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A BEHAVIORAL BUDGET OF PUGET SOUND KILLER WHALES

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INTRODUCTION

The surface behaviors of American inshore Pacific Northwest killer whales (Orcinus orca) have been observed by seafaring people of the region for some 8,000-10,000 years (Fladmark, 1979). Although these killer whales are probably the most thoroughly studied in the world, documentation of their behavior began only during the last few decades (Bigg et al., 1976; Hancock, 1965; MacAskie, 1966; Martinez and Klinghammer, 1970; Odlum, 1948; Scheffer, 1969; Scheffer and Slipp, 1948; Spong et al., 1970, 1972a, 1972b) and systematic analysis was not attempted until recently (Balcomb et al., 1980; Boran, et al., 1981; Haenel, J. Heimlich-Boran, S. Heimlich-Boran, Hoelzel and Osborne, and Jacobsen, this volume; Jepson, 1980; Martinez and Klinghammer, 1978; Osborne and Heimlich, 1981; Salden, 1979).

This paper is a report on five years of systematic behavioral observations collected by the Orca Survey (Moclips Cetological Society) research associates on the resident killer whale pods of Greater Puget Sound, Washington State (Balcomb and Goebel, 1976; Balcomb et al., 1980, 1982; Osborne and Heimlich, 1981). Photo identification of all resident whales was conducted in cooperation with Bigg's pioneering research on killer whale pod composition in British Columbia (Bigg, 1982; Bigg et al., 1976).

Longitudinal observation of identifiable inshore delphinids by Norris and Dohl (1980a,b); Saayman and Tayler (1979); Saayman et al. (1973); Wells et al. (1980); and Würsig and Würsig (1977, 1979, 1980) have documented many of the consistencies and variations of inshore dolphin socioecology. The three cohesive pods of killer whales designated J, K and L (after Bigg et al., 1976; see also Balcomb and Bigg, this volume) and numbering 19, 12 and 48 individuals, respectively, have been observed and behaviorally studied by Orca Survey personnel for 967 hr from April 1976 through August 1981, and to some extent during all months of the year (see also: Haenel, J. Heimlich-Boran and S. Heimlich-Boran, this volume). Most of the findings for killer whales are consistent with what is known about inshore dolphins (Norris and Dohl, 1980b) except in relation to social structure (S. Heimlich-Boran, this volume).

The sympatric populations of Pacific Northwest killer whales may have been socially and reproductively isolated for many generations. This is evidenced from (a) historical records (written and photographic) of pod composition and behavior of the past 15 yr (Balcomb et al., 1980; Balcomb and Bigg, this volume; Bigg, 1982; Bigg and Wolman, 1975; Hoyt, 1981); (b) from analysis of phonation dialects among socially and non-socially interacting pod communities (Ford, 1982; Ford and Fisher, 1981; Hoelzel and Osborne, this volume; Osborne and Heimlich, 1981); and (c) from chromosomal analysis of karyotypes within and between pod communities (Duffield, 1979, this volume). As a consequence, the behavioral characteristics of this specific population of killer whales may be geographically and socially unique (Bonner, 1980).

The resident community in Greater Puget Sound is composed of cohesive pod units of mixed age-sex classes that remain stable through preadolescence and perhaps the lifetime of most individuals (Bigg, 1982; Haenel, and S. Heimlich-Boran, this volume). The majority of their movements seem to be dictated by the seasonal abundance of food resources, primarily salmonids (*Onchorhyncus* sp.) (Balcomb, et al., 1980; Balcomb and Bigg, J. Heimlich-Boran, this volume). During periods of high salmon abundance (June through September) the three resident pods join together (in various pod and pod-subgroup configurations) and engage in cooperative foraging and intensive social interactions of sleep, play and mating (Balcomb et al., 1980; Haenel, J. Heimlich-Boran and S. Heimlich-Boran, this volume). Pods from a resident community have never been observed to interact with pods from other resident communities, or with any of the small transient pods which sporadically

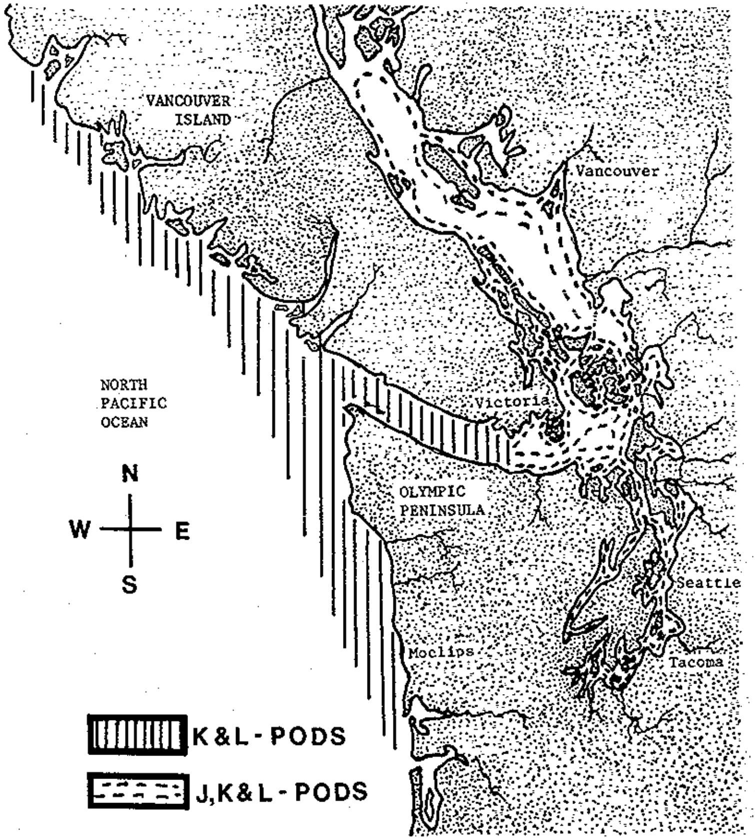


Fig. 10.1. A map showing the Orca Survey study area and the home ranges of the resident communities of pods J, K and L. Dashed line indicates the core area of the home ranges.

