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- p. 35 The last sentence of the page, which reads:
- "A total of 135.58 whale-hrs of *ad libitum* data (in five-min point samples) was collected."
- should read:
- "A total of 135.58 whale-hrs of *ad libitum* data (in five-min **scan** samples) was collected."
- p. 41 The third sentence from the end of the paragraph, which reads in part:
- "Adolescent males may also frequently be called upon as allofathers (Chapter Three: Part Two)..."
- should read:
- "Adolescent males may also frequently be called upon as **caretakers of young related juveniles, an activity known as allofathering** (Chapter Three: Part Two)..."
- p. 94 The first sentence of the page, which reads:
- "Male killer whales of the northern resident community of British Columbia encounter each other frequently, as a result the unusual social structure of the matrilineal group and the pod (General Introduction)."
- should read:
- "Male killer whales of the northern resident community of British Columbia encounter each other frequently, as a result **of** the unusual social structure of the matrilineal group and the pod (General Introduction)."
- p. 105 In the middle of the page, the part of the sentence that reads:
- "...slowly approached each other, picked up speed (essentially surfacing-swimming), and finally butted heads together..."
- should read:
- "...slowly approached each other, picked up speed (essentially **surface**-swimming), and finally butted heads together..."
- p. 126 From the top of the first column to the bottom, the alphanumeric male IDs should read:
- "A20, A31, **B02, C03, I05, A06**, A26, A27, A32, A33, A38, **A39, C09, D05**, A13, A15, A37, A46, C13, C14, **H07**, I43, B10."

p. 136 In the figure legend, where the top line reads:

"AMGs"

the top line should read:

"MOSIs."

p. 137 In the caption for Figure 3.3.a, where the sample sizes read:

"...(N = 5, 8, and 4, respectively)"

the sample sizes should read:

"...(N = 5, 8, and 3, respectively)."

p. 141 In the caption for Figure 3.4.a, the first sentence, which reads:

"A comparison of body-contact behavior rates in MOSIs vs. other behavioral contexts."

should read:

"A comparison of body-contact behavior rates in MOSIs vs. other behavioral contexts (N = 3, 8, and 3 respectively)."

p. 146 The first sentence of the second paragraph, which reads:

"Waite (1988) first hypothesized that the killer whales in Johnstone Strait show alloparenting behavior; she categorized the care being given as 'babysitting.'"

should read:

"Waite (1988) first hypothesized that the killer whales in Johnstone Strait show alloparenting behavior, **defined as care given to young by an individual other than the parent.** She categorized the care being given as 'babysitting,' **as opposed to, for example, provisioning.**"

p. 150 The last sentence of the page, which reads in part:

"...that is, older brothers keep an eye on younger sisters when the the latter begin to exercise independence, increasing the chances of an interaction with an inappropriate social partner."

should read:

"...that is, older brothers keep an eye on younger sisters when the latter begin to exercise **greater** independence. **This chaperonage decreases** the chances of an interaction with an inappropriate social partner."

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

THE SOCIAL DYNAMICS OF MALE KILLER WHALES, *ORCINUS ORCA*,
IN JOHNSTONE STRAIT, BRITISH COLUMBIA

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

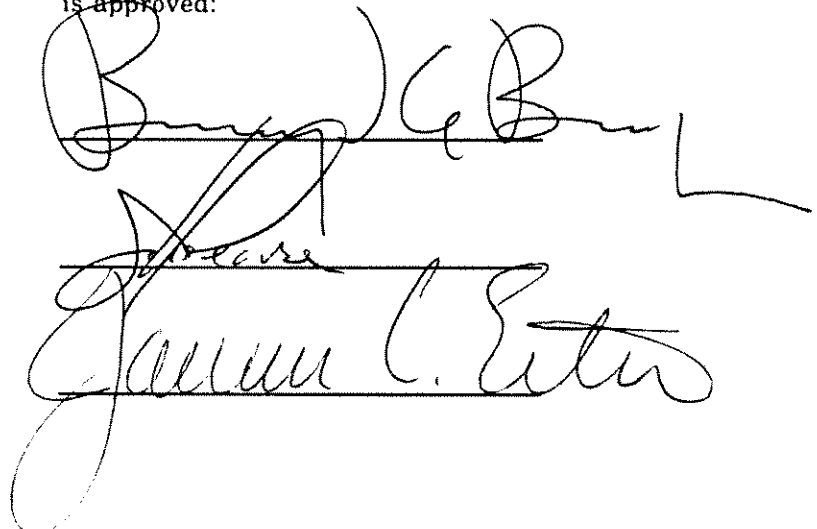
BIOLOGY

by

Naomi Anne Rose

December 1992

The dissertation of Naomi Anne Rose
is approved:



Dean of Graduate Studies and Research

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**THE SOCIAL DYNAMICS OF MALE KILLER WHALES, *ORCINUS ORCA*,
IN JOHNSTONE STRAIT, BRITISH COLUMBIA**

Naomi Anne Rose

ABSTRACT

Unlike other mammals, male killer whales in British Columbia maintain close spatial relationships with their mothers into adulthood. The aim of this study was to clarify the role that males play within this unusual social structure. To this end, the development with age of male behaviors and social interactions was described and compared to that of other species.

The study took place in Johnstone Strait during the summers of 1987-1990. Animals were encountered opportunistically and observed from a boat during daylight hours. Behaviors and distances between individuals were recorded continuously. Approximately 317 hours were spent observing whales, focusing on 32 males who were classified as juveniles, adolescents, or adults. Percent time spent traveling, foraging, resting, and interacting socially; respiration rates; frequency of body-contact, non-percussive aerial, and percussive behaviors; and percent time spent with various associates were calculated for these males and compared across age classes.

Adolescents interacted socially with others twice as often as did juveniles or adults. Juvenile behavior frequencies were as much as three times as high as those of adults. Juveniles and adolescents spent up to 65% of their time with their mothers. Adults spent about 35% of their time more than several meters from others, but also spent about 30% of their time interacting with unrelated adult females. Male-only social interactions primarily involved unrelated adolescents. Physical contact was frequent and mutual,

indicating a play function. Male-juvenile associations involved kin only and appeared to be an older male caretaking a younger animal.

Male killer whales play an integral role in the social structure throughout life. The behavior of juveniles is like that of most mammals and indicates they are still very dependent on the mother. Adolescents appear to have a central role as caregivers to juvenile siblings and maintain a non-aggressive social network amongst themselves. Adults have a somewhat peripheral position to the social group, but actively participate in probable reproductive interactions. The caretaking behavior and reduced aggression demonstrated by male killer whales are traits found in other species where male kin maintain bonds. However, unlike these other species, male killer whales treat kin and non-kin males similarly, a likely consequence of the mother-son relationship.

Dedicated to the memory of
Dr. Michael Andrew Bigg,
with affection and great respect

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GENERAL INTRODUCTION

Why study killer whales?

Among vertebrates, there are few taxonomic orders, outside of the fishes, without at least a few genera well-described and understood. Certainly among mammals, there are increasingly fewer opportunities for an aspiring behavioral ecologist to cover new ground. With the human population pushing the wilderness farther back, the twenty-first century bids fair to hold a relative paucity of mammalian mysteries for an ethological sleuth to solve. There is something to be said, therefore, that an entire mammalian order, the whales and dolphins or Cetacea, remains to a great extent a cipher to behavioral ecologists.

Long hidden behind a protective barrier of water, until recently cetaceans were described principally from dead animals collected in the whaling trade or from brief and furtive glimpses of quicksilver dolphins or long-diving and evasive whales. The quest to describe the behavioral ecology of these animals, to observe their social interactions in the wild, has been mostly a frustrating one, with few exceptions (Le Boeuf and Würsig 1985). A principal tool of the trade, focal animal observation (Altmann 1974), has been difficult, when not impossible, for cetologists to use. Most cetaceans spend less than twenty percent of their time at the water's surface (Stevick and Katona 1991), underwater observations are frequently impractical, and the methods of identifying individuals are often not conducive to repeated and continuous observations in the field (e.g. the underside of flukes: International Whaling Commission 1990). New technologies, such as radio and satellite tracking, have allowed limited entry into the cetacean world, but even they do not

provide a window onto social interactions. As a result, although detailed demographic and behavioral data have been collected on a handful of species (e.g. bottlenose dolphins, *Tursiops truncatus*: Würsig and Würsig 1977, Wells 1986, Shane *et al.* 1986, Wells *et al.* 1987; humpback whales, *Megaptera novaengliae*: Glockner-Ferrari and Venus 1983, Tyack and Whitehead 1983, Glockner-Ferrari and Ferrari 1990, Weinrich and Kuhlberg 1991; sperm whales, *Physeter macrocephalus*: Gordon 1987, Whitehead and Arnborn 1987, Arnborn and Whitehead 1989, Whitehead and Waters 1990; right whales, *Eubalaena australis*: Payne 1986, Payne *et al.* 1990), for the most part cetacean social dynamics are poorly understood (Evans 1987).

This is not a comfortable situation. It is clear that many cetaceans lead complex social lives, combining intelligence and sociality with an aquatic environment, possibly with unique results. The fine details of their social dynamics will undoubtedly shed considerable light on evolutionary and sociobiological theory and possibly open up new avenues of thought and speculation (Le Boeuf and Würsig 1985; Würsig 1991). Just as the study of primates, in its infancy in the 1960s, has now reached an established level of maturity (Smuts *et al.* 1987) and provided many evolutionary insights, the study of cetaceans must also mature (Lockard 1986).

An ideal candidate for more detailed examination is the killer whale, *Orcinus orca*. As recently as 20 years ago, virtually nothing was known of this largest of the dolphins (Hoyt 1984; Kirkevold and Lockard 1986). Over the past 19 years, two small populations, one in Puget Sound, Washington, and the other in British Columbia, have been studied intensively (Balcomb *et al.* 1982; Bigg 1982; Ford and Fisher 1982, 1983; Ford 1984; Balcomb and Bigg 1986; Felleman 1986; Osborne 1986; Baird and Stacey 1988; J.R.

Heimlich-Boran 1988; S.L. Heimlich-Boran 1986, 1988; Waite 1988; Bain 1989; Ford 1989; Jacobsen 1986, 1990; Bigg *et al.* 1987, 1990a, 1990b; Morton 1990; Nichol 1990; Olesiuk *et al.* 1990; Felleman *et al.* 1991). Using photo-identification, all individuals of both populations have been identified and named, using an alphanumeric system (Bigg 1982), and possess a known history, with many being of known age (Bigg 1982; Bigg *et al.* 1987; Bigg *et al.* 1990b). Genealogies, social structure, and life history parameters have been determined (Bigg *et al.* 1990b; Olesiuk *et al.* 1990). The situation is ripe for more exhaustive behavioral studies. Where should killer whales be placed in the continuum of mammalian social structures? With which other taxa do they share behavioral and social characteristics?

The aim of this study was to clarify the role that male killer whales play within the social structure. In British Columbia, males maintain close ties into adulthood with their mothers and kin of both sexes (see below). What are the consequences for males of these unusual permanent kinship bonds? To address this question, this study describes male behaviors and social interactions and how they develop with age. Throughout my analyses, I will compare and contrast the behavior of male killer whales with that of males of other species that share similar social structures (see Greenwood 1980; Liberg and von Schantz 1985; Chepko-Sade and Halpin 1987), notably canids (e.g. Bekoff *et al.* 1984), some primates (e.g. Blaffer-Hrdy 1976; Nishida and Hiraiwa-Hasegawa 1987; Pusey and Packer 1987), and many birds (e.g. Woolfenden and Fitzpatrick 1984; Brown 1987; Stacey and Koenig 1990). These terrestrial species in which males maintain bonds with kin have demonstrated certain consistent male behavioral traits, such as reduced male-male aggression and male caretaking of young (allofathering). Do male killer whales show these traits?

Review of life history and social structure:

Killer whales are long-lived members of the family Delphinidae, with females attaining an estimated maximum of 80 years of age and males 60 (Olesiuk *et al.* 1990). They are the most sexually dimorphic delphinid: Males are up to 1.3 times as long as females, they may weigh 1.5 times as much, and they possess several secondary sexual characteristics, most striking of which is a dorsal fin that is 1.5 times as tall as that of females (Matkin and Leatherwood 1986; Bigg *et al.* 1987). Like all delphinids, killer whales are highly social, traveling in groups of up to 100 individuals, although groups with from two to 50 members are most common (Matkin and Leatherwood 1986).

Sexual maturity for both males and females takes place on average at 15 years of age (Olesiuk *et al.* 1990). A female produces a calf approximately every five years; she may have up to five or six offspring during a 25 to 30-year reproductive lifespan and live for up to 30 years post-reproductively (Olesiuk *et al.* 1990). In the Pacific, along the northwest coast of North America (henceforth referred to as the Pacific Northwest), calving appears to take place year-round, with a diffuse peak from October through March; from captive animals, gestation has been determined to be approximately 17 months (Asper *et al.* 1990), meaning that peaks in mating probably take place from June through November (Olesiuk *et al.* 1990). Little is known about age at weaning in the wild, but there are several lines of evidence, both from captivity and from strandings, indicating that calves begin taking solid food very early (at less than two months of age) and may be nutritionally weaned by one to two years of age (Haenel 1986; Heyning 1988), although the interbirth interval suggests nursing may continue to some degree until four or five years of age.

Unfortunately, little is known about the mating system of the killer whales of the Pacific Northwest. Their sexual dimorphism suggests that they are polygynous (Darwin 1871; Trivers 1985), but their aquatic habitat has a low environmental potential for polygyny (Emlen and Oring 1977). That is, the three-dimensionality of the space that they inhabit and the typical dispersion of individuals over a wide area would make it difficult for a male killer whale to monopolize several females. In addition, their relatively high testes weight to body weight ratios suggest a promiscuous mating system with sperm competition (Kenagy and Trombulak 1986; Bain 1989). It is also assumed that there is no extreme inbreeding, although the small potential breeding population must be inbred to some degree. Even if the population is highly inbred, it would not necessarily suffer obvious disadvantages from inbreeding depression (Craig and Jamieson 1988). The question of mating system will probably not be resolved until DNA analyses have been conducted to determine paternity and degrees of relatedness between putative or known mates, parents, and offspring (see Stevens *et al.* 1989; Hoelzel *et al.* 1991).

The killer whales of the Pacific Northwest are divided into three communities and two forms or types. The northern *resident* community inhabits the inland waters north of mid-Vancouver Island up through southeast Alaska, the southern resident community inhabits the waters south of mid-Vancouver Island and into Puget Sound, Washington, while the *transient* community is sympatric with both resident communities (Fig. 0.1), although it apparently does not interact with them (Bigg 1982; Bigg *et al.* 1987; Morton 1990). The transients number only 80 individuals or so (Bigg *et al.* 1987); the northern resident community numbered at least 185 in 1990 (Bigg *et al.* 1987; M. Bigg, G. Ellis, pers.

comm.; pers. obs.), while the southern group was comprised of approximately 90 individuals in that year (M. Bigg, G. Ellis, pers. comm.).

The principal difference between transients and residents is that the former feed mainly on marine mammals while the latter feed mainly on fish (Felleman 1986; Bigg *et al.* 1987), principally salmonids (*Oncorhynchus* spp.) (Bigg *et al.* 1990a). Transients are seen sporadically throughout their range year-round and they do not linger for more than a few days in any one area. They travel in small groups of up to 12 individuals, with singletons not uncommon (Bigg *et al.* 1987; Morton 1990), and are rarely vocal (Ford 1984; Morton 1990; Ford and Morton 1991). Both resident communities inhabit core areas during the summer (Balcomb *et al.* 1982; Bigg 1982; Bigg *et al.* 1987; J.R. Heimlich-Boran 1988). They travel in groups of from two to 50 individuals, with aggregations of more than 100 whales occurring infrequently. True, isolated singletons are unknown (Bigg *et al.* 1987). They are highly vocal, using distinct dialects (Ford and Fisher 1982, 1983; Ford 1984, 1989; Ford and Morton 1991). In addition, there are minor morphological differences between the two types (Bigg *et al.* 1987; Baird and Stacey 1988; Bain 1989) and they also exhibit various other behavioral differences, leading some to conclude that they are reproductively isolated races (Bigg 1982; Bigg *et al.* 1987; Morton 1990; Ford and Morton 1991).

The resident communities are also different from each other, although their differences are more in degree than in kind. A live-capture fishery left the southern resident community heavily cropped (up to 48 animals removed) in the early 1970s, affecting the northern community comparatively much less (up to 15 removed) (Bigg and Wolman 1975; Bigg 1982; S.L. Heimlich-Boran 1988; Olesiuk *et al.* 1990). As a result of this differential cropping, the sex ratios and age distributions of the two communities are

dissimilar, as are their population numbers (Bigg *et al.* 1990b; Olesiuk *et al.* 1990). There are proportionally fewer adult males in the southern community (S.L. Heimlich-Boran 1986, 1988; Bigg *et al.* 1990b; Olesiuk *et al.* 1990) and there are some group behaviors observed in the southern group (e.g. intermingling: Osborne 1986) that are rarely seen in the northern group and vice versa (e.g. male-only social interactions in the northern community: Jacobsen 1990). Nevertheless, their similarities strongly support that these two groups, although they have never been observed to mix despite some overlap of their ranges (J.K.B. Ford, pers. comm.; see Fig. 0.1), have only recently become reproductively isolated (Bigg *et al.* 1990b; Olesiuk *et al.* 1990).

Residents travel in matrifocal units called matrilineal groups. A matrilineal group usually consists of a reproductive female (called the matriarch), her dependent calves, her juvenile and adolescent offspring, and her known or presumed adult sons. Occasionally an adult daughter with her first calf will still travel closely with her mother, but usually by the time she gives birth to a second calf, she will travel more independently as the matriarch of a newly founded matrilineal group within the same pod (see below). A matrilineal group can also consist of a non-reproductive matriarch, a female presumed to be older and post-reproductive, and her presumed adult son(s). Some matrilineal groups with a reproductive matriarch also contain a non-reproductive female (presumed to be the mother of the matriarch) who apparently has no sons, either because they have died or because she never had any. Some matrilineal groups contain older adult males who are less tightly bonded to the matriarch than known or presumed sons; these males may be brothers or uncles of the matriarch, who apparently have survived their mothers. One or more matrilineal groups that spend more time together than with other matrilineal groups and who share vocalization dialects are known as a pod (Bigg *et al.* 1987, 1990b). There are

16 pods in the northern resident community and three pods in the southern community (Bigg *et al.* 1987).

The outstanding feature of the social structure of the resident communities is that neither sex disperses from the large shared home range; that is, both sexes are philopatric. Transients appear to show a much greater degree of dispersal (Bigg *et al.* 1990b). This in itself is rarely seen in birds or mammals (Greenwood 1980), although Motro (1991) speculates that if the cost of inbreeding is low, both sexes will adopt the same dispersal strategy. However, the degree to which both sexes associate with their mothers, beyond sharing the home range with them, may be unique (Bain 1989), although preliminary analyses of demographics and social dynamics of bonobos (*Pan paniscus*) suggest that killer whales and this cousin to the chimpanzee share a permanent mother-son bond (e.g. Kano 1982; Furuichi 1989; Enomoto 1990).

Both sexes in killer whales show a rapid decline in time spent closely associated with their mothers through the first ten years of life. A daughter continues to show a sharp decline for five to ten more years, until the birth of her first or second calf, at which time her association with her mother stabilizes at a low level, when she becomes the matriarch of her own matrilineal group. A son, on the other hand, stabilizes his association with his mother at about ten years of age at a relatively high level (40-75% of his time is spent within a body-length of his mother) and appears to maintain this association throughout the rest of his life (Bigg *et al.* 1990b).

This study:

The ultimate question of why both sexes, especially males, are philopatric

in the resident communities of the Pacific Northwest will not be answered for some time yet. The most likely explanations link their dispersal pattern and grouping tendencies with their foraging ecology (see Packer and Rutman 1988; but see also Lamprecht 1981; Packer *et al.* 1990), but it may require another 10 to 20 years of longitudinal data to approach this question. Even then, it may never be possible to test empirically why these animals do not disperse, as the processes have probably been primarily historical (Koenig *et al.* 1992). However, it is certainly within reason to begin unraveling the intricacies of the consequences of the population's social structure and several studies in the past few years have begun this task (Haenel 1986; S.L. Heimlich-Boran 1986, 1988; Osborne 1986; J.R. Heimlich-Boran 1988; Waite 1988; Jacobsen 1986, 1990; Bain, 1989; Ford 1989; Felleman *et al.* 1991). These studies have focused on social theory, interpod relationships, general social behavior, and female-calf dynamics. My study focuses on the social dynamics of male killer whales of the northern resident community.

Chapter One addresses the ontogeny of male behavior. I identify those behavioral traits that coincide with physical signs of maturation. Describing how activity budgets and frequency of behaviors develop through different stages of the life cycle will address the following questions: What do males do? Where does killer whale behavior parallel and diverge from that of other species? The answers will contribute to understanding the role of males in the matrilineal group and the pod. These analyses should also help improve upon previous definitions of developmental stages that were fairly arbitrary.

Chapter Two analyzes male association patterns. I describe in detail with whom males associate on a daily basis and how these associations change with behavior state and as males mature. I compare my results with those of other studies on killer whales. By

clarifying association patterns and how they change over time and by specifying and emphasizing known relatedness in the analysis, I draw conclusions about the degree of social integration that males demonstrate within the community at different stages of development.

Chapter Three is an attempt to determine the nature of two specific social interactions that occur, that may be direct consequences of the permanent mother-son bond. Males participate in short-term male-only social interactions that often form in mid to late summer, when several pods have gathered in the strait (Jacobsen 1990; pers. obs.). I examine age composition, relatedness of participants, type and directionality of behaviors, group size, and timing of occurrence of these interactions in an attempt to determine their function. Males also associate tightly with related juveniles less than five years of age, while the mother is more than a body length (up to one to two kilometers) away. This has been hypothesized to be a form of allopaternal care (Haenel 1986; Waite 1988). Although I have few data, I offer a preliminary discussion as to whether the current evidence argues convincingly that such associations are allopaternal in nature.

GENERAL METHODS

The study area:

All observations were made in and adjacent to Western Johnstone Strait, British Columbia (Fig. 0.1). This region (approximate center: 50° 30' N, 126° 35' W), from the bottom of Queen Charlotte Strait, through Blackfish Sound, into Johnstone Strait and down to Adam River, is the summer core area (Bigg *et al.* 1987) for approximately half of the northern resident community at any one time. When not in the core area, whales are apparently north of Port Hardy, Vancouver Island (D. Bain, J. de Boeck, G. Ellis, J.K.B. Ford, pers. comm.). To maximize the number and duration of encounters, camp was set up on West Cracroft Island, directly across from Robson Bight, the site of pebbly beaches against which the whales rub their bodies. The function of beach rubbing has not been determined (Ford 1989), but whales visit these rubbing beaches regularly while in the core area (Ford 1989; Briggs 1988; pers. obs.), which guarantees a high rate of encounter.

Time period of observations and data collection:

The study was conducted over three summers, from 25 July 1988 to 14 September 1988, from 27 June 1989 to 3 September 1989, and from 30 June 1990 to 2 August 1990. Observations were attempted on 47 days in 1988, 57 days in 1989, and 27 days in 1990, for a total of 131 days. Going into town for supplies, rough water, severe storms, and mechanical breakdowns accounted for 21 lost observation days. Whales were encountered on 90% (118/131) of the days on which observations were attempted.

Observations were made from a 4.6 m Avon inflatable craft with a 35 hp outboard motor in 1988 and 1989 and from a 5.5 m fiberglass-hulled craft with a 130 hp inboard motor

in 1990. An observer day began at 0730 hrs and ended at 1830 hrs. Both visual and auditory scannings for whales began at 0730 hrs and were conducted either from camp, using a 60x-power spotting scope and a hydrophone sunk just offshore at the base of camp, or from the boat, using binoculars and a hydrophone placed over the side. Whales were spotted and/or heard and encountered opportunistically, precluding random sampling of animals and biasing the total sample toward those males that visited the study area most frequently.

Data collection depended on a number of factors. These included the number of commercial and private whale watching boats present (more than four or five boats watching a group made maneuvering difficult, frequently blocked my view, and appeared to alter the behavior of the whales), distance from camp (the amount of gas carried in the boat was limited and distances greater than 15-25 km from camp in either direction were prohibitive), and sea state (sudden squalls could arise and cut short an observation day, even if whales were within visual range).

Data to determine activity budgets, frequency of behaviors, and association patterns were collected by following focal animals (Altmann 1974) and keeping serial records of their activities. If the first group encountered contained one or more sample males and all of the above mentioned conditions permitted, I began an observation session. Overall, I feel this sampling regime gave a representative activity budget, as any and all whales were encountered and followed opportunistically at all times of day, throughout the study area, and for relatively standard periods of time (see below). From one to eight (more usually one to four) focal animals were followed at a time; one hour of following four focals, for instance, equalled four whale-hours of observation. The start times of the observation sessions were evenly distributed between the first and second half

of the observation day (Chi-square = 0.297, $df = 1$, $N = 165$, $P > 0.50$), so there was no bias in the sessions toward occurring early or late in the day. Density of boats in the whales' vicinity frequently prevented or interrupted continuous observations, resulting in a relatively small number of hours of serial record data compared to the total time spent observing each day.

Serial record data were taken as follows: All whales in visual range were identified before the session formally began; if there were individuals who could not be identified, photographs from within 10-20 m were taken to subsequently verify the tentative field ID assignments. Only three to four individuals from 165 sessions remained unidentified. Focal animals were chosen (as much as possible, all animals within a 300-400 m radius were followed). Observations were made from a distance of 10 to 1000 m, depending on activity, number of whales present, and familiarity with the focal animal(s). A session was generally 30 min in length, although infrequently sessions continued for up to 120 min (in approximately 15 min incremental increases) if there were no other whales present within observer range or other groups within observer range were being followed by large numbers of boats. A small number of sessions were less than 30 min in length due to unforeseen circumstances (e.g. mechanical breakdown).

Generally, if whales were continuously present, I waited at least one hour before beginning a second session with the same or a different group. This "downtime" minimized disturbance to the whales, who have been shown to alter their behavior when vessels approach closely and persistently follow them (Kruse 1991). From one to five sessions were completed in a day. An assistant recorded all of my spoken observations on data sheets that were divided into 10-sec intervals (Appendix A); thus, behavioral

sequences were accurate only to within 10 sec. Each surfacing was recorded, usually noted as a breath, and the distance between the focal animal(s) and any associates was estimated as tight, loose, or separate. Tight was within one body-length (< 8 m), loose was roughly one body-length (8-12 m), and separate was greater than one body-length apart.

The ethogram with its three-letter behavior codes (Appendix B) was based on that of Östman (1987). For each surfacing, all discrete behaviors (distinct, single event occurrences, such as a tailslap, a spyhop, or a body-rub) were recorded. These behaviors, plus estimated swimming speed, were subsequently used to determine the general behavior state of the sample male(s) (see Osborne 1986; J.R. Heimlich-Boran 1988; S.L. Heimlich-Boran 1986, 1988; and Jacobsen 1990 for comparative definitions of behavior states). I defined four behavior states:

- 1) **Rest:** defined as swimming at a speed generally less than 2 knots, often with bouts of remaining stationary at the surface, in tight association with matrilineal group members (for exceptions see Chapter Two), breathing synchronously. Discrete behaviors and milling were rarely observed; when they were, the whales were usually making the transition from resting to another behavior state or were changing direction.
- 2) **Milling/foraging:** defined as swimming at speeds varying from <1 to 8 knots, with occasional brief bursts of extreme speed, with frequent breaks in directional swimming to surface repeatedly in one area (the mill). Breathing was asynchronous, group movements were generally uncoordinated, and individuals were often spread out over a large area, although highly coordinated cooperative

fish herding (J.R. Heimlich-Boran 1988; Würsig and Würsig 1980; Bel'kovich *et al.* 1991) was infrequently observed. Foraging was frequently accompanied by percussive behaviors, positioning close to the shoreline, and rocking body motions and splashing at the surface. This was assumed to indicate active feeding, although fish-capture was rarely observed.

