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GROUP RAIDS: A MATING STRATEGY OF MALE SOUTHERN SEA LIONS

by

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(With 2 Figures)

(Acc. 30-X-1987)

Introduction

In most otariid species (sea lions and fur seals), males compete with each other to establish territories that females use as birthing sites. Females copulate in these territories a few days after parturition. Only large males acquire territories and monopolize mating (HAMILTON, 1934, 1939; BARTHOLOMEW & HOEL, 1953; RAND, 1967; BONNER, 1968; PETERSON & BARTHOLOMEW, 1967; GENTRY, 1970; MARLOW, 1975; GISINER, 1985). Two strategies for gaining access to females are evident among non-territorial males: (1) some individuals attempt to establish positions on the periphery of existing territories (KENYON, 1960; RAND, 1967; GISINER, 1985), and (2) some males acquire territories at the end of the breeding season, after most adult males have left the rookery and few or no females are in oestrus (KENYON, 1960; PETERSON, 1965; RAND, 1967;

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TRILLMICH, 1984; GISINER, 1985). An additional strategy occurs in southern sea lions, *Otaria byronia*. Groups of non-territorial males invade the territories where females reside, attempting to forcibly establish residence near females or to abduct females from the territories (VAZ-FERREIRA, 1965, 1975). Raids are disruptive for the breeding animals, resulting in interference with copulations in progress, mother-pup separation, pup abductions and pup death (VAZ-FERREIRA, 1965).

Group raids involve losers in conventional male-male competition banding together to attempt to obtain resources that are not available to each one of them acting alone. Raids are important insofar as they cause rearrangement in mating opportunities among competing males and they conflict with female mating strategies. Behaviour of this kind is unusual among pinnipeds. Group raids like those observed in *Otaria* have only been reported in one other species, the Australian sea lion, *Neophoca cinerea*, (MARLOW, 1975).

This paper addresses one aspect of male mating strategies in southern sea lions treated in CAMPAGNA & LE BOEUF (1988). We describe the form, composition, frequency, context and consequences of group raids. We emphasize the reproductive consequences of this behaviour on territorial males, breeding females and their pups, and on the raiders themselves.

Methods

Daily observations were conducted at the rookery of Punta Norte, Península Valdés, Argentina, from 0800 to 2100, during four breeding seasons (15 December to 10 February, 1983-1986) from a cliff seven metres above the colony and 30-40 m distant. We focused on male mating strategies during two weeks at the peak of the breeding season in mid-January 1984 (125 hrs of observation), and during the entire 1985 and 1986 breeding seasons (460 and 483 hrs of observation, respectively). In 1983, observations of group raids were made incidental to a study on male agonistic behaviour (CAMPAGNA & LE BOEUF, 1988).

At peak season, the Punta Norte rookery is composed of about 140 males, 350 females, and 430 pups (CAMPAGNA, 1985). Most females, pups, and adult males are located just above the high-tide line along a 200 m long, narrow stretch of open beach called the central breeding area (CBA). The beach is composed of small pebbles, and lacks topographical landmarks such as rocks or tidepools. Surf moistens the sea lions in the CBA at high tide; at other times, the animals are without shade or water. Access to the rookery is possible from all sides along the entire length of the breeding area.

Each breeding season, about 30 females and 60 males were marked individually with paint (CAMPAGNA & LE BOEUF, 1988). A serial record was kept of the presence and activities of each marked animal (*e.g.*, copulations).

For each group raid occurring during daylight hours, we recorded: location of the raiders previous to the attack, size and composition of the raiding party, and consequences of the event (*e.g.*, number and identity of raiders remaining in the CBA, identity

of resident males ousted, number of females redistributed, and number of females and pups seized or abducted).

By seizure, we mean that an adult female or a pup was forcibly held in position by a male who grabbed the animal in its jaws or prevented it from escaping by blocking its movements. When an animal was seized and carried or herded out of the CBA, we called it an abduction. In 1986, we paid special attention to pup seizures and abductions.

Each raid was ranked as mild, moderate or severe according to the number of females moved and the level of arousal in the CBA. The number of male threat vocalizations recorded during two-minute samples before, during, and after raids was used as an indicator of arousal. A male vocalizes when a territorial neighbour moves, or a non-territorial male approaches his territory (CAMPAGNA & LE BOEUF, 1988). Threat vocalizations were used to define the following categories of colony arousal: (a) Baseline (based on two-minute samples randomly distributed during the day), and (b) Raid (samples taken within five minutes from the start of a raid).

The breeding area was censused daily during low and high tide differentiating adults, subadults (estimated at 5-7 years of age), and pups. We determined the number and identity of males in each of three categories: 1) residents – adult territorial males with females in the CBA, 2) marginals – adult males with females on the periphery of the CBA, about eight metres from the nearest resident, and 3) itinerants – non-territorial adult and subadult males roving about outside the CBA or in the water. Itinerants made up the raiding parties. We counted the number of females associated with resident and marginal males. Females were considered associated with a particular resident male when they were closer to him than to any other neighbouring male. Mean instantaneous adult sex ratios were obtained in each of six equal-sized sectors of the CBA marked by poles. Weather and tidal conditions were recorded at hourly intervals.

The tenure of a male was defined as the number of daylight hours that he was observed in the CBA, or with a female on the periphery of the CBA. In calculating tenure we assumed that males were not leaving the rookery at night when we were not conducting observations. All copulations observed during daylight hours were recorded. Intromission was indicated by rhythmic pelvic thrusting lasting at least one minute and was used as a criterion for a successful copulation (CAMPAGNA & LE BOEUF, 1988). The oestrous period was defined as the day during the breeding season when a female copulated (about six days post-partum, CAMPAGNA & LE BOEUF, 1988).

To investigate the effect of the physical environment on raids, a group of 14 territorial males and 100 females was observed during January 1987 at Puerto Pirámide, a rookery with a different terrain and substrate than Punta Norte. Puerto Pirámide is located 70 km SW from Punta Norte and is similar in size. The animals are distributed on several flat rocky shelves containing boulders and tidepools. Access from the sea to the shelf, where the territories are located, is possible only during high tide, greatly limiting the movement of itinerants.

About twice per week, we recorded and described group raids during 1-2 hrs of observation conducted at the Faro rookery, located one km from Punta Norte (CAMPAGNA, 1985).

Results

I. Form, composition and frequency of group raids.

Context and initiation of raids.

In December, the first large, mature males to arrive at Punta Norte established positions where females came to be located, and the CBA was formed. Females gave birth in the territories of these males and copulated

one week later. By early January, 20-30 itinerant males milled about on the seaside and inland periphery of the CBA; approximately 60% of these males were subadults. Periodically, an itinerant male approached to within 15-20 m of females, and suddenly rushed into the CBA, moving directly to a female, attempting to cut her off from a resident male or grab her in his jaws and hurl her out of the CBA. These individual intrusions occurred throughout the breeding season with a frequency of about 25 per week.

