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First observations on colony structure, behavior, and vocal repertoire of the South American Fur Seal (Arctocephalus australis Zimmermann, 1783) in Peru

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Abstract

Studied were habitat, behavior and vocalization of *Arctocephalus australis* based on a short visit to Punta San Juan, Peru. The reproductive season reaches its peak in November/December. Thermore-gulatory movements had a pronounced effect on colony structure. Density varied between 0.5 and 1.5 animals/m². Territory size averaged about 50 m². It appears to be the rule that females nurse yearlings, leading in some cases to competition between yearling and its newborn sibling. Sonagrams show the vocalizations of this species to be similar o those of other *Arctocephalus* species, except *A. pusillus*. This corroborates the previously suggested intermediate position of *A. pusillus* between fur seals and sea lions.

Introduction

The South American Fur Seal is the least known of all *Arctocephalus* fur seals. As it is presumably the most primitive *Arctocephalus* species (REPENNING et al. 1971) its behavior and vocalizations are of considerable interest for the interpretation of the behavior of other species. We concentrated on the collection of basic data on colony structure and behavior of males, females and young, as well as on tape-recording their major calls when we obtained a permit to visit the largest colony of this species in Peru. Although our visit was very short and consequently our results are preliminary we feel it worth communicating them as so very little has been published on this species previously (VAZ-FERREIRA 1956; VAZ-FERREIRA and PALERM 1961; PIAZZA 1969; STIRLING and WARNEKE 1971).

Methods

We made a short stop in the evening of the 28th Nov. in Paracas, Punta Arquillo (13°55'S, 76°21'W), and stayed for the 30th Nov., 1st and the morning of the 2nd Dec. in Punta San Juan (15°22'S, 75°11.5'W). Total observation time at Punta San Juan was 34 hours; all observations described were made there unless otherwise stated. Photographs of parts of the colony were used to estimate animal density. Calls were recorded using an UHER 4200 portable tape recorder and a directional microphone (Sennheiser MKH 415 T) and sonagraphed on a Kay Electrics Sonagraph using the wideband filter setting.

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Habitat

Fur seals inhabit points and islands difficult of access on the Peruvian coast. Punta San Juan is a protected guano bird colony situated on a peninsula cut off from the hinterland by a concrete wall. Even so, poachers sometimes attempt to get in and kill seals. Just outside the area protected by the wall not a single fur seal female can be seen, although the habitat appears identical inside and outside the guarded area. In Paracas and Punta San Juan fur seals inhabit rocky and often quite steep slopes (Fig. 1). Many of the bays are exposed to heavy surf. The slopes are quite rugged and vertically structured so that for most of the day some places provide shade. At our main observation site the habitat consisted of almost level rock surface and the shingle beach. At low tide the rock shelf provided tidepools (Fig. 1, below; Fig. 2). Nearby, many fur seals lived in a huge cave where they had to climb about 15 m up and down; they found plenty of shade even during the noon hours.



Fig. 1. Habitat of fur seals at Punta San Juan. Above: Steep, highly vertically structured habitat providing many shaded sites. Below: Level rock with many tidepools and the adjacent pebble beach



Fig. 2. Thermoregulatory movements of fur seals. Above: Distribution of fur seals at 8:00 a.m. Below: Distribution over the same area at 12:00. Note that density is much higher at noon when the animals are forced into the intertidal zone

Reproductive season

During our stay at Punta San Juan we saw hundreds of young pups. Comparing their developmental stage with known-age Galápagos fur seal pups (*A. galapagoensis*) (TRILLMICH unpubl.), we think hardly any were older than one month. We also witnessed a few births. The warden, MARCIAL ROJO, told us that fur seals breed there between October and January, with the great majority of births occurring in November and December (see PIAZZA 1969). The breeding peak of the South American Sea Lion (*Otaria byronia*) is, according to M. ROJO around June. Because of this difference in peak breeding time between the two species, competition for space may never become serious even where the two species are closely sympatric.