3) **Travel:** defined as directional swimming at speeds varying from 2 to 12 knots, with moderate to high coordination of group movement, generally asynchronous breathing, and few discrete behaviors observed. If a mill commenced, an animal was not considered to be traveling again until more than ten sequential directional surfacings occurred. Occasional bouts of milling occurred while an animal was traveling, prior to a change in direction. These bouts of milling were distinguished from milling/foraging, as they usually occurred during slow swimming and were generally low energy mills, with frequent bouts of floating and hanging and slow surface swimming. An animal that milled for less than three surfacings during travel was not recorded as milling. Slow travel was distinguished from rest primarily by the asynchronous breathing and the greater distances (loose to separate) between individuals found in the former state.

4) **Sociosexual behavior and solo play:** generally involved at least two individuals, physical contact between animals, and an increased percussive and/or aerial behavior rate, including penile extrusions. Whales engaged in sociosexual behavior frequently alternated between remaining motionless at the surface, milling, and swimming directionally, but were distinguished from resting, foraging, or traveling animals by the frequent occurrence of body contact

or the overall context of the session. Interacting with objects, such as trailing a dorsal fin through kelp or riding the stern wave of a boat, were examples of solo play behavior.

Rubbing was not considered a separate activity in the activity budget (see Ford 1984), but was included in sociosexual behavior, due to recent governmental restrictions against approaching the rubbing beaches within 1 km. Whales did at times spend a considerable time rubbing (Ford 1984; Briggs 1988; pers. obs.), but as I could not approach closely enough to discern individual behaviors and interactions, I generally discontinued sessions if the whales began rubbing or waited to begin sessions until after they left the beaches. This produced a consistent bias toward underobserving time spent rubbing in my serial record data. Overall, rest and sociosexual behavior were relatively distinct, but traveling and milling/foraging were more difficult to distinguish from each other.

Ad libitum scan sampling data (Altmann 1974) were recorded continuously during waking hours, in a log I carried with me at all times. An entry was made upon first encountering a group or when reencountering a group after "downtime" between observation sessions. These entries were based on an instantaneous scan of all whales in visual range. The identity of all whales, associations, behavior states, and any discrete behaviors were noted. These data were used primarily for the individual profiles of Appendix C and the descriptions of specific associations of Chapter Two. I also made entries whenever the whales changed their behavior or their associations, did something highly visible, or merely persisted for unusually long periods at some behavior. As a result, these latter type of entries tended to be biased toward the obvious or spectacular. The principal value of these latter data is that unusual associations, such as adult

male/reproductive female, and rarely observed events, such as the capture of a fish, were recorded. These data were used primarily for the individual profiles of Appendix C and in Chapter Three analyses.

Ad libitum log entries were also made whenever whales passed by camp, either early in the morning before departing or later in the evening after returning. Such entries, with accurate whale identifications, were made as late as 2200 hrs, although generally they were made before 2100 hrs. I also continued to make entries when it was not possible to take serial record data due to too many other boats present, although I generally kept my distance at such times and such entries were highly irregular.

Sample males:

Ideally, I would have collected observations from all 78 of the males present in the northern resident community. However, only 45 of these males were regular visitors to Johnstone Strait. Regular visitors were defined as those individuals in matrilineal groups that visited the strait in at least one of the three years, for a total of at least ten days. There were 28 juveniles of unknown sex, nine known male juveniles, and two known female juveniles in this subsample of the population; assuming a 1:1 sex ratio prior to sexual maturity (Olesiuk *et al.* 1990), I considered 10 of the unknowns to be males, giving 19 male and 20 female juveniles. I only encountered 32 of the male regular visitors frequently enough to collect data from them. Table 0.1 lists these sample males, their pod affiliations, their presumed mother, their matrilineal group size and its matriarch, their estimated or known year of birth (Bigg *et al.* 1990b), and the total number of hours each male was observed. The 32 sample males represented nine pods and 16 matrilineal groups. Twenty-one males had at least one presumed or known brother/half-brother in the

sample and four had at least two presumed nephews in the sample. One male had three presumed great-nephews in the sample. Two additional males (A13, D05) were included in the male-only social interactions analyses (Chapter Three), but did not contribute to the serial record data set.

There was probably a bias toward older animals in the sample (see Fig. 1.1), in total number of individuals and certainly in total number of hours of observation per individual, since only a small number of younger animals were of known sex and older animals were easier to identify in the field.

Data analysis:

See each chapter for a complete description of analyses.

In all analyses, sample sizes were less than 20, one or two outliers in each sample were usually encountered, and variances were large (normality of data could not be assumed). As a result, robustness was favored over power and two-tailed non-parametric statistical tests were used (Kruskal-Wallis and Mann-Whitney U, where appropriate). Results of statistical analyses appear in figure and table captions and are not repeated in the text. If sample sizes were less than five, data were not statistically compared, as most non-parametric tests are not valid with such small sample sizes (W. Rice, pers. comm.). Non-significant results were discussed in the light of any trends present in the data. Data for all years for each individual were pooled for most analyses (each individual contributing one mean or data point to each analysis). It is unknown to what extent pooling affects the reliability of non-parametric tests (Machlis *et al.* 1985).

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Table 0.1. Identification of sample males, pod affiliation, mother (presumed or known), number of whales in matrilineal group and identification of matriarch, estimated or known year of birth, and total number of hours each male was observed during study (see General Introduction for definitions)

MALE ID	POD	MOTHER	MATRILINEAL GROUP SIZE (MATRIARCH)	YEAR OF BIRTH*	NUMBER OF HRS OBSERVED
B01	B01	PB11	8 (B07)	≤1951	4.29
B02	B01	?†	8 (B07)	≤1952	1.47
C03	C01	?†	5/6° (C06)	≤1952	4.26
A20	A01	PA01	5 (A36)	~1953	5.03
I05	I02	PI02	8 (I02)	≤1954	0.53
R01	R01	PR09	2 (R09)	≤1954	2.10
R03	R01	PR02	3 (R02)	~1956	1.89
A05	A05	PA09	3 (A09)	~1957	2.25
A31	A01	PA12	4/5° (A12)	~1958	13.55
I32	I31	PI31	4 (I31)	~1963	3.00
A32	A01	PA36	5 (A36)	~1964	7.70
A06	A01	PA30	5/6° (A30)	~1964	26.56
B08	B01	PB07	8 (B07)	~1964	1.50
H02	H01	PH06	80 (H06)	~1965	3.49
R12	R01	PR02	3 (R02)	~1966	1.89
A38	A01	A30	5/6° (A30)	1970-1	25.27
A33	A01	A12	4/5° (A12)	1971	13.47
A26	A05	A09	3 (A09)	1971-2	1.78
A27	A05	A23	3 (A23)	1971-2	5.07
C09	C01	C06	5/6° (C06)	1971-2	4.74
B06	B01	B11	8 (B07)	1973	2.20
H04	H01	H03	80 (H03)	1974-5	3.13
A39	A01	A30	5/6° (A30)	1975	21.72
A37	A01	A36	5 (A36)	1977∞	6.18
A15	A05	A14	40 (A14)	1979	1.73
B10	B01	B07	8 (B07)	1979	1.92
H07	H01	H03	80 (H03)	1981	1.50
A46	A01	A36	5 (A36)	1982	1.83
I43+	I11	I16	80 (I15)	1983	0.39
B12	B01	B07	8 (B07)	1984	2.54
C13	C01	C10	3/4° (C05)	1985	5.11
C14	C01	C06	5/6° (C06)	1985	3.03

Table 0.1 cont'd

* All birth years taken from Bigg *et al.* (1990b).

P Presumed mother, from Bigg *et al.* (1990b).

† Mother unknown--apparently died prior to 1971.

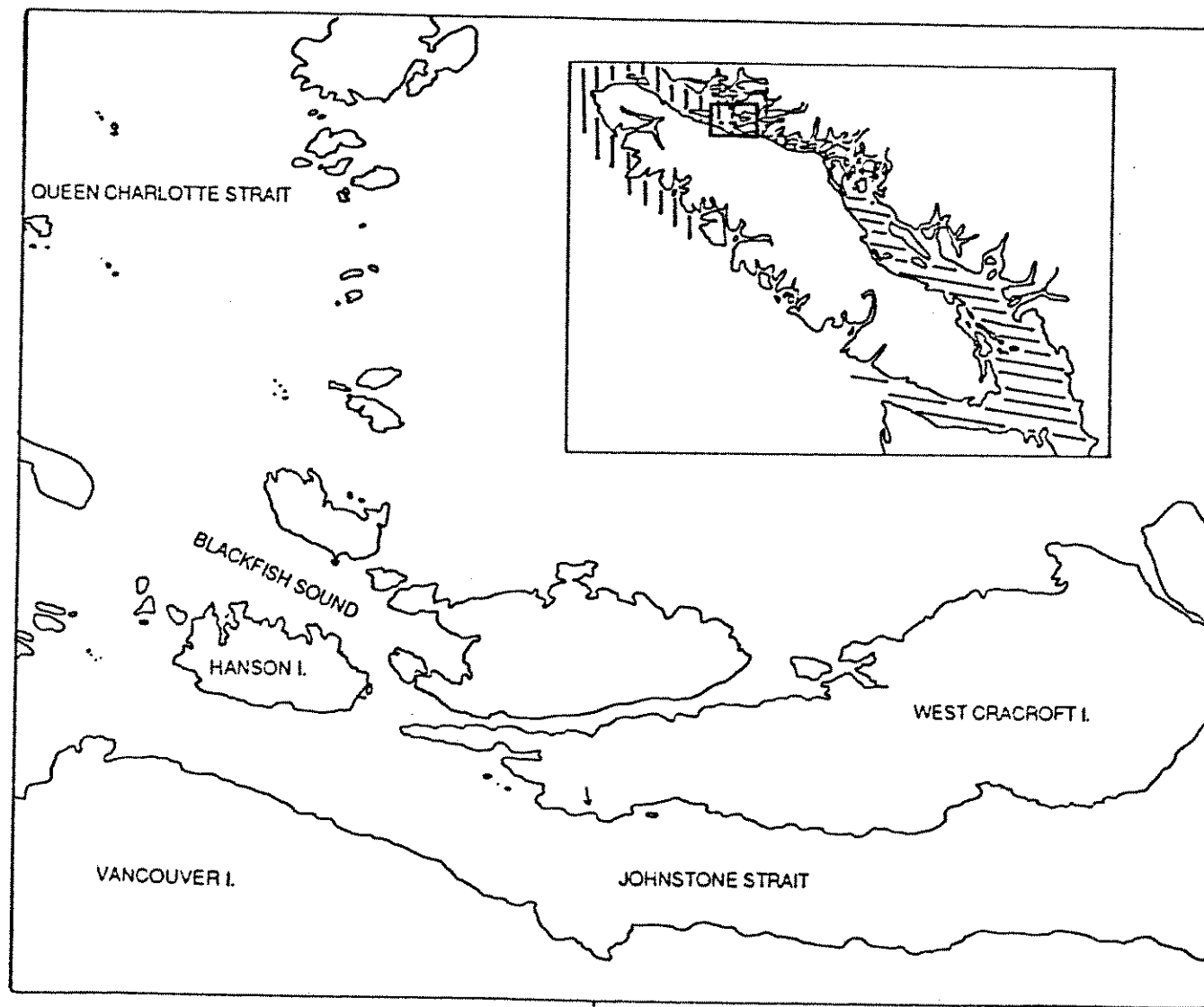
° Group size changed during study due to new birth.

◇ These matrilineal groups in the process of splitting apparently due to daughters having first calf--groups sizes variable both within and between years.

+ I43 presumed male based solely on behavior.

∞ A37 was the only male included in the Chapter Three analyses to span two age classes (juvenile in 1987-88 and adolescent in 1989) during that chapter's study period (1987-1989). For Chapter Three analyses, he was considered a juvenile, while in all other analyses, he was considered an adolescent. All males who matured into the next age class during the main study (1988-1990) were placed in the age class they occupied two out of the three years.

Figure 0.1. Map of study site: Johnstone Strait and its surrounding waters, with an arrow pointing to the research campsite on West Cracroft Island (inset: Vancouver Island with the study site indicated by a box and northern and southern resident communities' ranges indicated by hatch-marks).



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CHAPTER ONE
THE ONTOGENY OF BEHAVIOR

ABSTRACT

Behavioral development of male killer whales was studied in order to identify behavioral traits that coincide with physical signs of maturation and to demonstrate where the development of killer whale behaviors parallels and diverges from that of other species. The following predictions were made: 1) Younger males socialize (play) most and forage least; 2) for any given activity level, older males have lower respiration rates than younger males; and 3) activity levels decrease with age. Males were classified as juvenile (<12 years), adolescent (12-25 years), or adult (>25 years), based on known or estimated year of birth and age-related morphological changes. Animals were observed from a boat and surface behaviors were recorded continuously throughout daylight hours. Percent time spent traveling, foraging, resting, and socializing; respiration rates; and frequency of three types of behavior (body-contact, non-percussive aerial, and percussive) were calculated for 32 males. The first prediction was only partially confirmed; adolescents spent twice as much time playing as did adults, but also twice as much as did juveniles. The second prediction was not confirmed; respiration rates were the same for all age classes. The last prediction was confirmed; juveniles were up to three times as active at the surface as were older males. The inconclusive respiration results could be due to sampling biases. Body-contact and non-percussive aerial behavior rates paralleled the ontogeny of activity levels of most mammals. Activity budgets diverged from the pattern usually seen in mammals. Adolescents played more than juveniles, an apparent consequence of both the frequent encounters of kin and non-kin of all age and sex classes (in turn a consequence of the permanent mother-son bond) and the long period of adolescence in male killer whales.

INTRODUCTION

Behavioral development of male mammals:

Most mammals are polygynous (Eisenberg 1981). In these species, the behavioral development of males generally follows a similar pattern. As juveniles, males play more frequently and more actively than females (Chalmers 1980; Fagen 1981; Jamieson and Armitage 1987; Walters 1987; Biben 1989). As a correlate, males often achieve a greater degree of independence from their mothers at an earlier age than do females (but see Altmann 1980). This greater independence culminates just before or at puberty, when males disperse from their natal range (Greenwood 1980; Chepko-Sade and Halpin 1987). Males compete with each other for access to estrous females during adulthood, but otherwise have minimal interaction with conspecifics (Eisenberg 1981; Smuts 1987; but see Kano 1982). Finally, males contribute little or no parental care to offspring (Trivers 1972, 1985; Eisenberg 1981). The daily social fabric of mammalian societies is largely a matter of female kin relationships and interactions, as it is the females who are philopatric (Greenwood 1980). The basic social unit is a mother and her immature offspring.

Even in mammals with social groups that contain more than one adult male, this ontogenetical pattern generally holds (e.g. many cercopithecines: Melnick and Pearl 1987; but see Blaffer-Hrdy 1976; Sumatran long-tailed macaques, *Macaca fascicularis*: van Noordwijk and van Schaik 1988). However, certain steps in the sequence vary in some species whose basic social unit contains several adult males, such as in chimpanzees (*Pan troglodytes*: Nishida and Hiraawa-Hasegawa 1987) and some social carnivores, notably canids (Bekoff *et al.* 1984). In such species, the males are philopatric or both sexes disperse, often in kin units (Greenwood 1980). Thus males within a social group are usually related and behave cooperatively and affiliatively. Males may exhibit substantial

paternal and allopaternal care (Nishida 1983; Gittleman 1985). As with females in one-male social groups, kin relationships among males in these less typical multiple-male groups have fundamental effects on the development of behavior and the dynamics of social interactions.

This study:

In the killer whale population of Johnstone Strait, British Columbia, both sexes are philopatric, with males associating with their mothers for life (General Introduction). Males who are both kin and non-kin interact frequently. Research efforts into killer whale social dynamics have just begun and work so far has focused mainly on female-calf dynamics or group behaviors (Waite 1988; Ford 1989; Jacobsen 1990) and has provided more anecdotal than systematic observations of male behaviors. This study was the first attempt to examine systematically the behavior of male killer whales, in an effort to describe the behavioral consequences of their unusual social structure and to determine which, if any, developmental patterns they share with other mammals.

This chapter examines differences across age classes of activity budgets, respiration rates, and frequency of body-contact, non-percussive aerial, and percussive behaviors, in an effort to identify what elements of behavior change with age. It was difficult to predict what changes would occur, as no other male mammal was known to mature and live entirely within the social environment of both its male and female kin, while simultaneously interacting frequently with non-kin. However, the following predictions were made: 1) General activity budget results are similar to those of other studies that examined activity budgets for this population; 2) as with other mammals, younger males socialize (play) more and forage less than older males; 3) for any given

activity level, older, larger males have lower respiration rates than younger, smaller males, because the former have a lower mass-specific metabolic rate and also a much greater tidal volume than the latter (Schmidt-Nielsen 1979); and 4) activity rates overall decrease with age (see Burghardt 1988).

METHODS

See General Methods for a complete description of data collection.

Data analysis:

The data were analyzed for differences among age classes (defined by morphological changes: see below) in mean activity budgets (percent time spent in each of four behavior states) and mean respiration rate (number of breaths/min). The mean rates (number of behaviors/hr) of body contact behaviors (e.g. pushing, rubbing), non-percussive aerial behaviors (e.g. spyhops, taillifts), and percussive behaviors (e.g. tailslaps, breaches) were analyzed for differences among age classes. Only males observed for two or more hours were used in most analyses.

Definitions of age classes:

Age classes were used, rather than exact ages, as fewer than half of the sample males were of known age (Table 0.1). Table 1.1 compares three age class definitions; my definitions relied on the age-related physical changes described in Olesiuk *et al.* (1990), a description to which the studies of S.L. Heimlich-Boran (1988) and Jacobsen (1990) did not have complete access. Both Jacobsen and Heimlich-Boran defined a calf class (Heimlich-Boran used the term "immatures") that I combined with my juvenile class (Heimlich-Boran used the term "adolescents" for part of this age range), as so few calves have been sexed and only known males were included in my sample.

Heimlich-Boran considered the onset of sexual maturity, which takes place at 15 years of age on average for both sexes (Olesiuk *et al.* 1990), to be equivalent to adulthood in

males. Both Jacobsen and I considered that adulthood in males is not reached until a characteristic dorsal fin height-to-width ratio (an asymptote on the growth curve) and full body length have been achieved at 21 years of age on average (Olesiuk *et al.* 1990). This necessitated an adolescent class. I defined the lower boundary of this class to be 12 years of age, not 15, to account for the fact that secondary dorsal fin development (assumed to coincide with the onset of spermatogenesis) actually begins several years prior to the achievement of the dorsal fin height-to-width ratio that distinguishes young males from adult females. I defined the upper boundary to be 25 years of age, not 21, to account for those males in my sample whose dorsal fin growth was not complete until at least that age (Olesiuk *et al.* 1990). Although these decisions were somewhat arbitrary in themselves, I believed that certain of my sample males would have been miscategorized, based on physical appearance alone, had I not made them.

Behavioral categories:

I distinguished three categories of behaviors: body-contact, non-percussive aerial, and percussive. These behavioral categories, each of which comprises several discrete behaviors (see Appendix B, which groups categories of behaviors under behavior states), were chosen because they may have distinct functions. Body-contact behaviors, such as hitting and rubbing, may be a means by which social bonds are maintained; for example, dominance hierarchies may be determined and maintained through body-contact (Clutton-Brock *et al.* 1982; Hand 1986; Walters and Seyfarth 1987; Östman 1991; but see Chapter Three). Certain non-percussive aerial behaviors, such as spyhopping and gazing, may serve to orient an animal, by allowing it to locate landmarks in a maze of inlets and islands. They may also allow the animal to observe surface objects, such as boats or logs. During play, these behaviors may allow individuals to keep track of their play partners;

other behaviors, such as tail-waving or balancing kelp on the dorsal fin, may be seen exclusively during play (Evans 1987; Bel'kovich 1991). Finally, percussive behaviors, such as tailslapping and breaching, have been hypothesized to serve a function during foraging (stunning or herding prey) (Norris and Dohl 1980; Würsig and Würsig 1980; Würsig 1986; Bel'kovich 1991) or communication (Norris and Dohl 1980; Würsig and Würsig 1980; Alcock 1984; Baker and Herman 1984; Evans 1987). They have also been observed during periods of play, when they may indicate a state of high excitement.

Database:

The age distribution of the sample males (8 juveniles, 14 adolescents, 10 adults) was not significantly different from that expected based upon the age distribution of the potential pool of males (Fig. 1.1). The potential pool of 45 males included all of the males in the matrilineal groups that visited Johnstone Strait regularly throughout the study (see General Methods). To verify that my sample was randomly selected, I assigned each of the 45 males a consecutive number (the first juvenile male was 1, the last adult 45) and then used a random-numbers table to choose 32 males to simulate my sample. This gave a resultant age distribution that was not significantly different from the observed distribution (observed: 8:14:10; random sample: 13:10:9; Chi-square goodness-of-fit = 4.37, $df = 2$, $N = 32$, $p > 0.10$). Repeat trials gave similar results.

A total of 181.12 whale-hrs of serial record data was collected (see Table 0.1 for each male's total hours). A total of 135.58 whale-hrs of *ad libitum* data (in five-min point samples) was collected.

RESULTS

Activity budgets:

Only males observed for two or more hours were used in this analysis, except for one juvenile, B10, who was observed for 1.92 hrs (Table 0.1). Overall, males spent most of their time traveling (Table 1.2; Fig 1.2) and spent the least amount of time milling/foraging. When age classes were compared, the activity budgets of adults and juveniles were very similar (Fig. 1.3). Adolescent males spent significantly more time socializing than adults and tended to spend less time traveling; however, due to large variances within age classes, most differences were not significant.

Respiration rates:

Again, only males observed for two or more hours (plus B10) were used in this analysis. There were no differences in respiration rates (Fig. 1.4). Looking at respiration rates during rest, to control for activity level, juveniles tended to have higher rates, but the juvenile sample size was too small for statistical analysis (Fig. 1.5).

Behavior rates:

All males were used for these analyses, except for I05 and I43, who were only observed in male-only social interactions. For body-contact behaviors, there was a significant difference among age classes in rate (Fig. 1.6), with adults showing the lowest rate and juveniles the highest. For non-percussive aerial behaviors, the trend was the same and approached significance (Fig. 1.7). For percussive behaviors, an additional male, A27, was not used in the analysis, as he was an unusual outlier (see Appendix C). For this behavior category, differences were not significant (Fig. 1.8).

DISCUSSION

General activity budgets:

My activity budget results are in sharp contrast to previous studies using group scan sampling (Table 1.2; Fig. 1.2). These other studies estimate that killer whales spend at least half of their time foraging, if not more (J.R. Heimlich-Boran 1988; Ford 1989; Morton 1990; but see Nichol 1990). This discrepancy is probably not as extreme as it appears, however, since these studies, notably those of Ford (1989) and Morton (1990), undoubtedly classified what I considered traveling behavior as foraging. Although I was exceptionally conservative in classifying behavior as foraging, I do not dispute that animals could be feeding while traveling from point to point. I was attempting to distinguish between behavior states during which looking for food and feeding were paramount and during which food was acquired opportunistically. The abundance of food present in the strait during the summer makes it unlikely that foraging is difficult. Opportunistic feeding is probably common.

Furthermore, I was observing individuals to determine their behavior state, and on many occasions not all individuals in a group were doing the same thing. The group scan sampling of the other studies would assign a behavior state to a group based on what the majority were doing. From this point of view, my results may be more representative of the actual state of affairs, as ignoring the individual exceptions could overestimate time spent foraging. Nevertheless, it is clear from Table 1.2 that classifying the behavior states of killer whales has been a somewhat subjective exercise.

Despite biases in data collection that should have underestimated both time spent resting and socializing (see General Methods), my results for these two behavior states, the most objectively identifiable, are in general higher than those of the other studies (Table 1.2). However, it should be kept in mind that the other studies combined all age and sex classes, while my results were only for males. Consequently, I believe that the higher percentage for sociosexual behavior in my results is a real difference and should be even greater; males, especially young males, socialize more (certainly more obviously and physically) than females (pers. obs.).

Activity budgets by age class:

All evidence supports that it is adolescent males, not juveniles, who spend the most time in the sociosexual behavior state (Fig. 1.3; see Chapter Three: Part One). This is unexpected, since with most mammals, it is juveniles who socialize and play most (Fagen 1981). This increase in sociosexual behavior is the most notable behavioral difference that distinguishes the adolescent age class from the other two age classes. Whereas juveniles spend much of their time close by their mothers (Chapter Two; Appendix C) and adults socialize infrequently and are more often seen alone (Chapter Two; Chapter Three: Part One; Appendix C), adolescents socialize proportionally more often than they forage or rest (Fig. 1.3). They play with their younger siblings, with each other, with older, non-reproductive females, and less frequently with inanimate objects, such as boats (sternriding) (Chapter Two). It appears that adolescence signals an increase in such activity (Chapter Three). Adolescents are sexually but not physically (i.e. socially) mature (Olesiuk *et al.* 1990) and increased non-reproductive sociosexual behavior may be the result.

All three age classes spent similar proportions of their time foraging. This may be a result of the lack of very young juveniles in the study sample. The youngest juvenile in my sample was three years of age in 1988, an age at which dependence on solid food may be nearly complete. Evidence from captivity and strandings (e.g. Heyning 1988) indicates that killer whale calves begin taking solid food at a very young age (as young as two months), although complete nutritional independence from the mother is probably not achieved until four or five years of age (the average interbirth interval).

Respiration rates and metabolism:

Other studies on killer whales, controlling for activity level and/or swimming velocity, have found predicted differences in respiration rates correlated with various factors (e.g. sex: Kriete 1991; the presence of a certain class of associate: Waite 1988). This indicates that respiration rate can be used as a measure of metabolic rate in killer whales (see also e.g. gray whales, *Eschrichtius robustus*: Sumich 1983). However, males show no difference in mean respiration rates across age classes (Fig. 1.4). Apparently combining all behavior states and velocities introduces too many variables and masks any differences that may in fact exist. When looking at respiration rates during rest only, a behavior state that controls as well as possible for activity level and swimming velocity, the trend is as expected for juveniles (Fig. 1.5). It is probable that with a large enough sample size for analysis, this trend would be significant. One might also expect, with a larger sample size, that adolescents would have a respiration rate between that of juveniles and adults.

Behavior rates:

The rates at which males perform body-contact and non-percussive aerial behaviors correspond to age-related morphological changes (Figs. 1.6 and 1.7). Reaching adulthood appears to signal a decrease in activity level overall (see Chapter Three: Part One), as expected. However, percussive behavior does not follow this trend. If percussive behaviors are used for foraging, it makes sense that adults would perform them at least as often as juveniles. As mentioned above, three and four-year-old juveniles may still be nursing to some extent, and some of the percussive behaviors they perform could be attributed to their overall higher activity level. Adolescents and adults would maintain high percussive behavior rates, since these behaviors, used as a foraging technique, would continue to be an important component of their behavioral repertoire. This logic applies also if percussive behaviors are used as social signals; all age classes might be expected to use such signals.

Conclusion:

In some respects, male killer whales demonstrate developmental patterns that are typical of most mammals. In particular, juvenile males are more physically active than older males. However, in another respect, their behavior diverges from the general pattern. Adolescence does not signal dispersal, but rather an increase in sociosexual behavior. Sexual maturity in most other male mammals coincides with a decrease in general social interaction with conspecifics, although reproductive behaviors increase. However, sociosexual behavior in male adolescent killer whales does not appear to be reproductive in nature, as it is largely due to intrasexual play (Chapter Three: Part One) and only adult males are observed in physical contact with unrelated reproductive females (Chapter Two).

It is difficult to say whether this increase in sociosexual behavior is the result of male philopatry or the long adolescence of killer whales. Frequent encounters with other males, through association with the matriarch (Chapter Two), may increase the need for affiliative, aggression-reducing behavior (Chapter Three: Part One), but adults should exhibit similar levels of sociosexual behavior if this is so, and they do not. It is possible that intrasexual play is a means by which adolescent males acquire necessary social skills (Chapter Three: Part One) during their long adolescence. It may also allow them to relieve an active libido that frequent encounters with non-kin females may stimulate (e.g. Rose *et al.* 1991). Adolescent males may also frequently be called upon as allofathers (Chapter Three: Part Two), as they are the most likely to have young juveniles still in their matrilineal group. All of these factors may account for the increase in sociosexual behavior exhibited by adolescent males. A combination of philopatry and long adolescence may account for this behavioral pattern.

