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PUP ABDUCTION AND INFANTICIDE IN SOUTHERN SEA LIONS

by

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(With 3 Figures)
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Introduction

In some polygynous mammals, males start to reproduce later in life than females (*e.g.*, LAWS, 1956; GEIST, 1971; WITTENBERGER, 1979; CLUTTON-BROCK, 1982; LE BOEUF REITER, in press), and become sexually mature (*i.e.*, produce sperm) before they are physically and behaviourally in prime condition to compete with adult males for mates (HAMILTON, 1934). Consequently, although pubertal males are present on the breeding grounds, most of them are excluded from reproduction by large, dominant adults (CLUTTON-BROCK *et al.*, 1982; GISINER, 1985; CAMPAGNA *et al.*, 1988). One consequence of this exclusive arrangement is that subadult males engage in mating strategies which differ from those performed by the most successful individuals (LE BOEUF, 1974; RUBENSTEIN, 1982). Such mating restrictions on subadult males may also cause redirection of sexual-like behaviours by such males toward female substitute objects, such as other conspecifics of the same sex, infants, or members of other species (KUMMER, 1968).

In the otariids, one of the most polygynous mammalian groups (BARTHOLOMEW, 1970), large adult males monopolize mating, repelling

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younger males away from females (HAMILTON, 1934, 1939; BARTHOLOMEW & HOEL, 1953; GENTRY, 1970; GISINER, 1985). In some otariid species, while adult individuals are reproducing, outcast males engage in reproductive-like behaviours with pups. Males seize pups, abduct them away from females, hold and defend them against other males, and sometimes mount pups (VAZ-FERREIRA, 1965; MARLOW, 1975). This treatment may be detrimental to pups, who sometimes are traumatized and killed (MARLOW, 1975), and for the parents, who may suffer a reduction in their reproductive success, while it has uncertain consequences for the perpetrators. The behaviour of subadult males with pups suggest that, during the process of maturation of male reproductive behaviour, there is a conflict of interests in which infants and adults have something to lose due to the subadults' behaviour, at an apparent trivial cost to the latter.

This paper reports seizure of pups by male southern sea lions, *Otaria byronia* during the reproductive season. In this species, breeding males sequester females, defending them against competitors that band on the periphery of the breeding area (CAMPAGNA, 1985; CAMPAGNA & LE BOEUF, 1988). Adult and subadult peripheral males, excluded from the place where most females congregate, initiate group raids into the breeding area attempting to seize females. Raids result in some males losing females, others gaining females, and females being redistributed in the breeding area and separated from their pups (VAZ-FERREIRA, 1965, 1975; CAMPAGNA *et al.*, 1988). Subadult peripheral males are usually unsuccessful at securing females but, acting individually or as members of a raiding party, they seize pups, abduct them, and sometimes kill them (VAZ-FERREIRA, 1975; CAMPAGNA *et al.*, 1988). Here we describe in detail the context, form, frequency, and consequences of pup seizures and abductions, and compare this event in *Otaria* with infants being seized and killed in other marine and terrestrial mammals. We conclude that pups are used by southern sea lion subadult males as female substitutes; from this behaviour, males may gain experience in controlling and defending mates later in their life.

Methods

Daily observations were conducted at Punta Norte, Península Valdés, Argentina, from 0800 to 2100 hrs, during four breeding seasons, December 15 to February 10, 1983-1986.

In mid-January, peak of the breeding season, Punta Norte is composed of about 450 adult males and females, and 400 pups grouped just above the high tide line of a wide pebble beach (CAMPAGNA, 1985). We refer to this place as the central area (CBA). Females give birth to a single pup and most of them do so within three days of their

arrival at the rookery. Females copulate once, six days after giving birth, and go to sea to forage about eight days after parturition. Thereafter, females alternate periods of 2-3 days feeding at sea with similar periods of nursing their pups. Pups one to six days old spend most of the time near their mothers. Older pups are more mobile, but move within the limits of the CBA. Detailed information about the area and the breeding biology of males and females is summarized in CAMPAGNA (1985), CAMPAGNA & LE BOEUF (1988), and CAMPAGNA *et al.* (1988).

