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PROGRESS ON CALIFORNIAN OTTER RESEARCH

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Abstract: : My study has progressed well since some of us met at the International Otter Colloquium in September 1989. Occurrences of note are a 48-month-old female gave birth to her first offspring, while that female's sister remained nulliparous (and still cohabitating with her mother) after her second complete reproductive cycle; 2 matrilineally-related family units merged into a cooperative "Superfamily" comprising 3 generations; a copulation during which the male was in continuous intromission for 63 min., and during which the coupled pair came up on land 7 times; a single observation that finally disproved my oldest unmodified working null hypothesis (i.e. "adult males display no territoriality"); my ethogram now describes over 100 behaviors and action patterns that mediate intraspecific communication; and, some little-known literature references and personal communications that suggest the apparent behavioral anomalies I've documented at Trinidad Bay also occur in other marine coastal populations of *L. canadensis*. I also review the contribution of David Solf to otter observation. Finally I pose a question of scientific morality.

This is the first of an annual series of letters that will update my ongoing study of the marine coastal otters (*Lontra canadensis*) at Trinidad Bay, California (41°3'N, 124°8'W). The letter presents several new findings, rethinking of old findings, and concludes with a question of ethics that I wish to direct toward my colleagues for their considered response.

My study has progressed well since some of us met at the International Otter Colloquium in September 1989. Occurrences of note:

- a 48-month-old female gave birth to her first offspring, while that female's sister remained nulliparous (and still cohabitating with her mother) after her second complete reproductive cycle;
- 2 matrilineally-related family units merged into a cooperative "Superfamily" comprising 3 generations;
- a copulation during which the male was in continuous intromission for 63 min., and during which the coupled pair came up on land 7 times;
- a single observation that finally disproved my oldest unmodified working null hypothesis (i.e. "adult males display no territoriality");
- my ethogram now describes over 100 behaviors and action patterns that mediate intraspecific communication; and,
- some little-known literature references and personal communications that suggest the apparent behavioral anomalies I've documented at Trinidad Bay also occur in other marine coastal populations of *L. canadensis*.

Before I review these subjects in more detail, I'll describe my study briefly and summarize its principal findings, some of which were presented previously in Shannon (1989). I have observed the Trinidad Bay otter population since June 1983, and have studied it formally as a graduate research project since May 1986. The population is of relatively recent origin (circa 1955), and has never been the object of exploitation or deliberate harassment. As a result, the 12+3 otters at Trinidad Bay are sufficiently habituated to the presence and activity of people that they can be observed during daylight hours at relatively close distances (usually 5-100 in.). With an attentive eye and repeated observation, most

individuals can be identified by their own unique physical characteristics (particularly facial markings.); behavioral peculiarities may also "mark" individual otters. From May 1986 - December 1990, I conducted 1,082 sessions, and recorded more than 5,000 otter hours of direct observations.

The focus of my research has been to chronicle the behavioral development of wild otter pups from the nursery den to self sufficiency and independence, to sexual maturity, and on to those offsprings' own parenthood. To date, I have followed the development of 5 litters of pups (n=19) from the same mother, and 1 litter (n=2) from that mother's primiparous 4-year-old daughter. Summing both mothers' reproductive output to date, 10 pups were males, 8 were females, and 3 died before their gender could be determined.

Besides pup development, I have also studied the social organization of this marine coastal population. The otters at Trinidad Bay are conspicuously social, but not all adult members of this population interact freely. At Trinidad Bay, adult otters are segregated into 2 distinct social groups with mutually exclusive memberships: a maternal "Family" group that includes the elder female offspring of the dominant mother otter, and a "Clan" of socially-bonded, cohabiting males. My most general finding concerning the social behavior of this population is that adult members of 1 social group consistently avoid direct and prolonged mutual interaction with adult members of the other social group. Because all of the adult females are members of the Family, and all of the adult males are members of the Clan, their mutual avoidance results in a social segregation of the sexes. The strength of this segregation is remarkable. For example, as of the end of December 1990, it had been 1,017 sessions (9/9/86) since I saw an adult male forage and cohabit with the Family, and 685 sessions (9/6/88) since I saw an adult male and adult females interact playfully (play is a daily occurrence within a social group).