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Table 1.1. Age class definitions of S.L. Heimlich-Boran (1988), Jacobsen (1990), and this study.

	Heimlich-Boran 1988	Jacobsen 1990	This study
Calves	0 - 6 years (immatures)	0 - 3 years	---
Juveniles	7 - 14 years (adolescents)	4 - 10 years	< 12 years
Adolescents	---	11 - 21 years	12 - 25 years
Adults	≥ 15 years	> 21 years	> 25 years

Table 1.2. Comparison of activity budgets determined by J.R. Heimlich-Boran (1988), Ford (1989), Morton (1990), Nichol (1990), and this study. Numbers are percent of total time observed for all age and sex classes combined, except for this study (males only).

	Heimlich-Boran 1988	Ford 1989	Morton 1990	Nichol 1990	This study
Travel	25	4	8	32	43
Mill/Forage	47	66	50	38	13
Rest	13	13	21	15	24
Socialize	15	17	21	15	20

Figure 1.1. The age class distribution of sample males vs. that of males that were regular visitors to Johnstone Strait. The distributions were not significantly different (Chi-square goodness-of-fit = 3.82, $df = 2$, $N_1 = 32$, $N_2 = 45$, $p > 0.10$).

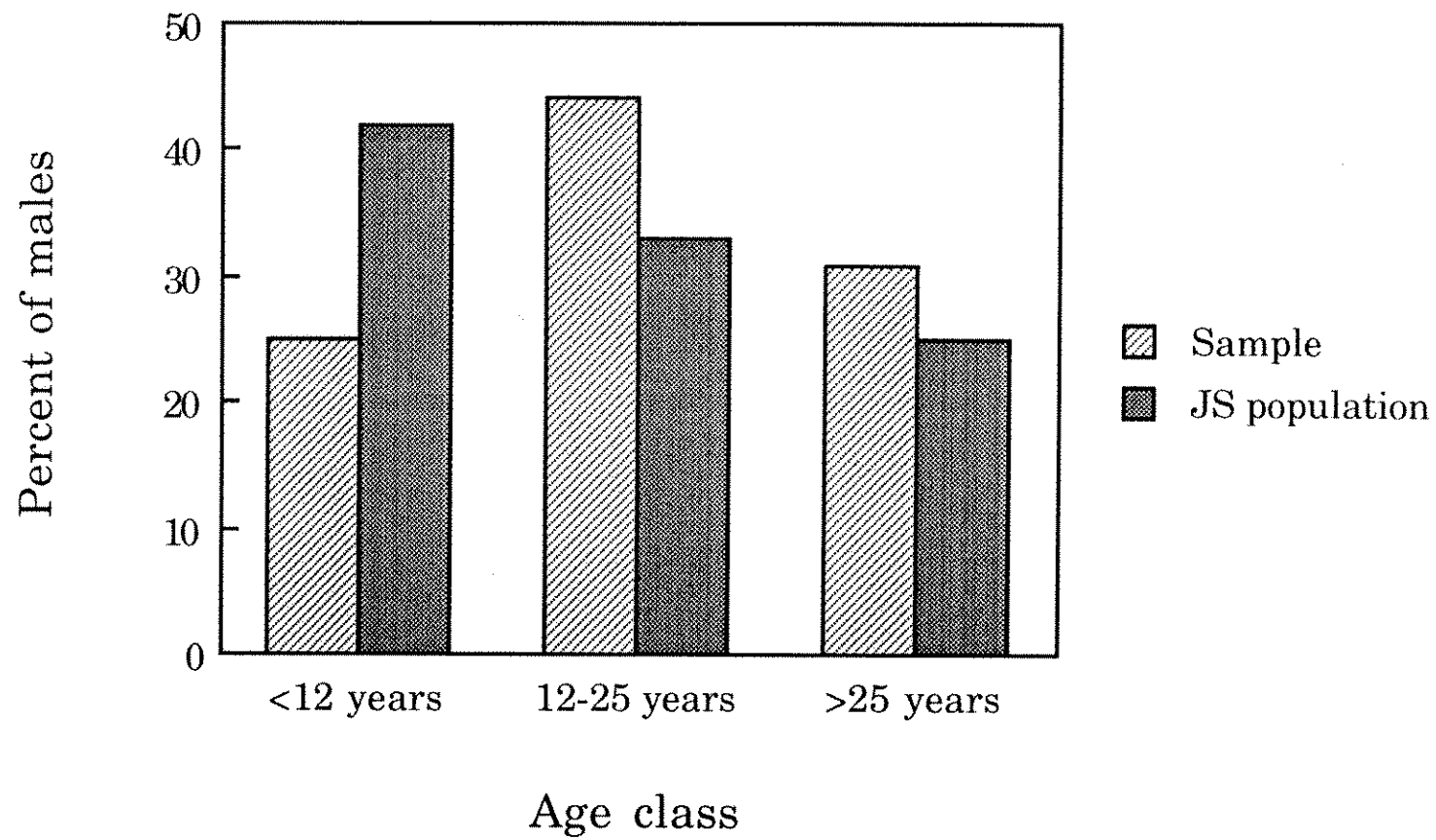


Figure 1.2. Percent of total observation time spent in each behavior state for all males combined (N = 22).

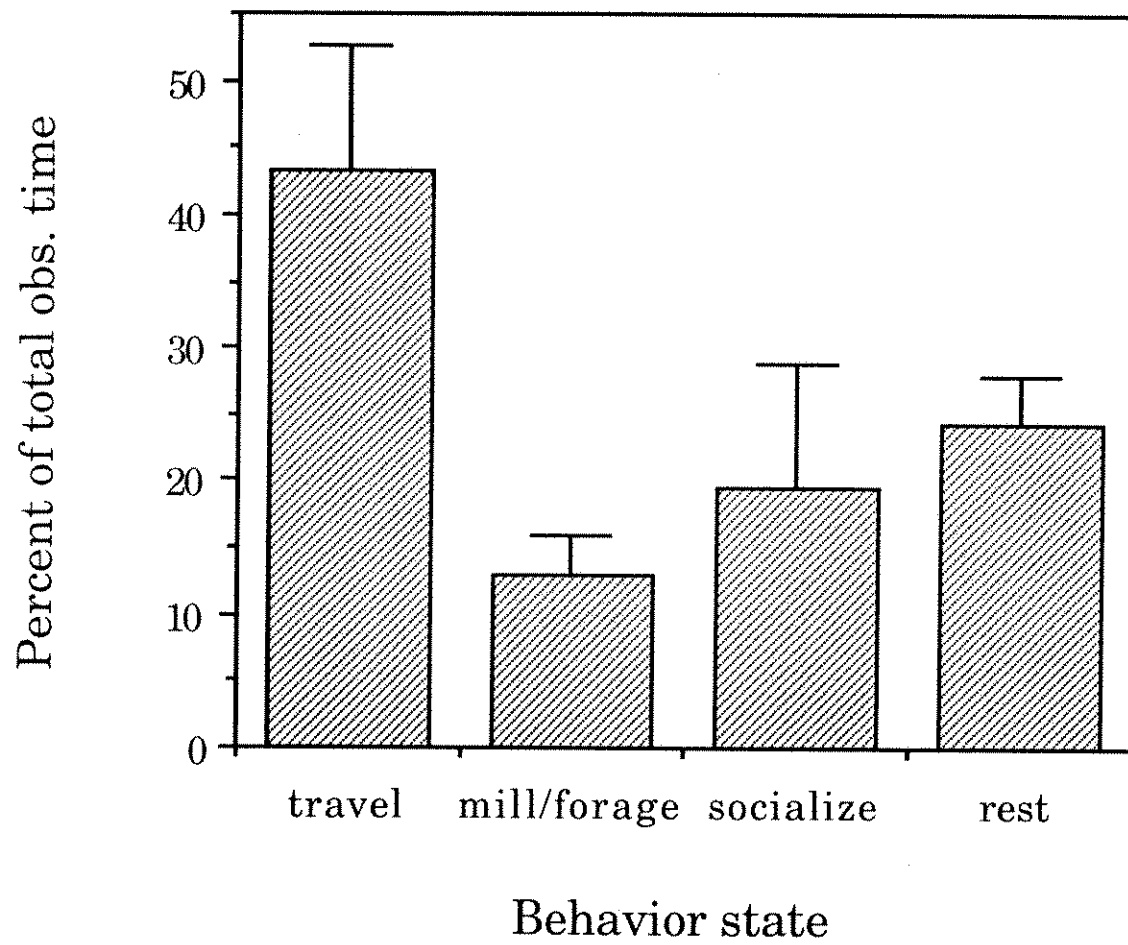


Figure 1.3. Percent of total observation time spent in each behavior state for each age class (N = 4, 11, and 7 respectively). The difference between age classes (juveniles were not used for analysis) was significant only for sociosexual behavior (sociosexual: Mann-Whitney U = 61, $p = 0.0410$; travel: Mann-Whitney U = 54.5, $p = 0.1569$; milling/foraging: Mann-Whitney U = 51.5, $p = 0.2548$; rest: Mann-Whitney U = 46, $p = 0.5189$).

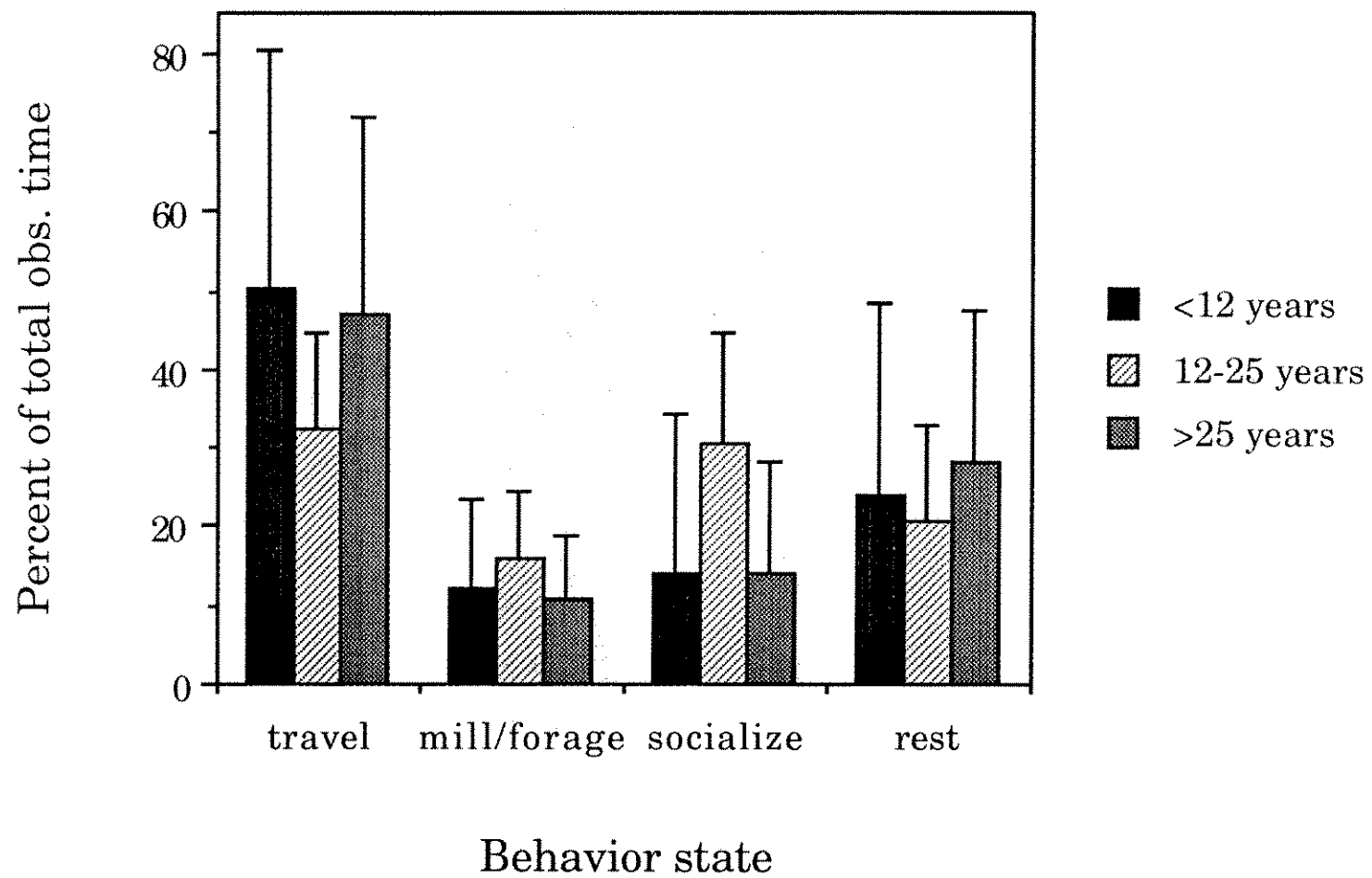


Figure 1.4. Respiration rates compared across age classes (sample sizes are the same as for Fig. 1.3). The difference between age classes (juveniles were not used for analysis) was not significant (Mann-Whitney $U = 41$, $p = 0.8601$).

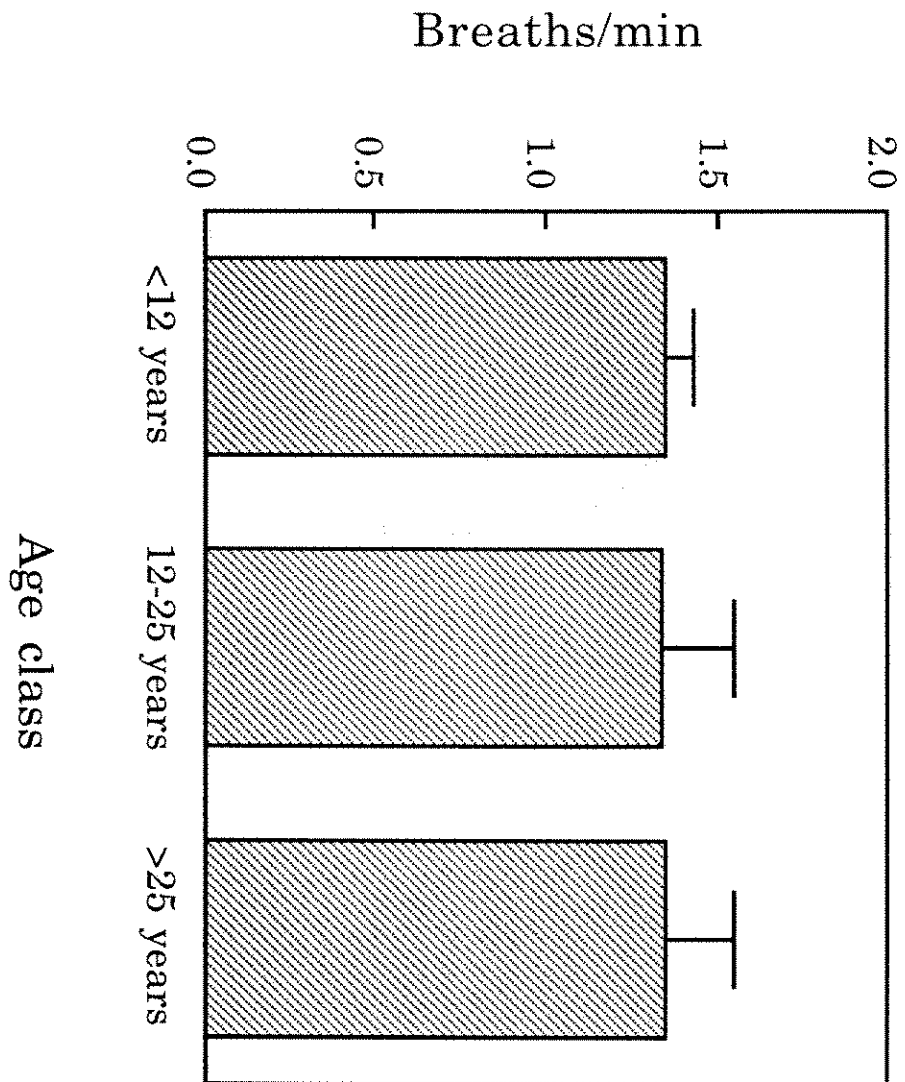


Figure 1.5. Respiration rates compared across age classes (N = 3, 10, and 7 respectively) for the resting behavior state only. The pertinent sample size (juveniles) was too small for statistical analysis.

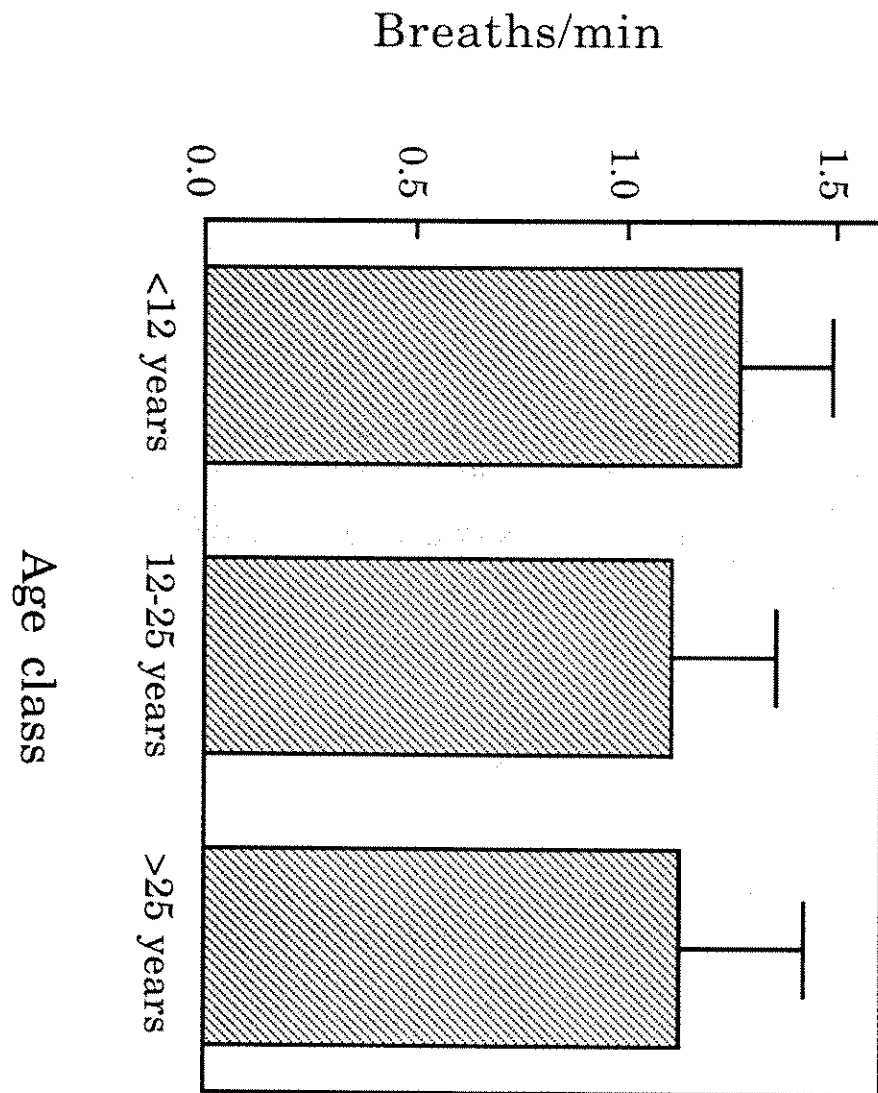


Figure 1.6. Number of body-contact behaviors performed per hour for each age class (N = 7, 14, and 9 respectively). Adults performed significantly fewer body-contact behaviors per hour than the other age classes (Kruskal-Wallis test, $H = 6.587$, $df = 2$, $p = 0.0371$).

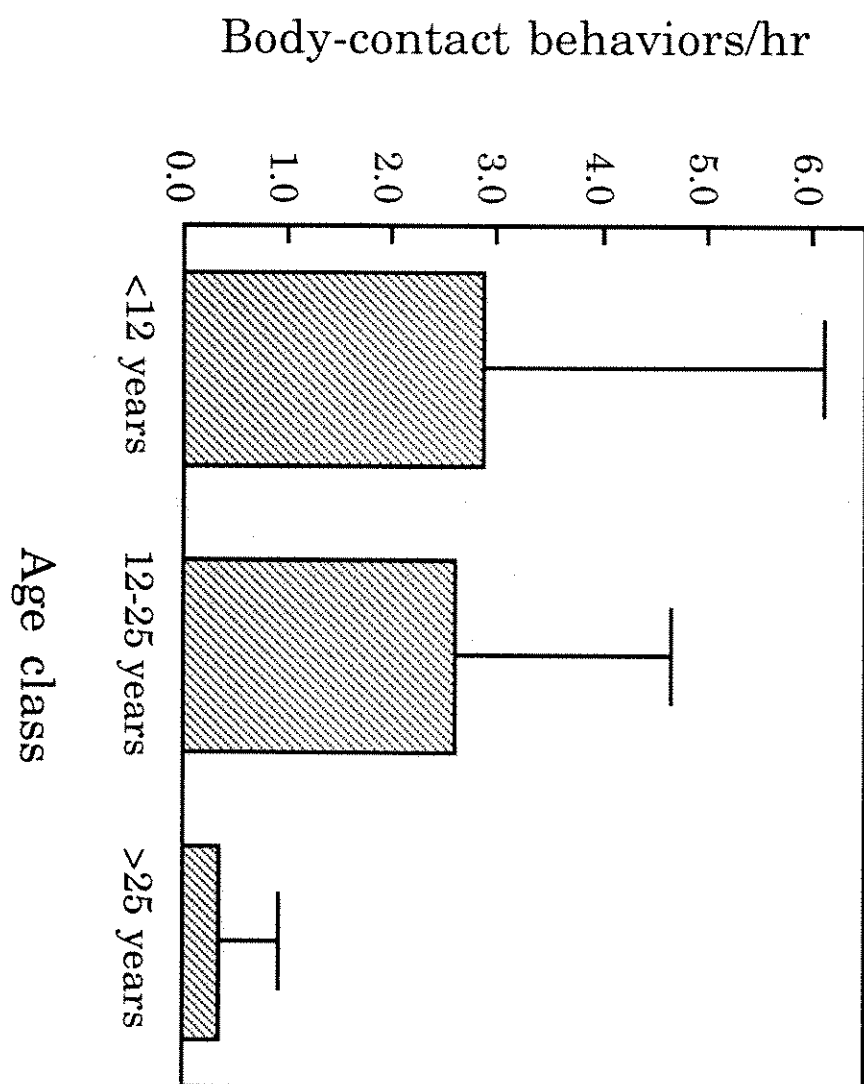


Figure 1.7. Number of non-percussive aerial behaviors performed per hour for each age class (sample sizes are the same as for Fig. 1.6). The differences among age classes approached significance, with adults performing fewer aerial behaviors per hour than the other age classes (Kruskal-Wallis test, $H = 5.489$, $df = 2$, $p = 0.0643$).

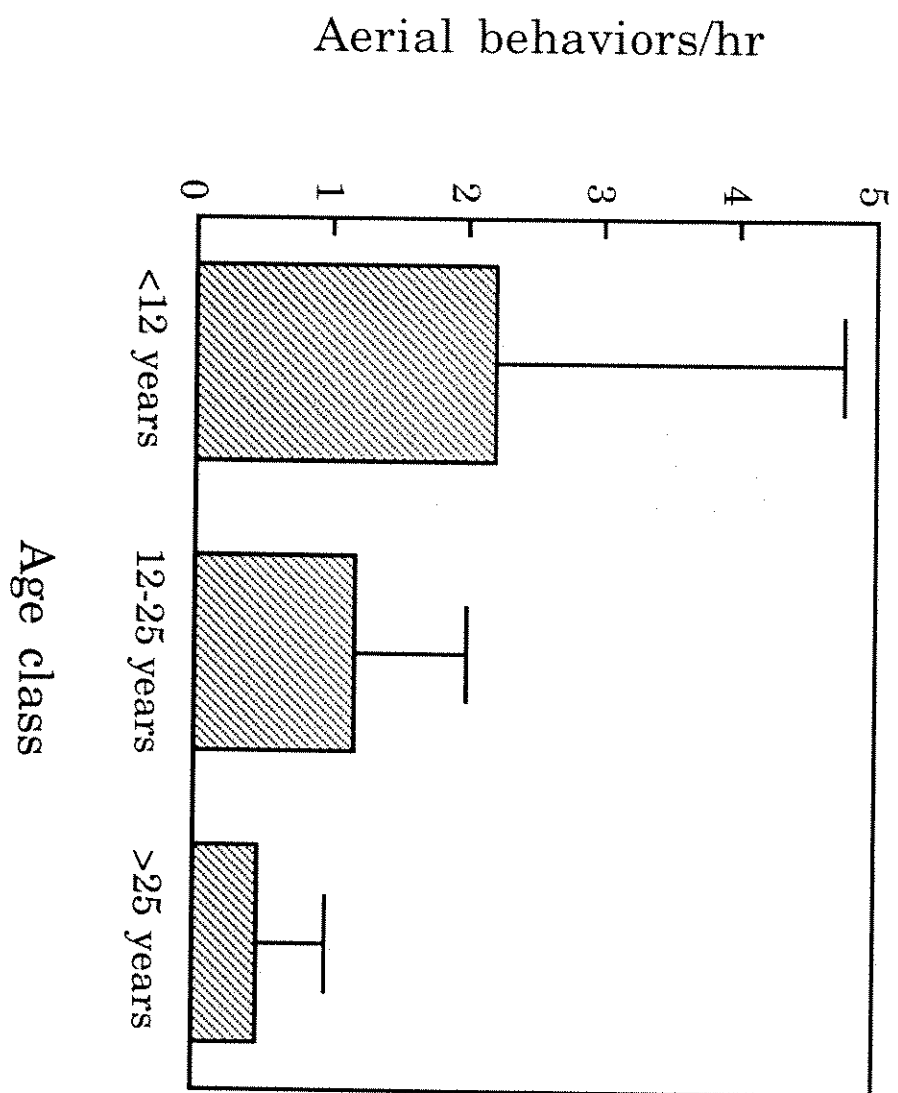
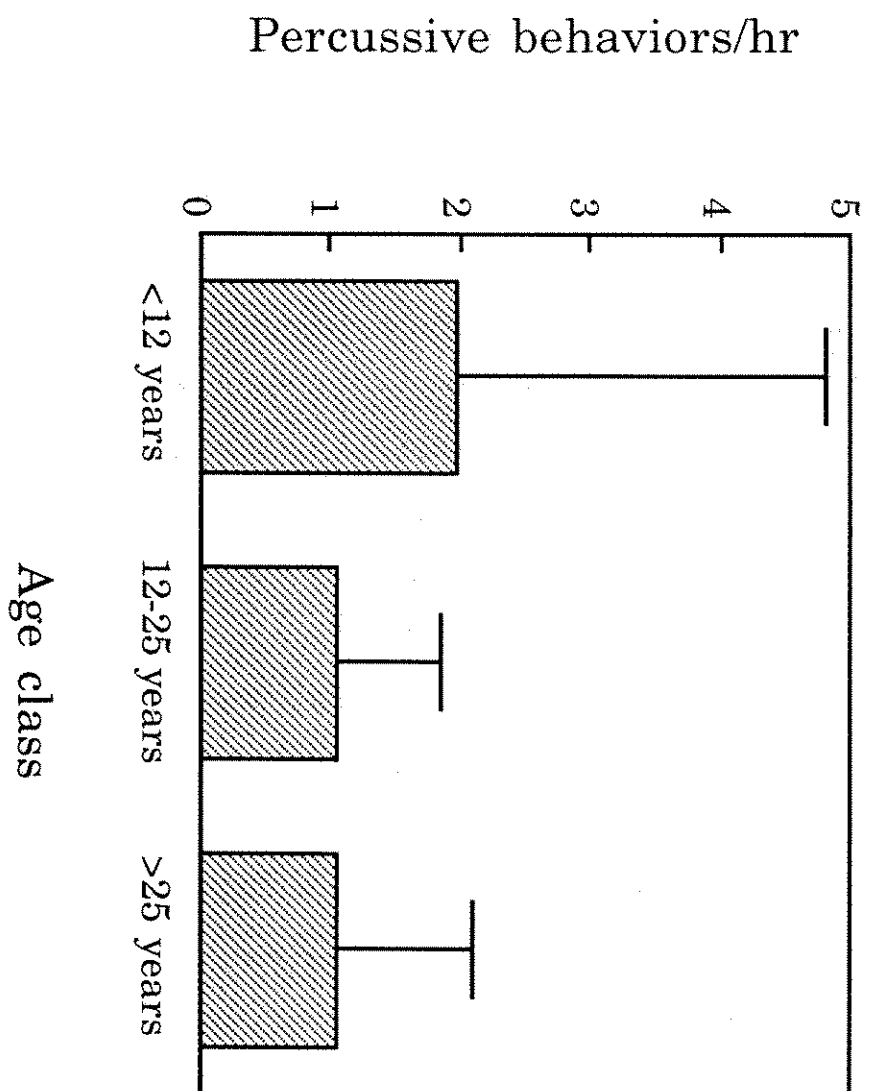


Figure 1.8. Number of percussive behaviors performed per hour for each age class (N = 7, 13, and 9 respectively). The differences among age classes were not significant (Kruskal-Wallis test, $H = 0.159$, $df = 2$, $p = 0.9237$).