There were two outcomes following individual intrusions by adult males: (1) Fifteen percent of the time, the intruder seized a female and held her for several days until she copulated. (2) Eighty five percent of the time, the intruder lost the female before copulating, or was rebuffed by the aggressive behaviour of the nearest resident males, each acting to defend his own females. About ten percent of the individual intrusions by adult males resulted in 1-10 females fleeing away from the intruder and being redistributed in the CBA. The rejection of individual intruders was often violent because they attracted immediate attention and were usually repelled simultaneously by several residents. The rebuffed intruder withdrew to the periphery of the CBA or moved to the water. Subadult males never held a seized female for more than a few minutes, nor copulated with her.

During some intrusions, peripheral males in the vicinity rushed after the instigator, which precipitated a group raid. Most group raids started so quickly that it was not possible to determine how they were triggered. However, raids were nearly always preceded by a gradual gathering of itinerant males on the periphery of the CBA, near the site of the raid. In 66 raids where the beginning was observed, 51% were triggered by individual intrusions, 29% by itinerant males pursuing females arriving and attempting to enter the CBA or departing to a feeding trip, 4% by itinerant males attracted to a fight between resident males, 8% by heat stressed peripheral males rushing through the CBA to go to the water, and 8% by resident males fighting over females. One raid was triggered by a thunder storm that caused sudden arousal of resident males.

Description of a group raid.

The typical group raid was conducted with great speed, generated much noise, and involved spatial rearrangement of males and females in the breeding group. All itinerant males in the vicinity rushed into the CBA and converged at the same point in a few seconds; some males coming

from as far away as 100 m (Fig. 1). Usually, females fled from the onrushing raiders, moving several metres laterally in the CBA. The progress of raiders was checked by resident males and females further from the point of attack. In the mêlée, one or more raiders usually singled out a female and attempted to mount her, separate her from a CBA resident male, or carry her away in his jaws. Resident males at the point of attack alternated between trying to halt the stampede of females from their territory and defending their females against the encroaching raiders. They mounted females, seized females from each other, bit and shook raiders, and ran over pups. As females stampeded in a group from the raiders, they momentarily abandoned their pups. In the turmoil, wandering pups were often seized by subadult male raiders and carried away from the breeding group where they were held for a few minutes to several hours and treated like adult females (CAMPAGNA & LE BOEUF, 1988). During the first few minutes of a raid, much noise resulted from males threatening each other and females and pups vocalizing. After 2-3 min of rushing about, fighting and milling around, most young raiders were rebuffed and driven out of the CBA. One or two adult raiders sometimes remained in the CBA for a few minutes, fighting off residents for a place or a female, and occasionally, one or two succeeded in establishing permanent residency. In about 30 min, there was a gradual return to normalcy.

Composition of raiding parties.

The mean number of males in 423 raids was 10 ($sd = 8$). Raiding party size reached a peak in mid-January, the peak of the breeding season, when raids were usually composed of 10-15 males and, sometimes, up to 40 individuals.

Raiders varied in age from subadults to fully grown adults, with the majority (66%) being subadults. In about 10% of the raids, all of the raiders were subadults.

Individuals participated in several raids during the breeding season. Seventy seven percent of 69 marked raiders participated in more than one raid. Thirteen percent of 60 adult marked males joined more than five raids during a single breeding season, and one male participated in 14 raids. At least ten males were involved in four raids during a single day. During the last three weeks of January, an itinerant marked male participated in a mean of one raid for every 22 daylight hours in the breeding area ($sd = 14$ hrs, $N = 32$). The most successful raiders par-

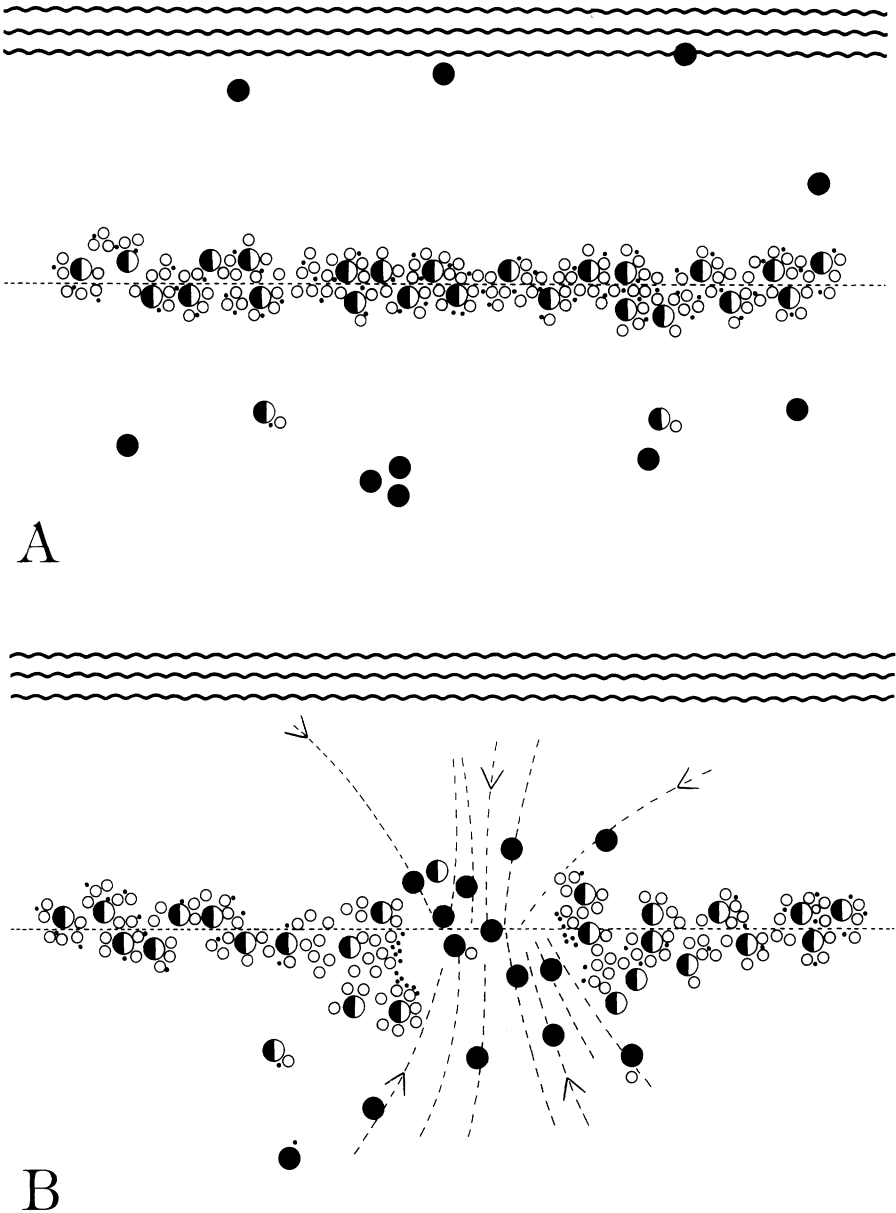


Fig. 1. A schematic showing the distribution of harem holding males (large half open circles), adult females (small open circles) and peripheral non-harem holding males (large black circles) before a raid (A) and after a raid (B). Note the location of the breeding area along the high water mark (dotted line). The schematic illustrates the convergent movement of raiders, a harem holding male being ousted, a female being held by a raider, and females moving away from the center of attack.

participated in few raids because they soon became established as residents in the CBA.