Behavioural observations were conducted from a cliff, seven metres above the colony and 30 m distant from it. We recorded the form, location, and consequences of every pup seizure and abduction that occurred during daylight hours during the entire breeding season. By seizure, we mean that a pup was grabbed by a male in his jaws and was forcibly held by him, for at least a few seconds. After a pup was seized, we called it an abduction if a pup was successfully carried off by force, five or more metres away from the CBA, and held there at least for a few minutes.

We attempted to identify the sex of seized and abducted pups to determine if there was a sex bias in the occurrence of these behaviours. To estimate if abducted pups were weak or abandoned individuals, susceptible to die independently of having been abducted, we interrupted eight abductions within ten minutes after they had started. These pups were sexed, marked with paint, and released near the CBA, and their presence and behaviour were recorded several times per day.

The breeding area was censused daily, differentiating pups, adult males in the CBA and the periphery, females, and subadult peripheral individuals. Males in the CBA were called residents. Binoculars and a spotting scope were used to census and record behavioural data.

Results

Context and description of pup seizures and abductions.

Most seizures took the following form. A male approached the CBA from the periphery, alone or as a member of a raiding party, and dashed into the breeding group moving toward a pup. The male grabbed the pup, and quickly attempted to take it away from the breeding group (Fig. 1). In the rush, the pup sometimes fell from the male's jaws while he was moving away from the CBA, and it scrambled back into the breeding group in a few seconds. More often, the male held the pup firmly while moving off, and carried it out, away from resident males (Fig. 2a, b). At this point, the abductor dropped the pup, remained at less than a metre from it, and ignored the pup so long as it stayed near him. But typically, when pups were released, they tried to escape. The abductor immediately reacted to a pup's movement by preventing it from moving further by interposing his body in the pup's way, and by holding the pup crushed against the pebbles (Fig. 2c). While being held, sometimes pups were grabbed, shaken violently from side to side, and tossed into the air. Pups were injured and sometimes killed in this manner. Abductors defended pups by threatening and occasionally fighting peripheral males who attempted to approach them.



Fig. 1. A subadult male abducting a pup.

