GENERATIONAL CHANGE IN AFFILIATION PATTERNS IN A SOCIETY OF MARINE COASTAL OTTERS (*Lutra canadensis*)

J. Scott SHANNON

Post Office Box 24, Arcata, California 95518, USA

Abstract: Affiliation patterns within a society of Canadian river otters changed from a regime of rigid sexual segregation to free intersexual interaction after a complete turnover in population membership. The author suggest that the change in this population's social "rules" was the result of collective choice by the otters themselves, rather than a result of habitat change or other ecological factors.

INTRODUCTION

Aspects of the social organization of the otter population at Trinidad Bay and some changes the author observed over his years of study have been described previously (SHANNON, 1989, 1991*a*, 1991b, 1992, 1993, 1997). To summarize, from 1988-1994, adult otters at Trinidad Bay practiced a ritualized behavioural segregation of the sexes. This sexual segregation was remarkably rigid.

A period of 70 months (1,481 observation sessions) elapsed between instances when the author saw an adult male and an adult female simply forage together, and 48 months (1,134 sessions) passed between observed episodes of intersexual play (SHANNON, 1993). The adult males were the primary enforcers of sexual segregation. A juvenile female could interact freely with the males and be accepted by them as a social co-equal, but after her first oestrus, she was thereafter shunned, and might be attacked, if she attempted to interact with an adult male. Although this pattern of sexual segregation was unequivocal and stable over many years, the author has been unable to explain the phenomenon in terms consistent with accepted biological theory (SHANNON, 1997). Some events that took place during the summer of 1997, however, have helped to better understand the process of sexual segregation witnessed at Trinidad Bay from 1988-1994.

STUDY AREA

The study area is Trinidad Bay (41°3'N, 124°8'W); a small, shallow marine bight on the far-northern Pacific seacoast of California. The otters' home range comprises approximately four linear km. of marine coastline that is predominated by thickly vegetated rocky shore cliffs. The otters at Trinidad Bay are exclusively marine in their habits. There are no streams or known bodies of standing fresh water within the otters' home range. The otters obtain their water by drinking from numerous springs and seeps, which flow year-round down the faces and crags of the shore cliffs.

MATERIAL AND METHODS

The author has been studying otters by direct observation. This study began informally in June 1983, was formalized in May 1986, and continues to the present day. Observations were conducted during the two hours preceding sunset; daily whenever possible. From May1986 until February 1998, over 3,165 sessions were conducted, and otters were observed at Trinidad Bay during 2,725 of those sessions (86% success). Since 1983, the author has documented the behavior of 63 otters of known identity or birth whose lives span five generations. During this study, the population has been comprised of 4-11 adults. Because the otters are diurnal and can be observed at close quarters (5-100 m.), they can be identified reliably by direct visual recognition. The author identifies the otters primarily by facial markings and other physical characteristics, but idiosyncrasies of behaviour are also reliable marks of individual identity. Equipment used consists of 10x28 binoculars, a tape recorder for dictating field notes, and a 35 mm camera and video camera for visual documentation. The otters have never been trapped, handled, monitored, or been subjected to any other invasive technique.

RESULTS

The event which initiated the change in this population's social system was the collapse of the resident matriarchy in July 1992, when all three of the maternal females died. Only one female remained: F91A[F'3], a yearling granddaughter of the old matriarch. Subsequently, F91A was accepted into the male Clan, and for the next ten months lived with the six resident males as their social co-equal and full-time cohabitant until the spring of 1993, when she had her first oestrus. After her oestrus ended, however, if she approached a male, instead of being greeted amicably as she was when she was a juvenile, she was shunned, often screamed at, and occasionally attacked, apparently without provocation, other than her mere presence. As spring turned to summer, even her littermate brother (M91) shunned her, and F91A became a complete social outcast. Despite being shunned, F91A persisted in attempting to interact with the males, always unsuccessfully. Finally, on 13 August 1993, as she followed the foraging males, they suddenly turned on her, and attacked her as a concerted group. Thus was F91A expelled from the males' society once and for all. F91A spent the entire third year of her life sharing the same home range with the males, but by virtue of her social ostracism, she was forced to live a completely involuntary solitary existence until she became a mother in the spring of 1994.

At the end of 1993, the male Clan lost two members, these were the last offspring of the old matriarch, and the last members of the third generation of otters the author studied. Two old males of the second generation still remained, however, as did two young adults of the fourth, but as of 1994, only two males remained who were adults during the peak years of sexual segregation (1988-1992).

After F91A attained motherhood, the author noted that one of the adult males ("Beady Eyes", the eldest male, and her brother M91) were visiting the mother and her new pup with increasing frequency. The interactions were

always brief, but clearly, these two males were no longer shunning the young mother as they did when she was an adult nullipara. However, the other two males, M90 (F91A's elder brother), and "Unk" (another old male), still reacted agonistically to the presence of F91A, shunning and sometimes attacking her as before. In 1995, F91A gave birth to two female pups. Now in her second season as a mother, it was clear that F91A was becoming a dominant social presence in the population, and was being accorded a noticeable degree of "respect". F91A's littermate brother began to visit his sister's family almost daily, as did old Beady Eyes. For the first time in years, the author was seeing occasional episodes of intersexual play and foraging between opposite-sex adults. M90 also started interacting more often with the family, but he did so only to play with the mother's young daughters; M90 still behaved agonistically toward F91A herself. Only old Unk continued to strictly avoid social interaction with the family group. By 1996, when F91A bore her first male pup, the author was seeing the adult males and the mother forage and play together at least once a fortnight. Obviously, the old regime of sexual segregation was no longer being rigidly enforced.

At the end of 1996, the last two old males died. A complete generational turnover had finally taken place. In the summer of 1997, F91A's only pup died early on. In the absence of pup-rearing activity, and with the daughters born in 1995 now adults themselves, the author saw the three adult females and two adult males forage and play together often. Behavioral episodes that the author once waited years to witness were now taking place virtually every day. In fact, during a three-week period in the summer of 1997, all of the adults in the population (including the now socially-dominant matriarch F91A) briefly formed a single cohesive social group - the first time in 14 years that the author had seen all of the resident adults live together. Even though the family and the males did not maintain their association beyond the summer, and once again largely go their separate ways, when they meet now, the males and females typically interact freely with each other.

CONCLUSIONS

The otters' habitat has not changed during the study period, indicating that factors in the otters' physical environment cannot be invoked to account for the change from sexual segregation to free interaction. Furthermore, all of the otters now living at Trinidad Bay are direct descendants of the sexually-segregated otters of the 1980s, so their form of sociality cannot be "hard wired". It is possible that the decline in the number of resident otters from 1991 to the present has contributed to the relaxation of sexual segregation. The formerly high population density may have "forced" the sexes to avoid each others' company. It is also possible that the current increased tendency for opposite-sex adults to interact may be due to the fact that all the otters now at Trinidad Bay are immediate matrilineal relatives; i.e., they are all members of the same genetic "family". For a number of reasons the author cannot elaborate upon here, the author also speculate that the old system of sexual segregation may have been caused to some degree by the presence of one particular individual: the favored eldest daughter of the old matriarch, for whom several of the males possessed an observable enmity (see also the other

article from the same author in this volume). In general, the author concludes that the observed change in this population's social organization may have been due to a combination of any or all of these factors. However, all of these disparate scenarios can be parsimoniously reduced to a single unifying concept: generational change. At any given time, the otters of Trinidad Bay determine for themselves how their society is to be ordered, and the social "rules" of generations past - however long and rigidly they were maintained and enforced - are not necessarily carried on by their descendants.

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