Density and thermoregulatory movements within the breeding colony

Density tends to be the same all year with perhaps minimum numbers ashore prior to the breeding season (M. ROJO, pers. comm.). As census methods are not standardized, considerable variation may go undetected. From photos (similar to Fig. 2) total density was estimated to be between 0.5 and 1.5 animals/m². In these measures we excluded the parts of the beach deserted by animals at the time of measurement.

On a rocky islet at Paracas pup density was about 0.1 pups/m²; in Punta San Juan, in the afternoon at high tide, it was about 0.2 pups/m². Males tend to maintain ample nearestneighbor distances; even in bachelor groups density never exceeded 0.4 males/m². Density of females is higher but depends on time of day, temperature, and tide level. It varies between 0.6 and 1.0 females/m².



Fig. 3. Changes in numbers of adults and pups counted on an inland area and an area near the water's edge (both of approximately equal size) at hourly intervals during the morning. The drop in numbers of pups at 12:00 near the water is an artifact due to the disappearance of some behind rocks and in smal canals where they could not be seen. The drop in numbers of adults near the water after 10:00 occurs because many are leaving the colony

In the evenings the animals spread out over the available habitat. A few males without territories rested far inland. The whole area used by females was claimed as territories during the night. During the hot hours of the day animals concentrated near tidepools or on the edge of the sea (Fig. 2, 3). Through this thermoregulatory behavior density within groups increased considerably from about 0.5–0.7 animals/m² in the mornings and evenings, to 1.3 or 1.5 animals/m² at noon when the fur seals rested near the water. Many adults and immatures left the colony during the day and returned in the evening. Numbers ashore were highest during the nights.

In thermoregulatory movements females sometimes cross many territorial boundaries. This thermoregulatory migration is most pronounced in females with recently-born pups. Lone pups also move to the tideline to spend the heat of the day and, towards dusk, begin

F. Trillmich and Patricia Majluf

to disperse and move inland again. Other animals are able to prolong their stay inland, away from the densest groupings near water, by making a quick trip to the water, and moving inland again.

Females and young

We observed one birth sufficiently closely to time the sequence of events. When we first saw the female come in from the water, she already showed signs of labor. 20 min later the pup was born, head first; 18 min after birth it began to search for the teats; the afterbirth was expelled 62 min after the birth of the pup. The female remained near her newborn all day. Presumably females stay with their pups for several days after birth, as in the other *Arctocephalus* species.



Fig. 4. Female nursing a yearling

Incoming females and their pups home in on each other through loud calls (see below for description and sonagrams of calls) and the identity of the pup is finally determined through an olfactory check, which seems to be the decisive one, as pups are sometimes rebuffed thereafter. Many females with older pups were observed to nurse their pups during the day, but many more were ashore during the night.

In the evenings and early mornings many females nursed yearlings (Fig. 4). In at least two cases body size and development of the canine teeth of the young suggested that females were nursing two-year-olds. From the abundance of females with immatures it appears that in *A. australis* – as in *A. galapagoensis* (TRILLMICH 1979) – young are nursed until they are at least one year old. In the early morning females with immatures were found farther inland than most females with pups. There was much less territorial activity of males in these groups. As may be expected with so long a nursing period, several females with pups were each accompanied by an immature as well. In a group of 41 pups in Paracas, three were in the company of immatures (7.3 %). Similarly, in Punta San Juan, of 39 pups with mothers, three (7.7 %) were accompanied by immatures sharing the milk.

The South American Fur Seal in Peru

Further cases were recorded outside this sample group. The sex of five such immatures could be determined (according to presence or absence of the penile opening): two were female, three male. One such female immature was clearly older than one year. These immature and newborn companions must be siblings, because in all otariid seals investigated, mothers nurse exclusively their own offspring (BARTHOLOMEW 1959; BONNER 1968; MCNAB and CRAWLEY 1975; PETERSON and BARTHOLOMEW 1967; RAND 1967; SANDEGREN 1970).

