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Lesions and Behavior Associated with Forced Copulation of Juvenile Pacific Harbor Seals (*Phoca vitulina richardsi*) by Southern Sea Otters (*Enhydra lutris nereis*)

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Abstract

Nineteen occurrences of interspecific sexual behavior between male southern sea otters (*Enhydra lutris nereis*) and juvenile Pacific harbor seals (*Phoca vitulina richardsi*) were reported in Monterey Bay, California, between 2000 and 2002. At least three different male sea otters were observed harassing, dragging, guarding, and copulating with harbor seals for up to 7 d postmortem. Carcasses of 15 juvenile harbor seals were recovered, and seven were necropsied in detail by a veterinary pathologist. Necropsy findings from two female sea otters that were recovered dead from male sea otters exhibiting similar behavior are also presented to facilitate a comparison of lesions. The most frequent lesions included superficial skin lacerations; hemorrhage around the nose, eyes, flippers, and perineum; and traumatic corneal erosions or ulcers. The harbor seals sustained severe genital trauma, ranging from vaginal perforation to vagino-cervical transection, and colorectal perforations as a result of penile penetration. One harbor seal developed severe pneumoperitoneum subsequent to vaginal perforation, which was also observed in both female sea otters and has been reported as a postcoital lesion in humans. This study represents the first description of lesions resulting from forced copulation of harbor seals by sea otters and is also the first report of pneumoperitoneum secondary to forced copulation in a nonhuman animal. Possible explanations for this behavior are discussed in the context of sea otter biology and population demographics.

Key Words: sea otter, *Enhydra lutris nereis*, harbor seal, *Phoca vitulina richardsi*, forced copulation, interspecific sexual behavior, mating trauma, pneumoperitoneum

Introduction

Sexual interactions between species have been well-documented among marine mammals (Wilson, 1975; Best et al., 1981; Harcourt, 1993; Hatfield et al., 1994; Miller et al., 1996; Mortenson & Follis, 1997; Cassini, 1998; Hayward, 2003). Such behavior has occasionally been observed among pinnipeds with overlapping breeding seasons that share the same rookeries, providing ample opportunities for interaction between adult or subadult males and heterospecific females (Miller et al., 1996). Documentation of hybrid offspring within mixed colonies of otariids (Miller et al., 1996) and phocids (Kovacs et al., 1997) further supports the occurrence of breeding events between pinniped species.

Reports also exist of interspecific sexual interactions occurring outside of the normal breeding season in which a single aggressive male opportunistically copulated with females or pups during periods when conspecific males were not present (Wilson, 1975; Best et al., 1981; Miller et al., 1996; Mortenson & Follis, 1997; Hayward, 2003). Large-scale mortality has resulted when females and juveniles were physically overpowered and forcibly copulated by much larger heterospecific males (Best et al., 1981; Miller et al., 1996; Mortenson & Follis, 1997; Cassini, 1998). In some cases, male pinnipeds have approached their subjects on land or in the water, mounted and attempted copulation (Wilson, 1975; Best et al., 1981; Harcourt, 1993; Miller et al., 1996; Mortenson & Follis, 1997; Hayward, 2003), killed the subject (Best et al., 1981; Harcourt, 1993; Miller et al., 1996; Mortenson & Follis, 1997), and then continued to guard and copulate with the carcass (Best et al., 1981; Miller et al., 1996).

Interspecific mating behavior involving southern sea otters (*Enhydra lutris nereis*) was documented previously in the California Channel Islands, where two different males were observed interacting sexually with weaned harbor seal pups (*Phoca vitulina richardsi*) (Hatfield et al., 1994). These sea otters hauled-out on the beach with harbor seals, harassed and herded pups into the water or approached them in the water, grasped them from behind with their teeth and forepaws, bit them on the nose and face, mounted them, and attempted copulation. The harbor seals escaped by diving or by slowly swimming away when the sea otters paused to groom. None of these interactions were known to have resulted in harbor seal mortality.

The primary objectives of this study were to document the behavior and lesions resulting from forced copulatory attempts by male sea otters on juvenile harbor seals. For purposes of comparison, two cases of female sea otters that were killed as a result of forced copulation by male sea otters are also presented. Observational data collected during these interactions is also included to help interpret this behavior in the context of observed lesions and southern sea otter biology and population demographics.

