

**IUCN OTTER SPECIALIST GROUP BULLETIN
VOLUME 15 ISSUE 2 PAGES 114 - 117**

Citation: Shannon, J.S. (1998) Behaviour of Otters in a Marine Coastal Habitat: Summary of a Work in Progress. *IUCN Otter Spec. Group Bull. 15(2):* 114 - 117

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

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(Received 15th December 1998, accepted 20th December 1998)

Abstract: Since 1983, I have studied 67 wild otters (*Lontra canadensis*) in Trinidad Bay, California, USA. The observations were made at short range (<100 m), and individuals were identified using a combination of facial and physical characteristics. In Trinidad Bay, the otters normally form two social groups: one maternal family and one "Clan" of males. The most noticeable pattern in this population's social organisation was that adult males and adult females led largely sexually-segregated lives. Since 1986, I have studied the behavioural ontogeny of otters, chronicling the development of 6 litters (22 pups) by one mother, 4 litters (9 pups) by that mother's daughters, and 5 litters (7 pups) by a granddaughter. The author summarises observations to date.

Since 1983, I have studied a marine coastal population of otters (*Lontra canadensis*), by naturalistic observation, at Trinidad Bay, California, USA. During this time, I have documented the behaviour of 67 free-ranging otters of known identity or birth, whose lives have spanned 5 otter generations. Thus far, I have conducted 3,457 sessions, recorded >8,500 otter-hours of direct observations, and seen otters at Trinidad Bay during 2,966 (86%) of my sessions. From 1983-1998, 5-18 otters shared a home range comprising 4 km. of marine coastline. At Trinidad Bay, otters were observable at very close distances (<100 m.). Individuals were identified reliably by noting each otter's unique combination of facial, physical, and behavioural characteristics.

The otters at Trinidad Bay typically formed 2 distinct social groups: a maternal "Family", and a male "Clan". The Family consisted of a dominant "matriarch" and her pups of the year, and usually, at least 1 elder daughter as a full-time cohabitant. Elder daughters provided socialisation, supervision, and some shared-food to the matriarch's pups, and helped defend their "home territory". Elder daughters were not alloparents in the strict sense, because they did not directly provision their mother's pups with food, nor did they assume true parental care in the matriarch's absence. When an elder daughter of the matriarch became a mother herself, the matriarch formed a "maternal alliance" with her daughter, combining their respective families into a stable, cohabiting, 3-generation "Super-family". Males at Trinidad Bay were highly gregarious, forming a seasonally-stable, cohabiting, socially-egalitarian "Clan". The Clan comprised all of the population's 2-8 adult males: the local fathers, sons, matrilineal brothers, unrelated immigrant males, and yearlings of both sexes. No adult females were observed to share the society of the males until summer 1997, when 2 elder uncles accepted their 2 nulliparous adult nieces into their company. Adult females aggressively expelled unrelated females from their home territory. Although the 2 mothers of the Super-family were usually tolerant of each other's dependent female pups, a maternal female usually aggressively expelled any independent yearling female that was not her own daughter. Expulsion attacks by territorial adult females were astonishingly fierce; even a grandmother attacked her yearling granddaughter with uninhibited ferocity. In the severest territorial attack, the eldest daughter of the matriarch killed the yearling daughter of the matriarch. Although territory literally meant life or death to females, males here displayed no intrasexual territoriality, except for brief fights during the females' oestrus.

The most noticeable pattern in this population's social organisation was that adult males and adult females led largely sexually-segregated lives. The strength of this behavioural segregation of the sexes was, at times, truly remarkable. For example, a period of 70 mon. elapsed between instances when I saw an adult male and an adult female simply forage together, and 58 mon. elapsed between episodes

of reciprocal play between opposite-sex adults. Typically, the primary enforcers of sexual segregation were the adult males. In general, the only prolonged social interaction that adult females and adult males engaged in was copulation, during the females' annual oestrus from late-March to mid-April. After all the adult females died in 1992, however, a new matriarchy was established by a female who had grown to adulthood as a Clan-mate and social co-equal with the males. When this female attained motherhood, the frequency of amicable interactions between the Family and Clan increased noticeably, to the extent that, in mid-1995, I concluded that the rigid regime of sexual segregation I documented here from 1988-1992 was no longer in effect. The Family and Clan still maintained essentially separate and independent existences, but free interaction between the sexes was observed frequently. In 1997, all of the otters here were direct matrilineal relatives, and amicable intersexual interactions reached an all-time high, and for a brief unprecedented period, all of the resident adults formed a single unified social group. In 1998, however, 2 unrelated yearling males joined the population, resulting in a re-emergence of segregation and agonism between the sexes. In this current manifestation of sexual segregation, though, the females are the principal enforcers of the social distance, and the females' aggressive attacks are directed exclusively against the new unrelated males.