pass through the region (Balcomb et al., 1980, 1982; Bigg, 1982). During the season of low salmon abundance (November through April) the resident pods spend most of their time separated into their more cohesive pod units (Balcomb, et al., 1980; Bigg, 1982). Two of the pods (K and L) spend the majority of this time in the outer limits of the resident community's home range (outer coast of the Olympic Penninsula and Vancouver Island; see Fig. 10.1). During the winter months, resident pod subgroups of specific age-sex classes occasionally separate from the pod and differentially forage for a few days at a time (J. Heimlich-Boran, this volume). This kind of foraging subdivision is similar to seasonal aggregation strategies documented for localized populations of coastal delphinids (Norris and Dohl, 1980b).

In the present paper longitudinal data on the basic configurations and variations in surface behavior and on levels of phonatory activity are presented for the resident southern population of killer whales inhabiting Greater Puget Sound. Categories of the consistent surface behaviors are presented along with observed sequential patterning, diurnal/nocturnal budgeting of activities and total-time activity expenditures. These categories are then considered in terms of a model that depicts the basic network of behavioral adaptation utilized by this community of killer whale pods.

METHODS

Study Area

The study area referred to as Greater Puget Sound lies between 47° and 49° north latitude and 122° and 123° west longitude and includes Puget Sound proper, waters east of Whidbey Island, Hood Canal, the Strait of Juan de Fuca, the San Juan Archipelago and southern Strait of Georgia (Fig. 10.1). On occasion whales were observed outside the study area in the Canadian Gulf Islands, the Strait of Georgia to Burrard Inlet and along the southeastern coastline of Vancouver Island.

Surveillance Methods

A toll-free telephone reporting system was advertised and used year round to receive sighting reports of whales from the public. These reports were very useful for determining geographic mobility of the whales in the study area, especially in peripheral regions. The sightings were used to locate whales for vessel encounters and served to partially compensate for seasonal bias in field observations.

Various configurations of fixed hydrophone arrays were installed and monitored on a 24 hr basis at the Orca Survey Research Facility on San Juan Island. From September 1978 through August 1981 several different hydrophone arrays were destroyed by winter storms and reinstalled. The most recent array was continuously operable during the last year of the study period. All utilized hydrophones, both from field vessels and in installed arrays, were either LAB CORE or Aquadyne. Vessel recorders were either Sony TC-152 SD or Sony TC-D5. Fixed array recorders were either Sony SRA-3, Akai 1730D-SS or Akai GX-365-D. Acoustic monitoring served as an audible surveillance of the whales' presence (approximately 8 km) and provided behavioral data in terms of relative levels of phonatory activity. Minimum system response was from 30 Hz to 16 kHz, which is within the range of fundamental frequencies utilized by killer whales (Hoelzel and Osborne, this volume).

Behavioral data were collected either from shore observation points (50 percent of the time) or from research vessels in proximity of the whales. The vessels utilized during the majority of whale encounters included two 19-ft Boston Whalers with outdrives and a 37-ft sailing trimaran. Behavioral observations were recorded in log books during encounters and later transcribed into code or were directly recorded in code while in the field.

Analytical Methods

The definitions of the behavioral codes are presented in Table 10.1. Code sentences were used to describe the variety of surface formations that consistently occurred.

Table 10.1. The definitions and coding system used to describe the surface behaviors of the pods encountered by Orca Survey.

BEHAVIOR CLASS	CODE	CATEGORY AND DEFINITION
POD STATUS	ASB	ASSEMBLAGE: More than one pod.
	POD	POD: One complete family unit with a stable membership.
	OTH	OTHER: Less than one pod, a lone whale, etc.
SOCIAL UNITS	GRP	GROUPED: All whales present are in a single homogeneous group.
	PSG	POD SUBGROUP: An aggregation of 2 or more whales, less than the sum of all whales present, containing members all from the same pod.
	MSG	MIXED SUBGROUP: An aggregation of 2 or more whales, less than the sum of all whales present, containing members from more than one pod.
	IND	INDIVIDUAL: A single whale by itself.
INDIVIDUAL SPACE	LOO	LOOSE: Individuals are approximately 5 meters or more apart.
	THT	TIGHT: Individuals are 0.5 to 3 meters apart.
	TCT	TOUCHING: Whales are in physical contact.
ACTIVITY LEVEL	FAS	FAST: Moving at approximately 6 knots or more (the whales are usually "porpoising" high out of the water when surfacing).
	AVR	AVERAGE: Moving at approximately 4 knots or less.
	SLO	SLOW: Moving at approximately 2 knots or less.
	STA	STATIONARY: Whales are motionless at the surface.
ORIENTATION	DIR	DIRECTIONAL: Moving with a nearly constant heading.
	NON	NON-DIRECTIONAL: Moving without an apparent heading.
SPECIFIC BEHAVIORS	SPL	SPLASHING: Any purposeful breaking of the water's surface with an appendage (excluding rising to the surface for respiration and "breaching" or "spy-hopping").
	BRE	BREACHING: A whale jumps vertically out of the water landing with a horizontal splash of at least 1/3 of its body.
	SPY	SPY-HOP: A whale rises vertically from the water exposing the rostrum and the eyes. The whale then slips back into the water in the same vertical plane.
	PEN	PENILE: A whale is observed with an erect penis.
	PRY	PREY: A food species is observed in the mouth or otherwise in the immediate vicinity.
ACOUSTIC ENVIRONMENT	SIL	SILENCE: Individuals are not producing any phonations.
	CLK	ECHOLOCATION CLICKS: Individuals are producing echolocation clicks and no other types of phonations.
	PHO	CLICKS AND OTHER PHONATIONS: Whales are producing phonations that include more than echolocation clicks.
INDIVIDUAL COMMENTS	M	MALE: An adult male.
	F	FEMALE: An adult female.
	C	CALF: A small young whale usually accompanied by an adult female.
	(A-X)	INDIVIDUAL ALPHA-NUMERIC DESIGNATION.
SENTENCE CONJUNCTIONS	&	PERIPHERAL: Behavioral outlier to the majority of whales present.
	/	OCCASIONAL: Occurence of non-continuous (sporadic) behavior.
		STOP: Go to next time period and/or encounter.