In Shannon (1989) and in my poster for the Otter Colloquium, I described this avoidance phenomenon nominally as "sexual segregation", but I now favor the more precise phrase: "a social segregation of the sexes". An otter's sex is not necessarily the sole determinant of social relationships at Trinidad Bay. Essentially, it is the presence or absence of a social bond between individuals that determines whether they interact amicably, agonistically, or simply avoid each other mutually. The basic "rule" of social interaction in this population appears to be: adult group members interact freely, and adults that are not members of the same social group do not interact freely. Although males at Trinidad Bay do indeed appear to bond preferentially with other males, regardless of familial relationship, a female will not bond socially with another female unless the other is her immediate matrilineal relative (i.e. her mother, sister, or daughter). Additionally, although it is very uncommon, adult females in this population have been observed to maintain both intermittent and long-term social bonds with individual adult males. That being said, I think this is the appropriate time to reveal that, during 1983 and 1984 (when there was a different resident mother, and the population was only half its current number), a very old adult male was a cohabitant member of the Family, and it was obvious that the male and the old female were permanently pair-bonded. Clearly, then, social bonding may be determined by factors other than gender, although the current gender "borderline" between the 2 social groups is, with few exceptions, strikingly rigid. Concerning dominance relationships, adult males are usually subordinate to the resident adult females, and the eldest maternal female is the *alpha*-otter of the population.

The Clan is an egalitarian confederation of 5-8 gregarious, cohabiting males. This year, I coined the term "egalitarian confederation" to phrase succinctly the essential social dynamic of this very interesting group: "confederation" defined here as "a body of independent entities united for joint action", and "egalitarian" referring to the apparent absence of social ranking among Clan members. Clan males den together, travel together, forage together, sometimes share food, and regularly engage in reciprocal comfort behaviors, such as mutual grooming and group play. Except for fights during the females' estrus, and brief squabbles over food, members of the Clan are remarkably unaggressive.

In 1990, all but 1 Clan member were adults, and only 2 were known to be related familiarly. Although I don't know the genealogy of most Clan members, the wide range of phenotypic variation displayed by these males makes it difficult for me to conclude that the Clan, as a group, is made up of close familial relatives. However,

I do have indirect evidence that 1 of the older males is the father of 2 of the younger males.

Until this April, I also referred to the Clan males as "non-territorial", because they appeared to cohabit year-round, even during the females' estrus. While it is true that some males do continue to cohabit during estrus, this season at least 2 older males established their own den quite separate from

the other males, and adjacent to the females' rendezvous site (I define "rendezvous site" as "a prominent physical feature in the population's core area where an estrous female waits for a potential partner"). On 13/4/90, during estrus proper, I saw an unambiguous demonstration of site-specific territoriality, when 1 of those self-isolated males excluded another male aggressively from a female's rendezvous site (the female was not there at the time). What made this encounter so unambiguously territorial was that, just 5 min. before, these same males were sharing food amicably at an apparently neutral location just a few meters from the rendezvous site. When both subsequently tried to occupy the rendezvous site, however, the male who got there first screamed and ran at the other and chased him away, ostensibly to monopolize the site for his own reproductive advantage.

Now to describe that marathon copulation. As I mentioned, the pair stayed coupled for 63 min., and the female dragged the clinging male up on land 7 times. Another noteworthy aspect of this mating was that it took place only 20-30 m. from my observation point, so I was able to identify both partners positively, something I'd not been able to do before. Also of interest: this was, at minimum, the pair's second copulation of the afternoon (the earlier episode began at 15:54:, and ended at 16:12:). And, as with every other mating I've observed thus far, both copulations were terminated by interference from a third otter, resulting in a fight.