In the observed cases pup and immature competed for the mother's milk. When they sucked simultaneously, which occurred only rarely, the immature sucked from the posterior and the pup from the anterior teats. Females defended the pup against attacks by its older sibling. Often the pup was merely manoeuvered behind the mother's back or in front of her head, while the yearling continued sucking. Immatures of both sexes were observed biting their younger siblings; one of the pups had a cut on its flipper which may have been caused by such an attack. One newborn pup never sucked during six hours of continuous observation, while its one-year old sibling (a male) was sucking almost continuously. The physical condition of seven pups who were together with their mothers and immatures was rated: 3 were healthy, 3 undernourished, and one was undernourished and injured. Very likely some of these pups will have died of starvation and/or infection, as observed in Galapagos fur seals (TRILLMICH 1979 and unpubl. data). If so, the percentage given above of 7-8 % of pups whose mother was still accompanied by a yearling must be a minimum estimate of the occurrence of this situation. General pup mortality was estimated by counting dead pups from the edge of the colony. The number of corpses amounted to about 10 % of the pups seen alive in the same areas. This is a minimum estimate of mortality as the corpses of pups disappear rapidly.

Male-female interactions, copulation

Quite frequently males attempt to herd females which cross their territories; but they almost never succeed if the females are moving for thermoregulation. Often the herding attempt of a bull precipitates its neighbor's boundary display and in the ensuing agitation the female slips into the next territory or out to sea. Females in estrus reacted differently, snapping at the bull. If a female showed this behavior the bull tried to mount. We observed three copulations of one territorial male which lasted 9.75, 10.75 and 11.5 min. One was recorded in detail. Intromission was achieved 3 min after mounting. After intromission the male made pelvic thrusts for about 6 min with a frequency of 54 thrusts/min. He then increased his thrusting frequency to about 160 thrusts/min. This lasted for 4.5 min after which the male dismounted. In all three copulations the females began to struggle shortly before the male dismounted. After copulations the females stayed for a while in the male's territory but were not particularly guarded.

The behavior of males

Territorial males

On an area of about 400 m² in Paracas we counted 9 territorial males (average territory size 44 m²). Similarly, in Punta San Juan, we observed 11 territorial males with an average territory size of 54.5 m². After two days of observation in the latter site it was clear that territory size varied considerably from about 25–30 m² to 100 m². The landward boundaries of inland territories were rather indistinct.

Territories varied not only in size but also in permanence of occupation. Two factors were obviously most important for the attendance of a male: 1. Thermoregulatory needs,

F. Trillmich and Patricia Majluf

and 2. Presence or absence of females on a territory. The importance of these factors varied for the three categories of males described in the following:

Landlocked males

About one third of the territorial males had no access to the water during low tide, and the majority of them not even during high tide. They were unable to endure the heat of the day on their dry territories. If the last female had left their area the males held out until increasing temperature forced them to depart (between 10:30 and 11:30) and did not return until the afternoon. They appeared to spend the noon hours resting in the water close to the coast. They returned to their territories between 14:30 and 15:30, shortly before at least part of their area became shaded and before the first female had moved there. The landlocked males resettled in their sites without serious fights with their neighbors, who may have recognized them by their full threat calls (see below, Fig. 6). Nevertheless, the course of the reoccupation of these territories looked like a quick-motion version of territory establishment by a newcomer. The bull could hardly move at first as any move induced a full threat call or a boundary display by one of his neighbors. Within about half an hour, however, he was again able to move normally within his territory, which by this time he had enlarged considerably around his initial center position. One inland male occupying a cave at the foot of a cliff remained on this territory over the noon hours.

"Water" males

"Water" males, whose territories were fully submerged at high tide. Another class of males became territorial only around low tide. These "water" males established themselves during daytime before low tide in areas still fully awash; they maintained territories there, which gradually filled with females escaping the heat, until about an hour after the incoming tide had pushed all females off inland again. Perhaps these bulls foraged at night, as they all looked very well fed. They appeared to be waiting mainly for a chance to take over a territory along the line between intertidal and dry land.