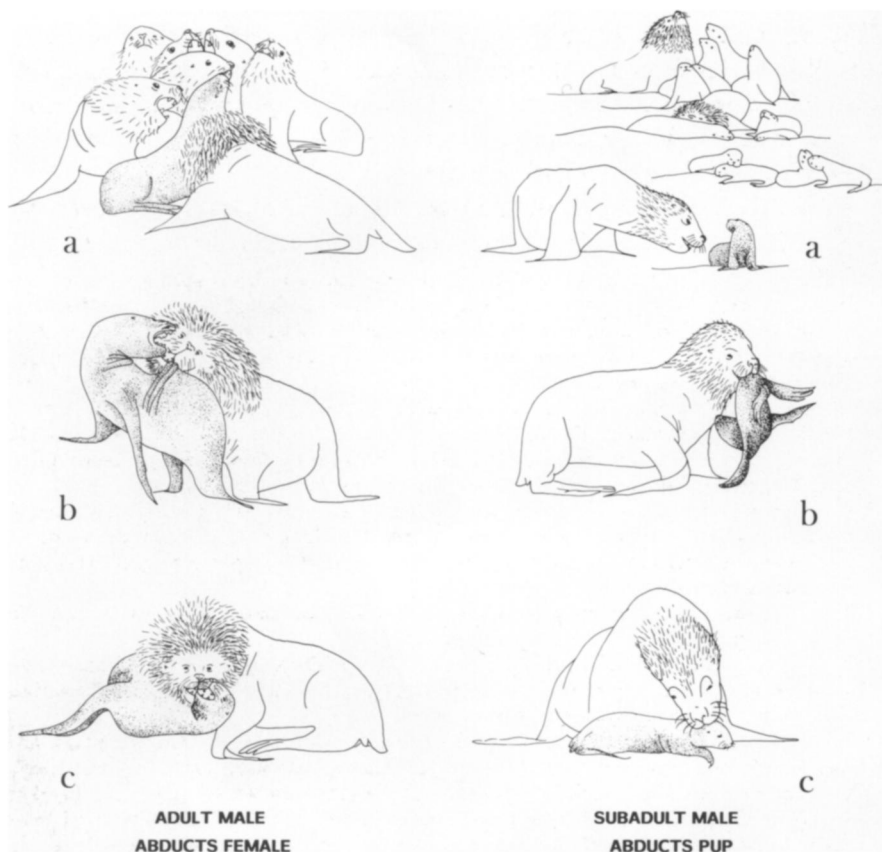


Fig. 2. Comparative schematic sequence of a pup and a female abduction.

Some males mounted pups, fully covering them with their massive bodies. Abductors sometimes held the flanks of pups with their foreflippers in the same manner that adult males sometimes held females that resisted copulation. While mounting pups, abductors performed pelvic thrusting movements and occasionally everted the penis. Intromission was not observed.

Some pups were taken to sea. Often the abductor and the pup were followed by other peripheral males. At times, the pup was surrounded in the water by several males, who competed to control it, grabbed it, and repeatedly submerged it. While swimming among the males, pups were bitten and tossed into the air several times. Pups swam frantically and erratically, stretching their necks out of the water. Tidal conditions par-

tially dictated a pup's fate. At high tide, pups had difficulty swimming through the surf back to the breeding group. They often ended up on the beach at a distance from the females. At low tide, pups could more easily return to the CBA by swimming and walking in the rocky intertidal channels located perpendicular to the beach.

Field notes on a pup abduction on January 22, 1983, illustrate this type of event and provide additional details of the behaviour:

- 1215 (p.m.). At low tide, a subadult male coming from seashore grabs a pup from the CBA. He takes the pup 10-15 m toward the sea. After shaking it vigorously, he drops the pup. A peripheral adult male chases the abductor, who moves momentarily away from the pup, but manages to recapture it. He grabs the pup in his jaws and carries it further away from the CBA, toward a group of seven young males resting at the seashore. The pup is isolated from the breeding animals, it is dropped on the beach, and disputed by the males. During the scramble, one male tosses it into the water and carries it, partially submerged, 60-70 m off the coast, straight away from the breeding area. The male with the pup is followed by three other males.
1223. The pup is in the water surrounded by four males. One of them carries it through channels in the intertidal, 100-150 m off the shore. The pup tries to climb out of the water, onto the rocks in the intertidal, without success. It is repeatedly grabbed by the abductors and thrown into the water.
1227. The abductors momentarily abandon the pup and move out, away from the shore. The pup swims slowly toward the shore.
1232. The pup arrives within a few metres from the pebble beach when it is approached by four other males. These males nose it and leave it alone. The pup finally arrives at the beach and rests. It is still isolated from the CBA.
1241. A new male approaches the pup. This time it is grabbed, shaken violently, and taken back to sea. Other males join the couple. The pup attempts to bite the abductors.
1250. The pup rests on a rock in the intertidal, close to several young males, 10-50 m away from the coast and 70-100 m from the site where it was originally abducted. Two males dispute the pup, pick it up once again, and carry it directly away from the breeding group.
1300. An adult male approaches from the sea and chases away the males surrounding the pup. The recently arrived male proceeds toward the coast, followed by the pup. Both are now about 150 m from the breeding group and keep moving toward the coast. The male ignores the pup.
1315. The pup moves towards the breeding group. It pauses frequently.
1340. The pup arrives at the beach almost in front of the breeding area. It approaches an adult male associated with a female. The female noses the pup and rejects it. The male ignores it. The pup goes towards a pod of pups and remains there until we lose track of it.

