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

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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

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

Space utilization and residency patterns

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

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

Location data were used to estimate home range size for each male observed at the colony for 10 or more days during the 2012, 2014, 2016-18 seasons. These data were compiled for 208 individuals (SA1 = 9, SA2 = 27, SA3 = 40, SA4 = 56, AD = 76). The occurrence probability distribution—or home range—for each male was calculated using the kernel density tool in the geospatial modeling environment module of ArcGIS (version 10.6.1) and QGIS (version 3.2.2). A polygon was created with a grid cell size of 1m² to encompass sighting locations within 95% and

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

Assessment of social relationships

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

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).

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

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

Acoustic playback experiments

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

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

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

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

Ethical Note

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

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

Results

Ontogeny of space utilization

Space use and movement patterns of male northern elephant seals change with successive maturational stages (Table 1, A1). As individuals get older, their home ranges within the terrestrial breeding colony decrease in size while their time spent ashore increases (Figure 1, A1, 2). Four-year old subadult males (class SA1) are the first to arrive and depart the breeding colony, coming ashore in late November and departing in early January (days ashore = 37 ± 11), prior to the arrival of most females. Five-year-old subadult males (class SA2) and 6-year-old subadult males (class SA3) arrive nearly a month later and stay ashore much longer ($49 \text{ days} \pm 12$ and $64 \text{ days} \pm 7$, respectively). Seven-year-old males (class SA4) and mature adults (8+ years old) spend the longest time ashore, arriving in mid-December and departing at the end of February ($71 \text{ days} \pm 4$ 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
Re-sights used for home-range analysis				Home range size kernel density estimates (KDE areas, km ²)						
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

Table 1. Male tenure and home range size at the Año Nuevo breeding colony. The upper panel provides a summary of attendance patterns exhibited by male seals (n=10 seals per age class) during the 2018 breeding season, including the number of days spent ashore for each age class (mean and SD, standard deviation). Male tenure increased with age class. The lower panel provides a summary of spatial patterns exhibited by 208 male seals sampled during five annual breeding seasons (n=9-76 seals per age class). Home ranges for each age class are expressed as both 95% and 50% mean kernel density estimate (KDE) areas (km²). With the exception of the youngest age class, male home range decreased with increasing age.

Fine-scale space utilization within the breeding colony also changes with developmental stage. The home ranges of males, measured as kernel density estimates (KDE), vary considerably between age classes (ANOVA: $F(4, 201) = 14.21, p < 0.0001$; 208 seals; Figure 1, Table 1, A1, 2). With the exception of the youngest subadult males (class SA1) who show little movement within the colony (50% KDE = 0.01 km²), home ranges decrease as individuals mature. The SA2 class has the largest home ranges (50% KDE = 0.07 km²), while adults occupy the smallest areas within the colony (50% KDE = 0.02 km²). This pattern of restriction in home ranges throughout development likely has a significant influence on the social associations of males as they mature.

