

VIOLENT INTERSPECIFIC SEXUAL BEHAVIOR BY  
MALE SEA LIONS (*OTARIIDAE*):  
EVOLUTIONARY AND PHYLOGENETIC  
IMPLICATIONS

Violent sexual behavior is widespread intraspecifically in pinnipeds, where it can injure breeding females and has important evolutionary consequences for social organization (Bartholomew 1952, 1953, 1970; Kenyon 1960; Marlow 1967, 1975; Peterson 1968; Le Boeuf and Mesnick 1990; Mesnick and Le Boeuf 1991; Hiruki *et al.* 1993 $a,b$ ; Gentry 1995). In this note we describe violent sexual behavior by adult male southern (*Otaria byronia*) and Steller (*Eumetopias jubatus*) sea lions towards breeding females of other otariid species. Such behavior seems to be highly individualistic. We interpret the behavior as an "excess" of sexual selection, which may be triggered by a communication breakdown beginning with subtle and inappropriate signals from females towards heterospecific males. Since it appears to be widespread, violent interspecific sexual behavior by sea lions may result in far more hybridization than has been recognized and may have resulted in substantial introgression throughout the evolutionary history of Otariidae, retarding or obscuring patterns of speciation and phylogenesis (Repenning *et al.* 1971, Stirling and Warneke 1971, Berta and Deméré 1986).

Observations of southern sea lions were made while studying South American fur seals (*Arctocephalus australis*) near Cabo Polonio, Uruguay (34°24'S, 53°46'W) in January 1993, 1994, and 1995. Detailed observations on that species (with photographic and videotape records) were made on Isla de Lobos, Uruguay (35°01'S, 54°53'W), 7-18 January 1995. Both species breed on those islands, with fur seals in the majority: about 6,000 *Arctocephalus* and 800 *Otaria* are born on Isla Encantada each year, and about 30,000 and 2,500, respectively, on Isla de Lobos. Fur seal births occur from mid-November to early January, peaking in early December (Vaz-Ferreira 1975, Ponce de León

1983). Sea lions pup from early January to late February, with most births in late January (Vaz-Ferreira 1975, Campagna 1985).

Observations were made on breeding Steller and California (*Zalophus californianus*) sea lions during a detailed study of northern fur seals (*Callorhinus ursinus*) on San Miguel Island, California (34°02'N, 120°23'W), 1969–1973 (DeLong 1982). All three species breed on the island; during the study the relative numbers of pups born were 5,000:250:10 (*Zalophus*: *Callorhinus*: *Eumetopias*). Pups of the three species are born, respectively, 25 May–25 June (peak mid-June), 1 June–10 August (peak early July), and June–July (peak mid-June).

On Isla Encantada (at Cabo Polonio), four, five, and one recently dead (<2 d old) adult female *A. australis* were found above the high-water level in the same small area (~100 m<sup>2</sup>) in 1993, 1994, and 1995 (respectively). The area was used for breeding by females of both species, though *A. australis* was much more abundant; it was defended by a single adult male *Otaria* in all years. No adult male *A. australis* were present, because that species' breeding season was advanced, and the males had abandoned their territories. Blood was observed on the rocks and the heads of the carcasses, but the carcasses were not examined closely. Also in 1995 we found four freshly dead adult females (three *A. australis*, one *Otaria*) in an area of 10 m<sup>2</sup>; a single adult male *Otaria* was nearby. On another island (Isla del Marco) in 1995, we found two concentrations of freshly dead adult female *A. australis*: 13 in an area of ~200 m<sup>2</sup>, and seven in another area of ~100 m<sup>2</sup>; one adult male *Otaria* was near each concentration. At a third location on this island, we observed an adult male *Otaria* copulating with a nearly dead adult female *A. australis*. He was disturbed by our presence and moved away; as his penis was fully inserted into the female, she was dragged along with him for a short distance before he could disengage.