Males with coastal territories

Males in an intermediate position had access to water (canals or tidepools) even at low tide during the day when females congregate just there. They also had a firm land base where females gathered at high tide during the day and remained during the night as well. Consequently they had at all times a high female density on their territories, giving them the best preconditions for high reproductive success. They remained permanently on their territories. It was one of these bulls we observed copulating three times. These bulls appeared to be involved in most male-male aggressive interactions with neighboring bulls and trespassing males.

Bachelor males

The majority of non-territorial males gathered in "bachelor" groups on beaches not used by females. These groups consisted of a few subadult and many adult bulls. Many of the adult bulls had obviously been territorial earlier or had fought for a territory unsuccessfully, as they were emaciated and showed great injuries. A lot of full threat calling went on in these groups, and some males defended a small area around themselves or perhaps rather reinforced individual distances. Incoming males often had to run the gauntlet to find a resting place. When withdrawing from an attacking male they uttered submissive calls with wide-open mouth and vibrissae either turned forward or flicking back and forth rapidly. Serious fights never developed.

Calls

We obtained slightly over an hour of tape recordings of fur seal calls. To describe these we use the nomenclature of STIRLING and WARNEKE (1971).

Calls of females and young

The Pup Attraction Call (PAC) of the female varies a lot between individuals (Fig. 5 D–F). PACs are rather constant intraindividually, not in their duration but in frequency distribution. Some females produce almost horizontal frequency bands with different spacing between the bands in different individuals (Fig. 5 E), others give highly frequency modulated calls (Fig. 5 F), and still others produce pulsed notes and only later in the call continuous frequency bands (Fig. 5 D). The last PAC-type reminds one of the full threat call of males (compare Fig. 6, 3rd from top). Frequency is lowest at the beginning of the PACs and the calls almost always end with a rapid drop in pitch. These calls are very similar to the calls of *A. gazella* and *A. forsteri* shown in Fig. 1 of STIRLING and WARNEKE (1971). They show about the same variability as in *A. galapagoensis* (TRILLMICH, in press.).



Fig. 5. a: Immature fur seal calling in search of its mother. b: Pup calling to its approaching mother; c: another pup; this is an example of the highly frequency modulated version of the mother-attraction call. The lowest continuous frequency band in this sonagram is from the call of a female; D: Pupattraction call (PAC) of a female. This call has a strongly pulsed beginning similar to the calls of some males; E: Longdrawn-out PAC of another female; F: Highly frequency modulated PAC of a third female



Fig. 6. Full threat calls of 4 different fur seal bulls

The calls of immatures and pups, uttered either when searching for their mothers or responding to their mother's calling from a distance, are very similar to the PACs but have a higher lowest frequency (Fig. 5, a-c). Lowest frequency is about 1.5–2.0 kHz in pups and about 1.0 kHz in yearlings, whereas it is about 500 to 800 Hz in females' PACs. Variation in all these calls seems sufficient to make individual recognition possible.

Calls of males

Fig. 6 shows four examples of full threat calls of males. Again interindividual variability is very pronounced so that individual recognition by these calls seems likely. Most of these calls were heard and tape-recorded in a bachelor group of males, making doubtful STIRLING and WARNEKE'S (1971) interpretation of this call as serving "to advertise territorial status". The full threat call is variable in length. It consists of two easily distinguished parts, a pulsed or growl-like beginning and a clear, higher frequency ending (Fig. 6). Either part can be, and often is, produced alone. The first part is varied to resemble either a growl or what STIRLING and WARNEKE (1971) describe as a low intensity threat (Fig. 7 A). The growl perhaps is more threatening, and was often used in the bachelor group when another male approached a resting bull to within about a body length. Low threat call and growl appear to be grades of essentially the same signal, the exact meaning of which is expressed through the accompanying facial expression (MILLER 1975). The growl can be given alone or with repeated puffs (strong exhalations). We are not sure if the latter combination is what STIRLING and WARNEKE (1971) described as bark. We never heard anything remotely resembling the barking of a sea lion (Zalophus californianus) or a South African fur seal (A. pusillus).