CHAPTER TWO

ASSOCIATION PATTERNS

ABSTRACT

The aim of this chapter was to determine if the bonds between specific male-female pairs established in previous studies persisted during this study and whether association patterns were the same in the northern as in the southern community. Animals were observed from a boat and estimated distances between individuals were recorded every ten seconds. The percent time that males spent within one body-length of nine categories of associate and that males spent separated from others by more than several meters were calculated for 32 males and compared across age classes. The female with whom a male associated most often was the same as identified previously in 91% of the pairs evaluated. Overall, juveniles and adolescents spent up to 65% of their time with their mothers, adults 40%, and adults spent the most time alone. Adolescents socialized frequently with other adolescents and juveniles. Adults spent more time socializing with unrelated reproductive females one-on-one than did juveniles or adolescents. Bonds between sons and known or presumed mothers have persisted for at least 17 years. The males of the northern community overall are more closely integrated into the social structure than are the males of the south. The association patterns of adolescents suggest an active social network among themselves, as well as an important role as allofathers of juvenile siblings. Adult males are somewhat peripheral to the matrilineal groups in both communities, but in the north, allofathering, intrasexual social behavior, and potential reproductive associations have apparently allowed them to maintain a more central position in the social structure.

INTRODUCTION

Definition of association:

In the past, researchers studying the killer whales of the Pacific Northwest used photographs to examine the association patterns of the various age and sex classes in the population (Bigg *et al.* 1990). Other studies used focal animal point sampling to determine patterns of association between individuals and groups (Heimlich-Boran 1988; Jacobsen 1990). Researchers were fairly uniform in defining associations; animals no more than a few tens of meters apart from each other were considered to be associated in a meaningful way. Similar definitions have long been accepted as appropriate in mammalian systems (lions, *Panthera leo*: Schaller 1972; elephants, *Loxodonta africana*: Moss and Poole 1983; primates: Smuts *et al.* 1987). Although it is clear that animals farther away than some specified distance are not necessarily separated (for instance, vocal communication is often possible), it has generally been accepted that physical proximity is the most socially relevant characteristic to measure when considering association patterns.

Previous killer whale studies:

Bigg *et al.* (1990) determined genealogies within the Pacific Northwest communities of killer whales. Using association indices and direct observations, they constructed positive, highly probable, and probable genealogies for most of the individuals they followed over 14 years. A seminal discovery of their study was that males remain strongly bonded to their mothers throughout their lives. For as much as 40% of his time, an adult male is within a body-length of his mother. If a son survives his mother, he appears to transfer a slightly weaker version of this bond to a close female relative, such as a sister, grandmother, aunt, or niece. This permanent mother-son bond raises a question: How and with whom do males spend the rest of their time?

Heimlich-Boran approached the answer to this question in her 1988 master's thesis study with the southern resident community of killer whales. Using focal-animal point sampling techniques, she determined association indices between all possible pairs in the community and grouped the results according to age/sex classes and behavior states. She pooled related and unrelated pairs and also both sexes for adolescents and immatures (see Table 1.1 for age class definitions), which makes it difficult to compare her results to the individual results of Bigg *et al.* (1990), and may have obscured some relevant aspects of social dynamics. However, she made several conclusions concerning males. Converting her age class definitions to their closest equivalent in this study, adolescent and adult males appeared to hold somewhat peripheral positions in the social structure. Their strongest affinity was for reproductive females. Older juveniles were also peripheral and relied heavily on older non-reproductive females for social integration and younger juveniles spent most of their time with their mothers and showed a tendency toward cohort formation. Do northern residents follow similar patterns?

This study:

This chapter sought to evaluate whether the specific mother-son bonds determined by Bigg *et al.* continued to persist and whether Heimlich-Boran's conclusions concerning the southern community applied to the northern residents and if not, to determine what patterns did exist. The following specific questions were addressed: 1) Does a methodology that attempts to take into account time-below-the-surface and asynchronous surface appearances produce the same association patterns between males and matriarchs as did the long-term, photographic methodology used in Bigg *et al.* (1990)? 2) Taking relatedness, sex, and age into account, with whom do males associate, overall and when

they are engaged in each of four defined behavior states? 3) What are some of the behavioral details of associations among males and others in the community?

I expected to observe the same pattern of association between matriarchs and males as was observed by Bigg *et al.* (1990). The bonds between males and certain females persisted over 14 years and therefore were expected to persist for the three years of this study. However, it was uncertain whether the more diverse patterns examined by Heimlich-Boran (1988) would be confirmed by this study. Heimlich-Boran looked only at the southern community, whose population demographics differ somewhat from those of the northern community (General Introduction). Positive and highly probable relationships were emphasized more in this study than in her study, age class definitions were not quite comparable (see above), and the sexes were clearly segregated in this study but not in hers. In addition, Heimlich-Boran did not directly measure the time individuals spent alone (that is, beyond the defined distance of association with any potential associate).

Nevertheless, I made the following predictions, based on the results of her study: 1) Due to the larger proportion of males in the northern resident community compared to the southern community, adult males do not show the same pattern of social integration as in the south; 2) as with the southern community, adult males show a strong affinity for reproductive females; and 3) based on activity budget results (Chapter One), adolescents spend less time separated from others than do adults and exhibit a higher degree of social integration, through contact with a variety of social partners, than is demonstrated by adolescents and juveniles in the southern community. There was no basis on which to predict whether or not younger juveniles show the same tendency toward cohort formation.

METHODS

See General Methods for a complete description of data collection.

Data analysis:

Associates were placed in the following associate categories: matriarch, non-matriarch reproductive female, non-matriarch non-reproductive female, matrilineal and non-matrilineal adolescent and adult males, and matrilineal and non-matrilineal juveniles (male, female, and unknown-sex combined, under 12 years of age). Known or presumed sisters who matured during the study were not included in analyses, as there were only three such females involved and males associated with them in much the same manner as they did with matriarchs. Thus, females from the same pod but not the same matrilineal group were included in the non-matriarch reproductive female category. Grandmothers were included in the non-matriarch non-reproductive female category.

The percent time that each individual spent in association with each associate category was determined for each behavior state. This was determined by adding up all of the 10-sec intervals during which an individual was in tight/loose association with each associate category for each behavior state and dividing by the total number of 10-sec intervals during which that individual was observed. Animals that were separate were categorized as "alone" or solitary. Mean percent times were calculated for each age class. For all behavior states and all associate categories, each male contributed only once to each mean, regardless of the number of individuals he associated with from each associate category. Individual associates were not distinguished. Thus, for each male, several individual associates could account for the final, single percentage value obtained for an

associate category. Time spent with the matriarch and time spent alone were analyzed for differences among age classes.

In the initial individual data summary, matrilineal and non-matrilineal juveniles were separated into male, female, and unknown sex categories. Since most juvenile associates were of unknown sex, however, these three categories were combined when calculating the final, age-class means (see above). The largest value of the three for each male was used in analyses.

A male only contributed to a mean if he had the opportunity to associate with an individual from an associate category (i.e. a male contributed a value to the matrilineal adolescent male category only if his matrilineal group contained an adolescent male). This resulted in sample sizes varying for the matrilineal associate categories. Also, males who were not observed in a behavior state did not contribute a value for that behavior state (i.e. a male who was never observed socializing contributed no value, rather than a zero value, to the sociosexual behavior state for all associate categories).

Relevant values were reciprocal, indicating that sampling effort was relatively unbiased.

Determining associations:

Occasionally a focal and its associate(s) were highly asynchronous in their breathing and distances between them could not be established for several surfacings; the association distances for the intervals in which an individual was underwater, as well as for the asynchronous surfacings, were assumed to be the same as the last established

association distance if and only if the next established distance was also the same. If the next established distance was different, half the intervening underwater intervals and asynchronous surfacings were assigned the previous distance and the other half were assigned the new distance.

Qualitative descriptions:

Qualitative descriptions were given of the following selected associations: Adolescent male/non-reproductive female; adult male/reproductive female; and male/juvenile (see Chapter Three: Part Two).

RESULTS

Matriarch assignments:

Overall, using the matriarch assignments from Bigg *et al.* (1990) gave association pattern results similar to those of the earlier study (Fig. 2.1). In 91% (29/32) of the cases, the matriarch determined by Bigg *et al.* (1990) was the adult female with whom the male was most closely associated overall. Two adults and one adolescent spent more time with adult females other than the female assigned as their matriarch by Bigg *et al.* One adult had been an older adolescent in 1973, one adult a young adolescent, and the adolescent had been an older juvenile. The relationship of the older adult with his matriarch was only probable and was a presumed sibling relationship. The relationships with the matriarchs for the other two were highly probable and were both filial relationships.

General association patterns:

Although individuals within age classes tended to behave similarly, each age class had at least one or two individuals who were a marked exception to the trend. Due to the very large variances that resulted from this and the small sample sizes, most statistical analyses of the results shown in Table 2.1 were not significant. Nevertheless, definite patterns did emerge.

Juvenile males spent most of their time with their matrilineal group members, especially their mothers and juvenile siblings (Table 2.1; Fig. 2.1). They spent significantly more time with their matriarchs than did adults. They spent little time alone (Fig. 2.2). There was a tendency toward cohort formation for this age class, at least

in comparison to the other two age classes (Table 2.2). Juvenile males spent more time with non-matriarch reproductive females than did any other age class.

Adolescents and adults showed little partiality for any particular associate category, other than for matriarchs and matrilineal juveniles. Adults spent significantly the most time separated from others (Fig. 2.2) and never spent more than half of their time with any particular associate category (Table 2.1). Their least preferred associates were non-matrilineal adolescent males and non-matrilineal adult males. In fact, non-matrilineal adult males were the least preferred associates for all three age classes.

Effects of behavior state on association patterns:

The single most striking result when behavior state was taken into account was that only adults ever rested alone (Fig. 2.3). Adolescents were occasionally seen swimming slowly when solitary, but they were generally alert and irregular in their breathing pattern. Only adults were ever seen separated from their matrilineal group when swimming slowly and non-responsively, with the regular breathing pattern that distinguishes resting. In most cases, the rest of the matrilineal group was observed resting simultaneously, although spatially separated.

Another consistent and striking result was that adult males almost always foraged alone (Table 2.1). Adolescents foraged alone half of the time, while juvenile males did so a third of the time. Juvenile males never foraged in the company of non-matrilineal individuals (Table 2.1).

Juvenile males spent little time traveling alone, while adolescents and adults spent approximately half of their time doing so (Table 2.1). Adolescent and adult males spent little time traveling with individuals from any particular associate category other than matrilineal juveniles and matriarchs.

Solitary play was infrequent (Table 2.1). Males of all three age classes socialized often with juveniles and adolescent males, both within and outside of the matriline. Adult males, especially non-matrilineal adult males, were among the least preferred social partners of juvenile and adolescent males. Adolescents socialized infrequently with non-matriarch non-reproductive females. Adult males found unrelated adults of both sexes relatively attractive as social partners. All three age classes spent about a third of the time that they were in the sociosexual behavior state with non-matriarch reproductive females (Table 2.3).

Behavioral details of specific associations:

Adolescent, and even less frequently juvenile and adult, males were occasionally observed, in the absence of their matriarchs, associating with older non-matriarch non-reproductive females, although the results of Table 2.1 do not indicate the absence of the matriarchs during these associations. Males usually socialized with unrelated non-reproductive females and foraged or traveled with their grandmothers. The social behaviors observed were less physical and aerial than those observed in male-only social interactions (Chapter Three: Part One), but there were usually frequent nose-to-tail orientation and gentle body-contact behaviors observed. On occasion, more than one male would follow and play with one or even two non-reproductive females. M. Bigg (pers. comm.) noted that when a matrilineal group contained both a grandmother and an

adolescent male, they would frequently pair when foraging (see A38's individual profile, Appendix C).

Each season, one or two reproductive females were involved in social interactions involving one to four unrelated (from different pods) adult males, consecutively pairing or simultaneously grouping. I termed such associations "consortships." Adult males swam closely with adult females and their juvenile offspring, for up to several hours. Body-contact occurred occasionally, but no penile extrusions were observed. Although older adolescent males were occasionally observed following unrelated reproductive females, these associations differed from adult consortships in that the adolescents were rarely if ever observed alongside the female and physical contact was rare or absent (see A06's individual profile, Appendix C).

Males of all three age classes were occasionally seen traveling or socializing with juveniles in the absence of any matriarch. When the juveniles were related, they were of either sex and both behavior states were observed (foraging was infrequently observed); when unrelated, they were always male and the only behavior state observed was sociosexual. See Chapter Three for an expanded discussion of these male/juvenile associations.

DISCUSSION

Matriarch assignments:

The association patterns between matriarchs and males found in this study conform exactly to the results of Bigg *et al.* (1990) (Table 2.1; Fig. 2.1), both on average and individually, with only three exceptions. At least two of these exceptions could have been sampling bias. The highly probable mother of the third male, the older adult, died in 1974 and his bond with his presumed sister is not particularly strong. Overall, juveniles spend approximately two-thirds of their time with their mother, adolescents spend about half of their time with their matriarch, and adult males spend about 40% of their time with their matriarch (Fig. 2.1). All three age classes spend more time with their matriarchs than with any other adult females. These association patterns have persisted over time (at least 17 years) and support the idea that physical proximity represents a meaningful social bond in this species.

General association patterns:

In contrast, although no animal in this population is probably ever socially isolated (due to vocal communication), I believe that an animal physically distant from its potential associates does have social barriers erected. An animal too far away for physical contact is probably solitary in some fundamental sense. Consequently, in accord with Heimlich-Boran (1988), adult males in the northern resident community do appear to occupy a somewhat peripheral position in the social structure, spending at least a third of their time alone (Fig. 2.2). Some even occasionally rest alone (Fig. 2.3), although such males have apparently survived their mothers and are not as tightly bonded to their matriarchs as males with living mothers.

However, adult males do spend about 40% of their time with members of their matrilineal groups (except fellow adult males, with whom they spend about 30% of their time) (Table 2.1) and observation indicates that these are not necessarily simultaneous associations. Some of the time they spend with matrilineal juveniles is in the absence of the matriarch, which may reflect an important role as allofathers within the matrilineal group (Chapter Three: Part Two). In addition, adult males, when socializing, do so often with adolescent males (Table 2.1; Chapter Three: Part One). Thus adult males appear to be slightly more integrated into the social structure in the northern community than in the southern community.

As in the southern community, adult males show a preference for reproductive females as social partners. Although it appears that juvenile and adolescent males socialize with unrelated reproductive females at least as often as do adult males, this is probably an artifact of the degree to which the former socialize with their matriarchs, who in turn frequently associate with other adult females (Bigg *et al.* 1990; pers. obs.) (Table 2.3). Adult males, on the other hand, almost never socialize with their matriarchs; this suggests that their socializing with unrelated reproductive females is less serendipity and more deliberate. This is expected if adult males are socializing with unrelated adult females for reproductive purposes. In addition, adult consortships frequently involve females with juvenile offspring, the youngest of which are usually between two and four years of age. Females, if they are to have another offspring within the typical interbirth interval, would be impregnated when their current youngest is in this age range. For the most part then, the results of this study for adult males coincide with those of Heimlich-Boran.

Adolescent males, on the other hand, do not seem to occupy as peripheral a position in the northern community as they appear to do in the southern community. Adolescent males socialize actively and frequently with juveniles and other adolescents (Table 2.1). Some of the associations with juveniles appear to be allopaternal in nature (Chapter Three: Part Two). Adolescent males only spend about a fifth of their time alone (Fig. 2.2). In addition, although this study did not directly address the association patterns of females, anecdotal evidence suggests that pre-pubertal females spend most of their time with their mothers or as allomothers for other adult females and their offspring (see also Waite 1988) and are rarely solitary. Thus the adolescents of the northern community appear to be considerably more integrated into the social structure than are those of the southern community.

Juveniles of both sexes in the northern community appear to conform to the pattern observed by Heimlich-Boran (1988) for young juveniles in the southern community. They spend most of their time within the confines of the matrilineal group, with their mothers and juvenile siblings. Overall, there is a tendency toward cohort formation (Table 2.2), although unlike the conclusion reached by Heimlich-Boran (1988), in the north this appears to be an artifact of the preference mothers have for each other's company. Heimlich-Boran observed that juveniles frequently associated with each other in the absence of their mothers, but other than in male-only social interactions, I did not particularly note this phenomenon in this study. Nursery groups formed, but were usually accompanied by at least one of the mothers.

Effects of rest and foraging on association patterns:

Resting behavior appears to have substantial social significance to these animals. Although several matrilineal groups may rest together (in fact, long resting lines comprising several pods occur at least once a season), each matrilineal group is distinct and all of its members participate in the behavior simultaneously, breathe synchronously, and keep physical contact with each other, although the rare adult male separates himself spatially. The coordination observed among individuals during resting behavior almost certainly reflects a kin relationship.

Foraging, at least during the summer, does not appear to be a group or cooperative endeavor for the most part. In fact, spreading out and lack of coordination are hallmarks of foraging in this population, at least during the summer, although on one occasion in 1987, I did observe group herding of salmon. The tendency for solitary foraging to increase with age may indicate a correlation with a decrease in dependence on the mother as a source of nourishment (either direct, in the form of lactation or indirect, in the form of training to forage).

Similarities with other species:

The permanent mother-son bond in killer whales may be unique (Bain 1989). However, preliminary analysis of the social structure of the pygmy chimpanzee, or bonobo (*Pan paniscus*), indicates that it may be remarkably similar to that of Pacific Northwest killer whales (e.g. Kano 1982; Furuichi 1989; Enomoto 1990). In bonobos, the mother-son bond appears to persist into adulthood and the social statuses of the two are closely linked. Both males and females are relatively highly integrated into the social structures of at least three populations (Badrian and Badrian 1984; Furuichi 1987; Uehara 1988). Sexual

behavior is used frequently, homo- and heterosexually, in both reproductive and non-reproductive contexts (de Waal 1987; Enomoto 1990). Furuichi (1989) mentions that, to his knowledge, human beings are the only other species to share the characteristic of a permanent mother-son bond.

Conclusion and future studies:

The greater number and proportion of males in the northern resident community as compared to the southern resident community appear to have created slightly different social dynamics in the two populations. Males appear to be more closely integrated into the social structure in the north than in the south. Other than a more independent demeanor, juvenile males do not seem to differ much from juvenile females, although future work needs to examine sex differences in behavior in more detail. Juveniles of both sexes rely largely on their matrilineal group as a source for social partners. The association patterns of adolescents suggest a fairly important role as allofathers to juvenile siblings, as well as an active social network among themselves. Adult males are somewhat peripheral to the matrilineal groups in both populations, but in the north, allofathering, intrasexual social behavior, as well as potential reproductive associations, have apparently allowed them to maintain a more central position in the social structure than appears to be the case in the south.

It may be that the heavy cropping of the southern community in the 1960s (General Introduction) left the remaining males with few of their principal social partners; namely each other. Another intriguing possibility is that the lack of males in the south may be a factor in the population's failure to match the growth rate of the north (Olesiuk *et al.* 1990).

Perhaps the dearth of potential allofathers has made it difficult for females to raise offspring successfully.

Future studies should examine who initiates associations; that is, who approaches and who departs? Continued observations of the increasing number of individuals with known genealogies who are reaching adulthood need to be made, to verify the conclusions drawn about probable genealogies from earlier studies. The age/sex class and kinship compositions of the various matrilineal groups need to be considered carefully to determine if these factors influence association patterns and behaviors. In time, the consequences of the persistent mother-son bond may be more fully understood. In fact, the consequences of this bond for killer whales may be found to be parallel to those for the taxonomically separate but behaviorally similar bonobos and even humans.

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Table 2.1. Association pattern results for all age classes, associate categories, and behavior states. Values are mean percents \pm 1 SD. Sample sizes are the same as for the matriarch, except where noted. Values do not add up to 100% because associations could be either simultaneous or sequential.

	Juveniles (N = 7)	Adolescents (N = 12)	Adults (N = 8)
MATRIARCH			
Travel	71 \pm 32 (N = 7)	44 \pm 31 (N = 12)	31 \pm 33 (N = 8)
Mill/Forage	63 \pm 14 (N = 4)	31 \pm 39 (N = 11)	11 \pm 11 (N = 7)
Sociosexual	59 \pm 37 (N = 4)	45 \pm 39 (N = 11)	3 \pm 7 (N = 6)
Rest	100 (N = 5)	100 (N = 11)	83 \pm 24 (N = 8)
Total	65 \pm 24	56 \pm 24	40 \pm 22
NON-MATRIARCH REPRODUCTIVE FEMALE			
Travel	23 \pm 23	18 \pm 27	19 \pm 36
Mill/Forage	0	14 \pm 30	6 \pm 9
Sociosexual	39 \pm 43	27 \pm 36	38 \pm 40
Rest	56 \pm 52	50 \pm 42	43 \pm 40
Total	41 \pm 31	27 \pm 28	28 \pm 20
NON-MATRIARCH NON-REPRODUCTIVE FEMALE			
Travel	22 \pm 33	11 \pm 16	8 \pm 16
Mill/Forage	0	8 \pm 21	3 \pm 7
Sociosexual	36 \pm 44	21 \pm 34	21 \pm 26
Rest	36 \pm 50	38 \pm 38	34 \pm 40
Total	28 \pm 31	20 \pm 24	21 \pm 21
MATRILINEAL JUVENILES			
Travel	65 \pm 36 (N = 5)	43 \pm 30	40 \pm 39 (N = 6)
Mill/Forage	45 \pm 32	23 \pm 32	15 \pm 14 (N = 5)
Sociosexual	67 \pm 58 (N = 3)	58 \pm 39	10 \pm 15 (N = 5)
Rest	100 (N = 4)	100	77 \pm 25 (N = 6)
Total	65 \pm 27 (N = 5)	58 \pm 21	46 \pm 25 (N = 6)
NON-MATRILINEAL JUVENILES			
Travel	23 \pm 23	18 \pm 28	8 \pm 13
Mill/Forage	0	14 \pm 30	0 \pm 1
Sociosexual	66 \pm 45	48 \pm 42	38 \pm 40
Rest	56 \pm 52	50 \pm 42	34 \pm 40
Total	50 \pm 32	34 \pm 31	22 \pm 17
MATRILINEAL ADOLESCENT MALES			
Travel	48 \pm 35 (N = 5)	26 \pm 25 (N = 7)	29 \pm 36 (N = 6)
Mill/Forage	26 \pm 44 (N = 3)	14 \pm 15 (N = 6)	17 \pm 27 (N = 5)
Sociosexual	91 \pm 15 (N = 3)	33 \pm 31 (N = 6)	44 \pm 49 (N = 5)
Rest	100 (N = 3)	100 (N = 7)	77 \pm 25 (N = 6)
Total	60 \pm 38 (N = 5)	43 \pm 19 (N = 7)	41 \pm 23 (N = 6)

Table 2.1 cont.

	NON-MATRILINEAL ADOLESCENT MALES		
Travel	14 ± 29	7 ± 13	2 ± 3
Mill/Forage	0	16 ± 35	3 ± 7
Sociosexual	72 ± 49	56 ± 42	33 ± 52
Rest	40 ± 55	18 ± 31	24 ± 39
Total	45 ± 35	26 ± 24	11 ± 14
	MATRILINEAL ADULT MALES		
Travel	42 ± 23 (N = 4)	23 ± 32 (N = 6)	4 ± 6 (N = 2)
Mill/Forage	12 ± 16 (N = 2)	11 ± 15 (N = 5)	0 (N = 1)
Sociosexual	16 ± 23 (N = 2)	27 ± 29 (N = 5)	0 (N = 1)
Rest	100 (N = 3)	82 ± 24 (N = 6)	58 ± 9 (N = 2)
Total	39 ± 29 (N = 4)	36 ± 21 (N = 6)	28 ± 9 (N = 2)
	NON-MATRILINEAL ADULT MALES		
Travel	7 ± 19	2 ± 2	2 ± 3
Mill/Forage	0	0	3 ± 7
Sociosexual	8 ± 15	11 ± 16	26 ± 43
Rest	8 ± 18	19 ± 32	26 ± 39
Total	9 ± 15	7 ± 9	15 ± 15
	ALONE		
Travel	14 ± 21	47 ± 28	57 ± 34
Mill/Forage	32 ± 12	51 ± 37	77 ± 22
Sociosexual	0	0 ± 1	4 ± 10
Rest	0	0	15 ± 22
Total	11 ± 14	23 ± 14	37 ± 15

Table 2.2. Mean percent time (± 1 SD) spent in association with both matrilineal and non-matrilineal peers (same-age class). Juvenile associates were male, female, and unknown sex; adolescent and adult associates were male only.

	Juveniles	Adolescents	Adults
Matrilineal peers	65 \pm 27	43 \pm 19	28 \pm 9
Non-matrilineal peers	50 \pm 32	26 \pm 24	15 \pm 15

Table 2.3. Mean percent time (± 1 SD) spent socializing with matriarchs and non-matriarch reproductive females for all three age classes.

	Juveniles	Adolescents	Adults
Matriarch	59 \pm 37	45 \pm 39	3 \pm 7
Non-matriarch reproductive female	39 \pm 43	27 \pm 36	38 \pm 40

Figure 2.1. The total percent time that males spent in association with matriarchs (N = 7, 12, and 8, respectively). The differences among age classes were not significant (Kruskal-Wallis test, $H = 3.902$, $df = 2$, $p = 0.1421$). However, the difference between juveniles and adults only was significant (Mann-Whitney $U = 45$, $p = 0.05$).