Particular males were sometimes seen together during raids. In 20% of 100 raids where more than two marked males participated, at least two of them had been seen together in a previous raid. Four pairs of males were seen together in five raids each during a two-week period.

Frequency, location and severity of raids.

We observed 484 raids during daylight hours, in four breeding seasons (Table 1). More than half (57%) of the raids occurred at peak season, January 14-26 (Table 1). During this period, about one raid occurred

TABLE 1. Number and rate of occurrence of group raids during four breeding seasons, at Punta Norte, Argentina

Breeding season	Total raids recorded	Raids at peak season	Raids per hour of observation at sex season
1983	(53)	53	0.43
1984	145	87	0.58
1985	165	89	0.64
1986	121	70	0.45
Total	484	299	
Mean \pm sd	144 \pm 22 ¹⁾	75 \pm 17	0.53 \pm 0.10

Peak of the season refers to the period 14-26 January.

¹⁾ Raids for 1983 were recorded at peak season only, and hence, are not included in the calculations.

every two hours of observation. Two to three times per season, two raids occurred simultaneously, affecting different sectors of the CBA. Raids were infrequent during February, and were not observed outside of the breeding season.

Raids occurred at all hours of the day but were significantly more frequent in late afternoon and early evening just before sunset (about 2100 hrs). Forty five percent of 375 raids recorded during three breeding seasons occurred between 1601 and 2000, 31% occurred between 1201 and 1600, and 25% occurred between 0800 and 1200 ($\chi^2 = 23.1$, d.f. = 2, $p < 0.01$). Raids also occurred at night but we do not have data on form and frequency of nocturnal raids.

Raids began more often from the seashore periphery of the CBA than

from the inland side (73% *vs* 27% of 258 raids respectively, $\chi^2 = 55.8$, d.f. = 1, $p < 0.01$). In 19% of 318 raids, the CBA was invaded from both sides simultaneously. The site of raids was associated with the location of peripheral males. The mean number of itinerant males was usually higher on the seashore than on the inland-side of the CBA ($\bar{X} = 15.2 \pm 7.8$ *vs* 6.2 ± 4.2 respectively, $t = 17.22$, d.f. = 627, $p < 0.01$).

Raids occurred during all tidal conditions, but were most frequent and disruptive at high tide. Sixty two percent of 291 raids occurred during high tides *versus* 38% during low tides ($\chi^2 = 15.4$, d.f. = 1, $p < 0.01$). In 53% of 48 high-tide raids recorded in 1986, at least one female was momentarily seized by a raider *versus* 26% of 39 low-tide raids ($\chi^2 = 6.28$, d.f. = 1, $0.025 < p < 0.01$).

All sectors of the CBA were raided, but the areas most frequently affected were those with the highest number of females. There was a positive correlation between a female-biased adult sex ratio in a sector of the CBA and the proportion of groups raids affecting it during a week (Kendall's $\tau = 0.65$, $N = 18$ weekly means, $p < 0.01$). The weekly occurrence of group raids was positively correlated with estimates of the mean daily number of females in oestrus (Kendall's $\tau = 1$, $N = 6$ weekly means, $p < 0.05$), and the sectors of the CBA most affected by raids were those where most copulations occurred (Kendall's $\tau = 0.87$, $N = 8$ weekly means, $p < 0.01$).

Raids varied in the degree of disruption created among resident males and females in the CBA. Forty four percent of 340 raids recorded in three breeding seasons were categorized as mild, 37% as moderate and 19% as severe. This skewed distribution was observed each week of each breeding season. Out of a total of 63 severe raids, the majority (52%) occurred at high tide, *versus* 34% at medium tide and 14% at low tide ($\chi^2 = 13.7$, d.f. = 2, $p < 0.01$). Mild *versus* moderate raids were not significantly different among tidal conditions ($\chi^2 = 0.01$ and 0.55 respectively, d.f. = 1, $p > 0.05$).

The effect of raiding party size for the 1985 breeding season is shown in Table 2. The mean number of females sitting up (a sign of arousal) and redistributed, and the proportion of raids that resulted in females or pups seized, increased with the number of males in the raiding party.

Behaviour during raids.

Raiders.

Adult raiders, like individual intruders, attempted to seize females. In 64% of the raids, all raiders were successfully repelled. In 36% of 355

TABLE 2. Number and consequences of raids as a function of size of raiding group

	Size of raiding group		
	Small (2-5)	Medium (6-10)	Large (> 10)
Number of raids	40	58	47
Size of raiding party	3.4 ± 1.1	7.6 ± 1.3	14.6 ± 3.9
Females sitting up	18.2 ± 7.1	26.2 ± 11.0	36.7 ± 11.4
Females redistributed	7.4 ± 6.2	11.6 ± 9.3	18.9 ± 14.2
Percentages of raids with:			
- At least one female seized	29	63	65
- At least one pup seized	13	22	26

Data recorded during the 1985 breeding season. Except for percentages, data represent mean \pm SD values.

raids, at least one female was seized. A male seized a female in the CBA at least momentarily by separating her from others or by seizing her in his jaws and hurling her behind him, then interposing his body between her and the resident males (Fig. 2). While facing the female and aggressively keeping her in place, he attempted to hold his ground, defending himself against the repeated bites and threats of 2-4 males. There were three outcomes to seizing a female: (1) In 53% of the seizures, the raider could not fend off residents biting his back and hind-quarters, and within a few minutes, he lost the female and was driven out of the CBA. (2) In 8% of the seizures, a raider held a female in the CBA for a few minutes but, when he could no longer defend himself against the attack of residents, he abducted the female 5-7 m to the periphery of the CBA, where he held her. He prevented her escape by stationing himself between her and the CBA, mounting her, or if she got out of position, grabbing her in his jaws and hurling her in the air with a violent twist of his head to a more defensible position. Males on the margin of the CBA usually held only one female. (3) In 39% of the seizures, the raider held the female for one or more hours while successfully defending himself in the CBA. Over the course of several hours, aggressive attacks on him decreased and he was accepted as a territorial neighbour by other residents. Once the seized female reunited with her pup (the pup moving to her, attracted by her calls), she did not persist in attempting to escape. With time the successful raider, now a resident, usually acquired other females as they arrived to breed.