Materials and Methods

Field Observations

Numerous observations of sexual interactions between male sea otters and juvenile harbor seals in Monterey Bay, California, were reported to local marine mammal stranding authorities between May 2000 and June 2002. Trained biologists from Moss Landing Marine Laboratories (MLML), the Monterey Bay Aquarium (MBA), and the California Department of Fish and Game (CDFG) independently confirmed these interactions and documented some events using video and still photography. Based on prior studies, available behavioral data for each observed interaction were coded into one or more categories, including harassing, herding, mate guarding, dragging the subject through the water, and forced copulation (Hatfield et al., 1994).

Carcass Collection

Carcasses of juvenile harbor seals were collected by the local marine mammal stranding network in Monterey Bay. Coastal stranding locations and corresponding latitudes and longitudes were recorded at the time of carcass recovery. Three criteria were utilized to select harbor seals for possible case inclusion: (1) carcasses recovered directly from male sea otters, (2) carcasses observed or reported in the immediate vicinity of a male sea otter, or (3) carcasses with lesions consistent with mating trauma that were recovered from sites where previous interspecific sexual interactions had been reported. In addition, carcasses of two adult female sea otters recovered directly from male sea otters by MBA and U.S. Geological Survey (USGS) biologists were included in this study to facilitate mating lesion identification and classification.

Necropsy and Lesion Classification

Harbor seal carcasses were necropsied by biologists at MLML or by a veterinary pathologist at CDFG. Sex was determined, and morphometric data were recorded, including standard length, axillary girth, and body mass. The age class of harbor seals was determined using the carcass recovery date relative to pupping season, standard length, body mass, pelage condition, tooth wear, the presence of milk or prey items in the stomach, and historical data for previously tagged animals (Bigg, 1969; Boulva & McLaren, 1979; Corpe et al., 1998). Both sea otters were necropsied by the same veterinary pathologist at CDFG as part of ongoing population health studies. Sea otter age class was determined using total length, dentition, and tooth wear according to categories previously established by Morejohn et al. (1975). For all carcasses necropsied at CDFG, the same systematic approach to measuring and quantifying gross lesions was employed to facilitate accurate comparison between cases. All fresh ($\leq$ 72 h postmortem) cases examined at CDFG included full-body radiographs, digital photographs, and microscopic examination of all major tissues. Formalin-fixed tissues were paraffin-embedded, sectioned at 5 μm, and stained with hematoxylin and eosin for examination by light microscopy. Vaginal and rectal cytology were performed in some cases to screen samples for the presence of spermatozoa.

Results

Field Observations

Observations of interactions between male sea otters and live and dead juvenile harbor seals are summarized in Table 1. The most common behaviors of male sea otters that were observed were mate guarding and dragging pups through the water (Figure 1). Mate guarding has been described in a variety of species as a male closely attending a female and defending her from rival males during the fertile period (Low, 2005; Willis & Dill, 2007). Male sea otters also were observed to feed, dive, groom, rest, and copulate with live and dead harbor seals. Interactions between sea otters and juvenile harbor seals lasted up to 7 d after the harbor seals had died. To initiate

Table 1. Demographic and observational data for documented cases of interspecific sexual interactions between male sea otters and juvenile harbor seals (n = 19)

Case number[a]	Age[b]	Sex[c]	Date[d]	Location	Male sea otter[e]	Summary of interaction
HS 1	W	M	12/5/2000	Monterey	N/A	
HS 2	P	F	21/5/2000	Monterey	696	Sea otter attempted copulation with live harbor seal that eventually died
HS 3	P	M	22/5/2000	Monterey	N/A	
HS 4	W	M	30/6/2000	Moss Landing	N/A	
HS 5	W	M	8/8/2000	Monterey	696	Sea otter in immediate vicinity of harbor seal carcass
HS 6	W	M	19/9/2000	Moss Landing	N/A	
HS 7	W	M	16/11/2000	Moss Landing	Untagged	Sea otter dragged harbor seal carcass through the water
HS 8	W	F	18/12/2000	Moss Landing	696	Sea otter dragged harbor seal carcass through the water
HS 9	W	F	21/12/2000	Monterey	696	Sea otter attempted copulation with harbor seal carcass
HS 10	SA	F	3/3/2001	Moss Landing	696	Sea otter in immediate vicinity of harbor seal carcass
HS 11	SA	M	28/3/2001	Moss Landing	N/A	
N/A	P	U	2/4/2001	Moss Landing	696	Sea otter harassed, guarded, and attempted copulation with live harbor seal that eventually swam off
N/A	P	U	20/4/2001	Moss Landing	Untagged	Sea otter dove and foraged with dead harbor seal; carcass not recovered
N/A	P	U	5/5/2001	Moss Landing	Untagged	Sea otter dove, foraged, and groomed with dead harbor seal; carcass not recovered
N/A	W	U	22/5/2001	Moss Landing	Untagged	Sea otter harassed, guarded, and attempted copulation with live harbor seal that eventually died; carcass not recovered
HS 12	P	M	11/4/2002	Moss Landing	224	Sea otter groomed next to harbor seal carcass and guarded it from others
HS 13	P	F	24/4/2002	Moss Landing	N/A	
HS 14	P	M	20/6/2002	Moss Landing	N/A	
HS 15	W	M	20/6/2002	Moss Landing	N/A	