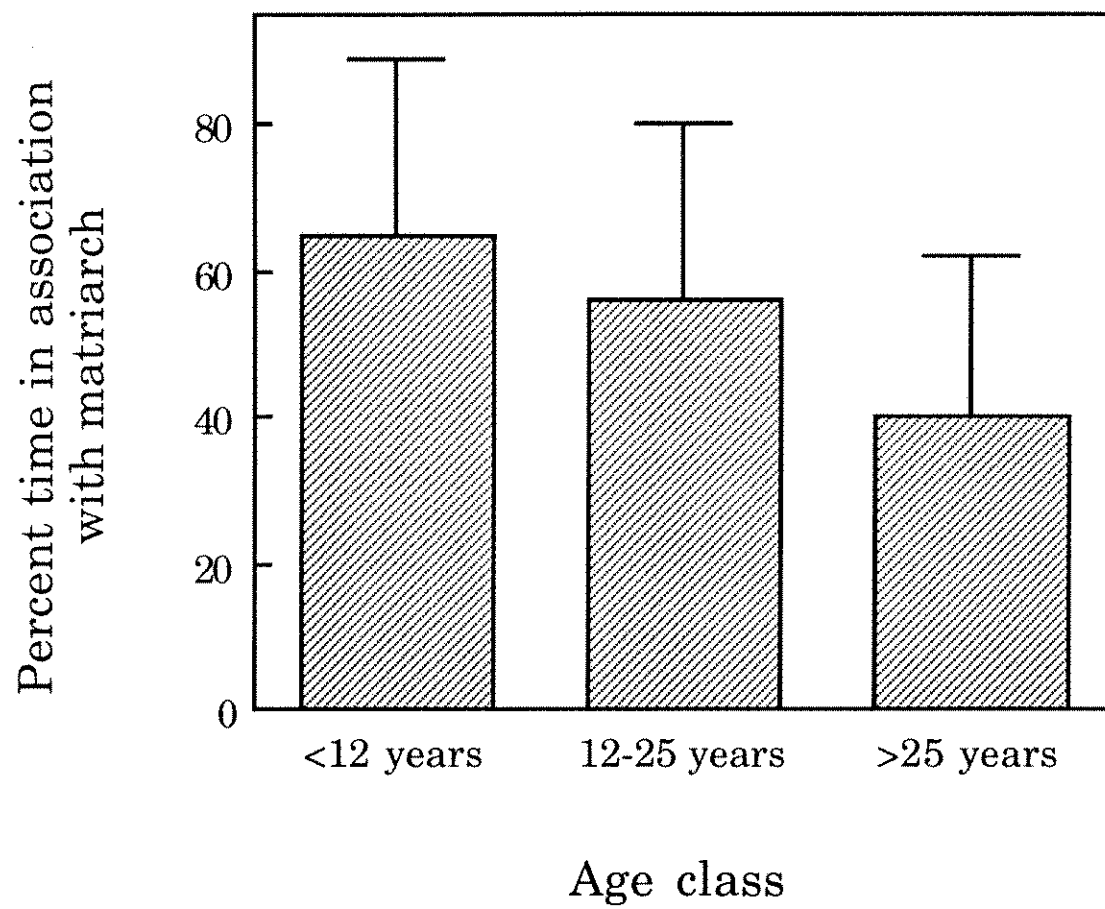


Figure 2.2. The total percent time that males were solitary (sample sizes are the same as for Fig. 2.1). The differences among age classes were significant (Kruskal-Wallis test, $H = 8.999$, $df = 2$, $p = 0.0111$).

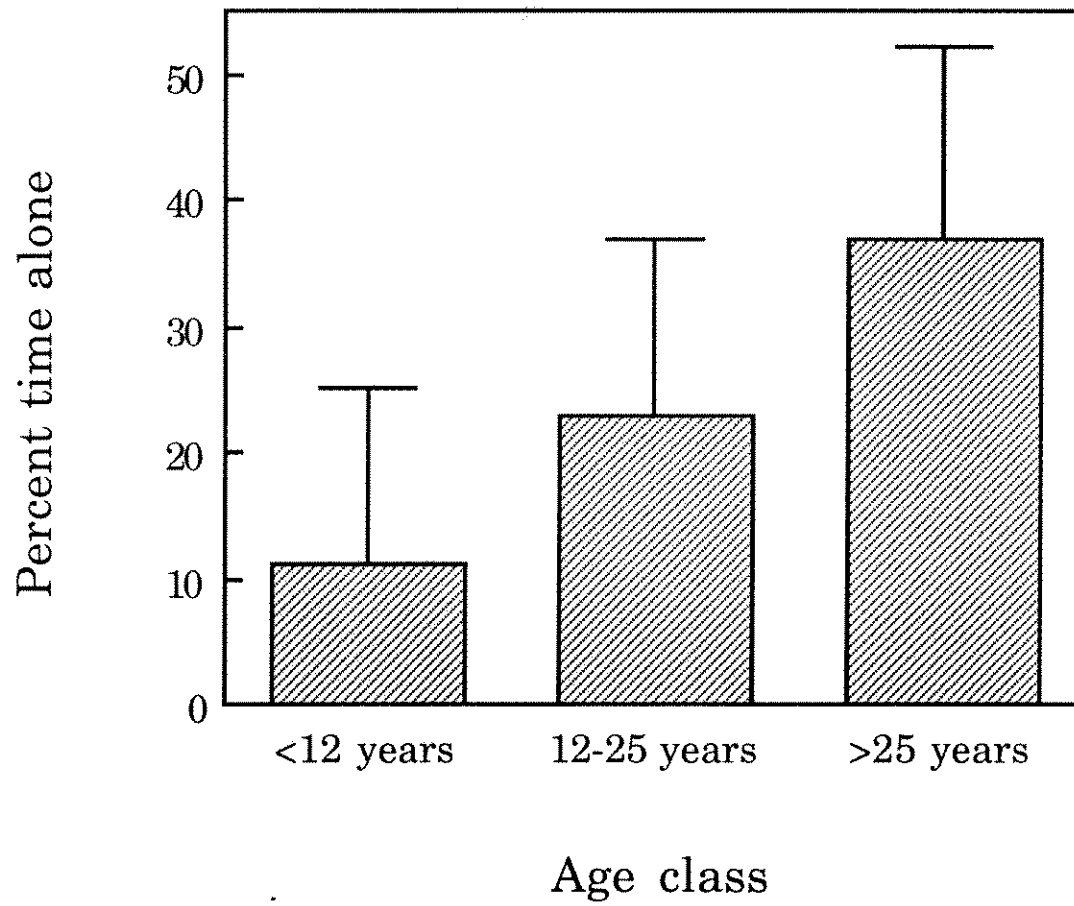
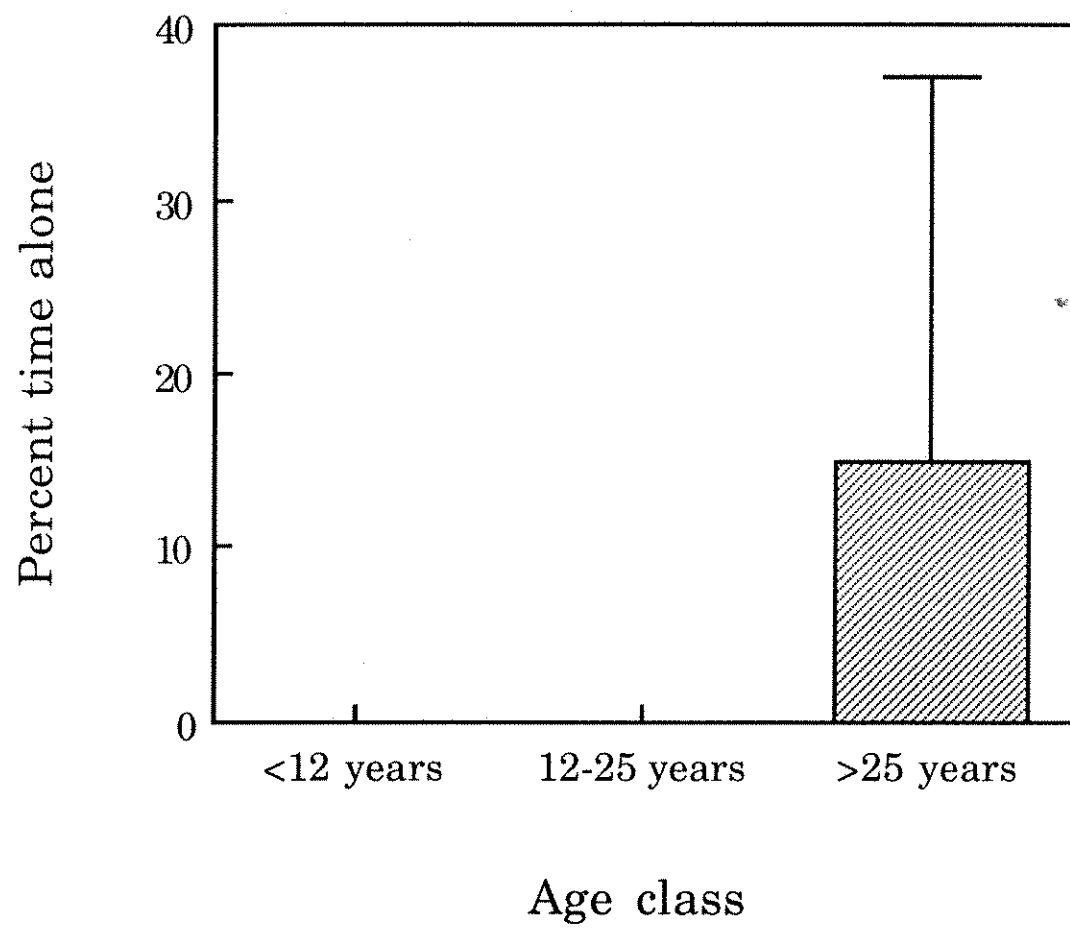


Figure 2.3. The percent time that males spent resting spatially separated from their matrilineal group (N = 5, 11, and 8, respectively). Juveniles and adolescents never rested solitarily. The standard deviation for adults was large (± 22), as most of them did in fact rest exclusively with their matrilineal group.



CHAPTER THREE

MALE-ONLY SOCIAL INTERACTIONS AND MALE/JUVENILE ASSOCIATIONS

PART ONE: MALE-ONLY SOCIAL INTERACTIONS: AGONISTIC OR AFFILIATIVE?

ABSTRACT

The aim of this chapter was to test two hypotheses, that short-term male-only social interactions (MOSIs) of male killer whales in British Columbia represent 1) dominance interactions or 2) play. Several predictions were made for each hypothesis. Approximately 25 hours were spent observing these male interactions and the following characteristics were examined to address the predictions: Age distribution and relatedness of participants, types of behaviors performed and their frequency, reciprocity of physical contact, group size, and percent time spent in interactions. Almost all MOSIs involved at least one adolescent male and adolescents participated four times as often as adults. Adults rarely participated. Participants were generally non-kin. Physical contact behaviors decreased in frequency with age and were almost always reciprocal between dyads. Pairs occurred most frequently, with trios and quartets occurring about a third of the time. Males spent just over 10% of their total activity budget in MOSIs, suggesting that they have an important role in the male behavioral repertoire. Results support the hypothesis that MOSIs are play interactions.

INTRODUCTION

Male-only social interactions in killer whales:

Male killer whales of the northern resident community of British Columbia encounter each other frequently, as a result the unusual social structure of the matrilineal group and the pod (General Introduction). Male-only social interactions (MOSIs) occur often in this population during the summer season in Johnstone Strait (Jacobsen 1990; D. Bain, G. Ellis, J.K.B. Ford, pers. comm.; this study). Such interactions involve males exclusively, with both kin and non-kin associating, and are short-term; none have ever been observed to endure for more than a few hours.

The principal behavior state observed in MOSIs is sociosexual and there are several consistent characteristics of these interactions that allow observers to distinguish them from other sociosexual interactions. MOSIs typically form when two or more males, at least one of whom is greater than 3-4 years of age (see below re: nursery groups), separate from their matrilineal groups, sometimes by a few meters, other times by as many as several kilometers. These males engage in activities that bring them into frequent body contact, often accompanied by percussive and aerial behaviors and penile displays, where the penis is extruded for several seconds but intromission into the genital slit of the other male(s) is not necessarily attempted (see Östman 1991; Jacobsen 1990; Nichol 1990). This last behavior, although not always observed, clearly distinguishes these groupings. The frequency and vigorousness of at-surface behaviors also distinguishes these interactions. Males may join and leave these groupings from moment to moment. After several minutes to a few hours, the group or pair disbands, when the males return to their matrilineal group or remain alone for a time. The rest of the matrilineal group may be

found in any behavior state other than rest while the males participate in MOSIs, but is usually completely disengaged from the activities of MOSIs (Fig. 3.1.a-d).

Males do not perform "essential" behaviors, such as foraging, resting, or directed traveling, during MOSIs. To emphasize further the distinct nature of MOSIs, females do not appear to form similar groupings, nor have mixed-sex groupings of this nature been observed (but see Jacobsen 1990). It has not been established whether occasional nursery pairs or groups containing dependent calves, where frequent body-contact behaviors occur, are mixed-sex or not, due to the large number of unsexed calves in the population. Pairs or groups form between juveniles of both sexes and older males from the same matrilineal group (i.e. older brothers or uncles), but these associations are considered allopaternal in nature (Chapter Three, Part Two; Haenel 1986; Waite 1988). Female juveniles have never been observed associated with unrelated older males except when two matrilineal groups come together with both matriarchs in close attendance.

Agonism or affiliation?:

Within social groups, aggression is disruptive and selection may favor its reduction or attenuation (Greenwood 1980; Hand 1986). For example, cercopithecine males, who are usually unrelated, maintain strict dominance hierarchies, which may reduce the need for overt aggression in competitive encounters (Hand 1986; Walters and Seyfarth 1987). They interact infrequently when no females are in estrus; to achieve access to estrous females, they may be aggressive toward each other or they may form cooperative agonistic alliances (Melnick and Pearl 1987). On the other hand, chimpanzee (*Pan troglodytes*) males in a community are usually kin and, although they may interact aggressively over access to resources, they reconcile afterward using various affiliative

behaviors (de Waal and van Roosmalen 1979). In general, their relatedness forms the basis for high levels of tolerance and affiliation (Nishida and Haraiwa-Hasegawa 1987). Are killer whale MOSIs primarily agonistic interactions or alliances, as is the case in unrelated cercopithecines, or are they affiliative, as in related chimpanzees?

What is the function of MOSIs?

This chapter seeks to determine the fundamental nature of killer whale MOSIs. The following four hypotheses as to the function of MOSIs are considered (Table 3.1 summarizes the associated predictions); it should be noted that these hypotheses are not necessarily mutually exclusive:

Hypothesis 1: Males participate in male-only social interactions in order to establish and maintain a dominance hierarchy.

If MOSIs are dominance interactions, adults should participate more frequently than any other age class, as a clearly defined rank within a hierarchy would be of greatest benefit to this age class. The main resource over which males in Johnstone Strait contend should be access to reproductive females; all other essential resources are acquired within the framework of the matrilineal group. Males should seek out like-size/age partners, as they would likely be dominant to smaller, younger individuals without contest. They should also seek out non-kin partners, as dominance relationships between kin should be age-based and should be defined daily within the matrilineal group. Lastly, if MOSIs are dominance interactions, behaviors should be aggressive and relatively high-energy and should be unidirectional. Unidirectional behaviors within dyads usually denote the existence of dominance relationships (Silk *et al.* 1981; Hausfater *et al.* 1982; Reinhardt *et*

al. 1986; Östman 1991). Penile displays could serve as a dominance signal, as they do in several other mammalian species (e.g. squirrel monkeys, *Saimiri sciureus*: Ploog and MacLean 1963; musk-ox, *Ovibos moschatus*: Reinhardt 1985; bottlenose dolphins, *Tursiops truncatus*: Caldwell and Caldwell 1977; Östman 1991).

Hypothesis 2: Male-only social interactions are play interactions that develop physical strength, endurance, and skill (motor training) (Fagen 1981; Smith 1982; but see Burghardt 1988).

If MOSIs enhance motor training, juveniles should benefit most. Adults should rarely if ever play and individuals should prefer like-age/size or larger partners in order to avoid excessive self-handicapping, which would decrease the efficacy of the exercise (e.g. Fagen 1981; Jamieson and Armitage 1987). There should be no tendency to prefer kin or non-kin as play partners, since the activity itself should be paramount; that is, animals should accept any available and willing partner(s). Behaviors should be bidirectional, as role-reversal or bidirectionality is considered a fundamental characteristic of play (Loizos 1966; Fagen 1981). Behaviors should also be vigorously energetic; that is, "rough and tumble," again to maximize physiological benefits (e.g. Barber 1991). The penile displays known to occur in MOSIs can be explained as a sign of excitement with this hypothesis.

Hypothesis 3: Male-only social interactions are play interactions that develop cognitive/social skills necessary for behavioral adaptability, flexibility, inventiveness, or versatility (Fagen 1981).

There is some evidence that males form consortships with females that may lead to mating (Chapter Two; Appendix C). If so, young males who are sexually but not socially mature (that is, adolescent males) need to develop courtship and mating skills. Adolescent males might learn such skills from older males or practice them on other males of any age in MOSIs. Once again, there should be no tendency to prefer kin or non-kin. Behaviors should be more controlled and ritualized than the random, high-energy "rough and tumble" behaviors predicted above and should be bidirectional. Penile erections would be consistent with this hypothesis.

Alternatively, if there is a dominance hierarchy among males, adolescents may experiment with dominance-related signals or behaviors among peers under less threatening, play conditions (e.g. Poirier and Smith 1974; Fagen 1981; Neill 1985; Pellis 1988). Thus, although MOSIs may not be serious dominance interactions, they may still be dominance-related. Males should prefer like-age/size partners, to simulate most closely an actual dominance interaction. Behaviors should still be bidirectional, as males would essentially be practicing with each other. There may be other cognitive/social skills males need to acquire, such as reconciliation skills (de Waal and Yoshihara 1983; Cords 1988; York and Rowell 1988), but the predictions would be similar.

Hypothesis 4: Male-only social interactions are play interactions that establish or strengthen social bonds (Fagen 1981; Poole 1985).

If maintaining positive relations or strengthening social bonds is the function of MOSIs, all ages should be involved, as any males whose matrilineal groups have come together can interact. Participants should be non-kin; kin-bonds should be maintained

daily within the matrilineal group. Activity rates should decrease with age (e.g. Burghardt 1988) and role reversal should be frequent.

This study:

In order to distinguish between dominance and play as the function of MOSIs and further to distinguish between the three play hypotheses, this study addressed the following specific questions: 1) Which age classes participate in MOSIs and in what combinations? 2) What is the relatedness of participants? 3) What behaviors are performed in MOSIs? How do the behavior types and rates compare to non-MOSI behavior types and rates? 4) Are there consistent directionalities to behaviors performed by specific dyads? That is, are there behaviors that can be scored as having an actor and a recipient and are these roles consistent for specific pairs of males over time? In addition, the following questions seek to clarify further the nature of MOSIs: 5) How does group size vary? 6) Do males have preferred partners? 7) What percentage of a male's total activity budget is devoted to MOSIs? 8) When do MOSIs occur, both seasonally and daily?

METHODS

See General methods for a complete description of data collection.

Data collection:

When observing a MOSI, I frequently brought my boat to within 10 m while males continued to interact, at times going under the keel. This was in contrast to the observation distances of 50-1000 m I typically maintained in other circumstances.

Surface penile displays were not always observed in MOSIs (although they rarely occurred at any other time) and only two were recorded in the serial record data. Therefore, I chose body-contact behaviors as the basis for determining reciprocity in dyads. I was able to score an actor and a recipient (or mutual actors) for most interactions involving the following behaviors: pushing, rubbing, hitting, gliding over back, and touching (see Appendix B for complete definitions). I believe that these behaviors might reasonably serve as cues for the existence of dominant/subordinate relationships, if in fact such relationships exist, since contact behaviors are often seen in aggressive or competitive interactions in mammals or serve as consistent determinants of dominance (Clutton-Brock *et al.* 1982; Hand 1986; Walters and Seyfarth 1987; Östman 1991).

The time during which any pair or group of males remained together continuously and without change in membership was termed a bout. A behavioral interaction between two males (a dyad) was considered bidirectional if Whale A pushed Whale B (one interaction) and sometime later within the same bout, Whale B pushed Whale A (a second interaction) or the push was mutual to begin with (one interaction).

Data analysis:

MOSIs were analyzed for composition (age and relatedness of participants), behavior and respiration rates (across age classes and in MOSIs vs. in all other behavioral contexts combined), and directionality of body-contact behaviors between specific dyads within a bout. Group size, percentage of total activity budget spent in MOSIs, and timing (seasonal and daily) of MOSIs were also examined, although concerning the last, the dates covered by this study (see General Methods) were not ideal to determine whether MOSIs were more likely to form early or late in the season. Killer whales begin visiting the core area of Johnstone Strait regularly in the last week of June or first week of July and continue to be regularly observed until the end of October (J. Borrowman, W. MacKay, pers. comm.; pers. obs.). Observations did not extend far into September and no observations were made in October.

Database:

No MOSIs were observed in 1990. Eighteen males were observed in MOSIs during the 1988 and 1989 seasons. Three additional males were observed in MOSIs during a pilot study in 1987. Two additional males were observed in MOSIs in the 1989 *ad libitum* samples. A total of 24.64 whale-hrs of serial record data was collected.

A total of 33 bouts was recorded; 18 were serial record bouts, 14 observed in 1988 and four in 1989. These bouts ranged in length from two minutes to over two hours. Seven bouts were recorded in the 1987 pilot study, but only the date, time of day, and ID of participants were recorded. Eight *ad libitum* bouts were recorded, two in 1988 and six in 1989, but again only dates, time of day, and IDs were recorded (Appendix D). Interactions were rarely

observed at formation or disbanding. Data did not therefore address whether any factors affected the duration of MOSIs.

The study group was made up of five adults (> 25 yrs), nine adolescents (12-25 yrs) and nine juveniles (< 12 yrs) (see Chapter One; Table 3.2). The age distribution of MOSI participants was not significantly different from the age distribution found among the 45 potential participants (Fig. 3.2; see General Methods). In addition, choosing males at random from this group of 45 potential participants (see Chapter One) gave a resultant age distribution that was not significantly different from the observed distribution (observed: 9:9:5; random sample: 11:7:5; Chi-square goodness-of-fit = 4.39, $df = 2$, $N = 23$, $p > 0.10$). Repeat trials gave similar results.

RESULTS

Age-class of participants:

Although the age distribution results (Fig. 3.2) implied that no age class predominated in the MOSIs, this assumed that each male contributed to the database only once, which was clearly not the case. On average, each male participated in over three MOSIs (mean \pm 1 SD = 3.78 ± 3.26 , $N = 23$). Adults tended to participate in MOSIs only once or twice during the study, while on average each adolescent male participated in a MOSI about four times as often and each juvenile 2.5 times as often (Table 3.3). One adolescent male participated in 13 of the 33 MOSIs observed! The tendency for younger males to participate in MOSIs more frequently than older males approached significance, but variance within groups was high.

Age/size characteristics of partners:

When males participated in a MOSI consisting exclusively of peers (that is, same-age class males), adolescent males did so significantly more than one-third of the time (Chi-square = 12.88, $df = 2$, $N = 16$, $p < 0.001$). Only one bout involved adult males exclusively. The age distribution of the observed 16 peer groups also significantly overrepresented adolescent males and underrepresented juvenile males when compared to the distribution resulting from randomly drawing 16 peer pairs of males (assuming all interactions were pairs to facilitate the analysis) from the potential pool of participants (observed: 3:12:1, random sample: 7:6:3, Chi-square goodness-of-fit = 9.62, $df = 2$, $N = 16$, $p < 0.005$). However, while half (16/33) of the MOSIs involved peers, fully 78% (25/32) of the interactions concerned males more than five years apart in age (each age class covers a range of approximately 12-13 years). Most MOSIs were thus mixed-age, although not

mixed-age class, using this 5-year criterion. All possible combinations of age classes occurred (Appendix D).

Relatedness of participants:

Participants represented nine of the potential 11 pods. Most MOSIs (64%) involved males from two pods; no MOSI involved males from more than two pods. Twelve of the groups (36%) involved members of the same matrilineal group (presumed or known brothers/half-brothers), but only three bouts (9%) involved brothers exclusively. Thus, males tended to join groups involving non-kin, and certainly groups involving only close kin were rare. Thirteen of the bouts (39%) involved males whose matrilineal group did not contain an older male; that is, males without older brothers or close male kin.

Behaviors:

Males in MOSIs were notably undisturbed by the close proximity of boats. I observed at least two underwater penile displays in this manner. Time spent at the surface appeared to increase during a MOSI; frequently, males would remain at the surface, fins showing, pushing and rubbing against each other for several seconds before diving. My impression was that they did not dive below 5-10 m, as an occasional fin-tip broke the surface of the water. In short, males appeared less attentive to their surroundings and increased their surface time (perhaps due to slightly increased respiratory rates; see Fig. 3.4.d) when in MOSIs than during any other behavior state or social interaction.

Although there was a tendency for behavior and respiration rates to decrease with age, differences among age classes were not significant (Figs. 3.3.a-d; see Chapter One). However, males overall performed more of all three behavior types (except adults, where

the trend for percussive behaviors was in the opposite direction: see Fig. 3.4.c) in MOSIs than in all other behavioral contexts combined and their respiration rates were slightly higher (these differences were significant for adolescents with body-contact and non-percussive aerial behaviors) (Figs. 3.4.a-d).

In 1988, I observed a unique sequence of behaviors between two pairs of males (A32/A26, A33/A38, all adolescents) on eight occasions (once between the first pair, seven times in one bout between the second). I did not observe this sequence in 1987 or 1989. The two males swam slowly side by side, dove simultaneously, surfaced to float facing each other about 20-25 m apart, slowly approached each other, picked up speed (essentially surfacing-swimming), and finally butted heads together, sometimes at high speed (a "ram"), sometimes more gently (a "bop"). After impact, they rubbed past each other, dove simultaneously, and surfaced seconds later again side by side, heading in the same direction as before. This sequence was observed at least twice more between other pairs of males by other researchers that same year (J. Jacobsen, J.K.B. Ford, pers. comm.).

Discrete behaviors observed in MOSIs did not differ in kind from those observed in all other behavioral contexts; only the rate at which they occurred was different (Figs. 3.4.a-c). Males did not rub at the beaches during MOSIs, nor did they make any obvious prey-capture movements.

Directionality of behaviors:

Of the 193 dyadic body-contact interactions where actors and recipients could be scored, 88% were reciprocal or bidirectional. Only 12% of the body-contact behaviors observed were not reciprocated during the bout in which they occurred.

Although data were few, other behaviors, such as beak-genital orientation (Jacobsen 1990; Östman 1991) and echelon-formation swimming (Kelly 1959), appeared to be reciprocal as well. Followers and leaders usually switched roles at least once during a bout. Also, all age-classes (and most individuals) performed percussive and aerial behaviors with high frequency. In short, there were no clear cases of unidirectionality in any observably directional behaviors. Of the two penile displays, a juvenile displayed among several adolescent males during one bout and an adolescent male displayed while with a juvenile male during another.

Group size:

Group size (mean \pm 1 SD) was 2.64 ± 0.9 participants. Twenty bouts (61%) involved pairs, six bouts (18%) involved three males, six (18%) involved four males, and only one bout (3%) involved five males. Looking only at the serial record data, the distribution was almost identical: 11 bouts (61%) involved pairs, for a total of 13.08 whale-hrs (an average observation session length of 1.19 whale-hr). Three bouts (17%) involved three males, three (17%) involved four males, and one (5%) involved five males, for a total of 11.56 whale-hrs (an average observation session length of 1.65 whale-hr). The implication of the session lengths was that pairs formed more often (11 pairs vs. 7 groups) but were on average shorter in duration than groups, but this was misleading. Session lengths did not correspond to MOSI duration times (see Methods). In fact, anecdotal observations suggested that pairs were more stable than groups, with the same two males remaining together persistently, sometimes for hours. Males tended to join and leave larger groups continuously. No other measurable differences distinguished dyadic from group interactions.

Frequent participants:

There was no clear indication that males had preferred partners, although nine males (three juveniles, six adolescents) participated in five or more groups (Table 3.3). These males may have solicited group formation or been solicited into groups more often than other males, but they had various partners (Appendix D). The two adolescent males who participated in the most MOSIs (A38 and A39: see Table 3.3) belonged to the most frequently observed matrilineal group, the A30 group (Jacobsen 1986, 1990; Nichol 1990; pers. obs.), so their frequent appearance in MOSIs may have been an artifact of the opportunistic sampling regime.

Percentage of activity budget and timing of MOSIs:

A mean (± 1 SD) of $12.5\% \pm 18.2\%$ of the total activity budget of all males combined ($N = 30$) was devoted to MOSIs.

Twenty-five (76%) of the total bouts recorded occurred during the second half of the observation day (see General Methods). Bouts were significantly more likely to occur in the afternoon than in the morning (Chi-square = 8.76, $df = 1$, $N = 33$, $p < 0.005$). Twenty-one of the 33 bouts observed took place after 7 August (the earliest occurring on 12 July), the approximate midpoint of the season. However, taking into account that the distribution of the total number of days actually spent in the field was not significantly biased toward early (≤ 7 August) or late (> 7 August) summer (Chi-square = 0.67, $df = 1$, $N = 121$, $p > 0.50$), the distribution of bouts was not significantly biased (Chi-square = 2.45, $df = 1$, $N = 33$, $p > 0.10$).

