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**BEHAVIOUR OF OTTERS IN A COASTAL MARINE HABITAT:
ABSTRACT OF WORK IN PROGRESS**

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Abstract: After reviewing the history of the study, the sudden and catastrophic loss of all three breeding females is described.

The behavior of a marine coastal population of otters, *Lontra* (= *Lutra*) *canadensis*, has been observed since 1983 and studied formally since 1986 at Trinidad Bay, California. From 1986-1992, I conducted >1,700 sessions, and recorded >6,000 otter-hours of direct visual observations. Since 1988, at least 1 otter was seen during 9 of 10 sessions. From 1983-1992, 6-18 otters shared a core area of <1 km². Otters were observable at close distances (5-100m). With repeated viewings, individuals were identified reliably by noting each otter's unique combination of facial, physical, and behavioral characteristics.

The otters at Trinidad Bay form 2 distinct societies: a maternal 'family', and a male-centered 'clan'. The family unit is matriarchal, enforcing female dominance and female intrasexual territoriality. An adult female defends a maternal territory from which she expels most other females. Elder daughters may return to live with their mother and her subsequent litters, serving as enforcers of their mother's territory, and providing comfort behaviors to their mother's pups. A dominant mother and an adult daughter with pups may form a 'maternal alliance', creating a cohesive, 3-generation 'super-family' unit. After females are 1 year old, however, a mother will usually attack and expel a yearling female of the other mother, even if the yearling she expels is her own granddaughter. Territorial attacks by females can be extremely fierce. In July, 1992, an elder daughter of the dominant female killed her mother's yearling daughter.

Adult males at Trinidad Bay are gregarious, forming a seasonally-stable, cohabitating, egalitarian 'clan'. Typically, the clan comprises all of the population's 5-8 adult males. Since 1983, no adult female has been a member of this wandering social group. Males are tolerated in the maternal territory as temporary residents and social subordinates, but the resident adult females and the adult males of the clan do not interact freely. The result of their mutual avoidance is a strict behavioral segregation of the sexes. The strength of this sexual segregation is remarkable: as of June, 1992, it had been 70 mon. since I saw an adult female and an adult male just forage together. Generally, the only prolonged social interaction that adult females and adult males engage in is copulation, during the females' annual estrus in mid-April.

From 1986-1991, I studied the behavioral development of otters. I chronicled the development of 6 litters (22 pups) by the same mother, and 3 litters (7 pups) by that mother's daughters. The 2 females born in 1986 were sexually mature at 24 mon., but remained nulliparous until 48 and 60 mon. respectively. The first daughter to give birth was accepted into a maternal alliance with her mother. When the other daughter became a primipara, her mother expelled her from the maternal territory.

At Trinidad Bay, otters achieve proficiency in aquatic locomotion only 9 wks. after leaving the natal nest, but proficiency in aquatic hunting requires over 9 mon. of trial-and-error learning. Basic self sufficiency in food procurement is attained at 37-42 wks., but the young do not achieve optimal utilization of food sources and habitat until after they are abandoned by their mother at 48 wks. Independent yearlings do not disperse from their home area voluntarily. After 3 mon. of independence, yearlings of both sexes usually join the clan. In her 16th mon., a yearling female either returns to her

mother or remains with the clan. A juvenile female may remain a member of the clan until she is expelled incidentally by a territorial female, or until the males shun her after sexual maturity. Males raised at Trinidad Bay travel widely along the coast, but most continue to base their activities at their home area. At times, however, adult males that were not raised at Trinidad Bay have joined the local clan, indicating that some males do disperse permanently from their home area. Elder adult males are noticeably less gregarious than younger adult males, and elders may leave the clan or be expelled after achieving seniority around age 10. The eldest known otter at Trinidad Bay, 'Old Mama', was estimated to be 11 years of age when she was last seen in July, 1992.

REPORT FROM TRINIDAD BAY : 1992

I never imagined that it would end so suddenly, so violently, or so absolutely. This summer, the ultimate calamity befell the otters at Trinidad Bay, California. Within 10 days in July, all 3 adult females in my study population died. Old Mama and both of her 6-year-old daughters. Mama Junior and Scarnose - all dead in less than a fortnight. The matriarchy that stood rock-stable for the last 6 years collapsed completely, virtually overnight, and the pivotal event was a *murder*. For the first time in my 9-year study, I documented an intraspecific killing, and I recorded, on videotape, a mother otter's cries of mourning for her slain daughter...