While being held by a male, pups often bit the male in the neck, face and flippers, but this had little effect on the male's behaviour. Pups vocalized, attracting the attention of other males and of females, who were alert, and sometimes replied to the call. Mothers responded to the approach of a peripheral male with an open mouth threat, and often bit peripheral males that came too close to them or their pups. However, females did not usually pursue pups once they had been abducted, so males did not gain a mate by abducting pups. The few females who

attempted to recover their pups from abductors made themselves vulnerable to injury by peripheral males. Twice we observed a female leaving the CBA in pursuit of a pup and its abductor. One of these females rushed quickly back to the CBA after being less than 10 m out of it, when peripheral males started to converge on her. The other female was intercepted by several peripheral males before she reached the pup, and before she was able to retreat to the CBA. Males fought over her, and bit, pushed and mounted her several times. She finally returned to the CBA without recovering the pup and with tooth punctures on her neck. In most episodes of pup abduction we did not see any reaction from the breeding females, but the mother of the abducted pup may have been at sea foraging. Adult resident males ignored pups and abductors unless the latter remained too close to the CBA, in which case resident males threatened or chased them away.

Pup holding was terminated when the abductors deliberately released the pup, or the latter escaped. Sometimes, after 10-30 minutes of holding a pup, males seemed to lose interest in it and allowed it to leave. More often, a pup escaped while several males disputed it, or when a resident male threatened abductors, chasing them off. Once the pup had escaped to within 5-10 m from the CBA, it was difficult for peripheral males to recover it because resident males prevented their approach.

Incidence and frequency data.

During four breeding seasons we recorded 285 pup seizures. Seizures occurred every breeding season (Table 1). Assuming that a different pup was affected in each episode, about 21% of the pups born each season were seized.

Seizures occurred every season at a similar rate (Table 1). Pups were seized throughout the breeding season at a mean frequency of about two

TABLE 1. Frequency distribution of 285 seizures recorded during four different breeding seasons (includes all recorded abduction attempts from December to February)

Breeding season	Pup seizures	Seizures per hour of observation
1982-83	30	0.25
1983-84	80	0.23
1984-85	59	0.16
1985-86	116	0.24
Mean \pm sd	71 \pm 36	0.22 \pm 0.04

pups per day. Seizure frequency peaked during the last week of January, when about six pups were seized per day. Only a few seizures were recorded after the second week of February (Fig. 3).

In 43% of 285 seizures, the pup fell from the male's jaws while he was moving away from the CBA, and scrambled back into the breeding group before the male recovered it. In the rest (57%), the male grabbed the pup firmly and carried it away (Table 2). Within 5-10 minutes, the duration of a typical holding episode, pups were grabbed, shaken, and thrown into the air 10-50 times. Some pups endured this treatment for as long as two hours. Nine (5.5%) of 163 pups abducted were mounted by males, and 19 (11.7%) were carried to sea. At least six times during three years, a pup was taken up to two kilometres off the coast. In 37% of the abductions, the male had to defend the pup against other males. Pups were usually released at a mean distance of about 20 m from where they had been abducted ($n = 35$, range = 10-80 m).

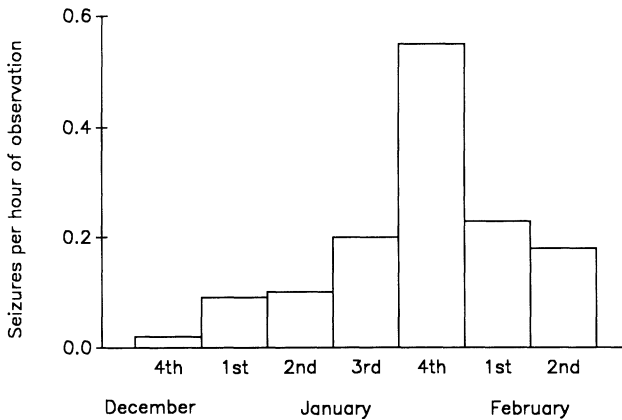


Fig. 3. Frequency distribution of 116 pup seizures that occurred weekly during the 1985-86 breeding season.

TABLE 2. Percentage of 285 pup seizures recorded during four breeding seasons in terms of the context and outcome

Context	Outcome		Total
	Lost	Abducted	
Raids	13	17	30
Solitary	30	40	70
Total	43	57	

In most pup seizures (70%), a solitary male rushed into the fringes of the breeding area and grabbed a pup. In the rest of the seizures (30%), the pup was grabbed by a male who was part of a raiding party (Table 2).