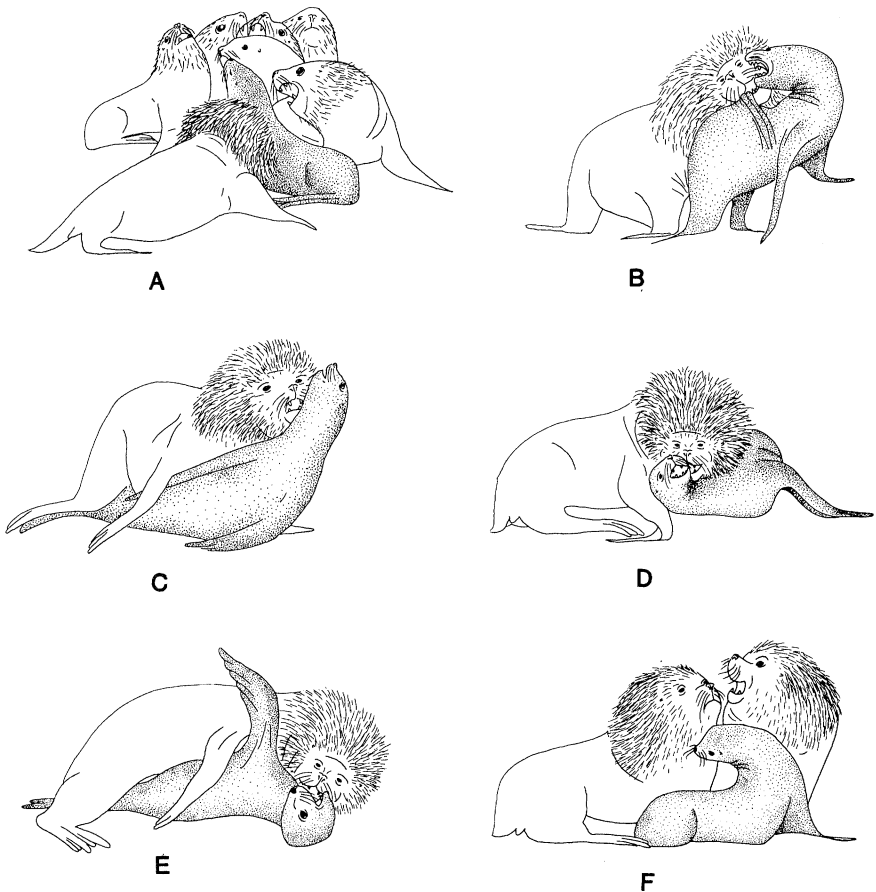


Fig. 2. A schematic of the typical sequence of events during a female abduction by a raider: (a) Several raiders surround a female, (b) a large adult male grabs her and moves her to the periphery of the breeding area, (c-e) he prevents her escape, (f) the abductor defends the female from other males.

The following field observations illustrate the behaviour of a typical adult raider.

January 3-8, 1986: Male F was an itinerant in the vicinity of the CBA. He participated in two raids, but did not seize a female and was repelled each time.

Jan. 9-12: F spent Jan. 9 alone, resting near the water 100 m from the CBA. On 10 Jan., he participated in two group raids but was repelled. On Jan. 11, he rested all day near the shore, 100 m away from the CBA.

Jan. 13: F invaded the CBA alone but was rebuffed and moved inland to rest.

Jan. 14-15: F rested during the morning of Jan. 14. In the afternoon, he invaded the CBA alone and seized a female, but lost her. In the evening, he participated in a group raid but was rebuffed. On Jan. 15, he rested all day.

- Jan. 16: F invaded the CBA alone but was rejected. Two hours later, he participated in a group raid and failed again.
- Jan. 17: During the morning, F triggered a raid by rushing into the CBA; he and the others were repelled. He rested in the shade during the afternoon. In the evening, he joined a raid into the CBA, seized a female, and got established in the CBA. He fought briefly with two residents but was not injured.
- Jan. 18-19: F copulated with the female seized during the raid. He did not associate with other females while in the CBA and went to sea after copulating.
- Jan. 20-21: F participated in two raids. In the second attempt, he seized and held a female in the CBA.
- Jan. 22-30: F was a resident in the CBA. He associated with five females and copulated five times.
- Jan. 31: F was absent from the CBA in the morning. He participated in a raid at noon but was repelled. He moved to the water and was not seen again.

The majority of raiders followed the first males that rushed into the CBA but were not able to secure females because they did not get the opportunity or were beaten off by resident males. Getting close to females during raids was positively correlated with the raider's age and size. The younger males rushed into the fray but their actions lacked focus, they seemed uncertain about what to do, and many of them were rebuffed by the threats of resident males. Rarely did a subadult male seize a female, and he always lost her in a few minutes.

Unable to secure females, subadult raiders paid attention to pups. In 18% (87) of 484 raids recorded during four breeding seasons, a subadult raider seized a pup and attempted to carry it out of the CBA. There were two outcomes to seizing a pup: (1) Forty three percent of the time, the raider lost the pup within a few minutes and the pup scampered back into the CBA. (2) Fifty seven percent of the time, the pup was abducted out of the CBA, to a distance of 10-80 m. Subadult males were dominating and possessive with pups, constraining their movements and defending them from other males.

Females.

Most females located near the raided area sat up and bolted away from the approaching raiders. Virtually every female that moved from the site of a raid ended up associated with a different resident male. Fleeing females left groups of pups in their wake; some females turned to call to their pups, others carried pups in their jaws. Female redistribution resulted in gaps in the CBA 10-30 m wide, where only a few males and females were left.

Abducted females vigorously resisted the attempts of males to carry them to the periphery, despite being hit, bitten, thrown and carried. They bit at males, and took advantage of fights to escape.

Residents.

The response of residents was divided between fighting raiders and holding or following fleeing females. Most males compromised; they bit at raiders, especially the adult raiders, and they retreated with their females. Most raids disrupted the territories of 4-8 residents. All of 39 resident males marked during the 1984-85 breeding season were directly involved in repelling raiders at least once during their tenure in the CBA. In 30% of 60 raids at least one female was moved out of the territory of a marked resident male. In severe raids, at least one resident lost all of the females located within five metres of him. Copulations in progress were terminated. If a male was copulating when a raid started, he dismounted either because: (1) he was attacked by other males, (2) he started to fight with a raider, (3) the female with whom he was copulating ran away from the raided area, or (4) females fleeing from the raiders jostled him.

In severe raids, one or two residents left their positions and pursued the females. Some males tried to prevent females from escaping by mounting them, and holding them in place. As residents crossed the territories of other CBA males they engaged in violent but brief aggressive encounters. Most fights were skirmishes lasting only a few seconds, but three or four times per season, males engaged in fights that lasted a few minutes. During these fights, males held their bites and shook the opponent violently (CAMPAGNA & LE BOEUF, 1988). Residents threatened raiders almost continuously during the first five minutes of a raid, but threats waned with time. For example, one raider attempting to get established in the CBA was threatened five times per minute during the first 5 min, but only once per minute 30 min later. About 10% of the threats involved contact. Subadult raiders, not holding a female, were not attacked as violently as adults. In about 10 raids per season, subadult males mounted residents while the latter were fighting.

Aftermath of raids.