The time blocks did not have a fixed interval so aggregrates of consistent behaviors varied in duration according to circumstance. In this system of behavioral coding, time blocks were composed of combinations of coded sentences joined by sentence conjunctions (Table 10.1). Categories of behavioral types were then sorted from the coded data by grouping time blocks that contained consistencies in sentence composition. Frequencies of occurrence of these behavioral categories were calculated to yield a measure of total activity time (i.e., a total time budget, Fig. 10.2).

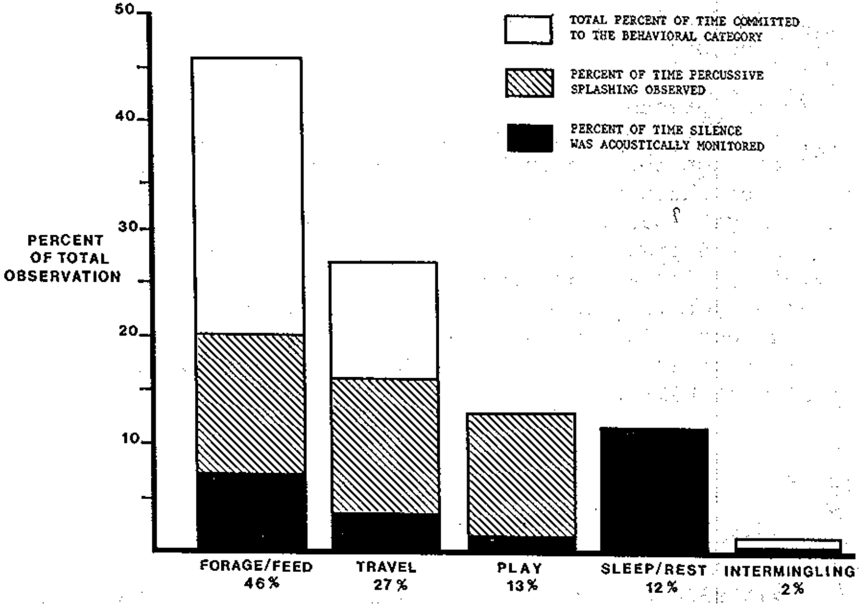


Fig. 10.2. A histogram showing total percent occurrence of categories of surface behaviors in the Greater Puget Sound resident communities of killer whale pods. Sample size equals 967 hr of observation during all seasons of the year (1976-1981). Percent occurrence of percussive splashing and phonating are also indicated for each general behavioral category.

Maximum, minimum and mean durations of the behaviors by categories were calculated from the number of samples in which the behaviors were observed from beginning to end. Sequences of these beginning to end samples were then analyzed for antecedence and subsequence in a first order Markov Chain (Fagen and Young, 1978). A first order contingency table was constructed and Chi-Square values were calculated to determine the significance of activities preceding and following each behavioral type ($p < .05$, Table 10.2). Values above expectation but not statistically significant were also ranked to distinguish secondary sequential contingencies.

Table 10.2. A first order Markov contingency table showing observed values, expected values and Chi-Square values for preceding and following characteristics of pod surface behaviors. Dark outlined boxes indicate significant values ($p < 0.05$).

FOLLOWING

PRECEDING	P	pT	pF	T	F	M	R	row sum$_2$
P	0	4 (5.1) [0.24]	8 (5.6) [1.02]	12 (6.2) [5.43]	4 (4.7) [0.10]	1 (3.0) [1.33]	4 (3.5) [0.07]	33
pT	9 (7.2) [0.45]	0	16 (8.3) [7.14]	11 (9.3) [0.31]	6 (7.0) [0.14]	7 (4.5) [1.39]	0 (5.3) [0]	49
pF	7 (6.9) [0.001]	13 (7.2) [4.67]	0	11 (8.9) [0.49]	7 (6.7) [0.01]	2 (4.3) [1.23]	7 (5.1) [0.70]	47
T	5 (8.2) [1.25]	9 (8.6) [0.02]	10 (9.5) [0.03]	0	15 (10.6) [1.83]	9 (5.1) [2.98]	8 (6.0) [0.66]	56
F	5 (8.2) [1.25]	10 (8.6) [0.23]	9 (9.5) [0.03]	13 (10.6) [0.54]	0	8 (5.1) [1.65]	11 (6.0) [4.10]	56
M	4 (3.8) [0.01]	5 (4.0) [0.002]	3 (4.4) [0.45]	6 (4.9) [0.25]	5 (3.7) [0.46]	0	3 (2.8) [0.14]	26
R	15 (5.9) [14.04]	6 (6.1) [0.002]	6 (6.8) [0.09]	5 (7.6) [0.89]	7 (5.7) [0.30]	1 (3.6) [1.88]	0	40
row sum$_1$	45	47	52	58	44	28	33	307