We recorded more episodes of abduction of male pups than of female pups (χ^2 -test = 4.18; d.f. = 1; $0.05 > P > 0.025$). The sex of 29 (18%) of 163 abducted pups was determined; 69% of them were males.

Age category of male abductors and risks involved in an abduction.

Males seizing pups were subadult individuals whose estimated age, based on size and secondary sexual characters, ranged between four and seven years. We never saw adult bulls seizing pups in the context of group raids or individual intrusions into the CBA. However, three times during three breeding seasons we observed adult males holding, biting, and tossing pups into the air. These males were not associated with females at the time that the pup was being held. One adult male had spent almost two days near a pup, apparently ignoring it, when he suddenly grabbed it, and took it into the water until we lost track of both.

Each breeding season, several different subadult males seized and abducted pups. For example, two of ten subadult males marked with paint pellets in 1984 abducted at least one pup. Five other males, identified by their size and fur color, also seized pups. These seven males together performed less than 20% of the 80 seizures observed during that season, so other males were also involved in seizing and abducting pups. One identified male seized three pups during the same group raid; another male abducted three pups during the same week.

Seizures and abductions were not usually hazardous events for males. During raids, subadult males gained safety in numbers, and exploited the chaos created in the CBA by raiders (CAMPAGNA *et al.*, 1988). Resident males rebuffing raiders concentrated on fighting adult males rather than subadult raiders (CAMPAGNA *et al.*, 1988). When acting alone rather than in a raid, pup abductors behaved quickly and unobtrusively. We never saw a male being wounded by another male or by a female while abducting a pup or holding it on the periphery.

Pup mortality associated with abductions.

Between 1983-1986, at least 16 pups died due to physical injuries caused by male abductors; 5.6% of the pups abducted and 1.3% of the pups born each year died due to harm caused by males during abduction. At

least once, a pup was killed, probably asphyxiated, when a subadult male mounted it for 20 min. Immediately after this episode, the same male mounted another pup, but released it in a few minutes without killing it. Pups were usually alive when the abduction occurred, but once, a male grabbed a pup carcass, defended it, and disputed it with another male.

Internal bleeding, due to physical trauma, was one apparent cause of pup death. We retrieved the carcasses of five pups that died a few hours after being abducted. All had bite wounds around the neck, face, head, back, and flippers. Extensive haematomas infiltrated the cervical muscles under the tooth puncture marks. Two of the carcasses had a partially dried umbilical cord attached, suggesting that the pups that had been abducted were a few days old.

Some abducted pups may have died from starvation. Every December, the first two to three pups born died due to mother-pup separation caused by adult males. The first females to arrive at the breeding area were the subjects of disputes between adult males who attempted to hold them. Sometimes, a female with a pup was abducted by a male and, while the abductor held her near him, another male held her pup. Pups were not mistreated by these males, but neither a pup nor the female were allowed to reunite, despite both being sometimes just a few metres apart.

In an unusual circumstance, a juvenile male killed a pup by sitting on it for about five minutes. The pup had been injured, presumably during a group raid. It was still alive, but was shaking its head from side to side without moving the rest of its body. A few minutes after we saw the pup, a young male approached slowly, and sat on it, maintaining a typical upright resting posture. When he moved away from the pup, five minutes later, it was dead.

Ours is a conservative estimation of pup mortality due to abduction because, although most pups did not die in most abductions, some of them may have died later due to internal trauma and injuries. Every season, we observed three to six pups with large lacerations on the head and back, and two or three pups with swollen necks, probably due to haematomas. These injuries may have been caused during abductions. Although pups were occasionally grabbed and tossed by females, we never saw a pup being killed or injured by a female. Adult males occasionally trampled pups during territorial disputes or raids, but this did not cause lacerations or bloody necks. In addition, we lost track of nine of the 19 pups taken to sea. Some of these pups may have drowned or drifted away from the breeding area due to strong parallel currents. Even

those who returned were not safe. At least five pups returned to the coast more than 100 m from the CBA. Two of them died after three days, and we lost track of the rest. During three seasons, 12 other pups were seen 100 or more metres away from the breeding area due to unknown reasons; all of them died after a few days.