Since 1986, I have studied the behavioural ontogeny of otters, chronicling the development of 6 litters (22 pups) by one mother, 4 litters (9 pups) by that mother's daughters, and 5 litters (7 pups) by a granddaughter. At Trinidad Bay, otters achieved proficient aquatic locomotion only 9 wks. after leaving the natal nest, but proficiency in aquatic hunting required >9 mon. of trial-and-error learning. Basic self-sufficiency in food procurement was attained at 37-42 wks., but the young did not achieve optimal utilisation of food sources and habitat until after they were abandoned by their mother at 48 wks. Yearlings did not disperse from their home area voluntarily. After 3 mon. of independence, yearlings of both sexes joined the Clan. Yearling females were accepted as fully co-equal members of the male Clan. In her 16th months, a yearling female either returned to her mother, remained with the Clan, or was expelled incidentally from the Clan by a territorial adult female. A female could remain a member of the Clan until she reached sexual maturity. After her first oestrus, however, most males would shun her socially, and some males attacked their former Clan-mate without apparent provocation. The 2 sisters born in 1986 were sexually mature at 24 months, but they remained nulliparous until 48 month and 60 month, respectively. The first daughter to give birth was accepted into a maternal alliance with her mother. When the lower-ranking daughter became a primipara, however, her mother expelled her aggressively from the home territory. In 1998, the 2 sisters born in 1995 should have had their first litters, but they remained nulliparous as their grandmother did, so my previous finding of reproductive suppression in socially-subordinate adult females was replicated. Males born at Trinidad Bay continued to base their activities at their home area well into adulthood. At times, though, males not born at Trinidad Bay joined the local Clan, indicating that some males do disperse permanently from their home area. Older males were noticeably less gregarious than young males, and 1 old male was expelled aggressively from the Clan at approximately 11 years of age; this exiled male died soon thereafter. The eldest female at Trinidad Bay was the former matriarch "Old Mama"; I estimated she was 11 years old when she terminated her own life in July 1992. The eldest male was "Beady Eyes", who joined the population as a young adult in 1987 and died in November 1996 at approximately 12 years of age.

RESÚMEN: COMPORTAMIENTO DE LAS NUTRIAS EN UN HÁBITAT MARINO COSTERO: RESUMEN DE UN TRABAJO EN PROGRESO.

Desde 1983 he registrado el comportamiento de 67 nutrias (*Lontra canadensis*) silvestres en Bahía Trinidad, California, USA. Las observaciones se han realizado a corta distancia (<100 m), y la identificación de individuos se ha basado en la combinación única de características faciales, físicas y comportamentales. En Bahía Trinidad la nutrias típicamente forman 2 grupos sociales distintos, una „Familia" maternal, que consiste en una „matriarca" y sus crías del año y generalmente al menos una hija mayor cohabitando permanentemente, y un „Clan" de machos. Las hermanas mayores colaboran con la madre en la socialización y supervisión de las crías, pero no las alimentan directamente ni les proveen de cuidados parentales en ausencia de la „matriarca". Cuando una de estas hermanas tiene sus propias crías forman una „alianza maternal" con aquella. Los machos son muy gregarios. Los „Clanes" son estacionalmente estables y socialmente igualitarios. El „Clan" incluye a todos los machos adultos de la población: padres locales, hijos, hermanos matrilineales, machos inmigrantes y juveniles de ambos sexos. A partir de 1997 2 hembras adultas nulíparas se sumaron al grupo. Las hembras adultas rechazan con mucha agresividad otras hembras de su territorio, incluso juveniles indirectamente emparentadas. Los machos no presentan territorialidad intrasexual fuera del período de estro de las hembras. El patrón social más evidente es que machos y hembras llevan vidas sexualmente segregadas.

Este patrón es principalmente impulsado por los machos adultos. La única interacción prolongada entre adultos de distintos sexos suele darse durante la cópula, entre fines de marzo y mediados de abril. Tras la muerte de todas las hembras adultas en 1992, un nuevo matriarcado fue establecido por una hembra que había crecido y llegado a su madurez como integrante del „Clan". A partir de entonces las interacciones amigables entre ambos grupos aumentaron evidentemente en frecuencia, hasta que a mediados de 1995 llegué la conclusión de que el rígido régimen de segregación sexual observado entre 1988 y 1992 había quedado sin efecto. En 1997 todas las nutrias eran parientes matrilineales y todos los adultos residentes conformaban un único grupo social. Con la llegada de 2 machos juveniles inmigrantes, se restableció la segregación de sexos, siendo en este caso las hembras las principales impulsoras de la misma, dirigiendo exclusivamente sus ataques hacia los 2 inmigrantes. En Bahía Trinidad las crías adquieren destreza en la locomoción acuática a las 9 semanas de abandonar el nido, y en la pesca después de los 9 meses. Adquieren autosuficiencia para procurarse la comida entre las 37 y 42 semanas, y llegan a utilizar óptimamente los recursos alimenticios recién después de ser abandonadas por sus madres a las 48 semanas. Los juveniles no se dispersan voluntariamente. Cuando la primera de 2 hermanas nacidas en 1986 tuvo crías, formó una alianza con la „matriarca", sin embargo, cuando la segunda tuvo su primer camada, fue expulsada agresivamente por la madre de su territorio. Probablemente exista supresión reproductiva sobre las hembras subordinadas. Los machos más viejos son menos gregarios que los más jóvenes, y uno de unos 11 años murió al poco tiempo de haber sido expulsado agresivamente del „Clan". Una hembra de aproximadamente 11 años y un macho de 12 fueron los animales más viejos registrados.