky RM (2005) The influence of social hierarchy on primate health. *Science* (80- )  
637 308(5722):648–652.
- 638 4. McDonald DB (2007) Predicting fate from early connectivity in a social network. *Proc Natl*  
639 *Acad Sci* 140(3617):1469–1470.
- 640 5. Croft DP, et al. (2009) Behavioural trait assortment in a social network: Patterns and  
641 implications. *Behav Ecol Sociobiol* 63(10):1495–1503.
- 642 6. Turner JW, Bills PS, Holekamp KE (2018) Ontogenetic change in determinants of social  
643 network position in the spotted hyena. *Behav Ecol Sociobiol* 72(1).
- 644 7. Williamson CM, Lee W, Curley JP (2016) Temporal dynamics of social hierarchy  
645 formation and maintenance in male mice. *Anim Behav* 115:259–272.
- 646 8. Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. *Trends Ecol*  
647 *Evol* 22(10):529–537.
- 648 9. Barnard CJ, Burk T (1979) Dominance hierarchies and the evolution of individual  
649 recognition. *J Theor Biol* 81:65–73.
- 650 10. Sheehan MJ, Tibbetts EA (2009) Evolution of identity signals: frequency-dependent  
651 benefits of distinctive phenotypes used for individual recognition. *Soc Study Evol*  
652 63(12):3106–3113.
- 653 11. Le Boeuf BJ (1974) Male-male competition and reproductive success in elephant seals. *Am*  
654 *Zool* 176:163–176.

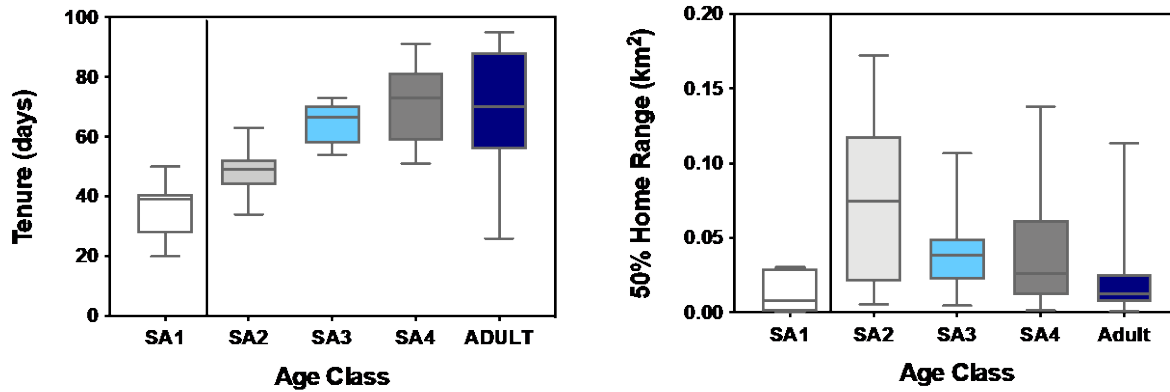
- 655 12. Le Boeuf BJ (1972) Sexual behavior in the northern elephant seal *Mirounga angustirostris*.  
656 *Behaviour* 41.1:1–26.
- 657 13. Deutsch CJ, Haley MP, Leboeuf BJ (1990) Reproductive effort of male northern elephant  
658 seals: estimates from mass loss. *Can J Zool* 68(12):2580–2593.
- 659 14. Shipley C, Strecker G (1986) Day and night patterns of vocal activity of northern elephant  
660 seal bulls. *Am Soc Mammal* 67(4):775–778.
- 661 15. Le Boeuf BJ, Laws RM (1994) *Elephant seals: population ecology, behavior, and*  
662 *physiology* (University of California Press).
- 663 16. Condit R, et al. (2014) Lifetime survival rates and senescence in northern elephant seals.  
664 *Mar Mammal Sci* 30(1):122–138.
- 665 17. Bartholomew GA, Collias NE (1962) The role of vocalization in the social behaviour of the  
666 northern elephant seal. *Anim Behav* 10(1–2):7–14.
- 667 18. Southall BL, Casey C, Holt MM, Insley SJ, Reichmuth CJ (2019) High-amplitude  
668 vocalizations of male northern elephant seals and associated ambient noise on a breeding  
669 rookery. *J Acoust Soc Am* 146(4513).
- 670 19. Insley SJ, Holt MM, Southall BL (2011) Vocal recognition of individuals versus relative  
671 dominance rank among breeding male northern elephant seals (*Mirounga angustirostris*). *J*  
672 *Acoust Soc Am* 129(4):2505.
- 673 20. Shipley C, Hines M, Buchwald JS (1981) Individual differences in threat calls of northern  
674 elephant seal bulls. *Anim Behav* 29(1):12–19.
- 675 21. Casey C, Charrier I, Mathevon N, Reichmuth C (2015) Rival assessment among northern  
676 elephant seals: Evidence of associative learning during male–male contests. *R Soc Open*  
677 *Sci* 2(8):150228.
- 678 22. Mathevon N, Casey C, Reichmuth C, Charrier I (2017) Northern elephant seals memorize  
679 the rhythm and timbre of their rivals' voices. *Curr Biol* 27:1–5.