[a]HS = harbor seal; N/A indicates that a carcass was not recovered
[b]P = dependent pup (0 to 1 mo); W = weaned pup (1 to 6 mo); SA = subadult (6 to 30 mo)
[c]M = male; F = female; U = sex unknown
[d]Date of observed behavior or date of carcass recovery if an interaction was not observed
[e]N/A = not applicable (harbor seal not recovered or interaction not observed)

contact, male sea otters were observed to haul-out near resting harbor seals and prevent them from entering the water by physically blocking their passage, biting them on the face, or wrestling with them. Male sea otters herded harbor seals into the water or targeted them in the water by grasping them by the head with their teeth and forepaws and then attempting copulation in the water.

In one case (included in Table 1 as an interaction dated 22 May 2001), a weaned harbor seal pup was resting onshore when an untagged male sea otter approached it, grasped it with its teeth and forepaws, bit it on the nose, and flipped it over. The harbor seal moved toward the water with the sea otter following closely. Once in the water, the sea otter gripped the harbor seal's head with its forepaws and repeatedly bit it on the nose, causing a deep laceration. The sea otter and pup rolled violently in the water for approximately 15 min, while the pup struggled to free itself from the sea otter's grasp. Finally, the sea otter positioned itself dorsal to the pup's smaller body while grasping it by the head and holding it underwater in a position typical of mating sea otters. As the sea otter thrust his pelvis, his penis was extruded and intromission was observed. At 105 min into the encounter, the

Figure 1. An untagged male sea otter guarding the carcass of an unidentified harbor seal pup while foraging in Elkhorn Slough, Moss Landing, on 20 April 2001; the pup was already dead when first observed, and the carcass was not recovered for necropsy.

sea otter released the pup, now dead, and began grooming. Unfortunately, this carcass was never recovered for necropsy.

Two male sea otters that initiated sexual interactions with juvenile harbor seals could be individually identified due to prior placement of flipper tags during rehabilitation at MBA. Sea otter 696 was a 6-y-old prime-aged adult that first stranded as a pup in 1995. After rehabilitation and release, he ranged along the central California coast within the southern half of Monterey Bay. Sea otter 696 was linked to five known harbor seal deaths (HS 2, 5, 8-10) and was attempting copulation with a sixth live harbor seal when he was captured in 2001 (Table 1). No significant abnormalities were noted on post-capture physical examination, complete blood count and chemistry panel, and plasma testosterone level. Sea otter 224 was an aged adult male (> 10 y) that initially stranded at Moss Landing harbor in January 2002. Physical examination at that time revealed a large paramedian subcutaneous abscess along the dorsal lumbar spine; a swollen, mildly lacerated penis; and multiple skin and soft tissue lacerations, all consistent with fight wounds inflicted by another male. This animal was treated and released 8 wks after the initial date of stranding. Later that same year, sea otter 224 was observed guarding a dead harbor seal pup (HS 12; Table 1). Additional interactions between untagged male sea otters and juvenile harbor seals were observed on multiple occasions (Table 1). The untagged sea otter(s) lacked any distinguishing characteristics, so the total number of sea otters interacting with juvenile harbor seals could not be determined.

Both female sea otters that were included for lesion comparison had been tagged previously and were being intensively monitored as part of ongoing research. SO 1 was recovered dead as an emaciated adult that had recently lost her 10-wk-old pup. She was observed mating with at least three different males over the 9 d preceding her death; two were study animals with flipper tags, while the third was untagged and might have been a transient that was passing through the territory of one of the tagged males. When this female was last observed alive 15 h before her death, she was floating on the surface with a markedly inflated abdomen and attempting unsuccessfully to dive. Her carcass was recovered the following day after biologists observed one of the tagged males dragging it through the water and attempting copulation. SO 2 was an adult female that was recovered dead after being dragged around by a tagged territorial male. She was last observed alive the day prior to carcass recovery, resting in a nearby kelp bed with another female. At the time of forced copulation and death, she had a full-term fetus

engaged in the pelvic canal, a patent and moderately dilated cervical os, well-developed mammary tissue with lactation, and protrusion of the chorioallantois from the vulva.