Critical Region = $X^2_{0.05,\ 1} = 3.841$ Sample = $R^2 6.3$

X= Observed Value (Xij)
()= Expected Value (Mij)
[]= Chi Square Calculated (X^2)

$$X^2 \text{ calc} = \sum_{i=1}^{R} \sum_{j=1}^{R} (x_{ij} - m_{ij})^2 / m_{ij}$$

An attempt was made to correlate behavior with time of day by subdividing the 24-hr diurnal/nocturnal cycle into 10 min intervals and seasonally tallying the occurrence of eight behavioral categories over the entire study period. The mean frequency for each behavioral category was then calculated as a percentage of a 30 min interval. This was done so that variations between 30 min time blocks could be compared with expected percentages based on the total sample independent of time. Sample bias disallowed both the seasonal analysis and diurnal/nocturnal analysis over an entire 24-hr cycle. A 9-hr diurnal period was the only continuous sequence of 10 min intervals of a large enough sample size to be considered adequate for comparison with expected percentages. Twenty-four hour acoustic monitoring from the fixed array was not as biased as visual data and was used as supplementary data to check preliminary hypotheses regarding circadian activity in killer whales.

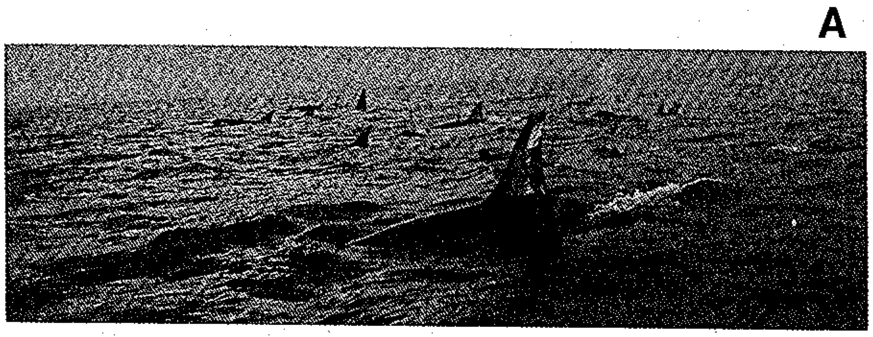
RESULTS

Six basic categories and nine variations of surface behaviors have been recognized in Puget Sound killer whales using the behavioral coding system described in Table 10.1. In Figures 10.3-10.8 examples of code are given for each basic behavioral category, accompanied by either a photograph and/or an aerial diagram visually depicting the behavior type. In the presentation that follows, each behavioral activity and its variations are briefly described in the statistical context of a total time budget (Fig. 10.2) and in terms of duration, sequence (Table 10.2) and level of phonatory activity (Fig. 10.2). Finally, a correlation of behavior by time of day is presented along with diurnal/nocturnal observations of phonatory activity.

Travel

The activity travel represents 27 percent of all observations (Fig. 10.2) and has a minimum duration of 0.4 hr, a maximum of 5.5 hr and a mean of 1.6 hr. Descriptively, pure travel is directional movement at a steady energetic pace (+3.5 kn) over a minimun distance of 2-3 km. Travel includes coordination of the entire autonomous group of whales present though they may be spatially distributed either individually, in subgroups, in multiple pod units, or as a single homogeneous assemblage. Surfacing patterns between individuals and subgroups are not necessarily synchronized, however, synchronization does occasionally occur. On such occasions the synchronization of respiration is usually associated with a reduction in speed and a subsequent shift to a sleep/rest category of behavior.

Travel was associated (but not statistically, $p > 0.05$) with foraging and milling/feeding behaviors that often either preceded or followed its occurrence (Table 10.2). During acoustic monitoring of travel, silence was documented 13 percent of the time; on all other occasions the whales were engaged in standard phonation activities (Hoelzel and Osborne, this volume). The most distinctive characteristic of travel was the noticeable absence of any novel surface activities such as milling or breaching.



B

ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #:______ DATE: TRAVEL EXAMPLE______ POD(s):______

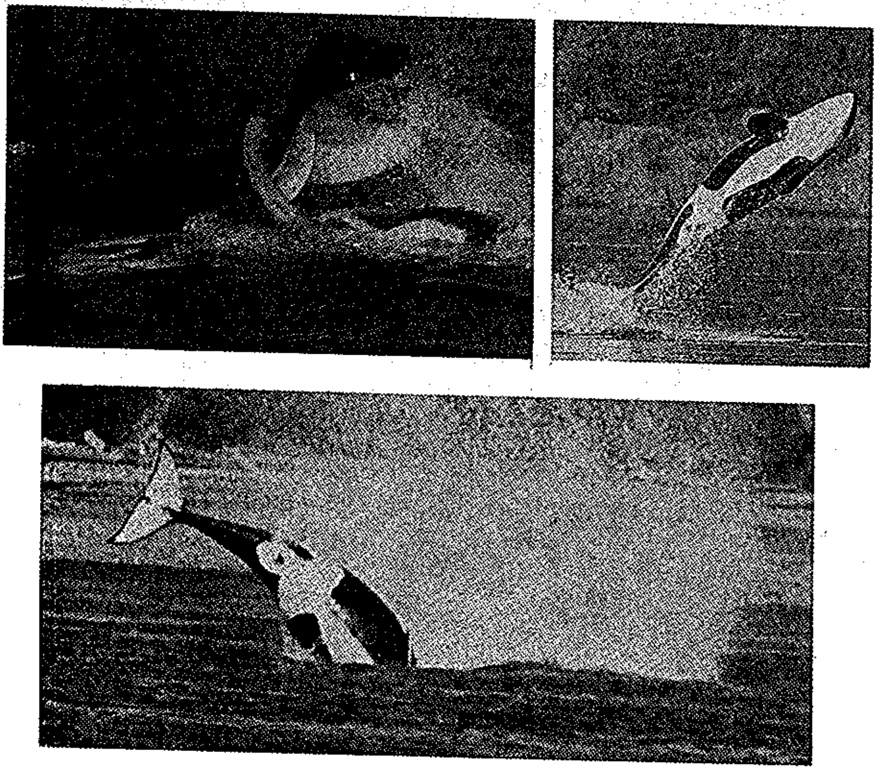
TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
	7	W	POD	GRP	LOO	AVR	DIR	-	-	-	-	-	-	PHO	M/F/C	
	7	W	ASB	PSG	LOO	AVR	DIR	-	-	-	-	-	-	PHO	M/F/C	
	7	W	POD	PSG	THT	FAS	DIR	-	-	-	-	-	-	PHO	M/F/C	