Abducted pups were not abandoned or weak individuals, likely to die even if not abducted. All eight pups whose abductions we interrupted were alive one week later. Seven of them nursed regularly. Apparently, one did not find its mother but stole milk from several females until we lost track of it.

Discussion

The abduction of pups by subadult males appears to be a low-cost epiphenomenon of male sexual motivation. An explanation for the observed 'pedophilia' is suggested by the similar treatment of pups by subadult males and adult females by adult males (Fig. 2). Subadult male southern sea lions appear to use pups as female substitutes to redirect their frustrated sexual and aggressive motivations. In the face of high sexual motivation, males that have little or no experience with the appropriate sexual stimuli, oestrus females, are likely to generalize to more easily obtained objects, such as pups. In addition, there is the possibility that the phenotypic characteristics that make mature females sexually attractive are juvenile-like. In any case, the combination of a stimulating environment, lack of experience with the appropriate sexual object, and stimulus generalization may cause subadult males to redirect their behaviour (TINBERGEN, 1952) and choose objects unsuitable for sexual behaviour. Males do not obtain obvious, immediate reproductive benefits from seizing pups but, by practicing with them, they may gain experience in securing females later in life.

Pup seizures and abductions are not restricted to one rookery, or to the genus, *Otaria*. These events have been observed at five other southern sea lion rookeries. Three of these are located on Península Valdés (E. CRESPO, pers. comm.; CAMPAGNA, unpubl. data); the other two are in Uruguay and Peru (VAZ FERREIRA, 1965, 1975; P. MAJLUF, pers. comm.). Among other otariids, male Australian sea lions, *Neophoca cinerea*, bite, toss, mount, injure, and sometimes kill pups. Pup mistreatment by males is an important cause of pup mortality in this species (MARLOW, 1975). Male New Zealand sea lions, *Phocarcos hookeri*, mount pups and perform pelvic thrusting movements on them (MARLOW, 1975).

In the context of agonistic territorial interactions, harem bull northern fur seals, *Callorhinus ursinus*, seize, shake, and toss pups in the air (BARTHOLOMEW, 1953). Among the phocids, the most dramatic similarities with *Otaria* are found with the northern elephant seal, *Mirounga angustirostris* (LE BOEUF, in press). Subadult elephant seal males approach weaned pups, bite them on the neck and back, and attempt copulation with them. About 50% of the weaners at Año Nuevo mainland have fresh tooth punctures or scars, particularly in the neck and back, suggesting they have been bitten by males (LE BOEUF, in press). Some weaners are killed by males. Male southern elephant seals, *M. leonina*, have also been reported to hold pups, attempt copulation, and sometimes kill them (CARRICK *et al.*, 1962). One southern elephant seal male killed several weaners in this manner at Península Valdés, Argentina (J. C. LÓPEZ, pers. comm.).

Among terrestrial mammals, male primates, particularly baboons and macaques, use infants for their own benefit during social interactions with other conspecifics (PACKER, 1980; STRUM, 1984). Infants serve as 'passports' to gain access to resources and as 'agonistic buffers' to turn off the aggression of an adversary (HRDY, 1976; STRUM, 1984). This is not the case in southern sea lions; subadult males do not gain access to the breeding area by abducting a pup. Seizure and abduction of pups by male southern sea lions more closely resembles kidnapping of infants by young male hamadryas baboons, *Papio hamadryas* (KUMMER, 1968). This behaviour in baboons is virtually restricted to young males that do not have their own females. However, hamadryas baboon kidnappers apparently do not injure and kill infants (KUMMER, 1968), as sea lions do.

Infant 'exploitation' in other primates sometimes leads to abuse, during which the infant can be injured (HRDY, 1976). Physical abuse of infants has been reported for several terrestrial mammals, mainly human and non-human primates (STEELE, 1977; GELLES & STRAUS, 1979; GREEN, 1980; NADLER, 1980; DALY & WILSON, 1981, 1984; LENINGTON, 1981; LIGHTCAP *et al.*, 1982; REITE & CAINE, 1983). The form and consequences of pup abductions in *Otaria* resemble descriptions of infant physical abuse in some primates (see: STRAUS *et al.*, 1980; COOK & HOWELLS, 1981; REITE & CAINE, 1983). Evidence from baboons, macaques, and langurs suggest that males, especially those who are peripheral to the breeding units, are most likely to exploit and abuse infants (HRDY, 1976).

