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**SOCIAL ORGANISATION AND BEHAVIOURAL ONTOGENY OF OTTERS (*Lutra canadensis*)
IN A COASTAL HABITAT IN NORTHERN CALIFORNIA**

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The following notes summarize an ongoing series of observations of the behavior of a coastal population of the Nearctic otter, *Lutra canadensis*. Study of this population began in June 1983, and became a graduate thesis project in May 1986. The study site is a boat harbor in the fishing village of Trinidad (41°3'N, 124°8'W) on the north coast of California. The harbor is located in the westernmost portion of a 1.5km-wide ocean bay, sheltered by the mainland on the north and east and a peninsular headland on the west. The otters occupy dens in the dense woody brush on the headland. From 1986 to 1988, total population ranged from ten to fourteen. Otters are present in the harbor year round but are most commonly seen during salmon fishing season (May through September), when they feed on fish remnants discarded off the pier. The otters are popular with the villagers and are valued as a scenic resource. Because the otters are seldom harassed, they display a remarkable indifference to the presence of people and the attendant bustle of a commercial fishing port. The otters' high visibility here greatly facilitates observation of their daily and seasonal activities, allowing for continuous, longitudinal study. Since 1986, I have logged over 1,200 hours of direct observations.

The focus of my thesis research is to document the behavioral ontogeny of the pups, and to follow changes in the pups' relationships with their mother and the other otters over time. Observations of the social organization of the otter population are also being recorded. It will be helpful to review some of the salient characteristics of this social structure before discussing the behavior of individuals.

Social Organisation

The most consistent finding of this study is that Trinidad otters are segregated into two distinct social groupings. One group is a family unit consisting of a maternal female, her pups, and adult female offspring. The other social group is a clan (*sensu* Arden-Clark, 1986) comprising the remaining six to eight of the population, and consists entirely of males. Because the otters are frequently observed out of the water at distances of less than 10m, secondary sexual characteristics and urine stream orientation are discernible. As a result, determining the sexual composition of those groups is a fairly straightforward task. During this study, I have never seen an adult female in regular, daily association with the male clan. Among adult members of this population, sexual segregation forms the foundation of the breeder social structure.

The most striking feature of this system of sexual segregation is the degree of gregariousness exhibited by members of the male clan. The clan occupies a common den. During much of their daily activity cycle, the males maintain a close association with other clan members. Episodes of group foraging, food sharing, mutual grooming, social mounting, and vigorous play are common. Clan males remain gregarious throughout the year, even during the females' estrus periods.

Within the clan, no dominance hierarchy is evident, though some group movements and activities appear to be initiated by older individuals. In terms of overall social rank, however, the males are subordinate to the adult females of the family group. The maternal female holds the highest social rank.

In keeping with the "rule" of sexual segregation, adult members of the clan and family avoid each other or interact with perfunctory brevity; consort relationships are the sole exceptions. Incidental encounters between the sexes are usually non-agonistic, but sometimes, especially when the pups are very young, the females may respond to the males' presence with aggressive attacks, and serious fights have resulted. Although they may initially engage the females, the males usually flee within a few seconds. Subsequent to such an attack, the entire clan may leave the harbor for several days. The behavior of the socially dominant adult females, then, appears to influence whether the clan is present in the harbor at any given time. The males may therefore be more properly regarded as temporary residents.

The clan's sporadic presence impedes detailed study of its internal dynamics, but over time, some general behavioral patterns can be discerned. A consistent observation is that, for most daily activities, clan members form affiliational subgroups, or "parties", of two or more individuals. Although the clan usually dens as a whole group and sometimes forages as a whole group, it is more common to see the males emerge from their den and travel about in parties of three to six. In many instances, these excursionary parties appear to be fortuitous in composition and transient in duration. Males may drift away from a party to forage alone or to join another party, or smaller parties may merge together.

At other times, however, a party's composition seems to reflect specific affiliational preferences among its members. For example, a male separated from his party will sometimes emit chirping contact calls which are attended to by his fellows but

ignored by males from another party. Similarly, a lost male in search of his party may encounter other males along his path, yet continue searching until he rejoins his original companions.

Some of these affectional parties have been seen to recur over periods of weeks or months. One such party is a closely-knit trio of younger males who repeatedly attempt to board and investigate pleasure boats in the harbor. Another is a more sedate party of four older males can sometimes be seen resting and grooming together on a particular dock. Such affiliational preferences are noted with regularity among clan members, as well as among members of the family group.

As might be expected, affiliational bonds tend to be stronger within the family. With few exceptions, family members remain in close proximity to one another throughout their daily activity cycle. The family's internal stability, along with its tendency to maintain a day to day presence in the harbor, provide the observational continuity necessary for detailed study of otter family life.

The Maternal Cycle

The term "maternal cycle" refers to the sequence of behavioral events in the female's reproductive cycle, and the concomitant behavioral development of the pups from birth through maturation to independence. At Trinidad, the maternal female, F' ("F-prime"), is approximately six years old, and has produced one litter each spring since 1986. The maternal cycle of F' has a period of twelve months.