Carcass Collection

Fifteen carcasses of juvenile harbor seals (HS 1 to 15) recovered in Monterey Bay between May 2000 and June 2002 met the case definition for inclusion in this study: three seals were recovered directly from a male sea otter, four were recovered dead in the immediate proximity of a male sea otter, and eight exhibited lesions consistent with mating trauma. Recovery locations for harbor seals ranged from central to southern Monterey Bay. Of the two carcasses of female sea otters (SO 1 and 2) recovered directly from males, SO 1 was recovered in September 2003 off the coast of Cambria (N35.579, W121.123) and SO 2 was found in February 2005 offshore of Monterey (N36.623, W121.904).

Necropsy and Lesion Classification

Postmortem examinations of the first seven harbor seal carcasses (HS 1 to 7) were performed by biologists at MLML, and the subsequent eight harbor seals (HS 8 to 15) and the two female sea otters were necropsied by a veterinary pathologist at CDFG. Gross lesions are summarized for the ten animals examined in detail by a veterinary pathologist (Table 2). Superficial lacerations and hemorrhages were the most consistent findings in all cases. Lacerations were present on the nose (n = 8), flippers (n = 5), eyes (n = 6), chest (n = 2), and around the mouth (n = 1). Nose wounds ranged from superficial punctures to full-thickness skin lacerations with significant hemorrhaging. Ocular and periocular trauma were unique to the stranded harbor seals and consisted of scleral hemorrhage, hyphema, corneal abrasions, corneal excoriations, and lacerations and periocular swelling with exophthalmia (Figure 2).

External genital and perineal trauma, characterized by hemorrhages, skin lacerations, and swelling

Figure 2. Face of harbor seal HS 8; periocular trauma and facial lacerations are typical of those sustained from forced sexual interactions with male sea otters.

Table 2. A summary of lesions associated with forced copulation by a male sea otter for all cases necropsied by a veterinary pathologist (n = 10)

Case number[a]	Nose wounds/ superficial lacerations[b]	Ocular/ periocular trauma	External genital trauma	Pneumo-peritoneum	Vaginal perforation/ avulsion	Colorectal perforation
HS 8	+	+	+	-	+	-
HS 9	+	+	+	+	+	-
HS 10	+	+	+	-	+	+
HS 11	+	+	-	-	N/A	+
HS 12	+	-	-	-	N/A	-
HS 13	-	+	+	-	+	-
HS 14	+	-	+	-	N/A	+
HS 15	+	+	+	-	N/A	+
SO 1	+	-	-	+	+	+
SO 2	+	-	+	+	+	-

[a]HS = harbor seal; SO = seal otter

[b]+ = lesion present; - = lesion absent; N/A = not applicable (individuals are male)

of perianal and perivulvar soft tissue was observed for six harbor seals and one sea otter (Figure 3). Trauma to the urinary system was present in three harbor seals, characterized by acute hemorrhages and mild fibrin deposition on the ventral serosal surface of the bladder and urethra.

Traumatic lesions to the genital tract in harbor seals and sea otters included vaginal perforation (n = 6) and vagino-cervical transection (n = 1), with secondary pneumoperitoneum (n = 3). Vaginal perforations were 1 to 3 cm diameter, round to elliptical, and were located on the dorsal and lateral vaginal walls approximately 10 cm from the vulvar opening and immediately adjacent to the cervical os (Figure 4). Adherent clotted blood often was noted at the perforation site, along with extensive mural hemorrhage in the surrounding vaginal wall. In the most severe case, the vaginal tract was avulsed from its connection to the cervix, and the wound edges were irregular and were partially coated with clotted blood.

Traumatic colorectal perforations (n = 5) with leakage of intestinal contents into the abdominal cavity or perirectal soft tissues were found in four harbor seals and one sea otter, with both male and female animals affected. Colorectal perforations were 1 to 2 cm diameter, round, and were located 3 to 12 cm proximal to the anus. HS 10 exhibited multiple rectal perforations. The force associated with these rectal perforations is exemplified by the lesions found in HS 14; the sea otter's penis had perforated through the rectum into the skeletal muscle of the left medial pelvic wall, forming an artificial pocket filled with tightly compacted feces.