Bulls retreating from an opponent's attack often produced a high-pitched scream-like call (Fig. 7, B and C) also described by VAZ-FERREIRA (1956). This is very similar to the submissive call of *A. forsteri* (STIRLING 1971) and *A. galapagoensis* (TRILLMICH unpubl.).



Fig. 7. Male calls. A: growling; B and C: submissive calls of two different males

F. Trillmich and Patricia Majluf

Discussion

The tropical conditions under which the Peruvian fur seals live are ameliorated by their choice of coastal areas where upwelling is strong and water and air temperatures, as a consequence, are comparatively low (ZUTA et al. 1978). The reproductive season does not, however, coincide with the period of lowest sea temperatures from August to October. Thermoregulatory problems clearly constrain the options of the animals because the habitat can be used in its entire area only at night and during the cool morning and evening hours. While e.g. *A. forsteri* forms territories five or six rows deep (GENTRY 1975), *A. australis* in our colony formed only three or four and even that only in the morning and evening. Further, thermoregulatory needs cause massive female movements in *A. australis* colonies (Fig. 2 and 3; VAZ-FERREIRA and PALERM 1961), leading to repeated shifting of the focus of activity even within the best territories every day.

The young of *A. australis* depend on their mothers for an unusually long period. Nursing of yearlings appears to be the rule rather than the exception. This is not found in any of the other medium-sized *Arctocephalus* species, which usually wean their young before the next pup is born. One reason for this long period of mother-young contact may be that the Peruvian and Uruguayan (VAZ-FERREIRA 1956) populations of this species are largely non-migratory. All three other otariid species with unusually long periods of mother-young contact (*A. pusillus*, RAND 1967; *A. galapagoensis* and *Zalophus californianus wollebaeki*, TRILLMICH 1979) are also largely non-migratory. It seems, however, unique in the Peruvian and Galápagos fur seals that the long-term bond between mother and young decreases the survival chances of a subsequently born young. The importance of this effect remains to be investigated in *A. australis*, but is considerable in *A. galapagoensis* (TRILLMICH 1979, and unpubl.).

The fact that *A. australis* and *A. galapagoensis* have almost identical vocalizations confirms their close relationship, suggested on the basis of skull morphology (KING 1954; REPENNING et al. 1971). STIRLING and WARNEKE (1971) tentatively reported that *A. australis* had a smaller vocal repertoire than most other *Arctocephalus* species. Our data show that this is not the case, and thus that all *Arctocephalus* species except *A. pusillus* have the same types of signals. This leaves *A. pusillus* as the only species of this group with a vocal repertoire similar to the sea lion.

The Otariidae were divided into Arctocephalinae (fur seals) and Otariinae (sea lions) solely on the basis of presence or absence of underfur. Using this criterion, *A. pusillus* was placed with the Arctocephalinae. However, the accumulated evidence of differences in skull morphology (REPENNING et al. 1971), behavior, and vocal repertoire (see review in STIRLING and WARNEKE 1971), besides his enormous size, make it most likely that *A. pusillus* occupies a systematic position intermediate between fur seals and sea lions.

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Zusammenfassung

Erste Beobachtungen über Koloniestruktur, Verhalten und Lautrepertoire des Südamerikanischen Seebären (Arctocephalus australis Zimmermann, 1783) in Peru

Auf Grund von Beobachtungen bei einem kurzen Besuch in der größten Kolonie des Südamerikanischen Seebären (Arctocephalus australis) in Peru werden Koloniestruktur und Verhalten dieser wenig bekannten Art beschrieben. Die Tiere leben meist an Steilküsten mit ausgeprägter Strukturierung. Die Fortpflanzungszeit dauert von Oktober bis Januar; das Maximum der Geburten liegt im November/ Dezember, der Zeit unseres Besuches. Die Dichte in der Kolonie liegt zwischen 0,5 und 1,5 Tiere/m². Alle Tiere müssen täglich aus thermoregulatorischen Gründen ans Wasser wandern.