For F', the maternal cycle comes full circle in the latter half of February. At this time, the actively gestating F' leaves her previous offspring in the harbor and establishes a natal den elsewhere. This finding corroborates Woollington (1986), who reported that, among coastal *L. canadensis* in Alaska, the maternal female utilizes a natal den outside her usual home range, away from other otters. In the present study, I do not know where F' goes during her natal period, only that she is very rarely seen in the harbor until June, when the new litter is brought from the natal den to the nursery den adjacent to the pier.

Because the pups' actual date of birth is unknown, their age when they leave the natal den must be estimated. In 1988, I last saw F' with her offspring on 23 February. F' was not seen in the harbor until 3 April when she was observed scent marking in front of a den entrance. It was noted that F' had distended mammae. The next day an adult male was seen displaying physical signs which I have come to associate with mating activity, these being the presence of small wounds on the face and extremities. Findings by Liers (1951), and Hamilton and Eadie (1964), suggested females of *L. canadensis* have a post-partum estrus. Assuming F' had returned to the harbor on 3 April to mate after the birth of her new litter, the pups were probably born sometime the previous week. If so, the pups would be in their eleventh week of life when they made their first appearance in the harbor on 7 June. This is consistent with Liers (1951), who noted that otter pups were ten to twelve weeks old when they left the natal nest. Before giving an account of the behavioral ontogeny of the pups, it is necessary to introduce the two females born to F' in the spring of 1986: F86A and F86B. In 1987, after F' produced her next litter, the F86 sisters returned to the family, and have since served as companions to their mother's 1987 and 1988 litters. At the present time (December 1988), despite being thirty-two months old (and reproductively active adults themselves), F86A and F86B continue to maintain a close familial bond to F' and her offspring.

Abbreviated summary of behavioral ontogeny data

Results are for the 1988 litter only. Observations made daily during last four to five hours of daylight.

Week 11 (7-13 VI) - Three pups moved from natal den to nursery den adjacent to pier. Swimming movements awkward. Pups paddle on surface using all four legs for forward propulsion, and can swim only 0.5m below surface for forward distances of 2 - 3 m. Deep-dives not attempted, frequently try to ride upon back of F' when swimming. F86 sisters loiter around nursery den. F' aggressively drives them away. F' often leaves pups alone in den for over an hour while foraging for herself. Day 1-4: One pup hesitates to enter water; must be dragged in. Pups display inconsistent interest in food. Begin self-exploration of surroundings. Play with other pups and F': wrestling, open-mouthed face-sparring on land, flurry-wrestling in water. May shake water off fur but make no attempt to rub dry in dirt as adults do. Day 5: All enter water readily. F86 sisters meet pups when F' away getting food. Rudimentary auto- and allo-grooming. One pup mounts and neck-bites another pup. Day 6: First see a pup soliciting food by sniffing at mouth of F'. F86A briefly interacts with F' and pups; F' bites her. One pup homes back to den from pier alone (approx. 70m). Day 7: Play with inanimate object.

Week 12 (14-20 VI) - Pups can swim below surface for forward distances of 3-5m; no deep-dives seen yet. Follow and try to imitate F' as she fishes and grubs along edge of headland. Regularly eat provided food. Dry fur by rubbing in dirt, though incompletely. F' and pups begin to play "pinning game"- F' pins pup to substrate by lying on top of it; "object" is for pup to squirm free. Day 1: Another mount and neck bite by pup. F86 sisters attempt to enter den, F' chases them out. Day 2: First vocal squabble over possession of food. One urinates in response to olfactory cues on rocks. Day 3: Amicable interaction between F' and F86B in presence of pups. Day 4: Several brief vocal squabbles over food. F' and pup allogroom. One autogrooms flank, belly. Day 5: All urinate in response to olfactory cues. All play with F86 sister in presence of F'. Day 6: F' drives clan from nursery den. Day 7: F' and both F86 sisters amicable; sisters mount F' and each other. All pups home back to headland from pier without F'. All autogroom most of body.

Week 13 (21-27 VI) - Pups swim with improved body and limb coordination, and dip below surface with proper arching of back. First deep-dives seen (approx 1m). Pups accompany F' on most foraging excursions. Begin chasing rockfish fry which school

under docks and in kelp. Nibble-groom fur like adults; rub dry most of body.. Nursery den used less often, primarily use main den 125m to the south. Day 1-3: Both F86 sisters spending more time with F' and pups, but F' still drives sisters from den. Day 4: F86 sisters officially rejoin family; sisters share den with pups, but may be bitten by F' if try to eat pups' food. Day 5: F86 sisters stay with pups while F' forages. Pup and elder sister allogroom. Day 6: F' catching rockfish fry and releasing in shallows for pups to chase; first fish capture seen. F' leaves pups with F86 sisters again. F86 sisters attack clan males. Day 7: First active refusal by a pup to share food with another.