Pneumoperitoneum in HS 9 and both sea otters was characterized by severe abdominal distension, a tympanic abdominal wall, and marked cranial displacement of the diaphragm (Figures 5a, 5b & 5c). In all three cases, marked compression of the chest cavity was noted along with severe pulmonary atelectasis, which was most prominent in the caudal lung fields. For HS 9 and SO 2, the air leakage was associated solely with vaginal perforation, while SO 1 had both vaginal and rectal perforations. Observations of SO 1 attempting unsuccessfully to dive with a grossly distended abdomen before being found dead confirmed that this lesion developed antemortem. Other potential routes for air entry into the abdomen, such as penetrating injuries through the body wall, perforation of the gastrointestinal tract, or internal cyst or abscess rupture, were ruled out through postmortem radiographs and necropsy.

Microscopic examination of all major tissues from six freshly dead harbor seals did not reveal significant lesions other than mild verminous pneumonia (*Otostrongylus* spp.) (n = 5) and nasopharyngeal acariasis (*Halarachne* sp.) (n = 4). Both necropsied sea otters had mild intestinal acanthocephalidiasis. SO 1 also had a small thyroid adenoma and focal cerebral lymphocytic meningoencephalitis. This latter lesion could be

Figure 3. Perineum of harbor seal HS 8; mucosal excoriations and erythema, vulvar swelling, and blood staining on the hair coat surrounding the vaginal and anal orifices.

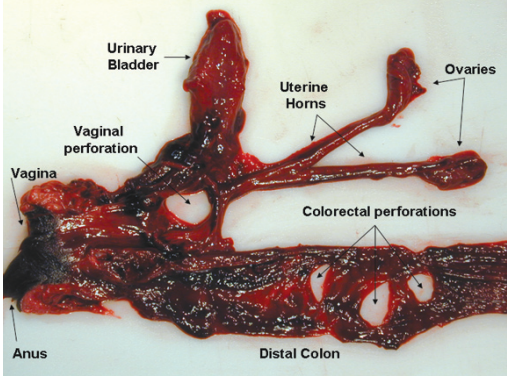

Figure 4. Genitourinary and distal gastrointestinal tracts of harbor seal HS 10; note the single vaginal perforation (3 × 3 cm) located just distal to the cervix, and three colorectal perforations (1.5 to 2.0 cm diameter) located 8.0 to 12.0 cm proximal to the anal opening. This animal had extensive mucosal hemorrhage of the cervix and vagina and leakage of intestinal contents (fish otoliths and bones) into the abdomen.