- 680 23. Shipley C, Hines M, Buchwald JS (1986) Vocalizations of northern elephant seal bulls :  
681 Development of adult call characteristics during puberty. *Am Soc Mammal* 67(3):526–536.
- 682 24. Le Boeuf BJ, Laws RM (1994) *Elephant seals: an introduction to the genus* ed Le Boeuf,  
683 Burney J., Laws RM (University of California Press, Berkeley/Los Angeles).
- 684 25. Clinton WL (1990) Sexual selection and the life history of male northern elephant seals.  
685 Dissertation (University of California, Santa Cruz).
- 686 26. Burt WH (1943) Territoriality and home range concepts as applied to mammals. *Am Soc*  
687 *Mammal* 24(3):346–352.
- 688 27. Csardi G, Nepusz T (2006) The igraph software package for complex network research.  
689 *InterJournal, Complex Syst* 1695(5):1–9.
- 690 28. Charrier I, Harcourt RG (2006) Individual vocal identity in mother and pup australian sea  
691 lions (*Neophoca Cinerea*). *J Mammal* 87(5):929–938.
- 692 29. Holt MM, Southall BL, Insley SJ, Schusterman RJ (2010) Call directionality and its  
693 behavioural significance in male northern elephant seals, *Mirounga angustirostris*. *Anim*  
694 *Behav* 80(3):351–361.
- 695 30. Barale CL, Rubenstein DI, Beehner JC (2015) Juvenile social relationships reflect adult  
696 patterns of behavior in wild geladas. *Am J Primatol* 77(10):1086–1096.
- 697 31. Holekamp KE, Smale L (1993) Ontogeny of dominance in free-living spotted hyaenas:  
698 Juvenile rank relations with other immature individuals. *Anim Behav* 46(3):451–466.
- 699 32. Madden JR, Drewe JA, Pearce GP, Clutton-Brock TH (2011) The social network structure  
700 of a wild meerkat population: 3. Position of individuals within networks. *Behav Ecol*  
701 *Sociobiol* 65(10):1857–1871.
- 702 33. Fitch TW (2006) Production of vocalizations in mammals. *Encycl Lang Linguist*  
703 (1972):115–121.
- 704 34. Reby D, et al. (2005) Red deer stags use formants as assessment cues during intrasexual

agonistic interactions. *Proc R Soc B Biol Sci* 272:941–947.