The first disaster of 1992 was a total reproductive failure by the adult females. None of the mothers had pups that survived their first weeks. Both Old Mama and Junior had shown signs of maternity early on, but when each returned from her natal exile, neither had pups, nor did they show signs of recent lactation.

The only good news of 1992 was that Scarnose - expelled by Old Mama last year when Scar became a primipara - survived her near-fatal battle with mastitis after all, and gave birth to at least 2 pups this spring. When Scar first returned from her banishment, she'd been gone from Trinidad Bay for *319 days*, and I'd long given her up for dead. I was thrilled to see her again! And I was amazed at how well her 5 cm. diam. self-inflicted 'surgery' wound had healed. She bore a noticeable depression on her belly where her right rear mamma used to be, and a 1 cm. diam. furless patch in place of the nipple. Scarnose thus became the first known otter to give herself a functional mastectomy, and survive!

Unfortunately, in late May, as Scar suckled her new pups, she experienced a recurrence of mastitis, this time involving her left mammae. In response, Scarnose abandoned her pups. She brought the pups to a vegetated ledge on a cliff face near the core den, and just left them. Numerous attempts were made to rescue the pups, but we were not successful. Thus did I obtain the grimmest datum of my study: if <10-week-old pups have access to a water source, they can survive 4 days without succor. As tragic as the deaths of those pups were, this was only the beginning.

The spring had started out hopefully, though, as 4 of last year's 6 pups survived to independence (I'd never had so many yearlings to observe). As has been the pattern, the yearlings gradually socialized more with the male clan. All 3 of Junior's yearlings eventually joined the clan (including Junior's yearling females Orange Lip and White Line), but Old Mama's yearling female, Little Porpoiser, never spent enough time with the males for me to regard her as a true clan member. In fact, during late winter and early spring, Porpoiser didn't seem to be resident here at all. I guessed that Porpoiser was living somewhere near Mama, who, like all adult females from March to May, was occupying a natal den away from her home area. (I say 'near' Mama, not 'with' Mama, as maternal females are aggressively intolerant of *all* other otters until after their pups are weaned. Numerous small bite wounds on Porpoiser's nose attested to her attempts to interact with her intolerant mother.)

When Old Mama re-established residence at Trinidad harbor On 3 June, though, she was already amicable and cohabitating with Porpoiser, more than a month earlier than I'd ever seen Mama tolerant of an elder offspring. That, along With Mama's regressed mammae, was clear proof she had no pups. After birthing 22 pups in 6 annual litters, Mama was finally getting a year off. This respite from pup-rearing transformed Mama behaviorally. In all the years I'd known her. Mama was a seriously task-oriented animal, with little time or inclination for play. If she did play, it was usually with her pups, much less with her adult daughters, and certainly *never* with any of the males. Old Mama was the stoic of the population, as befitted her *alpha* social rank and maternal responsibilities. This year, though, Old Mama had no maternal duties, and for the first time, I got to see her long-repressed playfulness. Mama and Little Porpoiser were each other's constant companions and playmates. The antics of this elderly

mother and her hyper-playful young daughter were a true delight to watch. I felt really good for Old Mama. Never in my life had I seen such a hard working mother, and how, at last, Grandma was finally free to simply enjoy life, and the company of her obviously beloved Porpoiser. During Mama's brief idyll, remarkable changes were to unfold in the social structure of the Trinidad otters.

In the last 2 letters in this series, I described the rigid social segregation of the sexes among adult otters in this population. To illustrate the strength of this segregation, I've been tracking 2 very long 'strings' in my behavior data. As of June 1992, it had been almost 6 years since I saw an adult female and an adult male just forage together, and 4 years since I saw adults of the opposite sex interact playfully. During Mama's idyll, this segregation began to crumble visibly - and it was the matriarch herself who took the initiative. The first record to fall was the 'no-play' string. On 10 June 1992, I saw Old Mama wrestle briefly with her adult grandson, Junior's'90. The last time I'd seen inter-sexual play by adults was 11 June 1983 (revised date), when the Two Sisters played with an adult male, 1,134 sessions ago. The 'no-forage' string ended 11 June 1992, when Mama, Junior's'90, and Mama's 4 yearling descendants entered the water as a group and fished under a dock. Old Mama and her adult grandson only stayed together foraging for 2 minutes, and nothing was captured, but that brief swim broke that longest of all strings at 1,481 sessions. The last time I'd seen Mama forage with an adult male was 9 Sep. 1986.