Infant abuse is sometimes a preface to infanticide (SPENCER-BOOTH, 1970; HAUSFATER & HRDY, 1984). An overwhelming amount of data sup-

port the contention that infanticide is widespread in nature (HRDY, 1974, 1977a, 1977b, 1979; HAUSFATER & HRDY, 1984). However, none of the theories of the adaptive significance of infanticide for the perpetrator that have been advanced for other species (see HAUSFATER & HRDY, 1984) are appropriate for *Otaria* for the following reasons. Sea lion abductors do not cannibalize pups as some other infanticidal mammals do (STRUHSAKER, 1977; HOOGLAND, 1985; TAKAHATA, 1985). Once an abducted pup is killed, males typically lose interest in it and abandon the carcass. Sea lion abductors cannot use pups to gain social control or dominance, as infanticidal leaders of a captive hamadryas baboon troop have been reported to do (RIJKSEN, 1981). One might expect that sea lion abductors would use pups as a mating strategy for luring their mothers out of the harem where they could mate with them, but this was never observed because females lacked the freedom to move easily. Perhaps shortage of food or breeding space is causally linked with pup stealing but there is no evidence that the food of sea lions is in short supply and breeding space was ample in all areas where infanticide was observed. Since females are also abducted and killed, males eliminate not only potential future reproductive competitors for them or their kin, but also potential mates. Pup killing cannot be a form of paternal manipulation of the progeny (*e.g.*, HRDY, 1979) because otariid males do not invest in offspring after insemination, and those who kill are in any case almost certainly never the sires, since they are too young. There is no need for males to kill pups to cause females to recycle, as suggested for African lions and hanuman langurs (HRDY, 1974, 1977a; PACKER & PUSEY, 1982, 1983). Otariid females enter into oestrus one to three weeks after parturition, despite nursing (CAMPAGNA & LE BOEUF, 1988) and again, the killers do not get to inseminate the mothers anyway. We do not know if females whose pups are killed have a better chance of weaning a pup next breeding season, as in female prairie dogs, *Cynomys ludovicianus*, (HOOGLAND, 1985). However, as female sea lions are inseminated shortly after parturition, a subadult male does not get a direct benefit from killing a pup.

Pup killing might be a spiteful behaviour that evolved because it decreases the reproductive success of others at a low cost for the actor (TRIVERS, 1985). Young males are unlikely to have fathered an abducted pup because they are rarely successful at copulating. The likelihood that a pup and its abductor are full or half siblings is unknown, although it is expected to be low. This is because the father of a male would probably be dead by the time his offspring is a subadult, and because only one out of several hundred pups in a rookery could have the same mother as the

abductor. Thus, it would be unlikely that subadult males are decreasing their inclusive fitness by killing or jeopardizing the life of pups. However, it is unclear what a male would gain from spiteful killing because, while reducing the fitness of others, he would also be benefiting many other unaffected individuals, diluting or eliminating his potential relative gain from interference competition.

Based on the present evidence, we conclude that infanticide in *Otaria* is of no particular adaptive value to their perpetrators. It appears to be a low-cost, nonadaptive byproduct of pups being treated as adult females. During competition for mates, *Otaria* males often injure and sometimes kill females (CAMPAGNA & LE BOEUF, 1988; CASSINI, pers. comm.). Pups would be even more vulnerable to harm than females because of the superior force and larger size and weight dimorphism between a subadult male and a pup, than between an adult male and a female. Evidently, males are not strongly motivated to kill pups because this would be an easy task and many more abductions would end in infanticide than we observe. Instead, pup killing is relatively rare, and occurs after a long series of interactions during which pups are physically subdued. Similarly, killing of pups by northern fur seal bulls seems to be the result of accident rather than of selected infanticidal behaviours.