Raids were most disruptive during the initial attack and the first 1-3 min that followed. The mean rate of male threat vocalizations during the first five minutes of a raid almost doubled from the baseline activity rate ($\bar{X} = 0.34 \pm 0.11$ vs 0.19 ± 0.12 vocalizations per male per minute; $t = 6.28$, d.f. = 356, $p < 0.01$). In about 10% of the raids, the baseline rate increased by a factor of five and remained elevated for at least 30 min.

Raiders that achieved residency stayed in the CBA until the end of the season, unless they were deposed during other raids or abandoned the CBA. Repulsed raiders and deposed residents moved to the periphery of the CBA where most of them rested or went into the water. A male that abducted a female to the periphery and became a marginal male continued to hold her, prevent her escape, and defend her from other peripheral males. These relationships were unstable due to tides and heat. The seashore was flooded twice a day during high tides, dissolving pairs on the periphery of the CBA. High temperatures precluded long tenure on the inland side of the CBA. After several hours of withstanding air temperatures above 30°C, and strong solar radiation (1-1.4 cal/cm²/min), marginal males with females on the inland periphery of the CBA showed evidence of heat stress. They burrowed into the pebbles with their foreflippers to reach the moist pebbles under the surface. They exposed the hindflippers to dissipate heat. After 3-5 hrs of exposure to high temperatures, these males forcefully attempted to copulate with the females. Forceful copulatory attempts were often a sign of heat stress for, regardless of whether the male copulated or not, he often abandoned the female and rushed to the sea to cool off. Males in the CBA did not abandon their positions at similar temperatures. Marginal males on the inland side of the CBA endured heat for longer periods than itinerant males. On hot days, when all itinerant males had moved to the water, marginal males with females maintained their positions. Two to four times per season, marginal males abandoned their females to join a raiding party.

Much pup movement occurred in the CBA within five minutes of the initiation of a raid. Pups attempted to reunite with their mothers who called to them persistently. Resident males did not pay attention to pups, but peripheral subadult males sometimes took advantage of the confusion to abduct isolated pups. Abducted pups were held for 10-20 minutes and treated in a similar way to the way that adult males treated females. For example, the pup was ignored so long as it remained near the abductor. When the pup attempted to escape, it was seized, shaken from side to side, bitten, or tossed into the air. This behaviour was often repeated 10-50 times during a 10-30 min period. In 9% of the abductions, the male mounted the pup, performing pelvic thrusting movements. Intromission was never observed. Pups bit the abductor's neck, face and flippers, but this had little effect on the male's behaviour. An abduction terminated when the pup was spontaneously abandoned, a resident male chased the abductor away, or the pup escaped by moving quickly into the CBA.

Gaps in the CBA caused by raids took several hours before being filled

TABLE 3. Mean values of copulatory success (\pm SD) of adult raiders that became residents in the CBA (raider-residents), founding males that lost their position in the CBA and re-gained it after raiding (ex-resident raiders), and founding males that secured residency in the CBA early in the breeding season

	Raider Residents	Ex-resident Raiders	Founding Residents
N	31	12	32
Mean number of copulations per male	2.2	4.9	5.3
Variance	6.0	9.7	12.3
Range	0-5	1-11	2-18
Mean percentage time in the CBA ¹⁾	35 \pm 23	69 \pm 17	76 \pm 17
Mean number of copulations in the CBA per 100 hrs with female in the CBA	1.5 \pm 1.4	2.0 \pm 1.2	2.0 \pm 1.0
Mean number of copulations per 100 hrs observed in the breeding area ²⁾	1.1 \pm 0.8	1.7 \pm 1.0	1.7 \pm 1.0

Data based on animals marked during two breeding seasons (1985, 1986). See text for statistical tests.

¹⁾ Percentage of time spent in the CBA in association with females in relation to total time observed in the breeding area.

²⁾ Includes all copulations achieved by males while they were observed in the breeding area, independently of their location and breeding status.

up again with breeding animals. Some gaps were re-occupied by females moving away from other raids in the opposite direction.

Raids at other sites.

Raids occurred at the other two rookeries observed. At Faro, where the topography was similar to Punta Norte, raids had the same form, frequency, and general consequences as at Punta Norte. Females and pups were seized and abducted, females were redistributed, and some raiders became established in the CBA.

In a small sector of the Puerto Pirámide rookery, where about 16 territorial males and 100 females reproduced, we observed nine raids during the last three weeks of January. This figure was low compared to sectors of Punta Norte rookery with a similar number of animals. All of them were repulsed by the resident males and no females or pups were seized.

The topography of this area precluded a massive and sudden invasion by raiders. Animals bred on a narrow rocky shelf backed up by a steep cliff. Lack of space prevented itinerant males from hauling-out inland; they had to stay in the water. Entrance to the breeding area from the water was limited to one narrow passage, where the edge of the shelf was less steep. The entrance was adjacent to two territories held by resident males. Only at high tide, when the water level ascended to the border of the shelf, was it possible for itinerants to approach the breeding group from other locations. Raids took the following form: 20-30 itinerant males milled around in the water for about one hour before two or three of them dashed toward the entrance, attempting to reach the shelf. They were always rejected by the territorial males a few seconds after landing on the rocky platform. Once the first few raiders were rejected the remaining raiders retreated. Raids had little influence on the behaviour of females or pups. No raiders gained a territory or displaced a territorial male.

In a different sector of the same rookery, where animals bred on a large flat shelf with ample space for itinerant males to haul out near the breeding animals, we observed 20 raids, a low number compared to Punta Norte. At this location, each raid caused redistribution of 20-40 females, and at least six territorial males were displaced. Females were seized, and four pups were abducted.

II. Reproductive consequences of group raids.

Tenure.

Raiders *versus* founding residents.

Forty three marked raiders that secured a female during raids remained in the CBA and established residency for a mean of 13 days ($sd = 9$). This is about half the length of the mean tenure of 33 founding residents, males that became established in the CBA at the beginning of the breeding season, ($\bar{X} = 24$ days, $sd = 5$, CAMPAGNA & LE BOEUF, 1988). The mean tenure of 32 raiders that abducted a female to the periphery of the CBA was 0.5 days ($sd = 0.4$ days). The length of tenure on the inland side of the CBA did not differ from that on the seashore side ($t = 1.49$, d.f. = 92, $p > 0.01$). Over the entire breeding season (all years), raiders spent a mean of 35% of the time they were present in the breeding area in association with females, versus 76% of the time by founding males (Table 3).

Deposition and re-establishment of residents.

Thirteen marked resident males were ousted from the CBA during raids in 1985 and 1986. Afterwards, all of them participated in group raids. Within 1-3 days of losing their residency, 12 of 18 marked ex-resident raiders re-established themselves in the CBA during raids. Five of these 12 males gained a position in virtually the same place where they were located previously.

Male mating success.