Development of social relationships

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

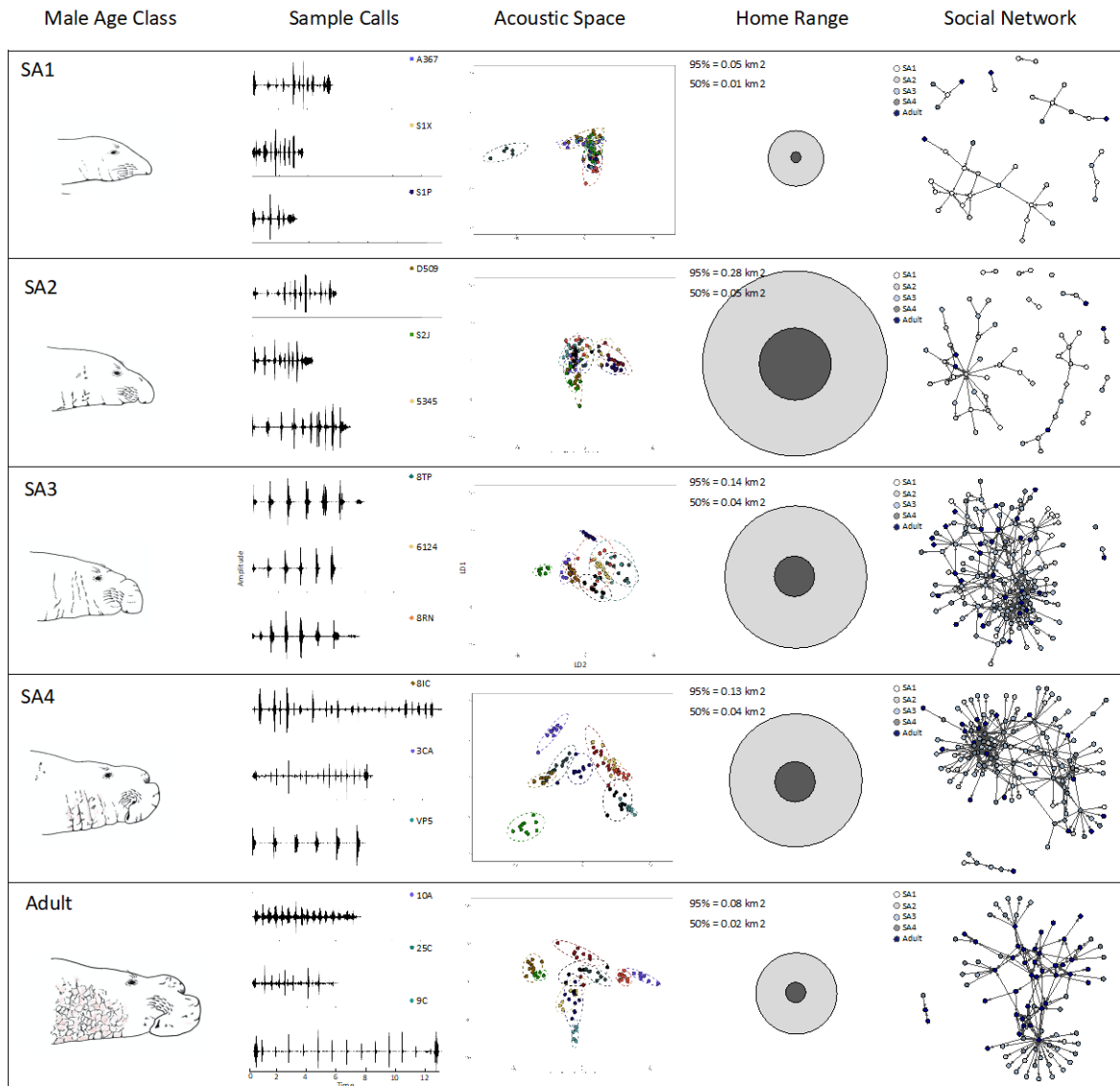


Figure 1. Development of male elephant seals. Several aspects of ontogeny are shown left to right pertaining to age class, call structure, call differentiation, home range, and social network. **Column 1** depicts the secondary sexual characteristics associated with each age class. Males categorized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

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

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

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

Description of vocal behaviour

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

	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 isocronicity
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
	$P > 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.01$	$P < 0.001$	$P = 0.237$	$P = 0.286$	$P = 0.366$	$P < 0.05$	$P = 0.366$