During the entire copulation, the male maintained a biting hold on the top of the female's neck near the back of her head, and he clasped her flanks tightly with his forelegs. During thrusting in the water, the male "rode" atop the usually passive female. The head of the female was submerged most of the time, and she raised her head for air only a few times per minute. The basic aquatic copulatory sequence was as follows. From the vertical, the male would roll the female and himself over to their left side until both their heads were submerged, emit 1-5 thrust-bursts, then roll himself and the female back up and over to their light side until both their heads were submerged, emit 1-5 thrust-bursts, then roll over to the left, thrust, over to the right, thrust, etc. Although the male continued thrusting during the entire copulation, there were 2 distinct "phases" of pelvic thrusting (cf. Liers 1951): a "quiescent" phase where intromission was maintained but thrusts were relaxed, and an "active" phase characterized by vigorous thrust-bursts, the force of which produced conspicuous splashing. Active thrusting occurred in bursts of 5 or 6 very rapid pelvic quivers, each burst lasting only about 1-1.5 seconds.

At 16:33: on 14/4/90, the estrous female, "Mama junior", was eating at her rendezvous site, when an older adult male, "Single-Lobe", approached from the rear. Junior saw Single-Lobe swimming toward her, and she torpedoed into the water away from him. Close to the headland, Junior fortuitously met her mate of the earlier encounter, "Complainer", a young adult male. They dove simultaneously, and surfaced coupled. (Instead of pursuing the estrous female, Single-Lobe simply sat down and ate the fish that she had just abandoned. Unless he was anosmic, he must have smelled the receptive female, but he did nothing about it.)

The copulation began at 16:35:25 with quiescent thrusting. At 16:44:41, the male began, his first active phase, which lasted until 17:00:12. At 17:06:53, the female dragged the male, still intromitted, up onto land. On land, the male was wrapped around and under the posterior of the female in what looked like an extremely uncomfortable posture; his scrotum was rubbing in direct contact with the rocks (the female exhibited little or no lordosis). The pair re-entered the water briefly from 17:07:13-17:07:32, then the female dragged the male back up on the rocks.

Soon after landfall, at 17:07:42, the male began his second active phase with a series of 10 extremely vigorous thrust-bursts about 3-6 sec. apart. The pair re-entered the water at 17:08:16, and the male continued his active thrusting until the female climbed up on land again at 17:19:07. Active thrusts stopped, but the male maintained intromission. During this landfall, the female made her first struggle to escape. At 17:19:36, they re-entered the water and the male resumed his active thrusting. At 17:21:03, they came back up on the rocks. Again, the female tried to escape. Back into the water at 17:21:14, active thrusting resumed, then back up on the rocks at 17:22:09. This time the female made a serious attempt to escape, jerking her head from side to side and turning to pull the male off balance. Into the water again at 17:23:37, the male resumed active thrusts. At 17:25:48, the male entered quiescence. Two more landfalls took place at 17:26:48-17:27:06 and 17:27:56-17:28:30. During the latter, the female vocalized for the first time: a brief scream. The copulation continued in quiescence until 17:38:30, when another adult male, "Moustache", interfered and terminated the copulation. A fight ensued.

Incidentally, it was only after the fight ended that I heard the "caterwaul" reported by others (e.g. Liers 1951). The female caterwauled, apparently to discourage another copulation. In fact, I have yet to hear any caterwauling during actual intromission; I have only heard this unmistakable vocalization after copulation ended, or to deter a unwanted suitor.

A footnote on Complainer's admirable stamina: keeping in mind what I wrote earlier about that being at least his second mating of the afternoon, believe it or not, Complainer returned for "thirds" at 18:08: Junior bolted from her rendezvous site and dove away, not to be seen again!

Now for news of the Family, or rather, the families, as there are now 2 mother otters at Trinidad Bay. At this point, let me introduce the 3 resident adult females. The dominant female is F2, a.k.a. "Old Mama", referred to as "F-prime" in Shannon (1989). In 1990, F2 was approx. 8 years old, and she's produced 1 litter here every Spring since 1986. (I have evidence that F2 had at least 1 litter prior to her residency at Trinidad Bay.) Mama's litter size was 4 every year except 1988, when she had 3. Thus far, of her 19 pups studied, only 2 females and 2 males have survived to sexual maturity. The 2 surviving females were born to Mama in 1986: F86A ("Mama Junior") and F86B ("Scarnose"), a.k.a. "The Two Sisters". Although both are reproductively-active adults (age 56 months in Dec. 1990), the Sisters have returned every Spring to live with their mother and her new pups.