Sixty three percent of 51 marked males who engaged in raids during two breeding seasons (1985 and 1986) copulated at least once as a result of raiding. All of them were adult resident males that held females in the CBA or were adult marginal males that held females on the periphery. None of the 15 marked subadult males secured females or copulations. Table 3 shows the mating success of raiders that became residents (raider-residents), founding residents that were deposed and reestablished residency during raids (ex-resident raiders), and founding residents. Raider-residents were less successful than ex-resident raiders ($t = 2.1$, d.f. = 41, $P < 0.05$) and founding males ($t = 2.4$, d.f. = 61, $p < 0.05$) with respect to the mean rate at which they copulated per 100 hrs spent at Punta Norte. This was because before they established themselves in the CBA, raider-residents spent potential reproductive time outside of the CBA participating in raids but being repelled. However, once they became residents, raiders copulated at rates similar to those achieved by founding residents ($t = 1.64$; d.f. = 61; $p > 0.05$), or ex-resident raiders ($t = 0.96$, d.f. = 41, $p > 0.05$).

Eighteen raiders that became marginal males copulated at an estimated rate of 9.5 times per 100 hrs spent on the periphery of the CBA associated with females ($sd = 7.4$). This rate was significantly higher than that of founding males ($t = 6.3$, d.f. = 61, $p < 0.01$), ex-resident raiders ($t = 3.6$, d.f. = 28, $p < 0.01$), and raider-residents ($t = 6.1$, d.f. = 47, $p < 0.01$) reported in Table 3.

The number of copulations achieved by raider-residents and ex-resident raiders was positively correlated with tenure in the CBA (Pearson's $r = 0.62$, d.f. = 41, $p < 0.01$). Raiders with the longest tenure in the CBA (≥ 250 hrs) copulated 1-5 times. The two most successful raiders that became residents during group raids copulated five times each, during 106 and 115 hrs in the CBA. The most successful founding male copulated 18 times during 350 hrs observed in the CBA.

It is instructive to compare the mating success of an individual

invading the CBA alone as opposed to raiding in the company of others. Over three breeding seasons, we recorded 34 marked, adult males invading the CBA alone and as a member of a group, both events occurring within three days of each other. When males acted alone, they were successful in seizing a female and eventually copulating with her on 11.8% of the attempts; as a member of a group, males achieved a copulation on 35.3% of their raiding attempts. This threefold difference is statistically significant ($\chi^2 = 4.0$, d.f. = 1, $p < 0.05$).

Injuries and mortality.

Raiders were injured by resident males while trying to secure and hold females. Lacerations on the neck, back, and face were observed a few minutes after raids began. Seized females bit the flippers, lips, and face of raiders. By the end of the season, all raiders had fresh wounds. Several males had broken canine teeth (CAMPAGNA & LE BOEUF, 1988).

Females were bitten by raiders as well as by residents. Seven times during two breeding seasons, raiders bit females on the head and lifted them by the face. Some females were disputed by several males who bit and tossed them from one male to another. One female lost an eye while being fought over by ten males. Females that left the CBA in pursuit of abducted pups were intercepted, held, bitten and mounted by peripheral males. By the end of the season, 26% of the females had fresh bloody punctures and bloody necks attributable to male bites (CAMPAGNA & LE BOEUF, 1988).

At least five pup deaths were attributed to physical injuries caused by males during or immediately following a raid. Victimized pups had bite wounds around the neck, face, head, back and flippers, and extensive hematomas in the cervical muscles. In five of 76 abductions during raids, the pup was taken to the sea, sometimes more than one km away from the coast. Pups were repeatedly submerged while being held. Two of these pups were not seen again and may have drowned.

Abducted pups were not abandoned or weak individuals, who would have been likely to die regardless of the abuse. All abducted pups appeared healthy. Eight pups who were captured and marked a few minutes after being abducted, returned to the CBA and were alive one week after the abduction. All of them nursed regularly.

Discussion

Group raids of female breeding aggregations by southern sea lion males are a frequently occurring and predictable behaviour that takes place in

several rookeries in the species' range. Raids observed at three rookeries in Península Valdés, Argentina, resemble those described by VAZ-FERREIRA (1965, 1975) at Lobos Island, Uruguay. VAZ-FERREIRA was the first to report the occurrence of raids in southern sea lions, but he did not investigate the role played by raids in the breeding behaviour of the species.

Group raids are a successful strategy for some males to obtain mates. Since virtually all copulations occur in the central breeding area, a male must obtain residence here in order to mate. Raids do not assure copulatory success but put some males in proximity to oestrous females. Once positions in the breeding area are taken up by the early arriving founder males, outside males have only two ways of obtaining residence near females. Males can invade the breeding area and attempt to seize a female alone or in a group. The latter strategy is more successful. For adult males, securing females in the breeding area during a raid is an alternative to arriving early in the season and defending a position that attracts parturient females (CAMPAGNA & LE BOEUF, 1988). Raiders do not copulate as much as founding males because of their shorter tenure near females.

The narrow physical boundaries within which males are successful in mating are indicated by the reduced mating success of raiders that become marginal males on the periphery rather than residents in the central breeding area. Marginal males force females out of the breeding area by just a few meters. This strategy allows a male to hold a female only a few hours to a few days. On the seaward side, high tidal conditions cause the pair to be inundated or overcome by swimming itinerant males, and on the inland side, high temperatures of the dry substrate cause the animals to suffer heat stress. Faced with this dilemma, marginal males attempt to force females to copulate. Although the estimated copulation rate of marginal males, per 100 hrs of association with females, is higher than that of resident males, their copulatory success by the end of the breeding season is lower than that of residents. This is because the tenure of marginal males with females is brief and they are rarely associated with more than one female at a time. In addition, the copulations achieved by these marginal males are probably unlikely to result in insemination of females because the latter may be forced to copulate at inappropriate stages of their breeding cycles.

Individuals that raid the breeding zone in groups rather than rushing in alone enjoy the benefit of surprise and confusion. A larger number of females flee from a group of raiders than from one individual invader.

Residents cannot deal with all of the raiders and a resident must decide which raider to focus upon. Like a predator preying on a individual fish in a school, there is difficulty in singling out an individual (SHAW, 1962). This not only gives the individual raider more time to seize a female, but also means that some raiders do not even come into contact with resident males. The risk of injury to the group raider appears to be lower than to that of the individual invading alone. Although the raiders compete among themselves for females, they facilitate each other's goals and decrease their risks by acting in concert.

What are the group dynamics that trigger and sustain raids? The first male to rush forward into the breeding zone instigates immediate participation by other males nearby. The males in the vicinity appear to be waiting for such an action and the stimulus of one male rushing in elicits the response of several others following. The participants do not seem to be cooperating but they are closely monitoring each other's behaviour. The aggregation is more like a group of individuals acting on their own using the actions of others as cover. There is some cohesiveness to the group in the sense that the same males may participate in raids together over a period of days. However, individuals that raid together were never seen aiding each other.