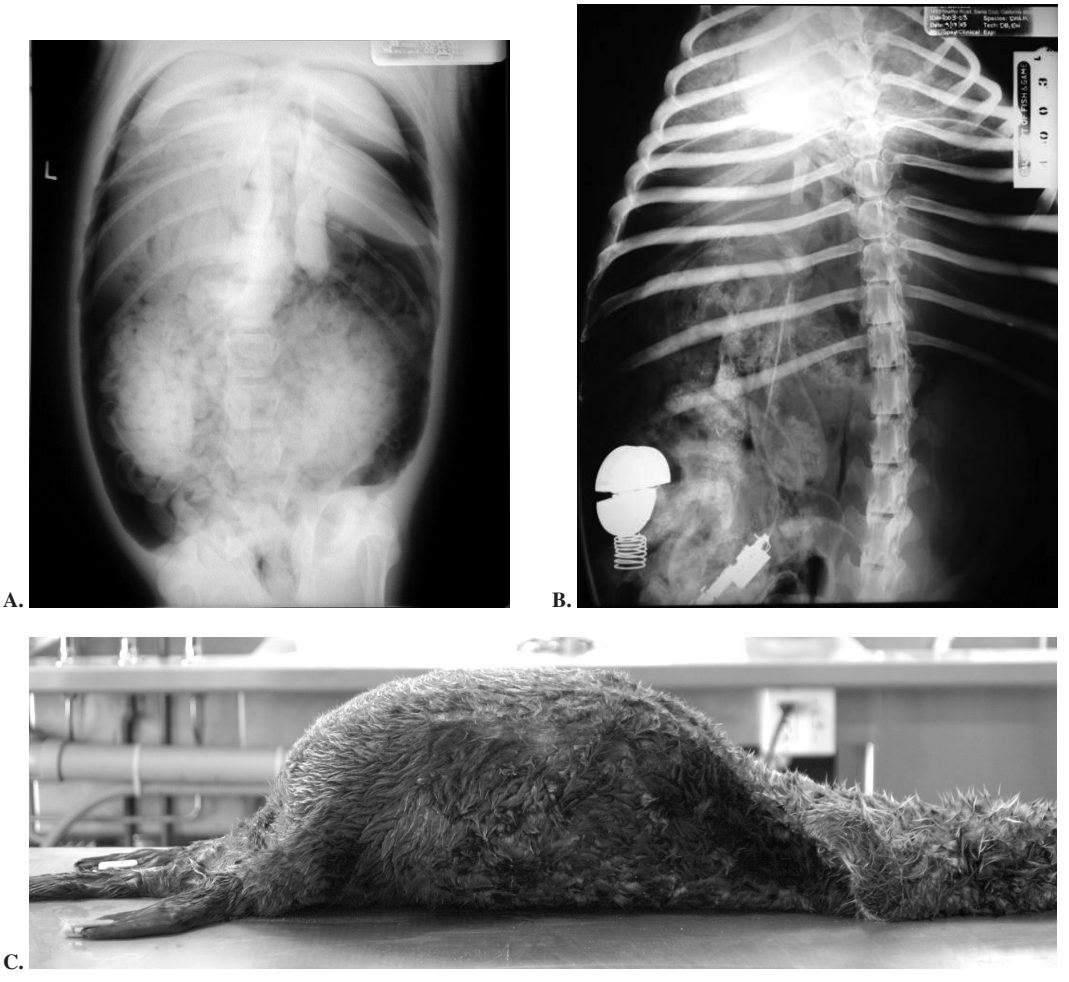

Figure 5. Radiographs and lateral view of torso in a harbor seal (A; HS 9) and a sea otter (B & C; SO 1), illustrating pneumoperitoneum secondary to vaginal perforation from forced copulation by a male sea otter; in the radiographs, note the cranial displacement of the diaphragm and free peritoneal air outlining the caudal border of the diaphragm, liver, intestines, and both kidneys. The intra-abdominal radio-transmitter and time-depth recorder in the sea otter (B) were surgically implanted 18 mo previously as part of ongoing sea otter health studies. This female sea otter was observed alive with gross abdominal distension, attempting unsuccessfully to dive the evening before it was found dead.

indicative of chronic *Toxoplasma gondii* infection, but no parasites were found near the lesion, and it was considered incidental. No spermatozoa were observed on vaginal or rectal cytology or microscopic examination of traumatized tissues.

Discussion

The behavioral observations and lesions described in this study are extreme examples of the spectrum of mating-associated trauma observed in southern sea otters. Copulation normally occurs in the water where the male sea otter will approach the female from behind, grip her around the chest with his forepaws, and grasp her nose or the side of her face with his teeth (Kenyon, 1969; Staedler & Riedman, 1993). Females often initially resist copulatory attempts, but eventually will submit, and the pair may roll and spin in the water, with the male positioned dorsal to the female during copulation (Kenyon, 1969). Immature males sometimes mimic this pre-copulatory behavior while playing with each other, including facial biting, spinning nose to nose, and mounting each other from behind (M. Staedler, unpub. data, 2000-2010). Facial biting by the male commonly results in the

development of skin and soft tissue lacerations of the female's nose and face that can occasionally be fatal (Foott, 1970; Staedler & Riedman, 1993). Trauma associated with mating was a primary or contributing cause of death for 11% of fresh dead southern sea otters examined between 2000 and 2003 (Kreuder et al., 2003). In one prior report on breeding-associated mortality, a tagged territorial male sea otter held a struggling female underwater until her body became limp and then copulated repeatedly with her carcass (Staedler & Riedman, 1993). Ten months later, this same male was observed with the carcass of another female sea otter. In both cases, the male was swimming, diving, guarding, and copulating with the carcass.

In other marine mammal species, females and juveniles of both sexes are sometimes injured or killed during mating attempts by male conspecifics (Campagna et al., 1988; Le Boeuf & Mesnick, 1991; Rose et al., 1991; Staedler & Riedman, 1993; Atkinson et al., 1994; Kiyota & Okamura, 2005). A male-biased adult sex ratio might increase the probability of these aggressive and sometimes fatal interactions (Le Boeuf & Mesnick, 1991). Mobbing, in which a group of males attempts to mount a single adult female or an immature seal of either sex, has been documented for Hawaiian monk seals (*Monachus schauinslandi*) (Johanos & Kam, 1986; Atkinson et al., 1994; Johanos et al., 1994). Associated with severe, sometimes fatal skin and soft tissue lacerations to the dorsal integument (Johanos et al., 1994), mobbing has most often been observed in monk seal populations that have a greater ratio of subadult and adult males compared to breeding-age females (Hiruki et al., 1993).