Week 14 (28 VI - 4 VII) - Pups make serious attempts to capture own fish; at least one successful. Swim underwater with well-coordinated body undulations and rear feet kicks. Front legs used less for forward propulsion. Can swim below surface for forward distances of 5-10m and dive to depths of 1-2m. Mammas of F' becoming less pendulous. Day 1: First solo fish capture. One bites another in squabble over food. Day 2: One swims alone from nursery den to main den and back (approx. 250m). Day 3: One stays out to explore after rest of family goes into den; returns to den on own. Day 4: All dive to bottom in shallows by beach (depth approx. 2m).

Week 15 (5-11 VII) - Three solo captures observed; all have probably caught first fish. Swimming movements and coordination functionally adult-like: swim on surface as fast as adults, and can swim underwater for forward distances of over 10m. Apparently not diving deeper than 3-4m, however, probably because of buoyancy of fur relative to body weight. Pup sexes confirmed: two males, one female. All groom, rub dry like adults. Begin treading back legs when eliminating. F86 sisters sharing food with F' and pups. Day 1: One leaves den alone, eats leftover fish, F' finds pup and scolds, F86 sister responds to a lost chirping pup. Day 4: One swims alone from beach to main den and back (approx. 450m). Day 7: Female pup (F88) stays out to forage on own, catches a fish in shallows by beach, F' retrieves her after 18 min.

Week 16 (12-18 VII) - F' takes pups on first foraging excursions beyond core area around pier (0.75-1.25km round trips). Scrotum discernable. Day 2: F86 sisters attack clan again. Day 7: Pup mounts F' with neck bites and pelvic thrusts.

Week 17 (19-25 VII) - The pups meet the clan. Day 1: Chirping pup and chirping male cross paths; brief but relaxed interaction. Day 3: Pups and six clan members interact in presence of adult females; no intersexual aggression. Pups mount adult males and vice versa. Day 4: Two males attempt interaction with pups: F' tolerates one, chases and screams at other, F86A "stands guard" between den and pups on dock. Pups participate in attack on common murre (*Uria aalge*). Day 6: One swims below surface for forward distance of approx. 20 m (as far as F86B).

Week 18 (26 VII-1 VIII) - Pups deep-diving as adults: first fish remnants and crabs retrieved from under pier (5m depth). F' continues to provide virtually all food, however. Mammas distension of F' less than half that of observed maximum.

Week 19 (2 - 8 VIII) - Day 1,2: F' takes pups on two-day excursion out of harbor, possibly to a den approx. 2.5 km down coast. Day 3: First hear pups emit affiliational "chuckle" vocalization.

Week 20 (9 - 15 VIII) Day 2: F88 leaves den alone, forages around pier area, returns to den after 40 mins. Day 3: - F88 injures right eye, keeps eye closed, reacts in pain when touched. Day 6: Family to northeast harbor to forage. F88 gets separated from others, finds own way back to main den (approx. 0.6km) with one good eye.

Week 21, 22 (16 - 29 VIII) - Pups remain clearly dependent on provided food; still occasional squabbles and refusals to share with siblings. F86 sisters increasingly solicitous: retrieve chirping pups, share food, family leaves on another two-day excursion. Male pups often mount F', F' rolls over on back in response. F88 opens injured eye occasionally but swims with eye closed, eye has bluish film.

Week 23, 24 (30 VIII- 12 IX) - F' still provides most food, but sometimes refuses to share her own food: may push at pup's face with paw or turn away. Foraging excursions out of core area at least three times a week. Mammas of F' flat. Eye of F88 apparently healed.

Week 25, 26 (13-26 IX) - Foraging excursions out of core area almost every day. End of daily observations; sessions held four days a week (or as weather permits) until next spring.

At six months, otter pups are efficient and dextrous swimmers, but they remain observably inefficient foragers. Considerable additional learning and refinement of fishing skills is required before self sufficiency is attained. Currently (Week 37), F' continues to provide supplemental food to pups.

In this study, "Independence" is arbitrarily defined as having occurred when a pup is seen living apart from F' for one week. From data obtained thus far, the pups of F' appear to achieve independence between 46-48 weeks of age. No pups have yet satisfied the Independence criterion by voluntary dispersion, however. In all cases, independence was the result of abandonment by F' when she led the harbor to begin her new maternal cycle. From the 1986 litter of four, a male, M86, joined the clan at independence; F86A and F86B, as stated, rejoined the family. From the 1987 litter of four, only M87B survived to independence. At thirteen months, M87B was still denning with the F86 sisters when he suddenly disappeared from the population.

Postscripts

Continued study of this population is planned. Compilation of data for the present thesis project will be completed in the spring of 1989 when the F86 sisters would be expected to produce their own first litters (F86B was observed copulating on 18 April 1988). Some interesting changes may be in store.

Highlights of sessions from the spring and summer of 1988 are recorded on video tape.

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