What are the conditions that select for these group efforts in this species? The following physical and social variables appear to be critical:

1. High temperatures and high solar radiation in an open habitat that offers few ways to reduce thermal stress constrain the animals to breed in a narrow zone near the water's edge. At Punta Norte, southern sea lions breed in mid-summer when solar radiation levels reach $1.40 \text{ cal/cm}^2/\text{min}$ and air temperatures may be as high as 39°C for several hours during the day. Solar heat impinging on the animals is magnified by conduction from the dry, pebbly substrate. The animals cannot cool themselves by behavioural adjustments such as seeking out shade or lying in standing water as do other otariid species (VAZ-FERREIRA & PALERM, 1961; RAND, 1967; MARLOW, 1975; PETERSON & BARTHOLOMEW, 1967), because the beaches are devoid of tidepools, trees, brush and boulders. They are constrained to breed along the high tide mark where the pebbles are wet and the animals are sprayed with surf at high tide. However, they cannot venture too near the water's edge because the pups of parturient nursing females would be in danger of being washed out to sea. Moreover, the large tidal range (5 m) adds to the narrowness of the useful zone. At high tides, the animals are nearly awash, and at low tides, they are 70 m from the water's edge, fully exposed to the sun. In straddling

this narrow zone, with disadvantages on both sides, the breeding animals are vulnerable to raiders from all sides.

2. Unlike some other otariids (*e.g.*, northern fur seals, *Callorhinus ursinus*, BARTHOLOMEW & HOEL, 1953, and Steller sea lions, *Eumetopias jubatus*, GENTRY, 1970), southern sea lion males give priority to defending females rather than a territory (CAMPAGNA & LE BOEUF, 1988). An adult male can effectively herd or prevent a female from moving away from him, unlike the case in other sea lions (*e.g.*, California sea lions, FRANCIS & HEATH, pers. comm.). However, sequestering females commits southern sea lion males to be vigilant and in close proximity to females to prevent them from straying or joining other males. When rival males approach, a male must compromise between keeping his females from fleeing and keeping the intruding competitors away. He cannot engage in long fights or fight far away from his females. The result is that marauding males are rarely hurt seriously. With the threat of serious injury and an all out fight removed, a male has little to lose in attacking the breeding area and incurs even less risk if he attacks in a group.

3. The ratio of potential breeding males to females at Punta Norte results in a surplus of near adult-size males that cannot obtain a position in the breeding area.

4. Numerous adult and subadult males have room to loiter on the periphery of the breeding area regardless of tidal conditions. Congregating near the breeding area allows these males to assess the reproductive status of females, monitor the vigilance and prowess of resident males, and weigh the probability that others nearby are set to initiate raids or follow in synchrony. Where the topography does not allow outside males to congregate or synchronize their attack, such as at Puerto Pirámide, raids are ineffective.

In summary, we expect the incidence of raids in this species to vary with the ratio of outside males to resident males and with climatological and topographical variables that affect the distribution of breeding animals. This statement is supported by our observations at different rookeries. At Puerto Pirámide, where the topography does not allow males to congregate or synchronize their attack, and fewer peripheral males are found in the vicinity of the breeding animals, raids are ineffective. At Lobos Island, Uruguay, ample beaches allow numerous peripheral males to gather near the breeding animals. The number of males involved in raids was much larger at this place than at the rookeries observed in Argentina (VAZ-FERREIRA, 1965, 1975).

The Australian sea lion breeding at Dangerous Reef is the only other

otariid species besides the southern sea lion for which raids have been reported. MARLOW (1975) observed "gangs of young males" harassing females and attempting to cut them out of territories while the territorial male was copulating or fighting. Judging from the descriptions available, the group raids of Australian sea lions are less disruptive than those of southern sea lions and have less significant consequences on the breeding behaviour of males and females. BARTHOLOMEW (1953) reported the invasion of harems by groups of two to four "idle bull" northern fur seals; the males seize, herd or toss females from neighbouring territories into their own. These males do not hold the females unless they abduct three or four of them at the same time. Recently, raid-like events have been observed in northern fur seals breeding on St. George Island but not on nearby St. Paul Island (GENTRY, pers. comm.). This difference may be due to the lack of subadult males in the colony of the latter island as a result of culling for commercial purposes.

As a mating strategy, group raids of male southern sea lions deviate from the typical behaviour of males of most mammalian species, namely that of competing on a one to one basis for females (WALTHER, 1958; GEIST, 1971; LE BOEUF, 1974; CLUTTON-BROCK *et al.*, 1982). In form, raids of southern sea lions resemble takeover attempts of bisexual troops by bands of male hanuman langurs, *Presbytis entellus* (HRDY, 1977). Both are collective revolts by the losers in male-male competition against the males who are associated with females and thus do most of the mating. These group actions of "desperadoes" bypass the asymmetry that exists between competing individuals undermining the "stability of respect" for the winners (GRAFEN, 1987). In at least 21 mammalian species, 81% of which are primates, males form alliances or coalitions related to gaining access to females (CAMPAGNA, 1986). In these groups, cooperation between group members is based on kinship (*e.g.*, BYGOTT *et al.*, 1979; PACKER & PUSEY, 1982) or reciprocation (*e.g.*, PACKER, 1977). In contrast, the apparent synchrony of effort of members of a raiding group of sea lions is not due to a complex cooperative network, but appears to be based solely on opportunity and social facilitation.

Although subadult males outnumber adults in raiding parties, only the latter secure females and eventually copulate with them. Subadult males abduct pups. There is no immediate benefit in doing this. Females are not lured out of the breeding area to retrieve their pups, allowing pup abductors to copulate with them. It is not possible for pup abductors to inseminate pups and they do not sequester them until adulthood as occurs in hamadryas baboons, *Papio hamadryas*, (KUMMER, 1968). A

potential long term benefit for males is to practice on pups for what they will do with adult females in future seasons. Controlling a pup is similar to controlling a female. Subadult males direct the same behaviours to pups as adult males do to adult females. They do this with relatively little risk of injury because most of them lag behind and are rarely the center of attention during a raid. The occasional infanticide that results appears inadvertent. An explanation for infanticide like that used for hanuman langurs (HRDY, 1974, 1977) and African lions, *Panthera leo*, (BERTRAM, 1975; PACKER & PUSEY, 1982, 1983), in which the pup's death benefits the assailant by causing the mother to return to sexual receptivity faster than she would otherwise, is not appropriate for this species. Southern sea lion females normally enter into oestrus while nursing, about six days after birth (CAMPAGNA & LE BOEUF, in press), and there is no evidence that the abduction of her pup causes a female to alter her reproductive cycle to make her available to subadult males later in the season, when most adult males are gone. Abduction or killing of pups by males has been observed at other southern sea lion rookeries (VAZ-FERREIRA, 1965, 1975; MAJLUF, pers. comm.), and in several other pinniped species (MARLOW, 1975; LE BOEUF & BRIGGS, 1977).

Summary

Southern sea lions, *Otaria byronia*, breed in a narrow zone along the high tide mark where males sequester females, defending them against competitors that congregate on the periphery. During four breeding seasons, 15 December to 10 February, 1983-1986, we observed marked animals at Punta Norte, Peninsula Valdes, Argentina, and recorded the form, frequency and consequences of an unusual mating strategy: groups of males raid the breeding area attempting to seize females from resident, territorial males.