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

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

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

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, $p < 0.05$

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

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

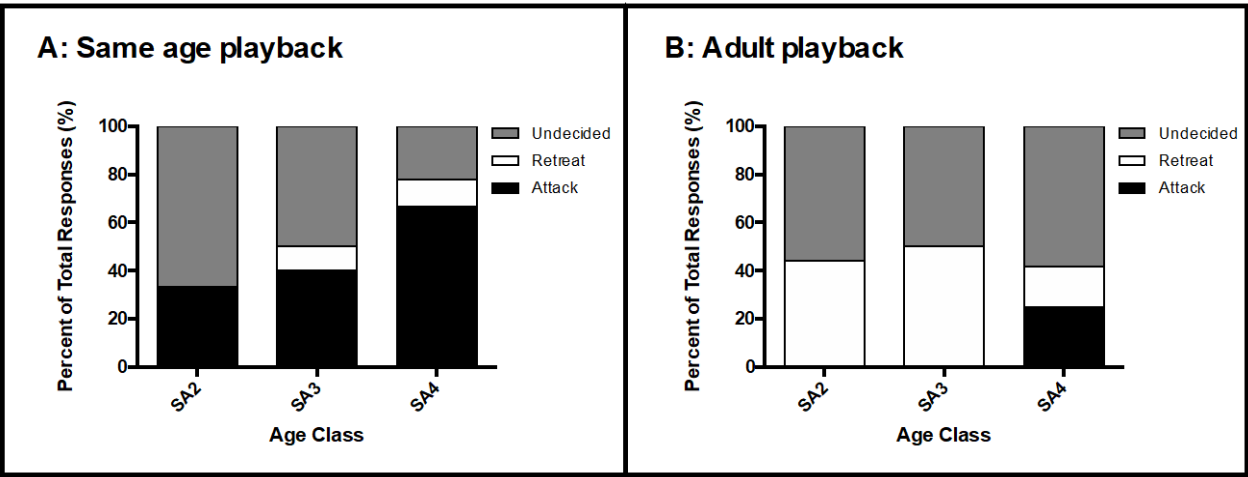


Figure 2. Of the males that responded to the playback, proportion of attack, retreat, and undecided responses of subadult males (SA2, SA3, SA4) exposed to calls from (A) unfamiliar same-age males and (B) unfamiliar adult males. Each column includes the percent of total responses scored from playback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

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

The emergence of individual vocal signatures

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

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

Discussion

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

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.

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611
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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.