## Appendices

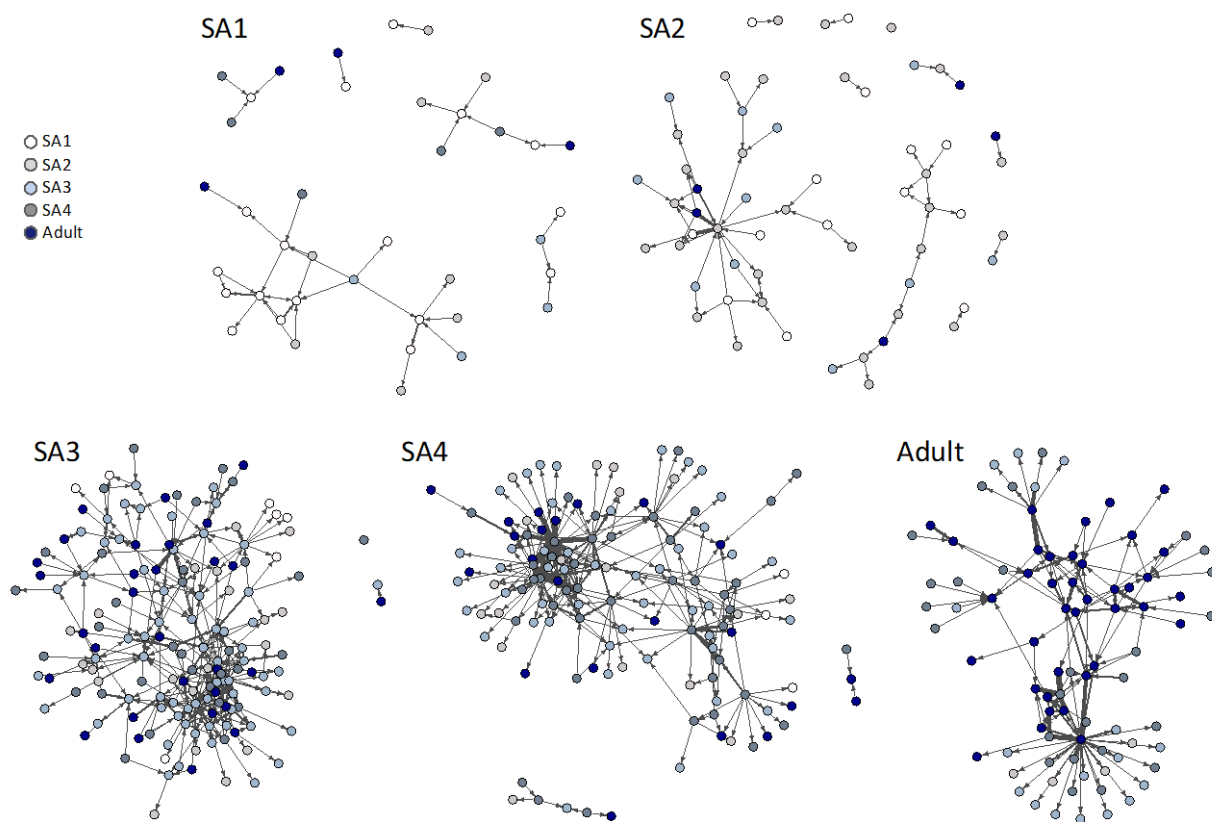


**A1. Male time spent ashore (left panel) and 50% home range size km<sup>2</sup> (right panel) for each age class.** Sample sizes are provided in Tables 1 and 2. Boxes show quartile data while whiskers show total range. Black vertical lines after the SA1 age class indicate the onset of sexual maturity. Male presence on the colony increases with age, while 50% home range declines with maturation. Statistical comparisons are provided in A2.

Age	Age	Time Ashore	95% HR	50% HR
AD	SA1	<.0001*	0.41	0.54
AD	SA2	<.001*	<.0001*	<.0001*
AD	SA3	0.36	<.001*	<.05*
AD	SA4	0.81	<.001*	<.001*
SA4	SA1	<.001*	<.05*	<.05*
SA4	SA2	<.01*	<.001*	<.001*
SA4	SA3	0.24	0.61	0.82
SA3	SA2	<.01*	<.05*	<.001*
SA3	SA1	<.0001*	<.001*	<.05*
SA2	SA1	<.05*	<.0001*	<.0001*