DISCUSSION

Evidence against agonism (dominance):

The data do not support the hypothesis that MOSIs in killer whales function to establish and maintain dominance hierarchies. Whether through choice or because of the relatively small number of potential same-age partners, mixed-age pairs and groups predominate. This indicates that self-handicapping by the older, larger male(s) occurs frequently. Directional behaviors are performed in a reciprocal manner. The relatively frequent occurrence of trios and quartets (one-third of all MOSIs) indicates that males are not seeking to "square off" with another male matched in size and strength. In addition, MOSIs may last an hour or more and all males apparently remain in a pair or group of their own accord, indicating that most participants actively choose to participate and are neither reluctant to stay nor anxious to leave (either might be more typical of dominance interactions, which in other species are usually short-lived, since the subordinate animal retreats quickly: e.g. bowl and doily spider, *Frontinella pyramitela*: Austad 1983; northern elephant seal, *Mirounga angustirostris*: Haley 1990).

This is not to say that there is no dominance hierarchy among males in Johnstone Strait. In a review, Hand (1986) discusses ways in which dominance may be asserted without aggression being involved. Smaller or younger animals can be dominant to larger or older individuals through leverage, the possession of a resource (or of status through kin relationships) the latter individual desires and cannot acquire through force. This is a complex concept that killer whales have the social sophistication to employ. Furthermore, I have observed two encounters between males that appeared to be aggressive, one between three males (two brothers and a third, unrelated male) in 1986 and one between

two brothers in 1990, involving pushing, shoving, hitting, and one animal fleeing. This apparent aggression did not result in obvious injuries, indicating that such encounters may occur more frequently without being detected. Thus, dominance interactions may occur, but all evidence suggests not during MOSIs as defined here.

In addition, some MOSIs may be dominance-related play. Some adolescent male pairs *are* matched in size and the "head-bopping" game of 1988 could be interpreted as a ritualized dominance interaction or aggression. Pre-adult play pairs observed in other mammals appear to be practice for or even to establish future dominance relationships (Fagen 1981; primates: Poirier and Smith 1974, Symons 1978; northern elephant seals, *Mirounga angustirostris*: Reiter *et al.* 1978; Galápagos fur seals, *Arctocephalus galapagoensis*: Arnold and Trillmich 1985; yellow-bellied marmots, *Marmota flaviventris*: Jamieson and Armitage 1987). In many species, younger males establish a provisional dominance hierarchy (Poirier and Smith 1974; Neill 1985), although rank is usually not rigorously contested until social maturity is achieved (Le Boeuf 1974; Clutton-Brock *et al.* 1982; Walters and Seyfarth 1987). In addition, male killer whales perform body-contact behaviors, the most likely type of behavior to be associated with dominance interactions, significantly more often in MOSIs than in other behavioral contexts. In effect, it may be that human observers cannot yet discern the subtleties of content among MOSIs; for instance, nuances that are relatively easy to detect in primate relationships, our close relatives, may not be as easy to perceive in cetacean interactions, far removed from us morphologically and ecologically. Nevertheless, the similarities that MOSIs share strongly suggest that they have a common underlying origin, which is not agonism.

Evidence for affiliation (play):

Although the dominance concept can be problematic when applied to empirical (vs. theoretical) situations (Hand 1986; Walters and Seyfarth 1987), there is much less controversy surrounding it than surrounds the concept of play (Loizos 1966; Fagen 1981; Martin and Caro 1985). Nevertheless, certain characteristics have come to be accepted as defining play, particularly in mammals. As already stated, social play is characterized by frequent role-reversals during a play sequence and self-handicapping by larger individuals (Fagen 1981). Play sequences do not achieve the biological end of any nonplay counterpart behavior (Müller-Schwarze 1978; Bekoff and Byers 1981) and play tends to occur when essential requirements, such as food acquisition, have been immediately satisfied (Loizos 1966; Burghardt 1988; Barber 1991). Finally, play behavior is similar but not necessarily identical to behavior that occurs in functional contexts, it is generally exaggerated, and individual acts within a play sequence are repeated more than they would be in the functional context (see review of literature in Fagen 1981). Martin and Caro (1985) stress that the benefits of play may not be large; that is, both the benefits and costs of play may be low, a balance that selection will nevertheless maintain.

The evidence strongly suggests that killer whale MOSIs are play interactions. As already mentioned, MOSIs are distinguished by the reciprocity of behaviors. In addition, they tend to occur in the afternoon and in the latter half of the summer. Although there has been no systematic examination of daily or seasonal activity patterns in this population, their arrival in the strait coincides with the return of their principal prey species, salmon (Bigg *et al.* 1990; Nichol 1990). Although MOSIs do occur early in the season, they tend to occur more frequently in August and September (with a larger sample size, this tendency might be significant), after the whales have been feeding in the Strait for several weeks.

In addition, almost all MOSIs occur later in the day; it may be that foraging takes precedence in the morning hours and once satiated, play and other sociosexual behavior are more likely to occur. Future work should test specifically for such a pattern. Finally, the high frequency of various body-contact, aerial, and percussive behaviors (Figs. 3.4.a-c) suggests exaggeration and repetition of otherwise functional behaviors (e.g. percussive behaviors as foraging techniques: Würsig and Würsig 1980; Bel'kovich 1991), as well as the existence of behaviors that are observed only during play (e.g. tail-waving).

It is interesting to note that percussive behavior rates are no different in MOSIs than in other behavioral contexts. In fact, adults seem to perform percussive behaviors more outside of MOSIs (the only case of such a reversal). This suggests to me that percussive behaviors serve extremely important functions and their occurrence during play is incidental. For instance, the lack of any correlation of percussive behaviors with age (Fig. 1.8) is in keeping with the hypotheses that they are social signals (Norris and Dohl 1980; Würsig and Würsig 1980; Alcock 1984; Baker and Herman 1984), that all age classes might be expected to use, or that they are foraging techniques, as mentioned above.

Play hypotheses:

There is evidence supporting all three play hypotheses (see Table 3.1). That the age distribution of participants is unbiased implies that participation is not a function of age, but a function of being male (Fig. 3.2). However, affinity for play groups, or the tendency to participate more than once, does appear to be a function of age. Younger animals play more often than adults, supporting the first two hypotheses. However, the large variance among individuals argues that personality has a role in determining how many MOSIs a male will participate in over time (Table 3.3; Appendix C). A few males join MOSIs very

frequently, suggesting that they are favorite partners of other males or that they themselves actively seek out partners. In support of the third hypothesis, adults vigorously participate and infrequently form adult-only pairs. Such adult-only associations may occur between males who seek to strengthen or reestablish social bonds after a separation; perhaps the term "friendship" can be applied to these relationships (Smuts 1985).

Non-kin are consistently favored partners in all MOSIs, suggesting that social cohesion plays a part for all age classes even when another function may be paramount. Intramatrilineal MOSIs occur very rarely, perhaps because play within the matriline involves all members, including mothers and sisters (Chapter Three: Part Two).

The overall tendency for the main participants of MOSIs to be males who have achieved puberty but who have not yet achieved full physical growth (Table 3.3) means that killer whale MOSIs run counter to the norm in mammals, where juveniles predominate in play situations (Fagen 1981). This supports the second hypothesis and suggests that the learning of cognitive/social skills plays a major role in the formation of MOSIs. It should also be kept in mind that adolescents are sexually mature, but probably not socially mature (Chapter One; Olesiuk *et al.* 1990). Participation in MOSIs may be an opportunity for these males to perform sexual behaviors that they may be socially restricted from performing with the appropriate target, reproductive females (e.g. Rose *et al.* 1991).

MOSIs are not formed more often by brotherless males who might have no other opportunity to associate with other males, which does not argue strongly that any skills learned in MOSIs are acquired there exclusively; however, most of the brotherless males who do not frequent MOSIs are juveniles. This suggests that puberty does trigger an

increase in MOSI participation and perhaps that adolescence is a critical period in which to acquire certain skills and that MOSIs are a critical social arena in which to acquire them. In further support of this, adolescents who are younger brothers will still seek to participate in MOSIs, even though they could learn social skills from their older brother(s). It should be kept in mind, however, that while play may aid in acquiring necessary cognitive/social skills, such skills are usually still acquired in the absence of play (Baldwin and Baldwin 1974; Caro 1980; Martin and Caro 1985).

Although behavior sequences tend not to change with age (see Meier and Devanney 1974), all of the measured behavior rates are highest for juveniles, although again variance is high and these differences are not significant (Figs. 3.3.a-c). Nevertheless, the trend is consistent across all measured behaviors, arguing that motor training through "rough and tumble" play is the goal in joining a MOSI for this age class (e.g. Chalmers 1980; Gomendio 1988). The choreographed behavior sequences observed in 1988 between adolescent males suggests either that males originate "games" or "fads" that do not necessarily persist over seasons, and/or that ritualized behaviors, that have functional consequences in non-play contexts, are practiced by this age class in MOSIs. Adults are much less energetic in MOSIs, suggesting that their main purpose in joining them is merely to associate with other males; that is, to promote social bonds.

Male-only groups in mammals:

Killer whales are certainly not the only mammal to form male-only groups. Non-breeding males of some ungulates form "bachelor" herds, away from groups of females and young (e.g. elands, *Taurotragus* spp.: Underwood 1981; red deer, *Cervus elaphus*: Clutton-Brock *et al.* 1982; African elephants, *Loxodonta africana*: Moss and Poole 1983).

These males appear to aggregate primarily as a defense against predators or in areas containing preferred resources. Relations are usually fluid and indifferent or mildly affiliative. Some cercopithecines, such as baboons and macaques, have extratroup males, who have yet to immigrate into an existing troop. These males band together rather than remain solitary, again apparently due to predation pressures (Struhsaker 1969; Pusey and Packer 1987). Some male primates emigrate in peer or kin groups (e.g. rhesus macaques, *Macaca mulatta*: Boelkins and Wilson 1972; patas monkeys, *Erythrocebus patas*: Gartlan 1975; gelada baboons, *Theropithecus gelada*: Dunbar and Dunbar 1975).

Male chimpanzees (*Pan troglodytes*) do not form groups outside of their troops or communities, but do form male coalitions (Bygott 1979; Goodall *et al.* 1979; Nishida 1979), within the larger, mixed-sex community, to defend territory boundaries. Unrelated male lions (*Panthera leo*) and red howler monkeys (*Alouatta seniculus*) may form small coalitions in order to increase their chances of success at a group takeover (Packer and Pusey 1982; Crockett and Sekulic 1984). Large coalitions of male lions are always composed of relatives (Packer and Pusey 1982; Packer and Pusey 1987). Male cheetahs (*Acinonyx jubatus*) occasionally form pairs or trios to hold territories (Caro and Collins 1987). Subadult bottlenose dolphin males (*Tursiops truncatus*) occasionally form bonds during "play" groups that endure for years between same-age pairs and trios. Wells (1986) speculates that these bonded males may be related. Adult bottlenose males form cooperative alliances to herd females in Australia (Connor *et al.* 1992). All of these examples are of relatively long-term groupings, enduring over days, a season, or over several seasons, although they may or may not be stable in moment-to-moment composition.

Another type of grouping can be characterized as short-term or transitory. All age classes of males in multiple-male social structures may find themselves in close proximity to each other while foraging, resting, playing, or traveling, as may immature males and an adult male in one-male social structures. Such short-term associations can be further distinguished from long-term associations in that the former tend to be non-exclusive, although there may be sex biases; for instance, although an immature rhesus macaque may seek out an adult male to be near while foraging, the immature might be male or female (Hill 1986). In many species, male pairs or groups are more likely to play together than are mixed-sex or female-female pairs or groups (Redican and Mitchell 1974; Lee 1983; Jamieson and Armitage 1987; Biben 1989), but usually all possible play partnerships occur at least occasionally.

MOSIs in killer whales appear to share characteristics of both long-term and short-term interactions found among these other male mammals. Overall, killer whale MOSIs appear more akin to the affiliative interactions found in related chimpanzee and dolphin males than to the agonistic alliances found in unrelated baboons and lions, although unlike in chimpanzees or dolphins, killer whale MOSIs are transitory and fluid in composition. It is quite possible that killer whales of Johnstone Strait are a unique variation on mammalian themes, as a result of their unique social structure. However, it will undoubtedly take several more years of study before the dynamics of the social bonds that exist between males of various ages and relatedness can be determined with more certainty.

Conclusion:

Over 10% of a male's activity budget is devoted to MOSIs, indicating that these interactions are an integral part of his behavioral repertoire. Each age class may have its own agenda in joining a MOSI; that is, the reason for joining MOSIs may change with age (Chalmers 1980; Martin and Caro 1985; Mendoza and Ramirez 1987; Gomendio 1988; Barber 1991). As a juvenile, a male may participate principally for motor training, although adequate motor training is probably achieved within the matrilineal group, since juveniles do not dominate the membership of MOSIs, some juvenile males do not frequent MOSIs, and female juveniles do not form similar groups. When he reaches puberty, he may actively seek to join MOSIs, primarily to learn and practice cognitive/social skills (for instance, courtship skills and reconciliation skills with potential rivals). Adolescents may also use MOSIs to relieve active libidos with fellow males, since access to reproductive females may be restricted, either by adult males or by the females themselves.

When a male achieves full social maturity, he participates much less frequently, perhaps as social skills become perfected. As an adult, he may join principally to strengthen social ties with "old friends" and to reconcile with erstwhile rivals, although the infrequency of adult participation suggests either that the latter activity is not performed exclusively within MOSIs or that it is not often required. It may also be possible that the adults who frequent MOSIs, such as A20 and A31 (Table 3.3), are in fact potential fathers of at least some of the adolescents and juveniles with whom they play (see Packer 1980; Fagen 1981; Nishida 1983; Whitten 1987). By serving as mentors to possible or probable sons, they may be directly enhancing their fitness through a form of parental care, with little cost incurred if in fact they are not the fathers. Although there is no empirical evidence to support this, it is an intriguing notion and one that DNA analysis

could address. In summary, I believe that social cohesion is at the heart of MOSI participation for all three age classes.

Future studies:

Future studies should continue longitudinal data collection on the males in this study. I predict that the juveniles who currently do not frequent MOSIs will increase their participation as adolescents. Many adolescents who are frequent participants should sharply decrease their participation as they enter their thirties. Certain adults should participate in MOSIs more than other adults in any given year, if probable paternity is a factor. Of course, paternities need to be determined.

It would be interesting if the affinity that some individuals appear to have for MOSIs could be confirmed, to determine if individual personality has a substantial effect on results and if there are indeed particularly attractive males or "nuclei." More careful examination of the initiation of MOSIs may show that there is a play signal, such as the play bow of dogs (Fagen 1981; Müller-Schwarze 1978), that all participants recognize. Such a signal could be visual or acoustic.

A practical application of this work is that it should be possible to sex juveniles through their participation in "male-only" social interactions; that is, pre-pubescent animals who are regular visitors to Johnstone Strait but who never participate in MOSIs may be with some confidence identified as females, while those who are observed in MOSIs may be considered males without anatomical verification.

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Table 3.1. Predicted characteristics of MOSIs according to dominance and each of three play-function hypotheses.

FUNCTION	PARTICIPANTS	AGE/SIZE OF PARTNERS	RELATEDNESS OF PARTNERS	BEHAVIORS
DOMINANCE	primarily adults	same-age/size	primarily non-kin	aggressive; unidirectional
MOTOR TRAINING	juveniles	same-age/size or larger	kin, non-kin	"rough and tumble"; bidirectional
COGNITIVE/ SOCIAL SKILLS	adolescents	courtship: all ages; dominance: same-age/size	kin, non-kin	ritualized; bidirectional
SOCIAL COHESION	all ages	all ages	non-kin	bidirectional

Table 3.2. Pod affiliation, identification of males, matrilineal group affiliation, estimated or known year of birth, total number of hours observed in MOSIs, and age class (see Chapter One).

POD	MALE ID	MATRILINEAL GROUP	YEAR OF BIRTH	NUMBER OF HRS OBS.	AGE CLASS
A01 C01 I02 B01	A20 A31 C03 I05 *B02	A36 A12 C06 I02 B07	~1953 ~1958 ~1952 ~1954 ~1952	0.93 1.02 0.17 0.53 --	>25 years (adult)
A01 A05 C01 D01	A06 A32 A38 A33 A39 A26 A27 C09 *D05	A30 A36 A30 A12 A30 A09 A23 C06 D03	~1964 ~1964 1970-1 1971 1975 1971-2 1971-2 1971-2 ~1964	1.24 2.34 2.96 3.49 2.86 0.95 0.80 1.02 --	12-25 yrs (adolescent)
A01 A05 C01 I11 A04 B01 C01 H01	A37 A46 A15 C14 I43 *A13 *B10 *C13 *H07	A36 A36 A14 C06 I16 A11 B07 C05 H03	1977 1982 1979 1985 1983 1978 1979 1985 1981	3.07 1.10 0.25 1.24 0.39 -- -- -- --	<12 years (juvenile)

* These males were observed only during the 1987 pilot study or in *ad libitum* samples

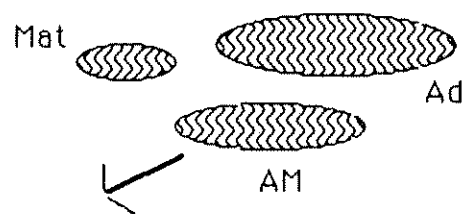
Table 3.3. Number of bouts observed per male, with the mean and SD for each age class. The difference among age classes approached significance (Kruskal-Wallis test, $H = 5.401$, $df = 2$, $p = 0.067$).

	MALE ID	NO. OF BOUTS
A D U L T S	A20	2
	A31	2
	B2	1
	C3	1
	I5	1
	N = 5	mean = 1.4 SD = 0.55
A D O L E S C E N T S	A6	5
	A26	2
	A27	6
	A32	6
	A33	6
	A38	10
	A33	13
	C9	1
	D5	1
	N = 9	mean = 5.56 SD = 4.03
J U V E N I L E S	A13	1
	A15	2
	A37	8
	A46	5
	C13	4
	C14	5
	H7	2
	I43	2
	B10	1
	N = 9	mean = 3.33 SD = 2.34

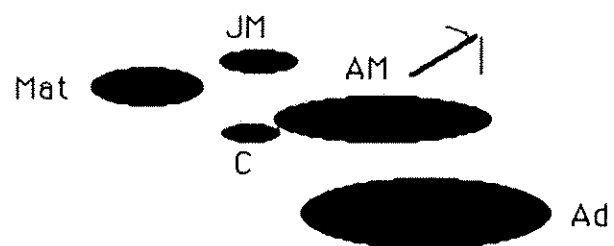
Figure 3.1.a. Hypothetical MOSI scenario: Two matrilineal groups, A and B, travel west about five body-lengths apart. Group A contains a matriarch (Mat), an adult male (Ad), and an adolescent male (AM). Group B contains in addition a juvenile male (JM) and a calf (C). At time 0:00 min, the adolescent males separate from and join up in between their respective matrilineal groups.

W ←

GROUP A



GROUP B



Time: 0 min

Figure 3.1.b. After 15 minutes, during which the two adolescent males push and rub each other and perform percussive and aerial behaviors, the juvenile male of Group B moves to join them.

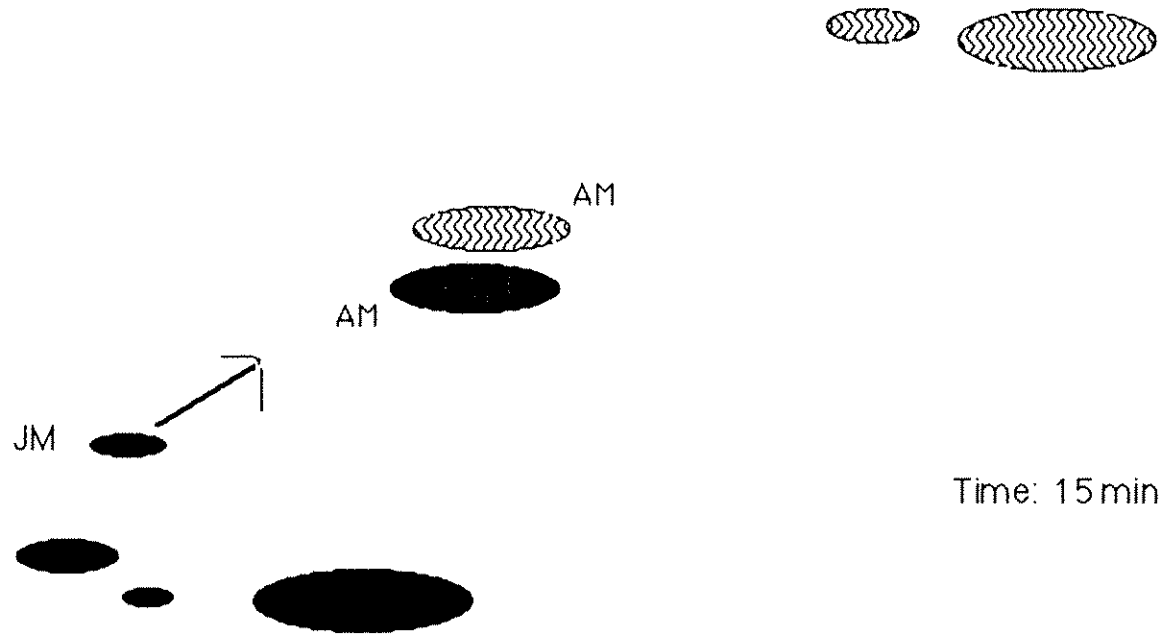


Figure 3.1.c. After only 5 minutes of interaction, the juvenile male moves back to join his matrilineal group, while the two adolescent males continue to interact.

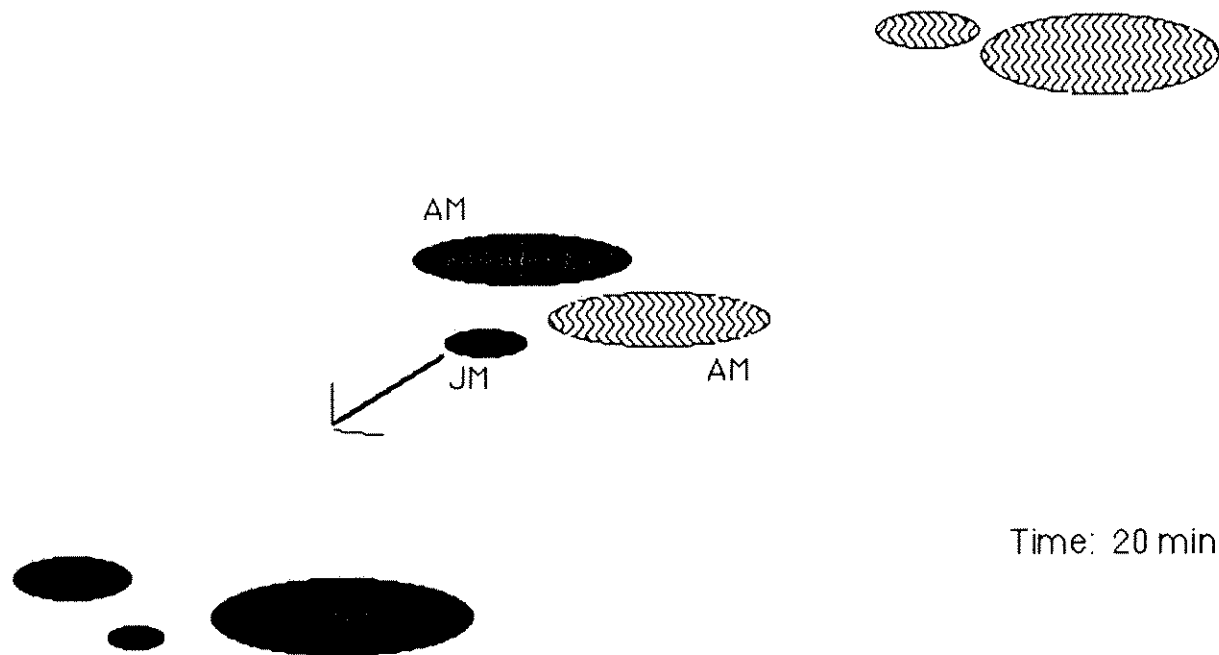
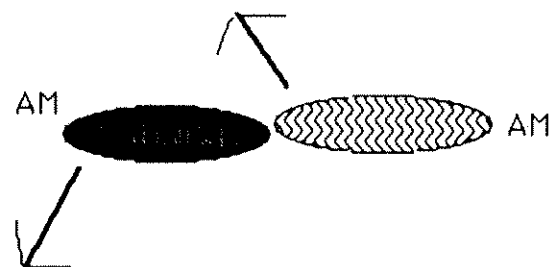
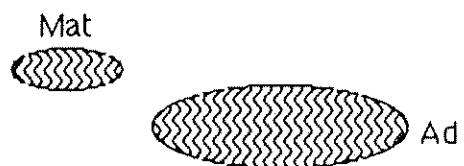
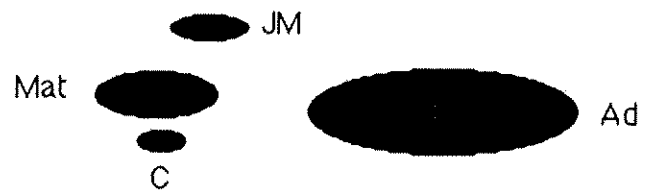


Figure 3.1.d. After a total of 60 minutes of interaction and a distance traveled of only 2 km (due to slow swimming and milling), the two adolescent males return to their respective matrilineal groups.

GROUP A

Distance covered: ~2 km

GROUP B

Time: 60 min

Figure 3.2. The age distribution of males who participated in MOSIs vs. that of males that visited Johnstone Strait regularly during the summer months of 1987-89. The distributions were not significantly different (Chi-square goodness-of-fit = 1.67, $df = 2$, $N_1 = 23$, $N_2 = 45$, $p > 0.10$).



Figure 3.3.a. The number of body-contact behaviors performed per hour for each age class (N = 5, 8, and 4, respectively). The difference between age classes (adults were not included in the analysis) was not significant (Mann-Whitney U = 29, $p = 0.2222$).

Figure 3.3.b. The number of non-percussive aerial behaviors performed per hour for each age class. The sample sizes are the same as in Fig. 3.3.a. The difference between age classes was not significant (Mann-Whitney U = 31, $p = 0.1274$).

Figure 3.3.a

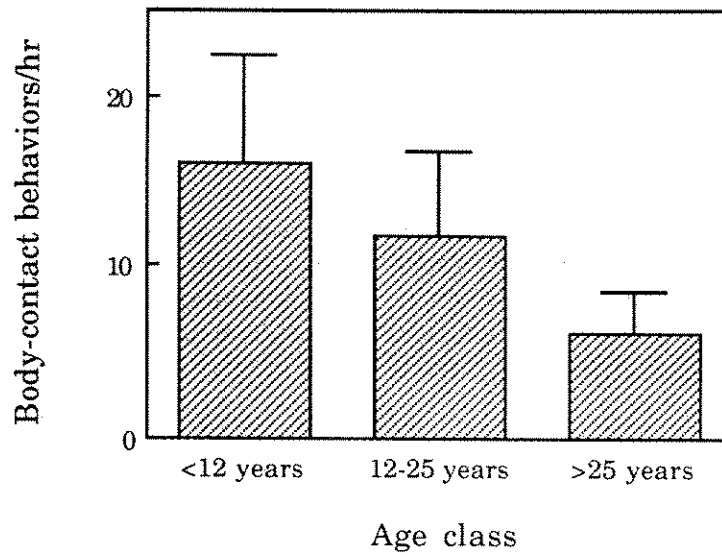


Figure 3.3.b

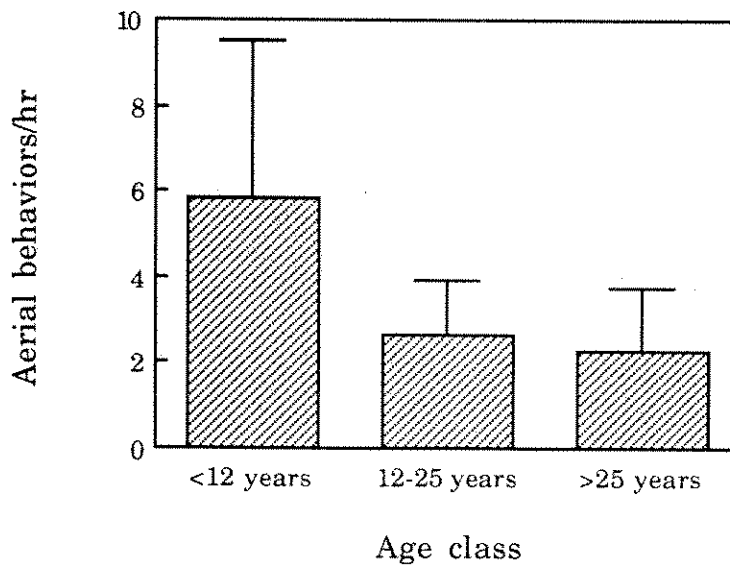


Figure 3.3.c. The number of percussive behaviors performed per hour for each age class. The difference between age classes was not significant (Mann-Whitney $U = 26.5$, $p = 0.3683$).