Our most detailed observations of *Otaria* were on 12–13 January 1995 on Isla de Lobos. On 12 January eight recently dead (from a few hours to <1 wk) adult female *A. australis* were found in an area of ~200 m<sup>2</sup>, from near shoreline to ~30 m inland. Two fresh carcasses were on a large flat rock near shoreline, where most female *A. australis* entered and exited the area. The area was used for breeding by both species and was defended by an adult male *Otaria*. He appeared to be healthy and in good condition, with a few minor fresh wounds on his neck and chest. No adult male *A. australis* were present because of the late date. At 0800 on 13 January the male *Otaria* and a female *A. australis* were on the large flat rock. The female started to move towards the sea, but she was immediately approached by the male who seized her by the nape, lifted her, flung her down, and mounted her. After 1 min the male seized the female by the nape again, dismounted (retaining his grip), then dragged the female a short distance and mounted her again. Two minutes later the female started to gape spasmodically every 5–10 sec; her spasmodic gaping continued for another 8 min, then her movements ceased. In this period, the male dismounted again, gripped the female by the nape, flung her down, then remounted, achieving insertion (insertion could not be ascertained earlier; Fig.

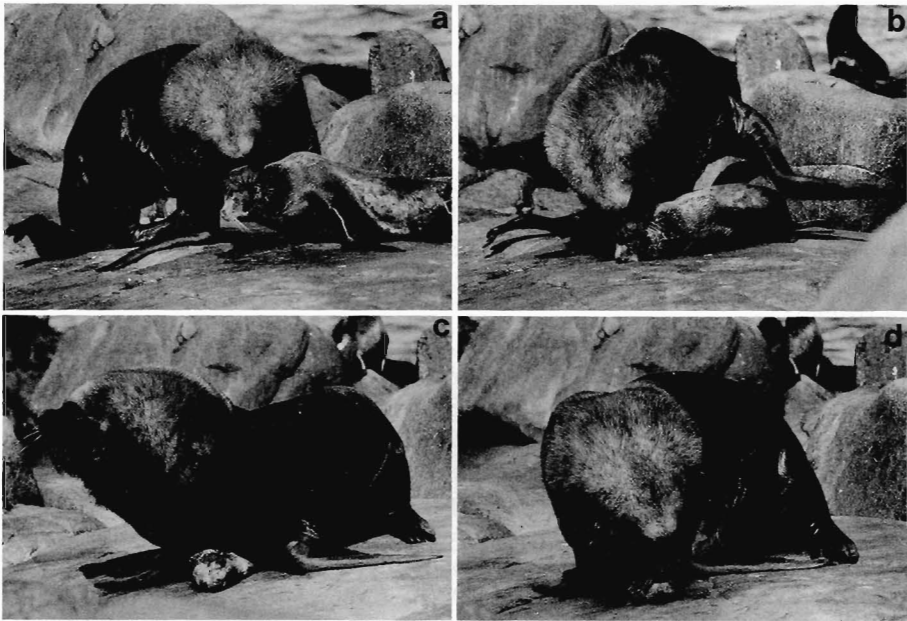


Figure 1. Forced copulation between adult male southern sea lion (*Otaria*) and adult female South American fur seal (*Arctocephalus australis*). The male gripped the female in the region of the right ear (a), then held her down as he mounted (b). After mounting, the male released his grip (c) and assumed a typical upright stance while barking (note the protracted mystacial vibrissae); the fur seal appeared to be dead by this time. The male leaned down several times to bite the female's crown or neck, as though to stimulate her to respond (d).

1). Bleeding wounds to the female's crown and nape were evident when the male picked the female up. The male's copulatory activity increased 1 min later, as evidenced by an increased rate of pelvic thrusting and "activation" of the female by biting her neck, as is typical of otariids (Le Boeuf 1972, Miller 1974). Several times the male gripped the female by the nape, lifted her slightly, and moved her forward  $\sim 1$  m, while remaining inserted. The male continued rapid thrusting for 7 min altogether, then remained mounted for another 30 sec before dismounting and moving away. The interaction lasted 23 min in total. Late on the morning of 14 January, we found another freshly dead female *A. australis* on the flat rock mentioned above; the same male *Otaria* (identified by natural markings) was still present.