Raids were often triggered by one male rushing into the breeding area. Females fled from the point of attack and were separated from their pups and were redistributed within the breeding area. Some resident males gained females, others were deposed and lost females, while some raiders gained females and residency in the breeding area. A mean of 144 (sd = 22) raids were observed per breeding season, with 57% of them occurring at peak season, 14-26 January. During this period, raids occurred at a rate of one every two hours of observation. Raids occurred at all hours of the day and at night, the rate, time and site of occurrence being associated with the location and number of females in oestrus, and with tide.

The mean size of the raiding party was 10 males (sd = 8, range = 2-40 males); 66% of the males were subadults. In 36% of 355 raids, at least one female was seized and held for at least a few minutes; in the remainder, all raiders were repelled. There were three outcomes when a raider seized a female: 1) In 53% of the seizures, the male lost the female in less than one hour and was driven out; 2) in 8% of the seizures, the raider could not withstand the attacks of resident males and herded the females a few metres to the periphery of the breeding area, and 3) in 39% of the seizures, the raider remained in the breeding area with one or more females.

Subadult raiders were not successful in securing females but in 18% of 484 raids, they seized a pup. Fifty seven percent of the time, pups were abducted from the breeding area and held forcibly like adult females. At least five of them were killed.

Raiders that secured a female during a raid remained in residency a mean of 13 days (sd = 9), a significantly shorter tenure than that of males that set up residence in the breeding area at the start of the season (\bar{X} = 24 days, sd = 5).

Group raids were an effective mating strategy for some participants. The probability of copulating was higher when a male raided the breeding area in a group than when alone. Raiders that seized females and became residents copulated 1.5 times per 100 hrs in the breeding area, achieving a mean of 2.2 copulations per male (variance = 6.0). Founder residents copulated at a similar rate, but were more successful than raider-residents due to longer tenures, achieving a mean of 5.3 copulations per male (variance = 12.3).

The incidence and success of raids as a mating strategy was partially dependent on topography. At Puerto Pirámide, where males defended territories containing tidepools and access to the breeding area was limited to a few sites at high tide, raids were infrequent and ineffective.

Raiders synchronized their rush into the breeding area, keying on the first male to move. However, no alliances or coalitions, suggesting cooperation, were formed.

Group raids consist of a collective revolt against the *status quo*, similar in form to troop takeovers by groups of male hanuman langurs. Outside males can achieve proximity to oestrous females with less risk of injury by raiding in a group rather than by attempting to seize a female by themselves.

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Resumen

Los lobos marinos del sur, *Otaria byronia*, se reproducen en una estrecha zona de playa, a lo largo de la línea de pleamar, donde los machos secuestran hembras, defendiéndolas de otros competidores agrupados en la periferia. Durante cuatro temporadas reproductivas, entre el 15 de diciembre y el 10 de febrero, 1983-1986, se observó animales marcados en Punta Norte, Península Valdés, Argentina, registrándose la forma, frecuencia y consecuencias de una estrategia de reproducción inusual: la invasión del área de reproducción por grupos de machos periféricos intentando obtener hembras.

Frecuentemente, una redada grupal se inició como resultado del ataque de un macho periférico moviéndose rápidamente en dirección al área de reproducción. Las hembras huían del lugar de ataque, y en el proceso, se separaban de sus crías y se redistribuían dentro de la agrupación. Algunos machos residentes obtenían hembras, otros las perdían, y algunos machos atacantes obtenían una posición y hembras. En cada temporada de reproducción se observó una media de 144 ($ds = 22$) redadas grupales, 57% de las cuales ocurrieron durante el pico de la temporada, 14-26 de enero. Durante este último período, se observó una redada grupal cada dos horas. Las redadas ocurrieron a toda hora del día y por la noche. La frecuencia, hora y sitio de ocurrencia de un ataque grupal se asociaron a la ubicación y distribución de las hembras en estro, y a la altura de la marea.

El número medio de machos componentes de una redada grupal fue de 10 ($ds = 8$, rango = 2-40 machos); el 66% de estos machos eran subadultos. En el 36% de 355 redadas grupales por lo menos una hembra fue raptada y retenida durante algunos minutos; en el resto de las redadas, todos los machos atacantes fueron rechazados por los machos residentes. El rapto de una hembra por un macho atacante tuvo tres desenlaces: 1) En el 53% de los casos, el macho peridió a la hembra en menos de una hora y fue rechazado del área, 2) En el 8% de los raptos, el macho raptor no pudo resistir los ataques de los machos residentes vecinos y abandonó el área, arreando a la hembra consigo hacia la periferia, y 3) En el 39% de los casos, el macho raptor mantuvo a la hembra, a pesar de los ataques de los machos vecinos, y permaneció en el área de reproducción.

Los machos subadultos no fueron exitosos en obtener hembras, pero en el 18% de 484 redadas un macho subadulto rapto a una cría. En el 55% de los raptos, la cría fue llevada hacia la periferia y retenida como si fuese una hembra adulta. Por lo menos cinco crías murieron en este proceso.

Los machos atacantes que obtuvieron y mantuvieron una hembra durante una redada permanecieron como residentes en el área de reproducción una media de 13 días ($ds = 9$), siendo esta una permanencia significativamente más corta que la de aquellos machos que se establecieron en dicha área desde el inicio de la temporada (media = 24 días, $ds = 5$).

Las redadas grupales demostraron ser una estrategia de apareamiento efectiva para algunos machos participantes. La probabilidad de copular fue mayor cuando un macho invadió el área de reproducción en grupo que cuando lo hizo en forma solitaria. Aquellos atacantes que obtuvieron hembras y permanecieron en residencia copularon 1.5 veces por cada 100 hrs de permanencia en la agrupación, obteniendo una media de 2.2 cópulas por individuo al final de la temporada (varianza = 6.0). Aquellos machos que llegaron al área de reproducción temprano en la temporada copularon a una frecuencia similar, pero fueron más exitosos que los atacantes debido a una permanencia más prolongada en la agrupación reproductora. Estos últimos machos obtuvieron una media de 5.3 cópulas por individuo (varianza = 12.3).

La incidencia y el éxito de una redada grupal como estrategia de apareamiento dependió en parte de la topografía de la lobería. En Puerto Pirámide, donde los machos defendían territorios conteniendo piletones con agua y el acceso a la agrupación estaba limitado a unos pocos sitios durante la marea alta, las redadas ocurrieron infrecuentemente y fueron ineficientes.

Si bien durante las redadas grupales los atacantes sincronizaron su invasión al área de reproducción, no se observó entre ellos la formación de alianzas o coaliciones que sugiriera cooperación. Una redada grupal consistió en una acción colectiva contra el *status quo* similar, en forma, al cambio de líderes en una tropa de langures. La participación en redadas grupales favoreció el acercamiento de machos periféricos a hembras en estro con una menor probabilidad de riesgo que los ataques solitarios.