In the polygynous mating systems of sea otters and many pinnipeds, males typically establish a dominance hierarchy based on age, size, and relative fitness such that subdominant males will have limited access to receptive females of the same species (Le Boeuf, 1972, 1974). Where species overlap geographically, interspecific sexual interactions could be the result of a subdominant male seeking a female surrogate. Male southern sea otters become sexually mature at approximately 5 y of age, although often they are unable to successfully defend territories for several more years (Riedman & Estes, 1990). Sexually mature male sea otters may establish and defend aquatic territories in kelp-dominated regions with high female density from which they exclude all other males except dependent pups and recently weaned immature sea otters. Subadult and adult males that are unable to establish territories are usually segregated from reproductive females and territorial males, aggregating with other nonterritorial males in "male areas" that occur at several locations throughout the range, often in sand-bottom habitats like Monterey Bay (Jameson, 1989; Riedman & Estes, 1990). Many nonterritorial male sea otters frequently move long distances between male areas and travel in winter toward the range peripheries where food resources might be more abundant (Jameson, 1989; Tinker et al., 2008).

During the 5 to 10 y leading up to this study, increases in age-specific mortality have disproportionately affected females, with the result that the sex ratio has become skewed toward males (Tinker et al., 2006). An increasingly male-biased sex ratio might have elevated the likelihood of intragender conflicts, including aggressive, forced matings that could result in significant morbidity and mortality. This gender shift in the sea otter population may have triggered the increased aggregation of transient, nonterritorial males in the Monterey Bay region throughout the study period, particularly around Moss Landing. The majority of observed forced copulatory events occurred in Elkhorn Slough in Moss Landing, a region characterized by both a major harbor seal rookery and a large population of nonterritorial male sea otters. Both tagged males that engaged in sexual behavior with harbor seals in the present study appeared to be nonterritorial transients based on direct observation of behavior over prolonged periods. These subdominant sea otters would have been denied access to female conspecifics by territorial males and may have simply redirected normal sexual responses toward sympatric phocids.

In the current study, strong links were established between observed interspecific copulatory behavior displayed by male sea otters toward harbor seals and specific lesions found during necropsy of the affected harbor seals. The distribution of superficial wounds in harbor seals preferentially over the nose, eyes, and sides of the face and neck is consistent with typical sea otter mating behavior and correlates with notes from direct observation of these interactions. Based on prior reports (Wilson, 1975; Best et al., 1981; Miller et al., 1996; Mortenson & Follis, 1997; Hayward, 2003), pinniped-initiated mating trauma typically has a more dorsal wound distribution because males grasp females from behind with their front flippers; bite them on the dorsal surface of the head, neck, and body to position them; and use the weight of their bodies on land to restrain females to facilitate copulation (Cline et al., 1971; Le Boeuf, 1972; Allen, 1985; Rose et al., 1991). Limited postmortem examinations of victims of forced copulatory behavior between pinniped species revealed bleeding skin and soft tissue lacerations and hemorrhage on the dorsal aspect of the head and nape (Miller et al., 1996; Mortenson & Follis, 1997), skull fractures with subcutaneous

hemorrhage and ocular proptosis (Miller et al., 1996), chest compression or collapse (Best et al., 1981; Miller et al., 1996), and bruising of the distal vagina (Miller et al., 1996), including one female whose intestines were forced out through the anus as a result of crush injury (Best et al., 1981). Ocular trauma, noted in six harbor seals, is an uncommon mating-associated lesion in female sea otters, presumably because sea otter eyes are much smaller and protrude less from the orbit than those of harbor seals. For affected harbor seals, vision loss due to ocular trauma might have restricted their ability to forage and to evade further attacks by male sea otters.

Nine animals examined in depth exhibited vaginal and/or colorectal perforation, which provides strong presumptive evidence for forced copulation. Although spermatozoa were not observed in the rectum/colon or vaginal tract on cytology or histopathology, the ejaculate could have been forced into the abdominal cavity or diluted by seawater or body fluids; the males might not have ejaculated; or they might not have been producing spermatozoa. All of these factors could be an effect of immaturity, advanced age, or incomplete species-specific copulatory behavior. In both harbor seals and sea otters, vaginal perforations and avulsions were invariably located at the junction of the vagina with the cervix as would be predicted with traumatic perforation due to forced penetration, particularly for immature harbor seals with small reproductive tracts. In contrast, perforations of the more fragile, thinner-walled gastrointestinal tract were often multiple and were spaced at variable sites along the distal colon and rectum. The average length for an adult male sea otter os penis is 15 cm (Kenyon, 1969), which correlates well with the depths of the perforations. As demonstrated by HS 14, penetration of the penis through the intestinal wall can result in severe bleeding and leakage of feces into the pelvic cavity and abdomen, leading to septic peritonitis.