All of the *A. australis* carcasses had puncture wounds on the crown and neck, consistent with being bitten. One female's eyeball was protruding from its socket, possibly due to the head being crushed. We skinned the female that we had observed in copulation, and noted an extensive subcutaneous hemorrhage covering dorsal and lateral surfaces of the right side of the skull. Her vagina was deep purple in color over most of its surface, up to and including the cervix. No semen was evident, suggesting that ejaculation had

not occurred. This is not surprising, as the dead female could not have participated in the species-typical interactive behavior with the male that normally occurs towards the end of copulation (Miller 1974). In keeping with this interpretation, the copulation that we observed was more than twice as long as the species' average (10.8 min; Campagna and Le Boeuf 1988).

All male *Otaria* that engaged in interspecific sexual behavior held territories that were isolated from conspecific males and held few or no breeding female *Otaria*.

Observations were made on interspecific sexual behavior by males of all three otariid species that breed on San Miguel Island (*Eumetopias*, *Zalophus*, and *Callorhinus*). *Callorhinus* males were seen to herd breeding female *Zalophus* that pupped on their territories and to interact aggressively with adult males of that species. No copulations were observed. Two instances of male *Zalophus* mounting female *Callorhinus* were noted. Both mountings were brief (<3 min), so intromission and ejaculation likely did not occur. Nevertheless, both genetic and phenotypic evidence of hybridization between the species was found (see below). More detailed observations were made on *Eumetopias*.

One territorial adult male *Eumetopias* was seen to copulate with a female *Zalophus* in seemingly normal fashion (DeLong 1982); the female survived. Another individually identifiable male *Eumetopias* was observed in many sexual interactions with female *Zalophus* in 1971–1973, a period when he held the same territory (he was present also in 1969–1970, but his behavior towards *Zalophus* escaped attention). He was observed to copulate with female *Zalophus* on 34 occasions and to attempt copulations with 61 others. Usually the male forcefully retained the females, for example by biting them on the head or neck. Most copulations involved pre-estrous females, but two involved females that solicited or were receptive to the male. Only 11 of the 34 females that copulated with the male survived; most died, apparently from suffocation or wounds to the head (12 of 45 skulls recovered from carcasses had punctures or broken elements). Over the three years of observation, at least 84 female *Zalophus* died as a direct result of interactions with this male (DeLong 1982). The same male *Eumetopias* often caught male (subadult and small adult) *Zalophus* and lay upon them until they died. He was seen to kill 12 *Zalophus* males in this way (DeLong 1982).

The two male *Eumetopias* that engaged in interspecific sexual behavior held territories in an area dominated by breeding *Zalophus* and were separated from other breeding *Eumetopias* by 500–800 km.

Scattered observations suggest that male otariids injure or kill females surprisingly often. They have been observed to defend, mount, and even copulate with carcasses of their own and other species (Peterson and Bartholomew 1967, Miller 1974, Wilson 1979). In some instances the males have not killed the females; however, *e.g.*, within a few seconds of the male *Otaria* on Isla de Lobos dismounting the female *A. australis*, a subadult male *A. australis* mounted the carcass. Harcourt (1993) observed a female *A. australis* to die from being mounted by a subadult male *Otaria*, and Wilson (1979) saw a male Hooker's sea lion (*Phocarcos hookeri*) copulating with the carcass of a female New Zea-

land fur seal (*Arctocephalus forsteri*) that he probably had killed by attempted copulation. Best *et al.* (1981) observed a male southern elephant seal (*Mirounga leonina*) kill >100 breeding female *A. pusillus* through his violent sexual behavior over several successive breeding seasons.