Weibchen säugen häufig einjährige Jungtiere. Das führt in einigen Fällen zu ernster Konkurrenz um die Milch der Mutter zwischen älteren und jüngeren Geschwistern.

Territorien messen im Mittel etwa 50 m². Die besten Territorien liegen an der Gezeitengrenze; nur in solchen Territorien halten sich Weibchen ganztägig auf. Männchen, deren Territorien keinen Zugang zum Wasser bieten, müssen sich über Mittag im Meer aufhalten.

Die Rufe von Weibchen, Jungtieren und Männchen werden an Hand von Sonagrammen beschrieben. Das Lautinventar von A. australis gleicht dem von A. galapagoensis weitgehend und entspricht dem aller mittelgroßen Arctocephalus-Arten. Dies macht die systematische Zuordnung von A. pusillus zu den Arctocephalinae weiter fragwürdig.

Resumen

De una visita a Punta San Juan, Perú, se da una descripción de la estructura de las colonias y del comportamiento del lobo Fino o de Dos Pelos de Sudamerica. La temporada de reproducción se halla en auge entre Noviembre y Diciembre. La densidad de la colonia está entre 0.5 y 1.5 animales por m². Hay un movimiento termoregulatorio muy pronunciado, el que se manifiesta todos los dias y afecta a todos los integrantes de la colonia.

Las hembras frecuentemente se las halla amamantando inmaduros de un año, lo que en algunos casos lleva a competencias serias por la leche materna entre éstos y los recién nacidos. El tamaño del territorio es de aproximadamente 50 m². Los territorios que poseen el mayor

número promedio de hembras a lo largo de todo el dia, se hallaron localizados a lo largo de la linea de marea alta. Algunos machos cuyos territorios se hallan aislados de la orilla, deben de abandonarlos durante las horas del mediodía en que el calor se les hace insoportable.

Se da una descripción asi como los sonogramas de las llamadas de hembras, juveniles y machos. El repertorio de vocalizaciones de A. australis se halló casi idéntico al de A. galapagoensis y de igual magnitud que el de otros lobos de dos pelos de mediano tamaño, lo que contribuye aun más a dudar de la clasificación de A. pusillus dentro de los Arctocephalinae.

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Development of the preputial gland of immature Fallow deer (Dama dama Linnaeus) with particular reference to puberty

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Abstract

Investigated the morphological changes in the preputial gland of immature Fallow deer in relation to puberty. The odour, and morphological and histological appearance of the prepuce of 66 immature deer, from birth to two years of age, were recorded. Pedicle and antler development were recorded also. The prepuce can be divided into three regions, namely an outer region, a transition zone and the penis sheath proper. Hypertrophy of the epidermis of the transition zone, together with some keratosis, is seen first when the animals are approximately 9-12 months old, the age at which pedicle development and the early stages of antler growth occur. During the period of rapid antler growth, at 12-14 months of age, epidermal hypertrophy is still apparent but keratosis is not detected. Hyperkeratosis occurs again at about 15 months of age, when the skin covering the mature antlers is being shed. Eversion of the transition zone, which is a rutting characteristic of adult Fallow, occurs for the first time when the deer are about 17 months old. These changes in the prepuce support the view that puberty in male Fallow commences at about 9 months of age, pauses, and then recommences at about 15 months.

Introduction

The specialised cutaneous glands of mammals are now known to affect the animal's behaviour and, in particular, to play an important part in sexual behaviour and social organisation (Cowley 1978; GRAU 1976; Keverne 1978; Shorey 1976). Deer in particular have a wide variety of such glands (POCOCK 1910, 1923) but, with a few exceptions, their

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