Not only was Old Mama becoming more tolerant of the males, she also became remarkably tolerant and accepting of Junior's yearlings. In almost all social interactions, Mama favored her Porpoiser, but as the first week of June passed, Junior's 3 yearlings, all members of the clan now, were treated with increasing grandmotherly affection. A picture I will treasure in my mind forever is the sight of this old matriarch, playfully beset on all sides by her 4 yearling descendants and her adult grandson. As fate would have it, though, these were to be the last happy days that Mama - and I - would know here.

The big mystery of June was the noticeable absence of Mama Junior. It was totally uncharacteristic for Junior not to be in residence at the harbor this time of the season. I had long ago concluded that Junior was Mama's 'heir apparent', and that Junior would remain in Mama's territory until she inherited it in her own right. But this June, Junior was definitely not living here. I reasoned that Junior - now a mother in her prime - had established her own territory adjacent to Mama's territory.

In a way, I was glad for Mama that Junior was not here, because I feared that Junior would attempt to expel Porpoiser. Last year, in 1991, Junior had asserted her ascending dominance by means of aggression toward other mothers' young. Junior attacked Mama's yearling daughter One Eye and her sister Scarnose' pups, expelling One Eye from the home area and contributing to Scar's forced banishment. Because Junior had this tendency to aggress against other females' young, I predicted that, if Junior ever returned, she would attack Porpoiser.

And so my prediction came true. On 16 June, after an absence of over 2 weeks, Junior returned to Trinidad harbor. The next day, Porpoiser was gone, and Mama sat alone in front of her den, peering, waiting. Junior attempted to interact with Mama, putting on a remarkably juvenile display of submission and play solicitation, but Mama ignored Junior totally. On the 18th, Porpoiser was back with Mama; Junior would not return for another 2 weeks. Then was the unimaginable to be realized. On 4 July, in their mother's presence. Junior attacked...and killed...Little Porpoiser.

Mama defended Porpoiser, biting a large chunk of flesh out of Junior's face, but the deadly deed was done. Porpoiser lay slain in Old Mama's den.

Mama's eldest daughter, her loyal lieutenant of the last 5 years, had killed Mania's youngest daughter, the joy of her life, in cold blood. For 3 days, Mama did not leave the place where her daughter lay. She stopped eating, stopped grooming, stopped all social interaction. This otter mother was doing just what a human mother would do: she mourned...and she cried. Atop her place of vigil at the death den, Old Mama would wail - a high, wavering, descending, almost loon-like wail - a truly haunting sound I'd never heard an otter make before. Her cries were audible 100 m. away. Mama's lamentation was the most piteous expression of grief I'd ever witnessed. There, far out on the headland, was a wild mother, dispossessed of love and utterly alone, wailing to the Four Winds over the murder of her lastborn daughter.

I last saw Mama 5 days after Porpoiser's death, and it was obvious she had lost the will to live. That last day, Mama looked absolutely wretched: she was emaciated and completely apathetic. By this time, her wailing had all but stopped, but up close, I could still hear her crying softly. As Old Mama visited the docks for the last time - the place where she had provided for her pups all those years - she would walk a few steps, sit immobile, close her moist eyes and emit a plaintive, wavering whimper. She paused at scenting places, her head bowed, perhaps sniffing the last traces of her daughter in life. When Mama returned to her den, I heard her give one last wailing lament, and then, nothing more. I never saw my dear Old Mama again.

After Junior killed Porpoiser, I expected her to return to the harbor permanently. If her attack was intended to displace the young rival for her mother's territory (and favor), then, logically, Junior should have moved back in. As it happened, I only saw Junior twice more in the harbor, and she was definitely not acting 'at home'. When Junior was here, she was constantly on alert, as if anticipating an attack at any time, zigging, and zagging back and forth in the water, looking this way and that, avoiding landfall, never marking. Junior probably had good reason to be wary. Having killed Porpoiser in her mother's presence, and having been attacked viciously by Mama in the process, I doubt Junior would ever have been accepted back by her mother, even had Mama lived. I saw Mama Junior for the last time just the day after I last saw Old Mama. Sometime between 11-14 July, Junior was killed on Indian Beach, north of the harbor. Another animal had torn open the right side of her neck. Magnificent Junior, by far the fittest of all Mama's daughters, did not live to inherit the territory she had defended so staunchly all her adult life. In the end, Junior died exiled, impelled in large measure by the consequences of her own actions to forfeit her lifelong home -and ultimately, to forfeit her life itself.