Despite the relatively low frequency of pup killing in southern sea lions, a pup killed or injured may represent a significant reduction in female reproductive success. As breeding is seasonal, females that lose a pup lose an entire breeding year. Males that father pups that are killed by other males also suffer a decrease in reproductive success. Therefore, the behaviour of subadults is in conflict with the interests of adults of both sexes and pups.

Summary

1. Southern sea lions, *Otaria byronia*, seize suckling pups, and take them away from the breeding animals. Females did not leave the central breeding area in pursuit of their pups.

2. During four breeding seasons we recorded 285 pup seizures. A mean of 21 % of 400 pups born each season were seized by subadult males. Fifty seven percent of the pups seized were abducted and held captive.

3. Subadult males treat pups in the same way that adult males treat adult females, sequestering them and preventing their escape. Males were possessive, held pups for up to two hours, and defended pups from other males. Pups attempting to escape were bitten, shaken from side to side, and tossed into the air. In 9 % of the abductions males mounted pups, but intromission did not occur.

4. Abducted pups were sometimes injured and killed. Some pups had bite wounds on the neck, back and flippers, and lacerations on the head and neck; 5.6 % of the pups seized, and 1.3 % of the pups born each season died due to physical abuse. Dead pups

had tooth puncture wounds and extensive haematomas. In addition, 19 pups abducted during four seasons were taken to sea; nine of these pups were not seen again and may have drowned. Since breeding is seasonal, females that lose a pup lose an entire breeding year.

5. Males do not obtain immediate reproductive benefits from pup abductions. Pups may be used as female substitutes by males that are sexually but not physically competitive with adults for mature mates. Through practice with pups, ousted males may gain experience in controlling adult females. Infanticide appears to be a by-product of males treating pups as females. Pups are vulnerable because of the superior force and larger size of abductors.

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Resumen

1. Los lobos marinos del sur, *Otaria byronia*, raptan crías lactantes de las agrupaciones reproductoras. Las hembras no abandonan el grupo reproductor para perseguir a sus crías.

2. Durante cuatro temporadas reproductivas registramos 285 intentos de rapto de crías. En promedio, el 21% de las 400 crías nacidas durante cada temporada se vieron expuestas a un intento de rapto por parte de machos subadultos. En el 57% de dichos intentos, una cría fue exitosamente raptada y conducida fuera de la agrupación reproductora.

3. Los machos subadultos trataron a las crías raptadas de una manera similar a como los machos adultos tratan a las hembras adultas, secuestrándolas, e impidiéndole escapar. Los machos raptadores mantuvieron a las crías cerca de ellos durante períodos de hasta dos horas, intentando impedir que otros machos se acerquen a ellas. Cuando una cría intentaba escapar ésta era mordida, sacudida de un lado a otro, y tirada por el aire. En el 9% de los raptos, el macho montó a la cría, pero no ocurrió cópula.

4. Los machos ocasionalmente lastimaron o mataron a las crías raptadas. Algunas crías tenían heridas de mordeduras en el cuello, el dorso y las aletas, y laceraciones en la cabeza y el cuello. El 5.6% de las crías raptadas, y el 1.3% de las crías nacidas en cada temporada murieron debido al trato recibido. Las crías muertas presentaban heridas de mordeduras y extensos hematomas. Más aún, un total de 19 crías raptadas durante cuatro temporadas de reproducción fueron conducidas al mar por los machos raptadores. No se volvió a ver a nueve de dichas crías, y es posible que estas últimas se hayan ahogado. Como la reproducción ocurre por temporadas, una hembra que perdió a su cría perdió un año entero de su vida reproductiva.

5. Los machos raptadores no obtuvieron un beneficio reproductivo inmediato por raptar crías. Las crías podrían servir como sustituto de las hembras para aquellos machos que están sexualmente maduros pero que no tienen las características físicas adecuadas para competir con machos adultos por hembras reproductoras. A través de la práctica con crías, los machos subadultos podrían obtener experiencia sobre cómo controlar hembras adultas. Durante este tratamiento, las crías son fácilmente heridas debido al mayor tamaño relativo y a la fuerza de los machos raptadores.