This Spring (circa 1-3/4/90), Junior birthed her first pups (1 male, 1 female), and as expected, Junior's new motherhood produced noticeable changes in her behavior and in her relationship with the other females. After mating with Complainer on 14/4, I did not see Junior again until 5/5. After her return, Junior displayed the postpartum intolerance typical of maternal carnivores. How ever typical, it was nonetheless a genuine novelty to see Junior avoid or drive away her life-long companion, Scarnose. Junior's period of intolerance toward Scar did not last long, however: Scar started cohabitating with Junior and her only surviving pup, m90', when the pup was 11 weeks old. (In years past, Mama wouldn't let the Sisters cohabit with the Family until her pups were 13 weeks old.)

On 6/6/90, Mama returned to the core area with her 4 10-week-old pups after a record absence of 89 days. At first, as in previous years, Mama shunned both daughters, but by the time Mama's 3 surviving pups (all females) were 12 weeks old, Scar was being tolerated. The 2 mothers, however, continued to avoid each other and each other's pup(s). It was not until week 14, when the pups' weaning was almost completed, that Junior and her pup began to cohabit and forage with Old Mama's family. During this period that the 2 families were bonding together, I began to see something entirely new: sometimes Junior provided food for the exclusive use of Mama's pups! In years past, the Sisters occasionally *shared* their food with Mama's pups, but they almost never *gave* them food. Even more surprisingly, sometimes Old Mama reciprocated and provided Junior's pup with food (as the weeks went by, however, each mother tended to avoid providing food for other than her own offspring). By the end of week 17, the 2 families had completed their merger into a unified, cohabitating, cooperative "Superfamily": a matriarchal maternal social group comprising 3 generations, 2 mothers, and 2 sets of offspring that were matrilineal grandsiblings. Old Mama maintained her dominant status as leader of the Superfamily, and Scarnose resumed her semi-alloparental role of "older sister" to both mothers' pups.

Comparing the maternal behavior of the naive mother. Junior, with the experienced, multiparous Mama, the most noticeable difference was that Junior allowed her pups to follow her out of the nursery den in their 9th week, while Mama kept hers inside until their 11th week. After seeing Junior's tiny, barely-ambulatory pups tumble repeatedly down the steep, rocky cliffs of the headland, it was clear that Junior allowed her pups to venture out much too soon (the little female, f90', apparently did not survive this severe battering).

By now, I'm sure the question has arisen: how do I know how old these pups are? Obviously, I cannot know the actual date of birth, but I have found it can be estimated behaviorally with some accuracy. Hamilton and Eadie (1964) stated "adult females mate not long after parturition", but that is not an operationally-useful statement. For my previous paper (Shannon 1989), I guesstimated that about a week elapsed from birth to the onset of copulatory behavior. Last Spring, I discussed this with Lee Roy Sevin, an expert on the husbandry of *L. canadensis*. He told me females come into heat "a week to a month after giving birth", with "10 days being about average." Adding a few days for the female to reach maximum receptivity, I changed my behavioral birth date estimator to "10-14 days prior to the onset of copulatory behavior." This has proven to be a very satisfactory criterion: if 4-5 days are added

to my daily development chronologies from 1988 and 1989, consistency with my 1990 chronology is reassuringly close.

The following is a brief summary of my pup development data from the litters of 1988, 1989 and 1990. Pups became aquatic during their 10th or 11th week of life, attained efficient coordination of their basic swimming movements by the end of week 14, possessed the complete adult repertoire of swimming behaviors by 16 weeks of age, and swam as proficiently as adults by week 19.