One surprising lesion that was observed only in female harbor seals and sea otters was the development of acute, severe pneumoperitoneum in animals with vaginal and/or gastrointestinal perforations. Forced copulation resulted in the passage of air from the vaginal lumen or rectum into the abdomen. These perforations appear to have functioned as one-way valves in some cases, allowing air that was forced in during and after copulation to become trapped in the peritoneum under high pressure. This resulted in a severely distended, tympanic abdominal wall and marked cranial displacement of the diaphragm, leading to tension pneumoperitoneum and increased intra-abdominal pressure. The end result was restricted diaphragmatic movement, compression of the thoracic cavity, and severe pulmonary atelectasis. In addition, secondary compression of the vena cava, as seen in SO 2, can also limit venous return, resulting in hypotension, hypoxia, and, in severe cases, acute respiratory distress and circulatory collapse (Kim et al., 2000). In all three cases, the diaphragm was displaced so far cranially and the thoracic cavity so tightly compressed by high-pressure air in the abdomen, it was deemed to be acutely life threatening. As observed for SO 1 while alive, free peritoneal air can also significantly increase buoyancy and negatively impact an animal's ability to dive and forage.

All three animals with pneumoperitoneum exhibited perforation or avulsion of the vaginal tract. One sea otter with pneumoperitoneum had perforations of both the vagina and distal colon, but none of the harbor seals with only colorectal perforations exhibited pneumoperitoneum, indicating that development of tension pneumoperitoneum was more closely associated with vaginal perforation in these animals. However, gastrointestinal perforation cannot be excluded as a potential cause of pneumoperitoneum. In humans, pneumoperitoneum has been reported secondary to colorectal perforation during colonoscopy (Marwan et al., 2007) and introduction of compressed air into the rectum (Kim et al., 2000) but has not been reported in association with anal intercourse.

Interestingly, postcoital pneumoperitoneum also has been reported in humans after vigorous sexual intercourse, both secondary to vaginal perforation (Lal et al., 2001; Manchanda & Refaie, 2005) and with an intact vaginal wall (Angel et al., 1988; Johnson et al., 2002). Patients have presented with abdominal distention, abdominal tenderness, vomiting, shoulder pain, dyspnea, and pain on inspiration. In all cases, radiographs revealed free intraperitoneal gas beneath the diaphragm. During sexual intercourse, the penis functioned like a piston, creating a closed system that forced air through a vaginal tear into the peritoneum (Lal et al., 2001; Manchanda & Refaie, 2005); or through the cervix, into the uterus, and out through the fallopian tubes (Angel et al., 1988; Johnson et al., 2002). In humans, this latter event might occur as a result of penile-vaginal disproportion (Manchanda & Refaie, 2005), or for patients in the recent postpartum period (4 to 9 wks postpartum), the cervix could be sufficiently dilated to facilitate passage of air into the uterus during coitus (Angel et al., 1988; Johnson et al., 2002). This could have been a contributing factor for both SO 1 (10 wks postpartum) and SO 2 (dilated cervical os and full-term fetus in the pelvic canal at the time of forced copulation).

In the present study, both harbor seals and female sea otters exhibited lesions consistent with forced copulation by male sea otters. Factors that resulted in the death of affected animals include

severe hemorrhage from external lacerations and bite wounds; loss of visual acuity due to ocular trauma; vaginal and rectal perforations that resulted in death due to peritonitis and sepsis; and development of progressive, severe pneumoperitoneum in some animals, severely compromising respiratory function and diving ability, and ultimately leading to cardiopulmonary collapse. In addition, the simple act of holding a victim underwater during forced copulation may have resulted in seawater aspiration and asphyxiation in some cases as has been reported previously in sea otters (Staedler & Riedman, 1993).

This study represents the first detailed account of mating-associated integumentary, ocular, genitourinary, and gastrointestinal lesions in harbor seals and sympatric sea otters. In addition, the first descriptions of fatal pneumoperitoneum as a result of forced copulation in any animal species are presented. Although postcoital pneumoperitoneum in humans does not commonly result in fatality due to medical intervention, the potential mechanisms for the development of this unusual lesion appear to be similar to those reported here for harbor seals and sea otters. Aggressive copulatory behavior in southern sea otters could reflect a recent demographic shift in the population, leading to a more male-biased sex ratio within Monterey Bay and resulting in misdirected sexual activity in the absence of available female conspecifics.

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