Figure 3.3.d. Respiration rates, in breaths per minute, for each age class. The difference between age classes was not significant (Mann-Whitney $U = 27$, $p = 0.3543$).

Figure 3.3.c

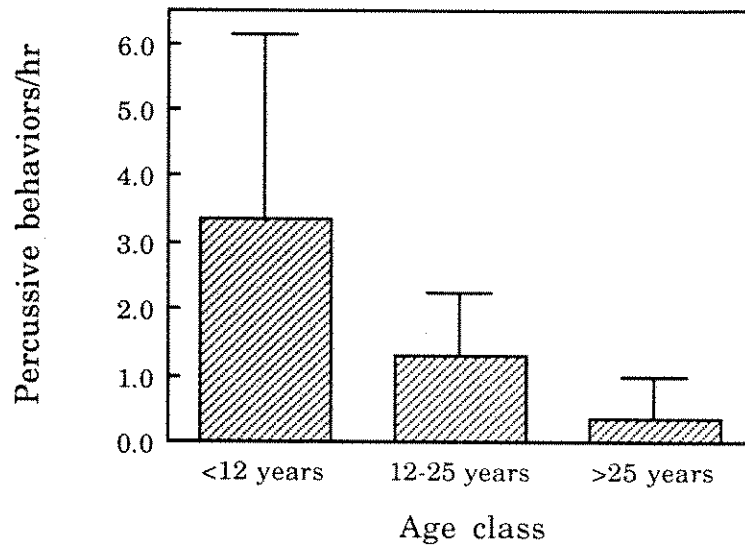


Figure 3.3.d

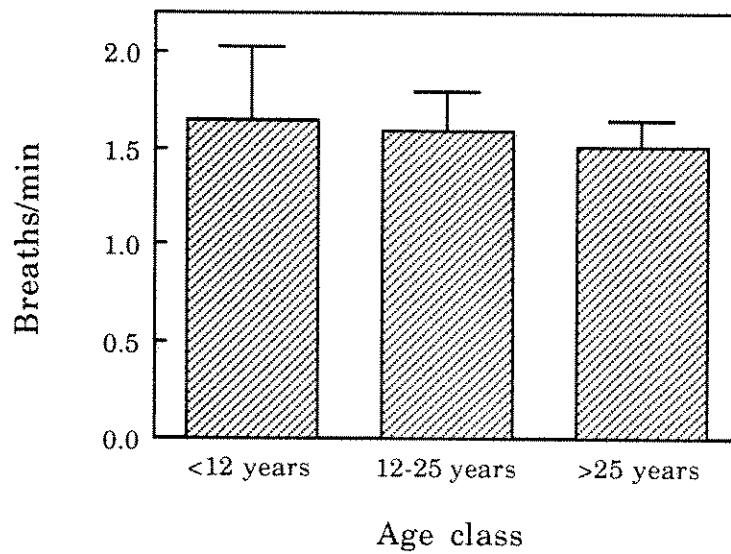


Figure 3.4.a. A comparison of body-contact behavior rates in MOSIs vs. other behavioral contexts. The difference for adolescent males (sample sizes of the other age classes were too small for analysis) was significant (Mann-Whitney $U = 64$, $N = 8$, $p = 0.0002$).

Figure 3.4.b. A comparison of non-percussive aerial behavior rates in MOSIs vs. other behavioral contexts. The difference for adolescent males was significant (Mann-Whitney $U = 59$, $N = 8$, $p = 0.003$).

Figure 3.4.a

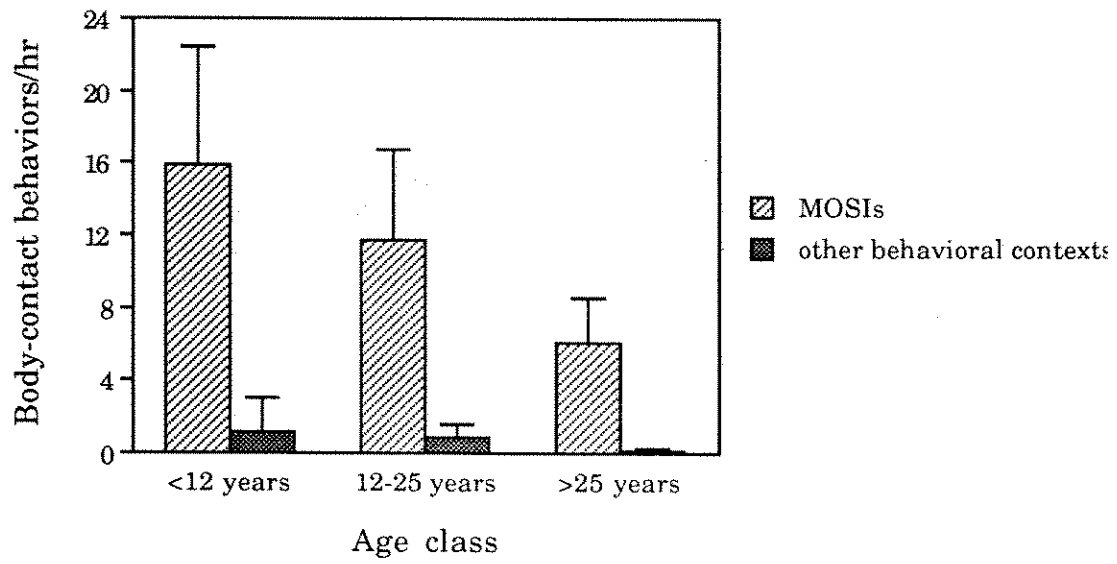


Figure 3.4.b

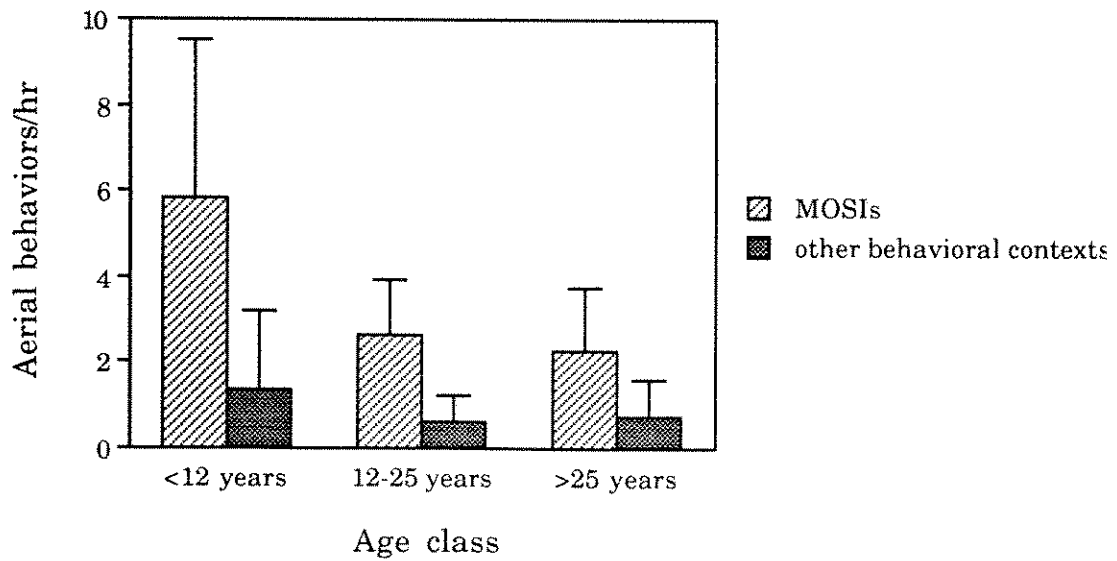


Figure 3.4.c. A comparison of percussive behavior rates in MOSIs vs. other behavioral contexts. The difference for adolescent males was not significant (Mann-Whitney $U = 44.5$, $N = 8$, $p = 0.1364$).

Figure 3.4.d. A comparison of respiration rates in MOSIs vs. other behavioral contexts. The difference for adolescent males was not significant (Mann-Whitney $U = 46$, $N = 8$, $p = 0.0802$).

Figure 3.4.c

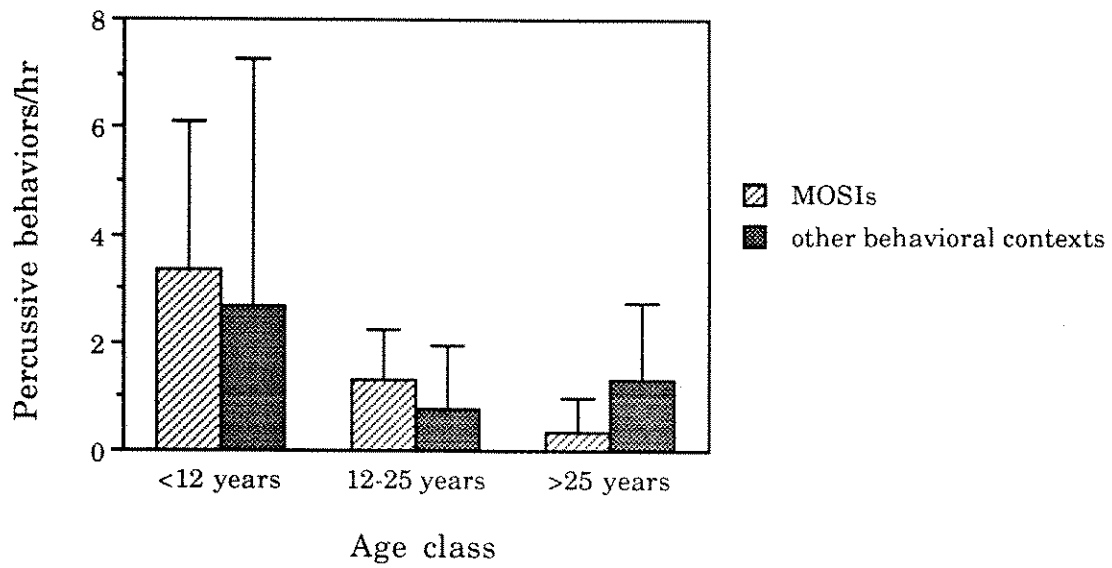
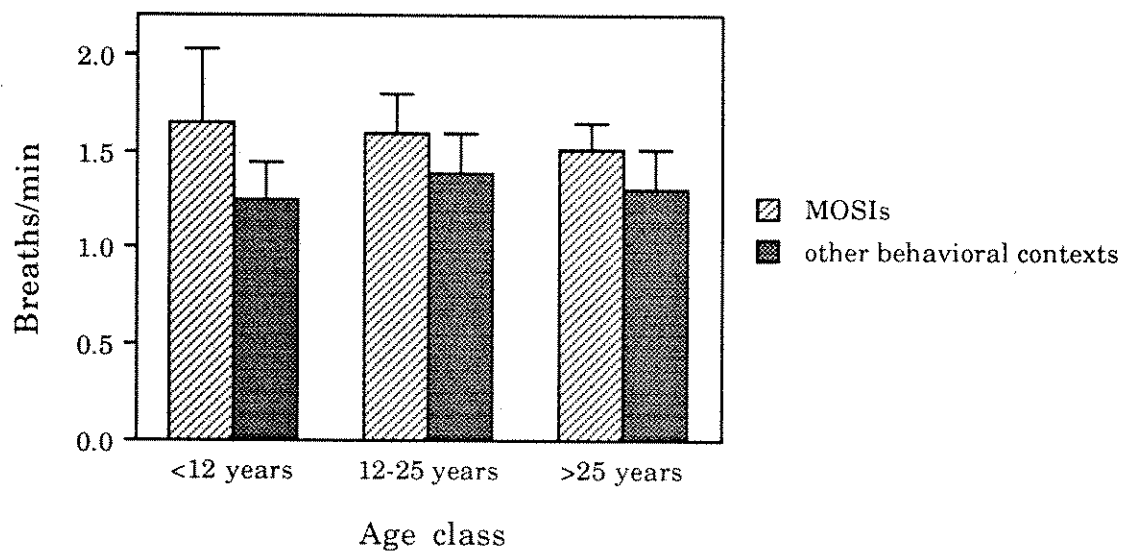


Figure 3.4.d



PART TWO: MALE/JUVENILE ASSOCIATIONS: ALLOPATERAL CARE?

ABSTRACT

Male killer whales occasionally associate with juveniles five years of age or younger in the absence of the juvenile's mother. These associations have been hypothesized to be forms of allopaternal care. The aim of this chapter was to evaluate the available data on these associations to determine if the evidence for allopaternal care was convincing. Thirty-eight male-juvenile associations observed over a period of seven years were examined to determine the following: The relatedness of the male and juvenile(s); the mother's distance from and orientation toward the juvenile(s); the behavior state during the association; whether or not the mother was currently nursing a younger juvenile; and how many pods were present in the area during the association. Male-juvenile associations involved kin only (either siblings or uncle-nephew). There was no pattern in the distance from or position of the mother from the juvenile(s). Traveling and sociosexual behavior were the most common behavior states observed. In 50% of the associations, the mother of the juvenile was nursing a younger calf. In two-thirds of the associations, at least one other pod was present in the area. The lack of any observed male-juvenile associations involving non-kin argues convincingly that these associations are allopaternal in nature, with males gaining inclusive fitness benefits. Males may guard juvenile kin from environmental hazards or from inappropriate non-kin social partners. They may also relieve the mother of energetic costs incurred by "carrying" the juvenile in the echelon-swimming formation or when engaging in rough-and-tumble play.

INTRODUCTION

Male/juvenile associations in killer whales:

In Johnstone Strait, males have occasionally been observed associated with juveniles five years of age or younger while the mother has been from several meters to one to two kilometers away (Waite 1988; see below). Five years is the average interbirth interval (Olesiuk *et al.* 1990), so these juveniles may be considered socially if not also physically dependent on the mother. Waite (1988) observed in particular that these associations, when the participants were traveling or foraging, were always between matrilineal group members; that is, while nulliparous females aged 10-15 years were often observed associated with calves from both the same and other matrilineal groups, males of all ages were only observed *traveling* or *foraging* with younger calves from the same matrilineal group. In addition, although males frequently *socialized* with unrelated male calves in male-only social interactions (Chapter Three: Part One), they were never observed to socialize with unrelated female calves or with calves of unknown sex (with one exception, I43; see Table 0.1). The purpose of this paper is to present a preliminary argument, based on observations from 1985 to 1992, that these associations are allopaternal in nature.

Waite (1988) first hypothesized that the killer whales in Johnstone Strait show alloparenting behavior; she categorized the care being given as "babysitting." After noting that males associated only with related calves and females associated with calves regardless of relatedness, she concluded that females gain mothering skills ("learning-to-mother;" Lancaster 1971) and males receive inclusive fitness benefits (Hamilton 1964). Her work also determined that mothers had lower respiratory rates when they were without their calves than when they were together. In addition, the amount of time that a calf spent

with its mother was negatively correlated with the number of older siblings the calf had, suggesting that mothers with potential alloparents allow their young offspring more independence. Although these results supported her hypothesis, they left several other assumptions untested. This paper attempts further tests of Waite's hypothesis, examining male/juvenile associations for patterns and trends.

This study:

If male/juvenile associations in killer whales are allopaternal in nature, the following predictions can be made (although not all need be met): 1) Males are members of the same matrilineal group as the juveniles (Waite 1988); 2) mothers are most vigilant with younger juveniles, positioning themselves behind or beside them and not moving too far away, as younger offspring are the least experienced and probably the most vulnerable to environmental hazards; 4) associations occur more when juveniles are extremely active, a condition more likely to fatigue the mother and during which juveniles are more likely to seek other social partners; and 5) associations occur more when the mother currently has two offspring under five years of age, as her attention may need to focus more on the younger, more dependent offspring.

RESULTS

From 1988 to 1992, I observed 33 instances where older males associated with juveniles five years of age or younger, with the mother farther than 10 m away. Ten of these associations fell under the definition of male-only social interactions (Chapter Three: Part One). Including the 15 instances observed by Waite in 1985, 1986, and 1987, animals from eight different matrilineal groups exhibited associations that did not come under the definition of male-only social interactions (Table 3.4). In these associations, the males were either brothers/half-brothers or presumed uncles and ranged from four to 35+ years of age. Juveniles were male, female, or of unknown sex and ranged from less than one to five years of age. There was no observable pattern in the position of the mother or in her distance from her calf. In 66% (25/38) of the cases, there was at least one other pod present in the strait during the association. The predominant behavior states were travel or sociosexual (play). In 19 cases, the mother had a younger calf. Duration of associations was not directly measured (see General Methods), but some were very brief (minutes) while others were quite long (hours).

DISCUSSION

Do killer whales demonstrate allopaternal care?

My results provide further evidence that males associate only with related juveniles (Table 3.4). Consequently, I agree with Waite (1988) that these male/juvenile associations are allopaternal in nature, although based on Waite's respiration rate results, costs and benefits may be low. In several other species with allofathering, the authors have concluded that the cost to the allofather is probably quite small (e.g. Hunt *et al.* 1978; Nishida 1983; Baker-Dittus 1985), with a concomitantly small benefit for the mother or parents.

In support of this conclusion, recent work with bottlenose dolphins (*Tursiops truncatus*) has determined that there is an energetic savings for an animal when riding the bow-wave of a larger animal (Williams *et al.* 1992), which also applies to echelon-swimming (Kelly 1959; Norris and Prescott 1961) behind a larger animal. The associated drag on a larger animal suggests that there is some energetic cost to an older killer whale accompanying a juvenile. In fact, echelon-swimming can be seen as a form of carrying, in the sense of allopaternal care in tamarins and marmosets (Goldizen 1987). Also, play is a common activity during male/juvenile associations (Table 3.4) and personal observations indicate that young calves can play very vigorously with an older companion, perhaps more vigorously with a companion than with the mother. When I have observed this, the companion appears a willing participant in this rough-and-tumble play, but such play undoubtedly requires considerable attention and energy. The benefit for the mother need be no more than the opposite of the cost to the allofather; that is, no drag from the calf and an energy savings when released from playing with the calf. The lower

respiratory rates exhibited by mothers when without their calves (Waite 1988) indicate that such a benefit may be realized for mothers.

Although there were no observable patterns to the mother's position in relation to and distance from her calf, it would be impossible at this stage to speculate as to the degree of a mother's vigilance toward a calf when it is with an allofather. Killer whales are highly acoustic and a mother could very well keep an "eye" on her offspring even when swimming several hundred meters ahead. Measuring position and distance demonstrates a bias toward the visual that may not have any significance for these animals.

Allopaternal scenarios:

My overall impression is that prior to puberty, a female does not find herself in close proximity to unrelated adolescent or adult males without her mother in close attendance. At this stage of study, it is difficult to say who initiates this segregation; the mother, the daughter, or an allofather. It is interesting to note that in one allopaternal bout between A38 and A50 (a 19-year-old brother and his five-year-old sister), A38 clearly exhibited sexual behavior toward A50. This may be inevitable in play-bouts between killer whales regardless of sex (see Chapter Three: Part One), and it may be this tendency that has created a social system that discourages associations between sexually mature males and unrelated female juveniles. In contrast, at least in the case of A50 and her brothers (Table 3.4), a sister may frequently travel, forage, or play with older brothers when the mother is at a distance. I suggest that this may be a kind of chaperonage; that is, older brothers keep an eye on younger sisters when the latter begin to exercise independence, increasing the chances of an interaction with an inappropriate social partner. That most

associations occur when there are unrelated whales present in the strait supports this argument. In contrast, male calves appear to exercise a great deal more independence at a younger age and may associate with unrelated older males in male-only social interactions (Chapter Three: Part One; see also Bigg *et al.* 1990).

Another situation where allofathering might occur, regardless of the sex of the juvenile, is when a female has another calf. Here, older male relatives may travel with the older calf to allow the mother to devote more time to the younger calf, as in the case of B01 and B12. B07, the mother of B12, was nursing a two-year-old, B13, during the summer of 1989 (Table 3.4). In 50% of the observed associations, the mother had a younger calf. Older males may also allofather both calves at once, as in the case of A38, A50, and A54 in 1989. In addition, very young calves, such as A54, C17, and H8 may be accompanied whenever they wander from their mother's side, due to their lack of experience and the intense curiosity that they tend to show toward their environment (Haenel 1986; pers. obs.). Young calves in Johnstone Strait occasionally follow directly in the engine wash of boats, an activity not without risks. If young calves show such indiscriminate curiosity toward natural dangers, such as sharks or potentially aggressive marine mammals (such as adult male Steller sea lions), then a constant caretaker may be imperative.

Allopaternal care in other species:

Male care directed toward conspecific young, whether paternal or allopaternal, is the exception rather than the rule in most animals. Paternal care is notable among most birds, certain insects, amphibians, and fish, and some social mammals (see Trivers 1985 for a review). Allopaternal care is even less frequently observed (perhaps because it is often difficult to define; in this paper, it refers only to benign or neutral behavior, as

opposed to behaviors that can be detrimental both to the young and the mother: see Blaffer-Hrdy 1976). Allopaternal care clearly occurs in many cooperatively breeding birds (see Brown 1987; Stacey and Koenig 1990 for reviews), in some fishes (e.g. fathead minnows, *Pimephales promelas*: Sargent 1989), in many social carnivores (e.g. dwarf mongoose, *Helogale* spp.: Rood 1978; African wild dogs, *Lycaon pictus*: Malcolm and Marten 1982; brown hyenas, *Hyaena brunnea*: Owens and Owens 1984; see Gittleman 1985 for a review), especially in the larger-bodied canids (Moehlman 1986), and in some primates (e.g. chimpanzees, *Pan troglodytes*: Nishida 1983; Barbary macaques, *Macaca sylvanus*: Small 1990), particularly tamarins and marmosets (Goldizen 1987). In these taxa, males who are not the father play with, carry, groom, feed, and guard/defend young. Killer whales travel, forage, and play with juveniles, but have not been observed to share food or defend actively against hazards.

Potential benefits to mothers and allofathers:

In many primates, allopaternal care, in the form of carrying and protecting, appears to be associated with an increased likelihood that the caregiver will mate with the mother (Hunt *et al.* 1978; Nishida 1983; Whitten 1987). In others, allopaternal care appears to promote the social skills of both the infant and the allofather (Baker-Dittus 1985; Small 1990). In some bird species, male alloparents, or helpers-at-the-nest, often inherit the territory of the pair they help (e.g. Florida scrub jays, *Aphelocoma coerulescens*: Woolfenden and Fitzpatrick 1978; acorn woodpeckers, *Melanerpes formicivorus*: Koenig and Mumme 1987). In other bird and mammal species, the allofathers are usually close kin, such as older brothers and uncles (in chimpanzees, they are potentially the fathers: Nishida 1983). The allofather receives inclusive fitness benefits and may also exchange allofathering for whatever benefits it receives by being allowed to remain in the natal

territory. This "repayment" model (Emlen *et al.* 1986; Emlen *et al.* 1991) states that the cost of producing the philopatric sex, increased through such factors as local resource competition (Clark 1978; Clutton-Brock *et al.* 1982; Silk 1984), has been offset by the evolution of alloparenting behavior; that is, the philopatric sex pays back some of its cost through caring for its parent's subsequent offspring. The philopatric sex may in fact become "cheaper" to produce over time, causing a bias toward that sex in the primary sex ratio (Emlen *et al.* 1986).

Although data are insufficient for a proper analysis and the lifetime reproductive success for any female has yet to be measured, I believe that both mother and allofather receive benefits from allofathering behavior in killer whales. As stated previously, mothers at a distance from their calves have lower respiration rates than mothers in echelon-swimming formation with their calves (Waite 1988). In addition, at least 10 reproductive females in the population with older males in their matrilineal groups have been very successful in both producing and rearing recent offspring. Conversely, one young female (A24) without any potential alloparents, and who has exhibited very brief interbirth intervals, has lost two of her last four offspring. The principal benefit to mothers may simply be temporary relief from constant vigilance or from rough-and-tumble play.

Because their mothers' reproductive success may be enhanced through allofathering, the allofathers would receive inclusive fitness benefits. The repayment model may also apply here; there are potential costs to the matriarch in allowing sons and other male relatives to remain in close association with her, notably local competition for fish. Allofathering may be a way to reduce these costs and its benefits may now in fact

outweigh these costs, as there is some preliminary evidence that there is a male bias in the primary sex ratio (Bain 1989; but see Olesiuk *et al.* 1990).

Alloparental associations, although not frequent, do occur measurably often. My overall impression is that calves with older matrilineal group members may be babysat as often as once or more a day during certain socially active periods of the summer. Alloparenting in this population would probably have very little impact on the direct survival of a calf (although it may have significant effects on the proper socialization of a calf), but its effect on the overall mental and physical health of the mother may be the principal selection pressure maintaining the behavior. Any conclusions based on such scant observations are clearly speculative, but I believe that this line of thought should influence the ultimate analysis of lifetime reproductive histories as they accumulate for this population.

Killer whale society and allopaternal care:

Several aspects of killer whale social organization have implications for any conclusions drawn concerning allofathering. First, several matrilineal groups have two or more older males who could serve as allofathers, leading to the following question: if there are several potential allofathers around, why would any one individual incur the costs of allofathering? Why not leave it to others? Eshel and Motro (1988) and Motro and Eshel (1988) have determined that in cases where there is more than one potential alloparent, the probability that any one individual will alloparent remains positive, if the cost/benefit ratio is favorable on a one-to-one basis. Also, personality appears to have an effect on behavior (Appendix C) and some males in a matrilineal group may be more

inclined to associate with juveniles than others. No problem need therefore exist with the cases where several brothers or uncles are available to the matriarch as allofathers.

Another characteristic of killer whale societies addresses the evolution of the behavior in this species. There appears to be no paternal care in the northern resident community. Any care-giving behavior exhibited by males could not therefore be explained as behavioral heterochrony, in the sense that Jamieson (1989, 1991) applied this concept to cooperatively breeding birds, unless paternal care occurred historically but has since been extinguished. Considering the typical mammalian parenting pattern, this seems unlikely, although it would be necessary to determine if other populations of killer whales show paternal care. Allopaternal behavior in the Johnstone Strait population may have evolved directly as such; that is, not as a derivative of paternal behavior. This idea needs further theoretical consideration.

Finally, it is interesting to note that there is no delayed dispersal or delayed breeding in the Johnstone Strait killer whales, a feature common to other species that show allopaternal care (Gittleman 1985; Brown 1987; Koenig *et al.* 1992). That is, at least some males actively breed even while remaining associated with their mothers (or matriarchs) for life. The evolution of allopaternal care under such circumstances, in my opinion, argues convincingly for a significant inclusive fitness benefit to the behavior. There appear to be no direct fitness costs to philopatry in this population, unlike, for instance, in birds with delayed dispersal and breeding. However, associated costs, such as local resource competition, may have selected for the evolution of male care-giving behavior toward matrilineal group calves, as a way to offset these costs. Males would have had *no predisposition* to such behavior.