719 **A2. Resulting p-values from Tukey-Kramer HSD post-hoc tests between each age class with respect to male**  
720 **time spent ashore, 95% home range, and 50% home range. Significant values are indicated by \*.**

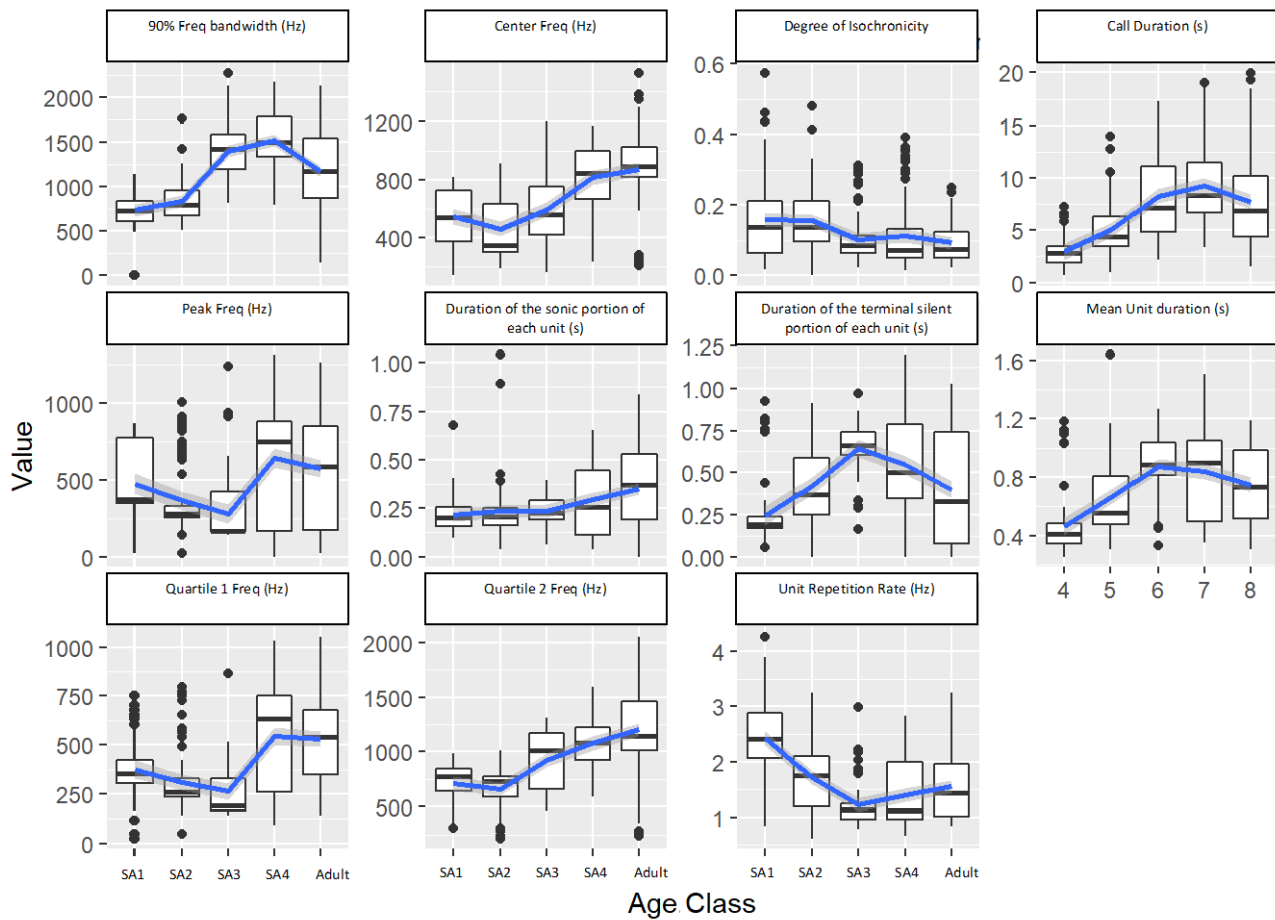
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725 **A3. An enlarged image of panel 4 from Figure 1 illustrating the social network of each age classes from one**  
726 **breeding season. Circles are males and directed lines are dyadic competitive interactions, with the thickness of each**  
727 **line corresponding to the number of interactions observed between two individuals. Age classes are separated by**  
728 **color.**