Although proficiency in aquatic locomotion is attained only 9 weeks after leaving the natal nest, proficiency in aquatic hunting requires almost a year of learning. The mother began presenting live fingerlings to pups in week 11; active interest in exploring for fishes increased markedly during the next 2 weeks. (Pups appear innately predisposed to seek and chase fishes, and will often continue in such exploration even after sated.) Last suckling was seen during week 14. As early as week 15, pups were taken on their first group foraging trip out of the core area. The earliest recorded solo* (sessile) fish capture took place at the beginning of week 17; earliest solo capture of a free-swimming fish occurred at the beginning of week 19. (*In Shannon (1989), I stated that first solo fish captures took place during weeks 14-15. This Summer, the waters of Trinidad Bay were unusually clear, and I could see that these early "solo" captures were actually instances in which the mother caught the fish underwater, and the pup had taken it out of her mouth as both swam up to the surface. Noting this, I revised my criterion so that only fish captures that took place at a reasonable distance from the mother were counted as solo captures.) Despite possessing adult-like swimming abilities at 19 weeks, however, pups' foraging efficiency remained functionally nil for several weeks thereafter. Even at 6 months, although pups had become active, agile fish-chasers, they remained noticeably inefficient at actually capturing fishes, and the mother still provided almost all the pups' food. During their 7th month, however, multiple prey captures became daily occurrences. The earliest recorded "competent" solo foraging excursion by a pup took place at the end of week 29 (sessile prey only). By the end of week 36, pups had become noticeably efficient capturers of small fishes (<25 an.), although they still relied upon food shared by the mother. Pups attained self sufficiency between weeks 37-42. (Instead of devising an artificial numerical criterion to define the period of self sufficiency, I let the mother define it behaviorally. Although she will continue to share some of her food with pups for as long as she remains with them, the mother stops providing food for the *exclusive* use of pups after week 37-38. After weeks 41-42, a mother might actually bite a pup that took food from her, and I have interpreted such unambiguous punishment as a clear indication that basic self sufficiency had been attained.) After self sufficiency, it became common to see pups and adults forage separately. The earliest observed killing of a seabird (Western Grebe *Aechmophorus occidentalis*) by a pup took place during week 43, and in week 45, the first large fish (>25 cm.) was seen captured by a pup. Although pups can satisfy their own food needs adequately by this time, they do not attain optimum efficiency in food procurement and habitat utilization until after they are abandoned by their mother at 48 weeks of age. Independent yearlings do not disperse from Trinidad Bay; after abandonment, males join the Clan (even yearling females may cohabitate with the Clan occasionally), but females rejoin their mother when she returns in late Spring with her new litter of pups.

After the Otter Colloquium, I began writing my thesis, and I made good progress until my mother passed away in February. Since that sad event, I've been preoccupied with estate matters, although I have managed to keep up with my field work.

I've also continued to add new behaviors to my ethogram (e.g. "run on water" , "emotional lacrimation", "cruciform mounting", etc.), and my ever-growing list of communicative behaviors finally topped 100 (114 described to date; 65 of which are mediated, in whole or part, by *vision*).

My continuing literature search also produced some rare gems. Actually, 2 of the more exciting finds I didn't find at all, they were given to me by friends. Pat Foster-Turley sent me a very interesting manuscript (Reid, Reid and Code, 1989) that described a cooperative social grouping of adult males in a bog habitat in boreal Alberta! (This reference, in particular, makes me suspect that male clans might be more common in *L. canadensis* than anyone might've expected. After all, I can think of few areas with less in common ecologically than a boreal bog mid a rocky seacoast! And yet, Jim Conroy has studied *Lutra lutra* in coastal habitats in Shetland that are, at least superficially, very similar ecologically to Trinidad Bay, but male groups are unknown from Shetland. Unpredictable creatures, these lutrines. But, after all, that's why they're so intriguing to work with, isn't it?)