Future studies:

Certainly it will be necessary to collect several lifetime reproductive histories of females, noting their availability of potential allofathers, before much can be said about the measurable benefits to allofathering. A better understanding of the dynamics between unrelated males and females needs to be developed as well (determining paternities would be a good step in this direction). Examining the finer nuances of who -- the mother, the calf, or the male associate -- instigates departures from and approaches toward the mother is also called for (a pilot study on this topic was conducted by a researcher at the University of British Columbia in the summer of 1992). It is clear at this time, however, that related males (older brothers and uncles) do associate with calves in a benign and consistent manner. Future work will determine how significant these associations are to all parties, but preliminary evidence suggests that the killer whale population of the Pacific Northwest has evolved an elaborate communal care-giving system for its young.

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Table 3.4. Summary of non-male-only social interaction male/juvenile associations: Date association observed, older male identity (with age in years in parentheses), juvenile identity (with age in years and sex, if known, in parentheses), relationship of male to juvenile, distance separating mother from juvenile, position (ahead, behind, or beside) of mother to juvenile, number of other pods in strait during association, and behavior state of associating male and juvenile.

DATE	MALE ID (AGE)	JUVENILE ID (AGE, SEX)	RELATION - SHIP	DISTANCE OF MOM	POSITION OF MOM	NO. OF PODS	BEHAVIOR STATE
24 July 85	A06 (21)	A50 (1, F)	sibling	?	?	0	?
23 Aug 88	A06 (24)	A50 (4, F)	sibling	> 1 km	beside	2	Travel
5 Sept 88	A06 (24)	A50 (4, F)	sibling	> 10 m	?	0	Milling
20 July 89	A06 (25) A38 (18) A39 (14)	A50 (5, F)	siblings	~60 m	ahead	1	Social
26 July 89	A06 (25) A38 (18)	A50 (5, F) A54 (<1, M?)	siblings	~40 m	beside	3	Travel
14 Aug 89	A06 (25)	A50 (5, F)	sibling	~15 m	beside	1	Travel
25 Aug 89	A06 (25)	A50 (5, F)	sibling	> 10 m	ahead	2	Milling
12 Aug 85	A32 (21)	A46 (3, M)	sibling	?	?	4	?
August 92	A33 (21)	A55 (3, ?)	uncle	~30 m	beside	?	Travel
29 Aug 86	A37 (9)	A46 (2, M)	sibling	?	?	4	?
27 July 87	A37 (10)	A46 (3, M)	sibling	?	?	1	?
12 Sept 87	A38 (16)	A50 (3, F)	sibling	?	?	1	?
2 July 89	A38 (18)	A50 (5, F) A54 (<1, M?)	sibling	~20 m	?	0	Social
15 Aug 89	A38 (18)	A50 (5, F)	sibling	> 30 m	behind	1	Travel
26 Aug 89	A38 (18)	A50 (5, F)	sibling	> 10 m	behind?	2 + 1 trans	Social
27 Aug 89	A38 (18)	A50 (5, F) A54 (<1, M?)	sibling	~10 m	?	1 + 1 trans	Social
22 July 90	A38 (19)	A54 (1, M?)	sibling	~30 m	behind	0	Social
26 July 90	A38 (19)	A54 (1, M?)	sibling	> 10 m	ahead	0	Social

Table 3.4 cont'd.

27 July 90	A38 (19)	A54 (1, M?)	sibling	> 10 m	ahead	0	Social
5 July 86	A39 (11)	A50 (2, F)	sibling	?	?	2	?
11 Sept 86	A39 (11)	A50 (2, F)	sibling	?	?	?	?
26 July 87	A39 (12)	A50 (3, F)	sibling	?	?	0	?
21 July 89	B01 (35+)	B12 (5, M)	uncle	~1 km	behind	7	Travel
26 July 89	B01 (35+)	B12 (5, M)	uncle	> 1 km	behind?	3	Travel
27 July 89	B01 (35+)	B12 (5, M)	uncle	?	?	3	Travel
28 July 89	B01 (35+)	B12 (5, M)	uncle	> 1 km	?	3	Travel
29 July 89	B01 (35+)	B12 (5, M)	uncle	> 500 m	behind	1	Travel
18 July 86	B06 (13)	B12 (2, M)	uncle	?	?	0	?
19 July 86	B08 (22)	B12 (2, M)	sibling	?	?	0	?
19 July 86	B08 (22)	B12 (2, M)	sibling	?	?	0	?
8 July 86	C02 (29)	C13 (1, M)	uncle	?	?	1	?
26 July 89	C03 (35+)	C14 (4, M)	uncle	~30 m	behind?	3	Travel
12 Aug 86	C09 (15)	C14 (1, M)	sibling	?	?	4	?
5 July 89	C13 (4)	C17 (<1, ?)	sibling	> 10 m	?	1	Social
19 July 89	C13 (4)	C17 (<1, ?)	sibling	?	?	1	Social
7 Aug 89	C13 (4)	C17 (<1, ?)	sibling	~30 m	ahead	0	Social
25 July 86	H07 (5)	H08 (<1, ?)	sibling	?	?	3	?
14 Aug 86	H07 (5)	H08 (<1, ?)	sibling	?	?	4	?

SUMMARY AND GENERAL CONCLUSIONS

What conclusions can be drawn about the roles males play within the matrilineal group and the pod at different stages of the life cycle? Juveniles associate more closely with their mothers than do older males, although they begin to exercise independence early (and earlier than females: Bigg *et al.* 1990). Their activity level is higher than that of older males; they socialize less than adolescents, but their behavior rates while in the sociosexual behavior state are very high. They demonstrate mature behavior patterns early, although relatively infrequently (e.g. participation in male-only social interactions, allofathering). In short, the behavior of juvenile males does not differ much from that observed in most juvenile mammals and indicates a role primarily dependent on the mother.

The adolescent stage is clearly distinct from the juvenile and adult periods. Adolescents demonstrate adult patterns of independence from their mothers, but occupy their time quite differently than adults do. They increase the amount of time that they spend socializing in non-reproductive contexts, although older adolescents may demonstrate the basic elements of adult "consortship" behavior with unrelated reproductive females. Adolescents are active in allofathering related calves, predominate in male-only social interactions, and are occasionally observed interacting with older, non-reproductive females. These associations may be an opportunity for these young males to relieve an active libido, that either adult males will not allow them to indulge with reproductive females, the appropriate target, or that the latter will not tolerate. Adolescents appear to be somewhat self-sufficient socially; that is, they rely on each other as social partners and may learn from and practice social skills (notably mating skills) on each

other. All evidence suggests that they play a major role as caregivers to juvenile siblings within the matrilineal group, while also playing a major role outside of it, broadening and strengthening their social contacts (e.g. Quiatt 1984), particularly among themselves.

The activity level of adults is low compared to younger males. Although some adult males continue to participate in male-only social interactions, most adult social behavior is performed either within the matrilineal group or in a reproductive context. If there is competition among adult males for access to estrous females within a dominance hierarchy, its form was not immediately apparent from the results of this study. However, observations suggest that some adults are more active reproductively than others. Adults continue to serve as allofathers if there are still young juveniles present in their matrilineal group. Older adults, especially those who are believed to be traveling with sisters or nieces, frequently travel, forage, and even rest alone. This last implies that older males who have lost their mothers are most peripheral to and the least integrated into the matrilineal group. Adults appear to have the central role in reproduction, as expected, but differ from adults in most other mammals by the degree and quality of their interactions with kin.

Males do share behavioral traits with the kin-influenced, multiple-male social structures of canids, certain primates, and birds. Reduced aggression within the social unit is apparent, although the existence of a dominance hierarchy is still undetermined. There is convincing evidence of allopaternal care. However, a major difference is that to some degree, males treat all other males, whether kin or non-kin, similarly. They interact with kin more often, not unexpectedly, but when they do interact with non-kin, there is no marked change in their behavior. This is not the case in other multiple-male

kin-based social systems; territorial dog packs and chimpanzee troops are very aggressive or ritualistically agonistic when they encounter unrelated neighbors. In killer whales, overt physical aggression between matrilineal groups and pods is not only attenuated, but apparently non-existent, unless the nature of underwater behaviors differs radically from that observed at the surface (the actual behaviors undoubtedly differ). This is possible but does not seem likely, as the nature of behaviors at the surface seems to be confirmed by what can be observed below the surface (pers. obs.). This almost total repression of aggression (which may be a result of males avoiding each other in some cases: see B01's individual profile, Appendix C) may be the most significant consequence of the mother-son bond.

Male killer whales are apparently guided by their matriarchs, similar to the case of matriarchs in African elephants (*Loxodonta africana*: Moss and Poole 1983). Anecdotal evidence suggests that killer whale matriarchs control where the matrilineal group goes and when it changes behavior states, especially moving into and coming out of the resting behavior state. However, the presence and behavior of males in matrilineal groups may be integral to the relationships that matriarchs maintain with each other. For instance, it would be beneficial for matriarchs with adult sons to associate as often as possible with unrelated reproductive females, to facilitate mating between their sons and these females in the interest of producing grand-offspring. Those with adolescent sons would benefit if they maintained close ties with females who also had adolescent sons, to facilitate interactions among these socially active males. It may be that social bonds community-wide, not just with kin, are equally important to males and females in the northern resident community of killer whales.

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Appendix A. Sample data sheet.

#59
 DATE: 12 Sept 88
 OBS: NR
 REC: GM
 LOC: West RE → F
 FILM: 8
 THEO?: 4.5
 WEATHER: Sun.
 Slt. Swell. 1.1

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BCC
 SUBS-H 1/4

Appendix B. Ethogram and behavior codes for *Orcinus orca*
in Johnstone Strait, British Columbia (after Östman 1987).

Rest

Rest SWS	swim slow (1-3 knots)
DSW	directional swimming
MIL	milling
HAN	hanging (body below surface, fin visible)
FLO	floating (body at surface, back visible)
RIS	rise (coming up, no forward movement)
SIN	sink (going below surface, no forward movement)
SDE	slow descent (fin visible for several seconds)
HOT	head oriented toward (e.g. another whale, a direction)
GAZ	gaze (head tilted, one eye up, above or below surface)

Milling/ foraging

MIL	milling
CIR	circle (swim in an arc at surface)
SWS	swim slow (1-3 knots)
SWM	swim moderate (4-6 knots)
SWF	swim fast (greater than 6 knots)
SSW	shark-swimming (rapid burst of speed at surface, fin constantly visible)
RAD	racing dive (lunge at surface)
UND	undulate in place (rostrum up against rock, stationary, gentle RIS-SIN, indicating a fish has been trapped)
HOT	head oriented toward (e.g. another whale, a direction)
GAZ	gaze (head tilted, one eye up, above or below surface)
TAT	tail throw (flinging tail from one side to the other)
CWH	cartwheel (full body TAT)
BRC	breach (e.g. belly BRC, side BRC)

Travel

SWS	swim slow (1-3 knots)
SWM	swim moderate (4-6 knots)
SWF	swim fast (greater than 6 knots)
DSW	directional swimming
SDE	slow descent (fin visible for several seconds)
RAD	racing dive (lunge at surface)

**Sociosexual
behavior and
solo play**

PLY	play (general)
FOL	follow (nose-to-tail orientation)
RBB	rubbing at beaches
PED	penile display
HOT	head oriented toward (e.g. another whale, a direction)
GAZ	gaze (head tilted, one eye up, above or below surface)
BOC	body contact (unspecified)
RUB	body-rub (friction)
TOU	touch (no friction)
PUS	push (e.g. flank-to-flank)
HIT	hit (e.g. HIT with tail)
GOB	glide over back (sliding over another whale's body)
TAO	tail out, vertically
TAS	tail out, horizontally
TWA	tail wave (TAO with back and forth movement)
FOU	pectoral flipper out
FWA	pectoral flipper wave (FOU with back and forth movement)
TAT	tail throw (flinging tail from one side to the other)
CWH	cartwheel (full body TAT)
POR	porpoise (leap, head-first reentry)
BRC	breach (e.g. belly BRC, side BRC)
BDR	body-roll (corkscrew at surface)
SRI	sternride (wakeride)
BDO	balancing object on dorsal fin (e.g. kelp)

All behavior states

T	tight (< 8 m between whales)
L	loose (8-12 m between whales)
S	separate (> 12 m between whales)

**Movement/ Body
Orientations:**

NDM	non-directional movement (zig-zag)
APP	approach (e.g. a location, another whale, an object)
PAS	pass (e.g. another whale, a landmark)
TUR	turn (+ direction)
-->	heading (e.g. in a direction or toward something)
INV	inverted
SBS	side-by-side
MCO	mother-calf orientation (echelon swimming)

Percussive
Behavior:

SPL	splash (unspecified)
TSL	tail slap
ITS	inverted tail slap
FSL	pectoral flipper slap
IFS	inverted pectoral flipper slap
DSL	dorsal fin slap

Non-percussive
Aerial Behavior:

NOU	nose out of water (rostrum just showing)
HEO	head out of water (vertical, eyes underwater)
SPY	spyhop (full HEO, eyes well above surface)
HSC	head scan (horizontal HEO, eyes at/just above surface, forward movement)
ARC	arch (head and tail bent ventrally)
VOC	vocalization in air
HBA	high-backed dive (sounding, before a long/deep dive)
TDI	tail-out dive (very arched HBA, tail comes above surface)
FIJ	fin jiggle (unspecified)
POP	"poppy", surfacing behavior of <1 year old calf

Breathing Pattern:

√	breath
UNB	up, no breath
SYB	synchronous breath (2 or more whales)
ASY	asynchronous breath (2 or more whales)

OUV	out of view
UNK	unknown behavior (describe)

Appendix C. Individual profiles of nine
selected males, three from each age class.

Adults:

B01: B01 was probably the oldest of the 32 sample males of this study (estimated year of birth 1951; see Table 0.1). He was a member of the only pod that had only one matriarch, B07, who was presumed to be his sister (Bigg *et al.* 1987). Other than B01 and B07, the B01 pod had one adult male, two adolescent males, two juvenile males, and one juvenile of unknown sex. According to the genealogy in Bigg *et al.* (1987, 1990), these were B01's uncle, brother, three nephews, and one nephew or niece. The B01 pod had an unusually large number of males, a situation that appeared to have had a significant effect on their relationships with other members of the northern resident community. During their short stays in the strait (usually about two weeks, twice per season), they would often be by themselves; other pods appeared to depart when the B01 pod was visiting the core area (Jacobsen 1990; M. Bigg, pers. comm.; pers. obs.).

B01 tended to travel alone and was often 1-3 km in front of his pod when they visited the strait. His predominant behavior state was traveling and in general he did not tend to be active at the surface, which was typical for his age class (Figs. 1.6, 1.7, 1.8). He swam very directionally, on straight courses. He usually rested with his pod. B01 was never observed socializing (all other males in his pod were seen socializing at least once). He was never seen associating with unrelated reproductive females without other members of his family in close attendance.

On five different occasions in 1989, B01 was seen traveling tightly, in echelon-swimming formation, with B12, the five-year-old male calf of his putative sister, B07 (Table 3.4). These associations were possibly allopaternal in nature (see Chapter Three: Part Two), as B07 at that time was nursing a two-year-old calf, B13.

A20: A20 was also one of the older males of the northern resident community (estimated year of birth 1953). He traveled predominantly with the A36 matrilineal group and Bigg *et al.* (1987, 1990) presumed that he was the brother of A36, as his probable mother, A01, was alive in 1973 but died early in the Bigg study. Other than A20 and A36, the A36s had two adolescent males and one juvenile male. A20 was presumed to be the uncle of these individuals. The A36s were one of three matrilineal groups that made up the A01 pod.

A20 was perhaps the most independent of all the adult males in the population; he was often seen several hundred meters from any group. He was the closest thing the residents had to a singleton (see General Introduction), as his bond with his presumed sister was relatively weak. On several occasions, he was found traveling with unrelated reproductive females. In an unusual break from the general pattern, A20 was occasionally seen resting simultaneously but spatially separated from the other A36s (see Chapter Two). He was more active at the surface than most adults. He was also one of five adult males seen in male-only social interactions (Table 3.2). He was one of two adults to form an exclusively adult male pair.

On one occasion in 1988, swimming 200 m ahead of any other whales, A20 was seen performing a series of inverted pectoral fin slaps and a penile display in the presence of several whale-watching vessels. One boat with a very noisy motor approached to within 15

m of A20 just before the penile display. He continued to perform percussive behaviors, including tailslaps and dorsal fin slaps, for the next five minutes while swimming slowly westward, accompanied by the boats. Considering the sequence of events, it seems reasonable to speculate that these behaviors were a display, possibly aggressive (Baker and Herman 1984), toward the boats, especially the boat with the noisy motor.

A31: A31 was a member of the A12 matrilineal group. With the A30s (see next profile), the A12s were the most frequent visitors to Johnstone Strait. In addition to A31, who was a young adult male (estimated year of birth 1958), and A12, the non-reproductive matriarch, the A12s had an older adolescent male and a pubescent female (who gave birth to her first calf in 1989), who were presumed to be the younger brother and sister of A31. The A12s were one of three matrilineal groups to make up the A01 pod.

A31 was one of the least independent of the adult males in the sample. He was never observed with unrelated reproductive females without other members of his family in close attendance. He was observed traveling or foraging alone on several occasions, but participated in only two male-only social interactions (Table 3.3) in over 13 hrs of observation. His activity level was typical for his age class. He was never observed resting alone. Unlike his younger brother, A33, A31 was never observed traveling alone with his sister, A34, or with his sister's offspring, A55.

Adolescents:

A06: A06 was one of three males who spanned two age classes during the study; however, based on his estimated year of birth (1964), he was considered an older adolescent

(see last note of Table 0.1). He was the putative eldest son of A30; she also had two younger sons, a daughter, and an unsexed calf, who was born in 1989. The A30s were the most frequently observed matrilineal group in each year of the study and A06 was the most frequently observed of the three brothers (see Table 0.1). At least once each season, this group was the only one observed for several days at a stretch. The A30s, with the A36s and A12s, made up the A01 pod.

A06 was a very peripatetic individual. He was observed on several occasions following unrelated reproductive females, traveling with older, non-reproductive females, associating with his younger sister (Table 3.4), playing with other males (Table 3.2), and traveling/foraging with his brothers. He was never observed resting alone. For his age class, he was not very percussive or active at the surface, especially considering the number of hours he was under observation. Along with his brothers, he tended to travel offshore while his mother and youngest siblings traveled onshore.

In the second year of the study, A06 was observed with his youngest sibling, A54, only once in the absence of their mother, and his next youngest brother, A38, was also with them. By himself, he only accompanied his sister, A50 (Table 3.4). A06 was never observed alone with his youngest siblings during the third year of the study. On several occasions in 1988 and 1989, he was observed following unrelated reproductive females, but he was never seen side-by-side with them (as were adult males); his position was always slightly to the side and behind, up to 30 m. On one occasion, he was observed breaching several times just behind the I15s, a group of several reproductive females and their calves. A06 was also observed on several occasions traveling tightly and socializing with C05, an older, non-reproductive female.

A38: See A06's family description; A38 was his next youngest brother (estimated year of birth 1970-71).

A38 was one of the most physical males in the sample, with 103 body-contact behaviors recorded in 25 hrs of observation. He was also, along with his younger brother, A39, the most active male in male-only social interactions (Table 3.3). He was observed associating with his two youngest siblings on several occasions, almost always playing with them, unlike his older brother, A06, who usually traveled when with them (Table 3.4). On the one occasion when he (with his brothers) was seen with C05, the three males surrounded her and were very physical in their association. A38 was never observed following or otherwise associating with unrelated reproductive females except when in the company of his mother. Compared to other males his age, he was not often seen alone. A38 was frequently observed in the company of his putative grandmother, A02, in the two years before her death in 1987.

A27: A27 was estimated to have been born in either 1971 or 1972. He was the son of A23, who also had a juvenile offspring of unknown sex, A43. A23 was believed to be the mother of two of the juveniles removed from the population during the live-capture fishery of 1969 (Bigg and Wolman 1975; Bigg *et al.* 1990). She had another calf in 1992. The A23s were one of four matrilineal groups that made up the A05 pod.

Two qualities distinguished A27 from the other males of this study. First, although A27 had predictably shown the first stage of secondary dorsal fin growth by the mid-1980s, he had not grown much more by 1990. His dorsal fin was notably shorter than other males

his age, such as A33 and A38. Secondly, he was the most percussive individual observed during the study, of any age or sex. His percussive behavior rate was 22.68 per hour, mostly tailslaps. This was roughly 10 times the juvenile male mean rate (Fig. 1.8), the highest shown. A27 would often perform a long series of tailslaps, of five, 10, even 20 in a row. He was particularly percussive in male-only social interactions (36.25 behaviors/hr). A27 was never observed alone; he was usually with his family or with other males, although on one notable occasion he and an older A05 pod juvenile (A15) were observed tightly associated with two older, non-reproductive females (C05 and R09).

Although this is highly speculative, his small dorsal fin and his unusual percussive behavior lead me to suspect that A27 was somehow retarded or aberrant in physiological and/or psychological growth. The repetitive nature of his tailslaps was markedly different from the pattern observed in other animals and had all of the earmarks of a tantrum or fit of some kind. That he was always in the company of other animals, unusual for a male his age, supports this idea. However, it is impossible to verify, although his future behavior, throughout his 20s and 30s, will be most interesting to observe.

Juveniles:

B10: B10 was the third youngest offspring of B07 (year of birth 1979). He was one of three members of the B01 pod born after the beginning of the Bigg study, thus of known age and known relatedness to his two younger siblings and his mother. In the genealogy of Bigg *et al.* (1987, 1990), he also had another brother, two uncles, and a great-uncle (see B01's family description, above).

B10 tended to travel with his mother and younger siblings. He was usually seen in loose formation with them when the pod was first sighted on an observation day. The B01 pod as a whole tended to travel back and forth in the strait, making a roundtrip circuit several times a day between the west end of Hanson Island and the east end of West Cracroft Island (see Fig. 0.1). B10's pod was not often observed with other pods in the strait, but in 1989, they were more social than in the previous three years and B10 was seen in a male-only social interaction (Appendix D). His behavior rates were typical for his age class. B10 experienced a slight dorsal fin growth spurt in 1988 at nine years of age, but had another larger spurt in 1990, when he was 11 years of age.

A46: See A20's family description; A46 was his youngest nephew, born in 1982. A46 had two older brothers.

A46 was observed away from his mother on several occasions. He was observed traveling in echelon-swimming formation with a pregnant nulliparous female from another A01 pod matrilineal group in 1988, at six years of age. He was seen playing with other males (Table 3.2), traveling by himself, and foraging with his brothers. He was relatively active at the surface and was observed on several occasions with an erect penis when playing, especially with his brothers. For the most part, however, A46 traveled closely with his mother. He was never seen alone with A20. He had not yet experienced an observable dorsal fin growth spurt by 1992, at ten years of age.

C13: C13 was born in 1985. He was the first offspring of C10, who in turn was born in 1971-72 to C05. The C05s were the first matrilineal group to be reliably identified in the northern resident community, when they were photographed in 1965. C05 was reidentified in 1973, when the long-term study began (see General Introduction), and she was accompanied at that time by C02 (a young male) and by a young female calf (C10) (Bigg *et al.* 1990). C02 was an adult when he died between 1986 and 1987. After his death, C05 continued to travel with C10. In 1989, C10 had another calf, C17, of unknown sex. The C05s were one of two matrilineal groups that made up the C01 pod.

C13 was the most frequently observed juvenile in the study (Table 0.1). He was rarely observed without his mother (and never alone) in 1988, when he was three years of age, but in 1989, he was observed both in male-only social interactions (Appendix D) and alone with his newborn sibling, C17 (Table 3.4). He was also observed by himself on a few occasions; in one incident, he moved rapidly ahead of his matrilineal group and was located several minutes later over a mile away, sternriding one of the commercial whale-watchers. He was observed occasionally in nursery-groups, which entailed playing with other juveniles while an adult (usually one of the mothers) was in close attendance. Overall, however, he was less active at the surface than was typical for his age class and spent most of his time traveling and resting with his mother and sibling. C13 was never observed alone with his grandmother, C05.

Appendix D. Data from male-only social interactions.

IDs of bout participants:	codes:	pods:	date:	approx. start and stop time
1. A13 - A37 (< 5 yrs)	x +	A1/A4	3-Aug-87	10:05/-
2. A15 - A27 (> 5 yrs)	+	A5	3-Aug-87	17:00/-
3. A27 - A32 (> 5 yrs)	x +	A1/A5	8-Aug-87	14:07/-
4. H7 - A38 - A39 (> 5 yrs)	!	A1/H1	8-Aug-87	10:23/-
5. A26 - A27 - D5 (> 5 yrs)	x +	A5/D1	9-Aug-87	14:00/-
6. A39 - H7 (> 5 yrs)		A1/H1	27-Aug-87	15:15/-
7. A33 - A37 - A38 - A39 (> 5 yrs)	!	A1	16-Sep-87	15:28/-
8. A6 - A37 (> 5 yrs)		A1	10-Aug-88	11:49/12:50
9. A33 - A39? (< 5 yrs)	x #	A1	10-Aug-88	11:39/-
10. A33 - A38 (< 5 yrs)	x	A1	12-Aug-88	14:33/16:03
11. A33 - A39 (< 5 yrs)	x	A1	13-Aug-88	13:04/14:30
12. A20 - I5 (?)	x *	A1/I2	21-Aug-88	13:12/13:43
13. A38 - A39 - A15 (> 5 yrs)	! +	A1/A5	22-Aug-88	10:03/10:18

Appendix D. Data from male-only social interactions.

14. A6 - A38 - A39 - A27 (> 5 yrs)	I + x	A1/A5	23-Aug-88	10:06/10:09
15. A6 - A27 (> 5 yrs)	x +	A1/A5	23-Aug-88	10:11/10:17
16. A20 - A27 (> 5 yrs)	+ *	A1/A5	23-Aug-88	14:57/15:20
17. A32 - A26 (> 5 yrs)	x	A1/A5	23-Aug-88	12:58/13:55
18. A37 - A46 (< 5 yrs)	!! x	A1	30-Aug-88	14:40/14:42
19. A37 - A46 - C9 - C14 (> 5 yrs)	I	A1/C1	30-Aug-88	16:24/17:25 (19:00)
20. A46 - C13 (< 5 yrs)	x + #	A1/C1	6-Sep-88	15:14/-
21. A31 - A39 (> 5 yrs)	*	A1	12-Sep-88	16:05/16:08
22. A31 - A39 - A37 - A33 (> 5 yrs)	I *	A1	12-Sep-88	16:09/17:05
23. A32 - A38 (> 5 yrs)	x	A1	12-Sep-88	15:29/15:59
24. A38 - A39 (< 5 yrs)	!! x #	A1	12-Jul-89	18:30/-
25. A6 - A39 (> 5 yrs)	!! x #	A1	13-Jul-89	17:48/-
26. A38 - A39 - I43 (> 5 yrs)	I +	A1/I11	20-Jul-89	17:59/18:22

Appendix D. Data from male-only social interactions.

27. A6 - A38 - A39 - I43 (> 5 yrs)	! #	A1/I11	20-Jul-89	13:40/-
28. A37 - B10 - B2? (> 5 yrs)	x * #	A1/B1	23-Jul-89	15:50/-
29. C3 - A32 - C14 (> 5 yrs)	*	A1/C1	26-Jul-89	13:58/14:06
30. A32 - A37 - A46 - C13 - C14 (> 5 yrs)! +	! +	A1/C1	26-Jul-89	12:32/12:59
31. A32 - C14 (> 5 yrs)		A1/C1	26-Jul-89	13:40/13:57
32. A33 - A46? - C13? - C14? (> 5 yrs)	# +	A1/C1	26-Jul-89	14:43/-
33. A38 - C13 (> 5 yrs)	# +	A1/C1	7-Aug-89	18:04/-
Key:				
! = bouts with brothers participating (!! = brothers only participating)				
+ = bouts with brotherless males				
x = bouts with males from same age category only (peer groups)				
* = bouts with adult males participating				
# = bouts from 1988-89 ad lib. data				