630

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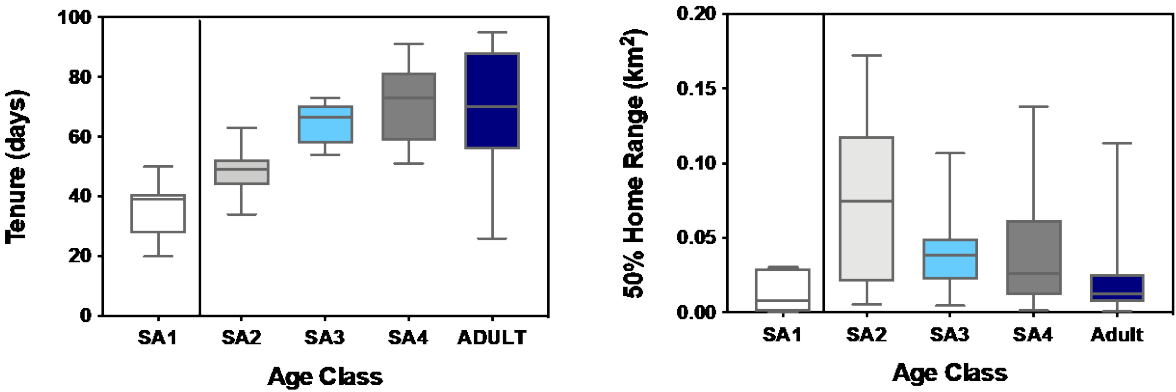
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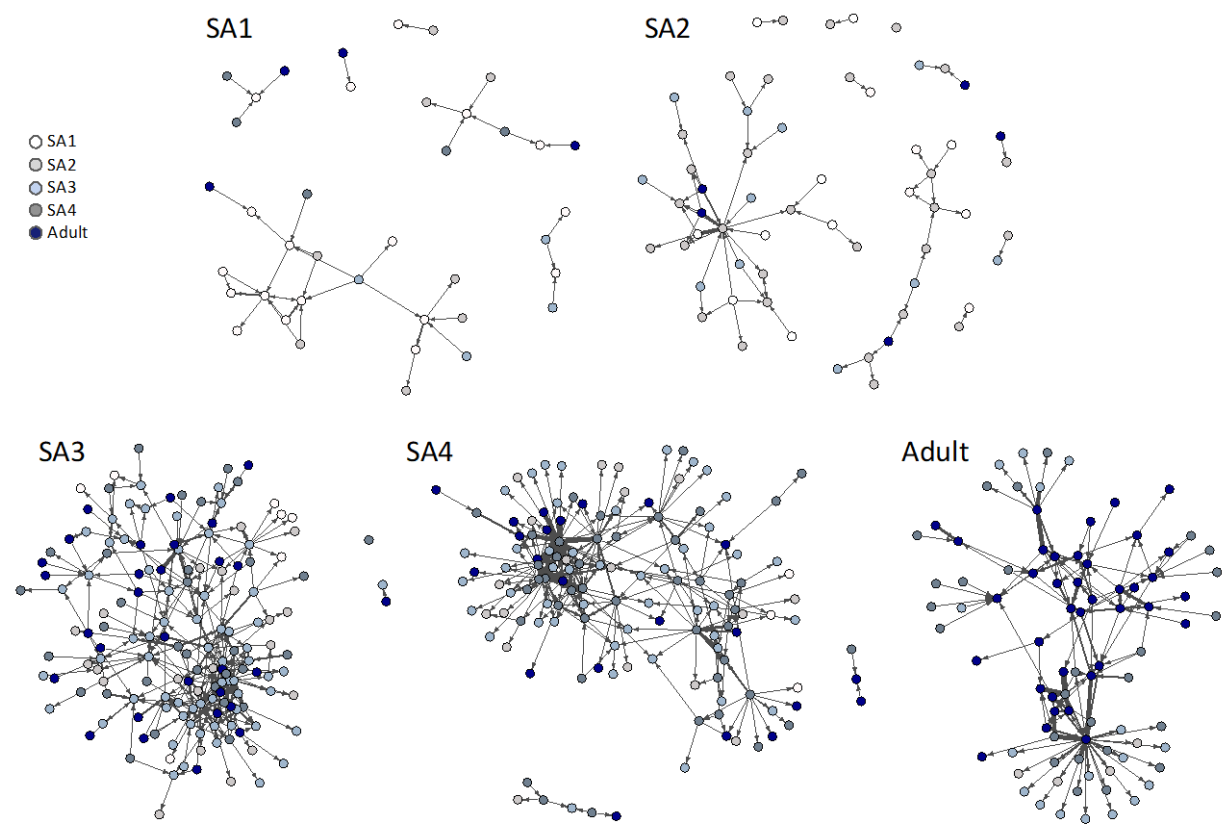
Appendices