Another interesting account (Osborne, Calambokidis and Dorsey 1988) was called to my attention by Alan Baldrige at Hopkins Marine Station. In this guide to marine mammals of Puget Sound, Washington State, the chapter on the river otter contained a statement that grabbed my attention immediately: "...in the San Juan Islands, some preliminary research suggests that males will occasionally band together to form bachelor groups of up to 10 or 15 individuals." - Male clans! No authorship was ascribed to the chapter, but its accompanying photographs were credited to Timothy Ransom, a former correspondent of mine. I recalled the last time Dr. Ransom and I spoke in 1985, he'd mentioned his intention to spend more time studying the otters in the San Juans, and after seeing his name associated with the chapter in Osborne, et al. (1988), I wondered if this "preliminary research" might be his. It was! Turns out his ideas about "bachelor groups" evolved over 10 years ago to account for his observation that adult males are not usually found in company with the females (sound familiar?), and occasional sightings of large groups of otters ("13+") moving through the ranges of smaller family groups. According to Ransom, assuming equal sexual mortality in young otters, and the apparent absence of males from family groups, where do they all go? These large, mobile groups seemed to offer the logical answer for the males' collective absence.

I spoke with some of you at the Otter Colloquium about the fascinating unpublished work of a biologist, J. David Solf, who studied the marine coastal *L. canadensis* at Eshamy on Chenega Island in Alaska's Prince William Sound from 1958-1974. During his years tracking otters, Solf logged, by his own account, "approximately 15,000 hours" of field observations (Solf 1969). The only printed summary of his work was Solf (1972), a deceptively ordinary-appearing general information pamphlet, that, for its time, contained more new findings on the behavior of *L. canadensis* than any published account since Liers (1951). Most notably, Solf (1972) first described the existence of "group(s) of bachelor males", the members of which "travel together and operate as a social unit", "have no apparent leader", "have no exclusive territories", and among which "fighting...is extremely rare." Additionally, "male groups usually consist of fewer than 10 individuals. Larger numbers that are occasionally seen together may represent a temporary association of neighboring groups."

Excited by the similarity of Solf's observations and my own, I tried to contact him through Alaska Dept. of Fish & Game. I was disappointed to learn that Mr. Solf died in 1974, but fortunately, an old college friend of his at Fish & Game helped me get in touch with Solf's family. Thanks to the gracious cooperation of his sister, Bettijane Solf Boltmann, I was given copies of David's transcribed field journal (Solf 1954-1967), and 4 personal letters (Solf 1969, 1970a, 1970b, no date), 3 of which were written to C. J. Harris (author of the reference, *Otters: a study of the Recent L. uirinae*), that described in greater detail the social and reproductive behavior of the otters at Eshamy.

Solf's writings comprise a wealth of findings never reported previously for *L. canadensis*, and on almost every page, I found more affirmation that the behavior patterns I'd documented at Trinidad Bay were not local anomalies.

Here are a few highlights from Solf's writings. Perhaps you might think my 63 min. copulation is a record? From Solf (1969): "on the 5 occasions I've seen the complete performance, it has lasted from 65 to 73 minutes." Also, Solf (no date) described a copulation with a total on-land time of :36:50. Or perhaps you might think Ransom's bachelor group of 13+ is the largest male clan documented? From Solf 1970a: "the largest of these groups I have seen was of 17 animals."

Truly, David Solf was an unheralded pioneer in our field, and one of the keenest, most knowledgeable, and most dedicated observers of wild otters ever. Ironically, and tragically, Solf paid the ultimate price for his dedication, for he lost his life while tracking his "critters". Solf was following otter tracks at a frozen stream when he fell through thin ice. Although he managed to climb out, and his companions tried to warm him, he succumbed to hypothermia. John David Solf was 39 years old.

In closing, I'd like to discuss a question of ethics with you, my colleagues and friends. This might come as a surprise, but I have serious misgivings about publishing many of my findings formally, particularly those describing social groupings, patterns of cohabitation and den usage. I am concerned that what I have learned could be employed to the detriment of other populations of marine coastal otters. It seems to me that it would be very harmful to disseminate the knowledge that, for example, a dozen or more otters might share 1 den, or that all of a population's reproductive females might do likewise. Consider this sobering thought: if I wanted the pelts of the Trinidad otters, knowing their secrets as I do, be assured, my friends, that I could take them all with thoroughly lethal efficiency. A trapper could make

very profitable use of what I've learned. How do we handle such sensitive knowledge responsibly? Must the scientific community's "right to know", or a researcher's "duty to publish", always take precedence over the better interests of one's subjects?

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