With Mama and Junior gone, there was nothing now to prevent Scarnose from re-establishing residence. I saw Scar here on 7 of the 10 days after Mama was last seen, and I was really glad she was coming back. Even if Scar turned out to be an unfit mother because of her recurrent mastitis, she was still my favorite of all Mama's 22 offspring, and I welcomed her return. There was an amusing irony that the scrawny runt from the litter of 1986 would become the matriarch of Trinidad Day. During the period she was reconnoitring the harbor, I remember thinking; "The queen is dead. Long live the queen." But there would be no 'Queen Scarnose'. My miracle girl, Scarnose-Little Pup, swam out of my life forever on 19 July. Some time the next day, she was killed by poachers. Those thoroughly despicable people had no conception of what bright a light they snuffed out with their hateful ignorance.

So it was that, in only 10 days, all of the adult females died: the old matriarch herself, and the entire generation of daughters that should have inherited Mama's territory and carried on her maternal line. The population was reproductively dead. At one point in July 1991, there were 18 otters at Trinidad Day; 13 of whom were known descendants of Old Mama. As of Dec. 1992, only a year and a half later, there were no resident otters. None. Even the males were no longer using the harbor dens. From 18 otters to nil in 18 months. I'd never imagined such a debacle were possible.

Of all the female descendants of Old Mama, only 1 granddaughter is known to still be alive: Junior's daughter Orange Lip. If she survives to maturity this spring, she may be the new resident adult female at Trinidad (and I'll rename her Junior, Jr.). I say 'may' because, as of Jan. 1993, the little girl was still a full-fledged member of the male clan. She goes where the males go, and lately, the males are just not living here. Another adult female could move in and displace Orange Lip at any time. This is too prime a territory to remain vacant. How ironic it would be if, after producing 31 known descendants, the lineage of Old Mama were to die out here. How very fragile even an apparently thriving otter population can be...

Before I close, I must make an important point, lest noble Mama Junior be vilified wrongly. You must know that Junior's aggressive behavior to her young kin was not an aberration. Ever since there has been more than one mother resident here, it has been a noticeable pattern for a mother to behave agonistically toward the young of other mothers. Even Mama attacked her own granddaughters: in one case with no less savage intensity than Junior employed on Porpoiser. In mid-June, after Junior attacked Mama's yearling daughter for the first time, Mama's previously amicable behavior toward Junior's yearling daughters turned suddenly violent. On 20 June, Mama bit off the front of Orange Lip's nose, and on the 22nd, I watched as Mama attacked White Line with absolutely astonishing ferocity. For 2 terrifying minutes, Mama tore at the back of White Line's head with unrestrained fury. It truly looked like Mama would kill her granddaughter, apparently for no other reason than White Line had

approached Porpoiser and Mama for social interaction. After Mama's attack, White Line disappeared from Trinidad harbor for almost 2 months: expelled from her home area by her own grandmother. White Line did not return until long after Mama's death, but she was still traumatized behaviorally. I never again saw White Line interact socially with any of the other otters, even with her own sister. White Line was last seen on 1 Oct.

Until this year, I thought I understood this social system and its ecological and evolutionary significance. This was a matriarchy in which a dominant mother allowed her eldest, fittest daughter to share and enforce her territory, to join her in a maternal alliance (comprising the dominant mother's grandpups), and to inherit her territory after her. But this year, in the absence of pups, the stable mother-daughter alliance degenerated into violent intrafamilial warfare, and everything came apart. Perhaps there were just too many otters here. Perhaps that's why the mothers failed this year, and why they turned so aggressively on each other's daughters. Those are logical and parsimonious conclusions, to be sure, but they do not encompass the totality of the actual events. The complexity of behavior can defy tidy reduction.

But now it's my task to attempt just that: to translate the wonders I've witnessed to words, so that all - scientists and laymen alike - may enter the world of these extraordinary otters. Old Mama and the Two Sisters are gone now, but in my thoughts, and in my works, this treasure of Trinidad Day shall live on.