729



730

731

732 **A5. Acoustic parameters measured for call exemplars from each age class, as provided in**

733 **Table A6.** Boxes show the mean and quartile data while whiskers show total range, with a

734 LOESS smooth applied across age class.

735

## SA1s

	Range	Mean	Std. Dev.
<b>Spectral Parameters</b>			
Quartile 1 frequency (Hz)	273-506	378	87
Center frequency (Hz)	367-661	539	107
Quartile 3 frequency	539-823	700	109
90% frequency bandwidth (Hz)	612-841	720	81
Peak frequency (Hz)	335-691	496	123
<b>Temporal Parameters</b>			
Call duration (s)	1.6-5.7	2.9	1.3
Unit duration (s)	0.33-0.5	0.41	0.06
Duration of sonic portion in each unit (s)	0.15-0.28	0.2	0.04
Duration of silent portion of each unit (s)	0.17-0.27	0.2	0.04
Unit repetition rate (Hz)	2.06-3.18	2.54	0.37
Degree of isocronicity	0.08-0.24	0.41	0.06
<b>Descriptive Characteristics</b>			
Number of elements in each unit	1	1	
Number of different elements in each unit	1-2	1	
Percentage of calls that contain introductory snorts/rumbles	0-30%	6%	5%
Percentage of calls that contain terminal snorts/rumbles	10-80%	53%	52%
Percentage of calls that contain harmonics	10-70%	29%	28%
Fundamental frequency (Hz)	59-86	75	74

## SA2s

	Range	Mean	Std. Dev.
<b>Spectral Parameters</b>			
Quartile 1 frequency (Hz)	183-640	305	130

Center frequency (Hz)	302-841	455	164
Quartile 3 frequency	502-938	654	129
90% frequency bandwidth (Hz)	677-1109	818	140
Peak frequency (Hz)	185-823	367	178

**Temporal Parameters**

Call duration (s)	3.0-8.68	4.9	1.7
Unit duration (s)	0.42-1.12	0.68	0.24
Duration of sonic portion in each unit (s)	0.14-0.35	0.24	0.07
Duration of silent portion of each unit (s)	0.21-0.78	0.44	0.19
Unit repetition rate (Hz)	0.89-2.49	1.67	0.54
Degree of isochronicity	0.05-0.25	0.16	0.05

**Descriptive Characteristics**

Number of elements in each unit	1	1	
Number of different elements in each unit	1-2	1	
Percentage of calls that contain introductory snorts/rumbles	0-30%	3%	10%
Percentage of calls that contain terminal snorts/rumbles	0-100%	57%	46%
Percentage of calls that contain harmonics	0%	0%	<i>n/a</i>
Fundamental frequency (Hz)	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>

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**SA3s**

	<b>Range</b>	<b>Mean</b>	<b>Std. Dev.</b>
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**Spectral Parameters**

Quartile 1 frequency (Hz)	155-347	258	78
Center frequency (Hz)	314-894	586	206
Quartile 3 frequency	476-1274	915	256
90% frequency bandwidth (Hz)	935-1895	1419	265
Peak frequency (Hz)	164-403	276	73

**Temporal Parameters**

Call duration (s)	4.76-12.11	8.04	3.07
Unit duration (s)	0.55-1.14	0.88	0.2

Duration of sonic portion in each unit (s)	0.08-0.34	0.24	0.08
Duration of silent portion of each unit (s)	0.41-0.86	0.65	0.13
Unit repetition rate (Hz)	0.88-1.81	1.22	0.33
Degree of isocronicity	0.06-0.24	0.1	0.05