Fig. 10.3. Travel. (A) Photograph (by N.J. Haenel) and (B) examples of coded sentences used to indicate travel behavior.

Play

Play behavior that was not concurrent with any other category of surface behavior represented 13 percent of the total observation time. Its minimum duration of continuous occurrence was 0.3 hr with a maximum of 7.1 hr and a mean of 1.7 hr. Play was distinguished from other activities primarily by the performance of explosive surface acrobatics by adults as well as calves and juveniles. These most consistently included full body breaches, short duration high speed synchronized porpoising by tight subgroups of females, and cartwheels (Fig. 10.4A). Usually the acrobatics were also accompanied by variations in low level percussive activities such as tail lobs, pectoral slaps, dorsal fin slaps, spyhops and other splashing antics commonly observed in killer whales both in captivity and in the wild (Martinez and Klinghammer, 1978). During play, geographic progression of the whales noticeably decreased or occasionally ceased altogether. Play usually occurred at a prominent location such as a peninsula, underwater seamount, or kelp bed. When play was observed in and around kelp beds individual adults and calves would roll around in the kelp and surface with it draped on their dorsal fins or appendages. "Kelping," like many other play behaviors, was also exhibited by the more peripheral subgroups during other behavioral activities such as travel or foraging. Pure play was also characteristic of tightly formed calf subgroups involved in energetic chase sequences and/or sexual activity.

Sexual behavior. Sexual activity was defined primarily by the observation of an erect penis accompanied by tactile activity and rolling at the surface (Fig. 10.4A). Nearly all observations of erect penises (82 percent) occurred in association with more than one pod and always in association with either peripheral or pure play activities. The occurrences of erect penises fell roughly into three categories: (a) calf/adult or calf/juvenile play-chase groups; (b) all adult male groups of mixed pod status rolling at the surface; or (c) adult male/female pairs and groups of mixed pod status engaging in suspected reproductive behavior. The first



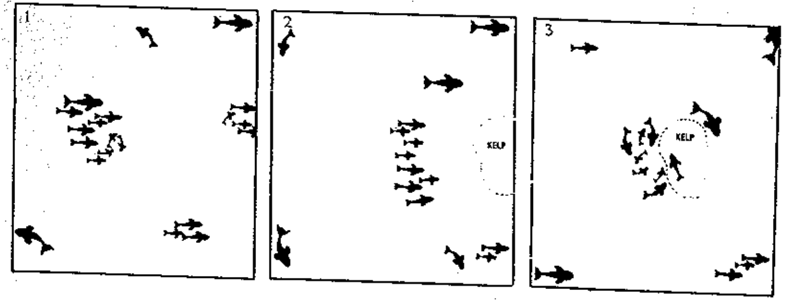
ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #: ____________ DATE: PLAY EXAMPLES ____________ POD(s): ____________

B

TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
	7	A	ASB	MSG	LOO	SLO	NON	+	+	+	+	+	-	PHO	M/F/C	&
	7	A	ASB	PSG	THT	FAS	DIR	+	-	-	-	-	-	PHO	P	&
	7	A	ASB	IND	LOO	AVR	NON	+	+	+	+	+	-	PHO	M/F/C	&
	7	A	ASB	PSG	TCH	SLO	NON	+	+	+	+	+	-	PHO	M/F/C	

Fig. 10.4. Play. (A) Upper photographs by B. Todd; lower photograph by K.C. Balcomb. (B) examples of coded sentences used to indicate play behavior.