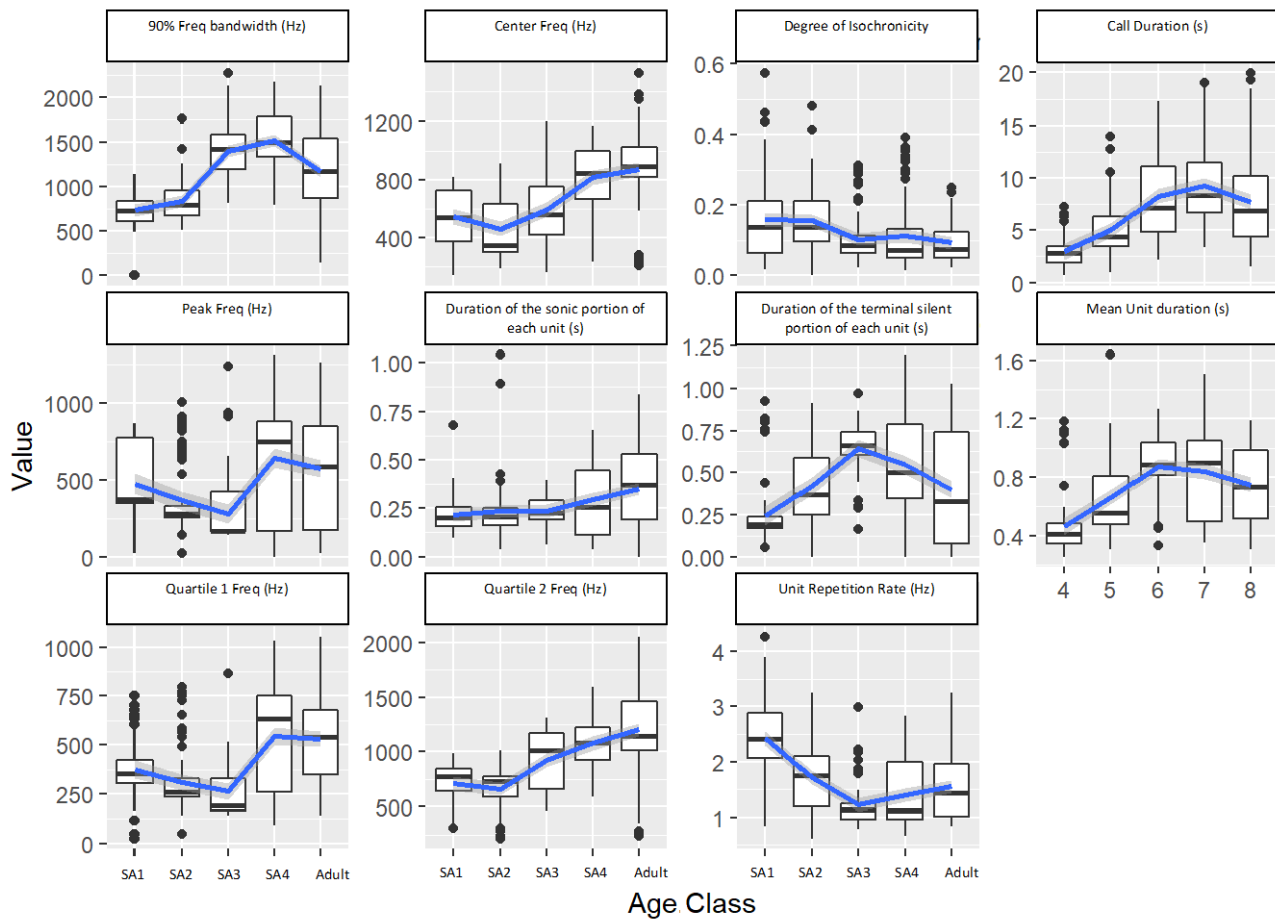
A1. Male time spent ashore (left panel) and 50% home range size km² (right panel) for each age class. Sample sizes are provided in Tables 1 and 2. Boxes show quartile data while whiskers show total range. Black vertical lines after the SA1 age class indicate the onset of sexual maturity. Male presence 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*

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



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



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

Table A6. Boxes show the mean and quartile data while whiskers show total range, with a LOESS smooth applied across age class.

736

737

SA1s			
	Range	Mean	Std. Dev.
Spectral Parameters			
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
Temporal Parameters			
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
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%	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.
Spectral Parameters			
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 isocronicity	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>

SA3s

	Range	Mean	Std. Dev.
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>
<hr/>			
SA4s			
	Range	Mean	Std. Dev.
<hr/>			
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>

Adults

	Range	Mean	Std. Dev.
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Spectral Parameters

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

Temporal Parameters

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 isocronicity	0.04-0.18	0.09	0.04

Descriptive Characteristics

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

Supplementary Material

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

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

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

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

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