#### Descriptive Characteristics

Number of elements in each unit	1	1	
Number of different elements in each unit	1	1	
Percentage of calls that contain introductory snorts/rumbles	0-40%	10%	10%
Percentage of calls that contain terminal snorts/rumbles	0-80%	20%	30%
Percentage of calls that contain harmonics	0%	<i>n/a</i>	<i>n/a</i>
Fundamental frequency (Hz)	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>

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#### SA4s

	Range	Mean	Std. Dev.
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#### Spectral Parameters

Quartile 1 frequency (Hz)	117-783	544	247
Center frequency (Hz)	466-1069	819	208
Quartile 3 frequency	766-1292	1089	167
90% frequency bandwidth (Hz)	1024-1781	1544	225
Peak frequency (Hz)	122-921	627	265

#### Temporal Parameters

Call duration (s)	6.44-14.17	9.21	2.27
Unit duration (s)	0.4-1.41	0.86	0.32
Duration of sonic portion in each unit (s)	0.08-0.62	0.3	0.19
Duration of silent portion of each unit (s)	0.16-1.13	0.57	0.29
Unit repetition rate (Hz)	0.71-2.51	1.36	0.58
Degree of isocronicity	0.04-0.31	0.11	0.09

#### Descriptive Characteristics

Number of elements in each unit	1-2	1	
Number of different elements in each unit	1-2	1	

Percentage of calls that contain snorts/rumbles	0-100%	46%	46%
Percentage of calls that contain snorts/rumbles	0-100%	11%	31%
Percentage of calls that contain harmonics	0%	<i>n/a</i>	<i>n/a</i>
Fundamental frequency (Hz)	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>

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**Adults**

	<b>Range</b>	<b>Mean</b>	<b>Std. Dev.</b>
<b>Spectral Parameters</b>			
Quartile 1 frequency (Hz)	192-766	575	167
Center frequency (Hz)	220-1253	924	278
Quartile 3 frequency	328-1971	1332	481
90% frequency bandwidth (Hz)	523-1603	1197	371
Peak frequency (Hz)	211-914	579	238
<b>Temporal Parameters</b>			
Call duration (s)	5.02-13.98	7.68	2.56
Unit duration (s)	0.38-1.06	0.75	0.26
Duration of sonic portion in each unit (s)	0.15-0.28	0.2	0.04
Duration of silent portion of each unit (s)	0.01-0.62	0.35	0.22
Unit repetition rate (Hz)	0.95-2.84	1.55	0.62
Degree of isochronicity	0.04-0.18	0.09	0.04
<b>Descriptive Characteristics</b>			
Number of elements in each unit	1-3	1	
Number of different elements in each unit	1-2	2	
Percentage of calls that contain snorts/rumbles	0-100%	79%	42%
Percentage of calls that contain snorts/rumbles	0-100%	28%	39%
Percentage of calls that contain harmonics	0%	<i>n/a</i>	<i>n/a</i>
Fundamental frequency (Hz)	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>

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740 **A6. Mean, range, and standard deviations of spectral and temporal measurements obtained from males**  
741 **representing each age class.** For discrete parameters, we report the range, mean, and standard deviation of each  
742 variable; for continuous data, we report the mode and range. The sample sizes for each age class are as follows:  
743 SA1s—8 individuals, 75 calls total, SA2s—9 individuals, 94 calls total, SA3s—10 individuals, 10 calls total, SA4s—  
744 10 individuals, 82 calls total, and Adults—10 individuals, 100 calls total.

745

## 746 **Supplementary Material**

747

748 **Supplementary Audio 1.** Three example calls from the same SA1 male A367.

749

750 **Supplementary Audio 2.** Three example calls from the same SA2 male D509.

751

752 **Supplementary Audio 3.** Three example calls from the same SA3 male 8TP.

753

754 **Supplementary Audio 4.** Three example calls from the same SA4 male 3CA.

755

756 **Supplementary Audio 5.** Three example calls from the same Adult male 10A.