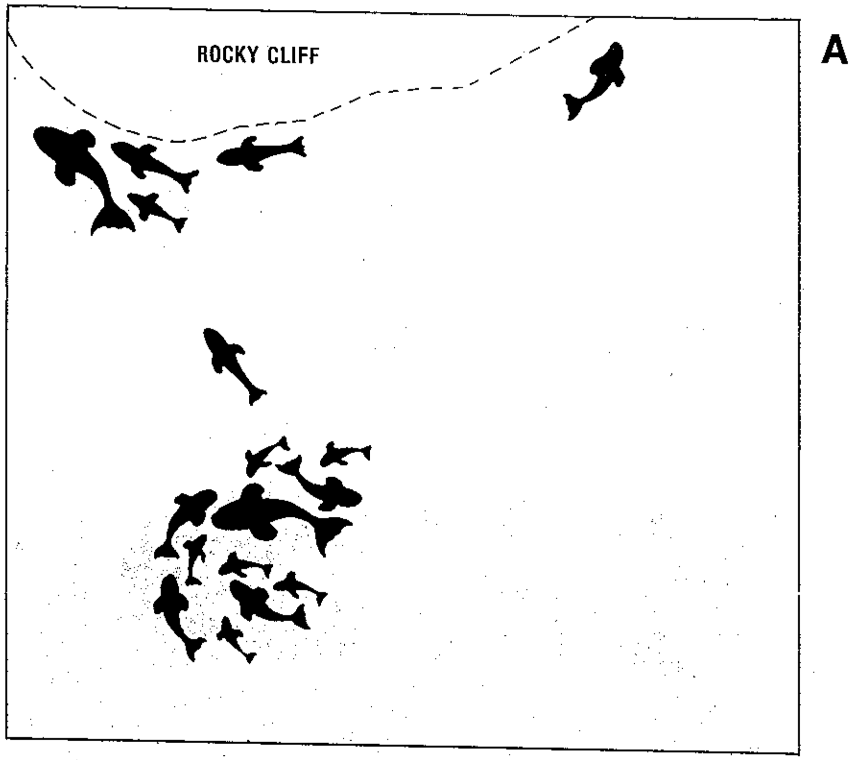
ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #: ____________ DATE: FORAGING/FEEDING ____________ POD(s): ____________

C

TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
	7	W	POD	PSG	LOO	AVR	DIR	+	-	-	-	-	-	PHO	M/F/C	/
	7	W	POD	PSG	THT	SLO	NON	-	-	-	-	-	-	PHO	M/F/C	/
	7	W	POD	IND	LOO	SLO	NON	-	-	-	-	-	-	PHO	M/F	/
	7	W	POD	IND	LOO	FAS	NON	-	-	-	-	-	-	PHO	M	.

Fig. 10.5. Foraging-Feeding. (A) Sequential aerial diagrams showing characteristics of foraging-feeding behavior, (B) photograph (K.C. Balcomb) of this behavior against a shoreline and (C) examples of coded sentences. Pod size and age/sex composition in the aerial diagrams are modeled after J-pod.



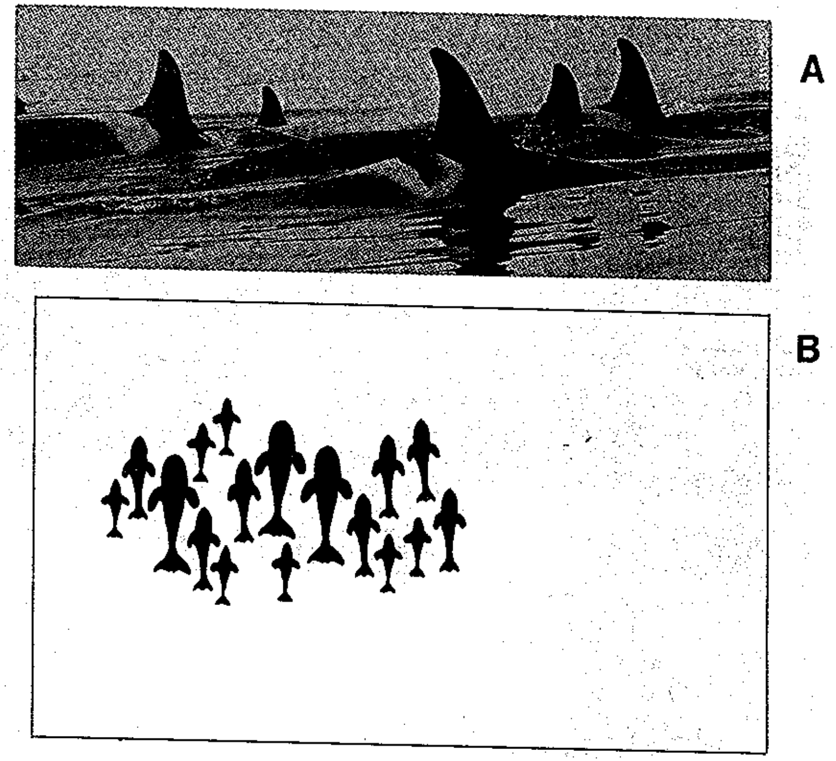
B

ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #:________ DATE: MILLING POD(s):________

TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
	7	A	POD	PSG	LOO	SLO	NON	-	-	-	-	-	+	PHO	M/F/C	a
	7	A	POD	PSG	THT	SLO	NON	+	-	-	-	-	+	PHO	F/C	a
	7	A	POD	IND	LOO	FAS	NON	-	-	-	-	-	+	PHO	M/F	

Fig. 10.6. Milling. (A) An aerial diagram and (B) examples of coded sentences showing characteristics of milling behavior. Pod size and age/sex composition in the aerial diagram are modeled after J-pod.



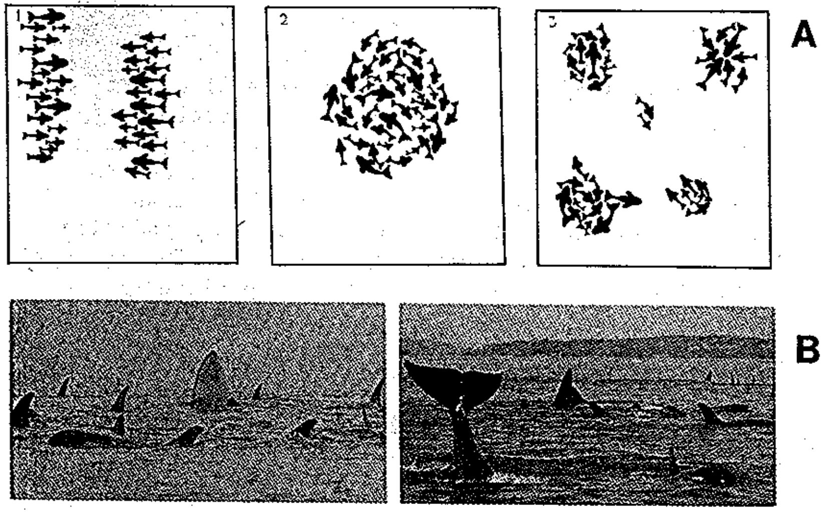
C

ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #:________ DATE: SLEEP/REST EXAMPLES POD(s):________

TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
	7	W	POD	PSG	THT	SLO	DIR	-	-	-	-	-	-	SIL	M/F/C	
	7	W	POD	IND	LOO	STA	DIR	-	-	-	-	-	-	SIL	M/F	
	7	W	ASB	GRP	THT	SLO	DIR	-	-	-	-	-	-	SIL	M/F/C	

Fig. 10.7. Sleep/rest. (A) Photograph (B. Todd), of a tight resting formation, (B) an aerial diagram and (C) examples of coded sentences showing characteristics of sleep/rest behavior. Pod size and age/sex composition in the aerial diagram are modeled after J-pod.



C

ORCA SURVEY BASIC BEHAVIOR DATA

ENCOUNTER #: ______ DATE: INTERMINGLING EXAMPLES POD(s): ______

TIME	FISHERIES AREA	TIDE	POD STATUS	SOCIAL STATUS	INDIVIDUAL SPACE	ACTIVITY LEVEL	ORIENTATION	SPLASHING	BELLY-UP	SPYHOP	BREECHING	PENILE	PREY	ACOUSTIC ENVIRONMENT	COMMENTS	SENTENCE CONJUNCTIONS
1	7	S	ASB	GRP	THT	STA	DIR	-	-	-	-	-	-	SIL	J&K- PODS GREETING	
2	7	S	ASB	GRP	TCH	SLO	NON	-	-	-	-	-	-	SIL	M/F/C	
3a	7	S	ASB	MSG	TCH	SLO	NON	-	-	-	-	-	-	PHO	M/F/C	&
3b	7	S	ASB	MSG	TCH	SLO	NON	-	+	+	-	-	-	PHO	F/C	

Fig. 10.8. Greeting ceremony and intermingling session. (A) Sequential aerial diagrams, (B) photographs, (left, by K.C. Balcomb from Osborne and Heimlich, 1981; right, by K. Wood) and (C) examples of coded sentences showing characteristics of a greeting ceremony and subsequent intermingling session. Pod sizes and age/sex composition in the aerial diagrams are modeled after a greeting ceremony between J- and K-pods including the L-pod subgroup which has recently become a part of K-pod.

category is primarily the only type of sexual activity that has been observed in groups of individuals from the same pod. The second and third categories have mainly been observed during play sessions in the summer through fall seasons when the community of J-, K- and L-pods join together and gregariously feed on the local salmon runs (Balcomb, et al., 1980; J. Heimlich-Boran, this volume). Play behaviors exclusive of sexual activity were observed equally often whether pods were traveling alone or with another pod.

Peripheral play. During 50 percent of all behavioral observations some degree of percussive splashing and sporadic breaching has been observed. Such peripheral play has occurred during 17 percent of the observations of travel behavior and during 20 percent of the observations of foraging behavior. Most of this sporadic peripheral play is attributed to subgroups of females and calves. Calves, in particular, often unexpectedly exhibit short bouts of breaching, splashing and rolling at the surface. This activity becomes especially noticeable when all or most calves are traveling in a single subgroup with only one or two adults. Occasionally calf subgroups are accompanied by only a single adult male who is presumably "baby-sitting" (see Haenel, this volume). However, 38 percent of the peripheral splashing that occurred during travel and foraging also involved adults, though these were primarily females traveling in subgroups with calves and other adult females. Such percussive splashing by female/calf subgroups almost exclusively involved tail lobbing and pectoral fin slapping and most often preceded milling/feeding behavior and non-percussive foraging (Table 10.2). Therefore, this particular activity has been designated as probable "herding" behavior of aquatic prey.

Pure play behavior that was simultaneously exhibited by all members of the group was preceded significantly ($p < 0.001$) by resting and interpod greeting ceremonies. Travel and percussive foraging somewhat less frequently followed ($p < 0.05$) play behavior (Table 10.2). During 85 percent of the time that whales were acoustically monitored while exhibiting play behavior they were found to be actively phonating.

Foraging/Feeding Behaviors

Foraging behavior comprised 46 percent of all observations with a minimum observed duration of 0.5 hr, a maximum of 7.0 hr and a mean of 2.3 hr. Foraging was characterized by a loose forward orienting formation with subgroups and individuals occasionally varying their progress and engaging in non-directional milling activity (Fig. 10.5A). This sporadic milling is presumed to indicate the location of patchy food sources and the subsequent capture of prey. Prey capture during this activity was suggested by the occasional observation of fish in the immediate presence of milling whales.

Milling/feeding behavior. Sometimes during foraging behavior all whales present would engage in continuous milling behavior for extended periods of time. Beginning-to-end samples of this continuous milling yielded a minimum duration of 0.2 hr, a maximum of 4.0 hr and a mean of 1.5 hr. Simultaneous milling by all whales present o[redacted]ost often around peninsulas, kelp reefs and under mounts notorious for salmon abundance among loc men (see J. Heimlich-Boran, this volume). Milling behavior was frequently preceded by percussive splashing travel as the group approached one of these geographic regions. At such times it was presumed to represent a type of cooperative herding (Fig. 10.6).