The extreme sexual behavior that we observed seems to occur regularly though at low frequency in sea lions and may be important for our understanding of otariid genetics and phylogeny. Most of the female *A. australis* and *Zalophus* that we observed in interspecific copulations died, but some survived so they could have produced hybrid offspring. In addition, several probable hybrids were noted. At Cabo Polonio a likely hybrid between *Otaria* and *A. australis* was captured and handled by F. Machado, a sealer of 50 years' experience (personal communication). The animal was a juvenile male, with a sea-lion-like face and head (large head, thick short snout), but fur-seal-like pelage. On San Miguel Island in 1972 and 1981, three ostensible *Callorhinus* pups were seen with the odd characteristic of fur extending onto the foreflipper beyond the wrist (DeLong 1982; E. Jameyson, personal communication)—a diagnostic feature of sea lions and *Arctocephalus* that contrasts with the sharp demarcation between pelage and bare skin at the wrist in *Callorhinus* (Repenning *et al.* 1971, King 1983). Electrophoretic evidence suggests that the 1972 animal was a *Callorhinus/Zalophus* hybrid (D. Duffield, personal communication). Natural hybridization between antarctic (*Arctocephalus gazella*) and subantarctic (*A. tropicalis*) fur seals occurs regularly in some places (Condy 1978, Shaughnessy *et al.* 1988, Gales *et al.* 1992); hybridization between other *Arctocephalus* species likely occurs but has gone unnoticed until recently because no other species is as strikingly marked as *A. tropicalis* (S. D. Goldsworthy, personal communication). In captivity, hybrids between female *Zalophus* and male *A. pusillus*, and between female *Zalophus* and male *Otaria*, have been born (Jennison 1914, Schliemann 1968, Kirchshofer 1968). In summary, there is abundant evidence of interspecific sexual behavior and hybridization in otariids, and some wild hybrids are viable and survive to maturity (*e.g.*, Condy 1978). We suggest that some of this hybridization is attributable to violent sexual behavior by male sea lions towards heterospecific females.

Several features of otariid life history and behavior promote interspecific contact during the breeding period, setting the stage for interspecific sexual behavior and hybridization. Otariids exhibit high dispersal and notable long-distance movements (Shaughnessy 1970, Shaughnessy and Ross 1980, Taylor 1990, Gales *et al.* 1992, David *et al.* 1993), rapidly colonize breeding sites (Peterson *et al.* 1968; Taylor 1982, 1992; Shaughnessy *et al.* 1988; Dix 1993), and occur in mixed colonies (Orr 1965, Condy 1978, DeLong 1982, Shaughnessy *et al.* 1988). Some pups in mixed colonies (particularly those in the minority species; see Arnold 1992) must be exposed to numerous interspecific social interactions throughout development. They may thereby acquire a social preference for heterospecific pups that influences them as adults (Gentry 1974, DeLong 1982), when their social and nonsocial behavior is highly individualistic (Kenyon 1960; M. W. Cawthorne and D. S. Horning, cited by Matlin 1978; Gentry and Johnson 1981; Harcourt 1992, 1993; Gentry 1995). Finally,

geographic isolation probably reinforces any tendencies of minority species towards heterospecific interaction (e.g., *Eumetopias* on San Miguel Island).

Intense sexual selection may lead to rapid divergence in mating signals between allopatric conspecific populations, thereby accelerating speciation (Sibley 1957, West-Eberhard 1983). Otariids might be expected to conform to this generalization because of the pronounced polygyny in the group. However, otariids differ from animal groups that most sexual-selection theory is based on (anurans, birds, acoustic insects), where long-distance mate-attraction signals prevail. In otariids, sexual selection acts mainly on male attributes that promote access to breeding females and control of them; little or no direct mate choice occurs (Miller 1974, 1975; Gentry 1995). Consequently, sexual selection has led to the evolution of aggressive sexual behavior in males (notably in the highly derived sea lions) that may injure or kill conspecific or heterospecific females, and that females may be physically unable to resist [pregnant female *Otaria* and unreceptive female Australian sea lions (*Neophoca cinerea*) may be physically overpowered by males, who then copulate with them: Marlow 1975, personal observation]. We do not wish to downplay the important role that female behavior may play in instances of natural hybridization between otariid species. Females may provide inappropriate signals to heterospecific males during social interactions, leading to abnormal escalation of male behavior. We focussed on male behavior because it is so dramatic and conspicuous, yet the key to understanding our observations may lie in the subtle reactions of heterospecific females, including pheromonal cues and unobservable internal interactions during copulation (Eberhard 1996). This may be particularly true of *Arctocephalus* fur seals, where hybridization and introgression are common, and where non-violent sexual behavior by males towards heterospecific females is the norm—in contrast to the larger and more recently derived sea lions (S. D. Goldsworthy, personal communication).

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EDWARD H. MILLER, Biology Department, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada; ALBERTO PONCE DE LEÓN, Instituto Nacional de Pesca, División Mamíferos Marinos, Constituyente 1497, C.P. 11200, Montevideo, Uruguay; ROBERT L. DELONG, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115, U.S.A. Received 8 May 1995. Accepted 25 September 1995.