Foraging. The majority (89 percent) of feeding-oriented behavior was foraging behavior where only subgroups and individuals sporadically engaged in opportunistic milling and where the group as a whole remained consistently directional in orientation. The basic foraging pattern exhibited by these whales typically covers a 3-10 km^2 region where small clusters of females and calves travel in either loose or tight subgroups and adult males and females travel individually or in pairs (Fig. 10.5A). For J-Pod (composed of three males, nine females and seven calves and/or juveniles), a common foraging formation would have the lead animals in a subgroup of two adult females and three calves with two other subgroups of adult females and calves and maybe one adult male 1-2 km behind; the rest of the adults would be foraging alone or in pairs on the periphery. In foraging, each group or individual occasionally exhibited milling behavior presumably as a response to opportunistically encountering prey. During this kind of foraging behavior adult female/calf groups commonly engaged in percussive splashing just prior to milling. Again this percussive activity is suggestive of a form of cooperative herding and is almost exclusively characteristic of subgroups that contain calves (Figs. 10.5A and 10.5C).

The foraging strategy of the peripheral adults traveling as individuals or pairs is more typical of males than females. Females do exhibit this behavior but more usually in pairs. Adult males tend to forage on the extreme periphery as much as 3 km from the nearest animal. Milling activity in these peripheral individuals tends to be more active, sometimes resulting in high speed chases at the surface (Fig. 10.5B). In peripheral foraging it is not known to what degree, if any, there is cooperative facilitation in the capture of prey.

Foraging was followed significantly by resting ($p < 0.001$) and was associated, but less frequently ($p < .05$), with travel as either an antecedent or subsequent activity (Table 10.2). Acoustic monitoring revealed phonatory activity 83 percent of the time for all instances of foraging and 91 percent of the time specifically for milling, the latter was the highest percentage of phonatory activity recorded for any behavioral category (see Hoelzel and Osborne, this volume).

Resting

Sleep/rest. A tight slow moving group with all individuals in one or two synchronized assemblages was observed 12 percent of the time. It is the most common variation of resting and has been labeled sleep/rest. It is always exhibited by every individual in the group and is presumed to be the means by which these whales satisfy their physiological requirement for sleep. The minimum duration for a sleep/rest session was 0.5 hr with a maximum of 6.6 hr and mean of 1.8 hr.

During sleep/rest, respiration was synchronized so that all whales came to the surface within 20 sec of each other, usually in 2-4 simultaneous waves of surfacing individuals. Respiration rates were of the typical pattern exhibited in orca during most other behavioral categories (except for the irregular respiration patterns of play and milling). The typical respiration pattern is 3-5 min submerged, followed by 2-4 respirations at 20-40 sec intervals and submerged again for 3-5 min. In sleep/rest, intervals between breaths tend to be slightly longer than during other behavioral activities. The number of simultaneously surfacing individuals is proportional to the number of individuals present. A single small pod will have 1-2 waves of simultaneously surfacing whales (J- or K-pods) and if all 3 pods (J, K and L) are sleeping together (approximately 80 whales) there may be as many as 5 waves of simultaneously surfacing whales.

The coordinated sleep/rest group travels with a specific orientation at a speed of 1-2 kn and all individuals are either touching or within a few meters of their immediate neighbors. The spatial formation of sleep/rest tends to be a more latitudinal than longitudinal pattern, with individuals surfacing abreast of each other (Figs. 10.7A and 10.7B). The spatial arrangement of age-sex classes in sleep/rest groups do not indicate whether adult males, females or calves are on the outer perimeter. However, preliminary analysis of individual sleep/rest configurations indicates there may be a non-random pattern based on individual preference and/or social structure (Bateson, 1965; S. Heimlich-Boran, personal communication).

Peripheral resting. Two other types of apparent resting that involved exclusively peripheral subgroups or single individuals have also been observed. The first type was observed only on a few occasions, lasting from 20-60 min and involved classic sleep/rest as already described. Under that circumstance the peripherally resting subgroup was usually 3-7 km away from the main body of whales who were engaged in foraging or some other behavior.

The second type of peripheral resting behavior involved only one to a few individuals who hovered in one spot at the surface for up to 1.5 min at a time. Sometimes the individual hovering at the surface would take more than one respiration before submerging again. This type of stationary resting at the surface has never been observed to be repeated more than three to four times in succession by the same individual. Individual stationary resting appears to be contingent upon calm water conditions (although observation bias may be operating here) and is generally sporadic and independent of what the other whales are doing.

When all whales present are engaged in sleep/rest it is preceded significantly ($p < 0.05$) by foraging and to a lesser extent by milling (Table 10.2). Play is the only behavioral category that predictably ($p < 0.05$) follows sleep/rest. If more than one pod is involved in sleep/rest it is nearly always followed by intermingling or play ($p < 0.001$). On all occasions in which there was acoustic monitoring of sleep/rest the whales were found to be silent.

Intermingling

Intermingling is a loosely defined category of behavior but it is easily discernible from other surface activities and has some very consistent social contexts within which it occurs. It is characterized by slow moving and tight milling clumps of whales. Many of the whales in any one clump are in actual physical contact, rolling and brushing against each other at or near the surface, giving the appearance of swarming. Intermingling has been observed 2 percent of the time, with a minimum duration of 0.7 hr, a maximum of 3.2 hr and a mean of 1.5 hr. It only occurs when more than one pod is present, with the independent clumps of milling whales composed of individuals from different pods. Clumps of milling whales may be of any age-sex composition with what appears to be a constant flux of individuals moving from one swarming clump to another. For example, on one occasion in September, 1980 the female J8 was found to occur in four out of seven clumps of intermingling whales as the research vessel moved from one aggregate to the others over a 20-min period.

In addition to milling swarms of individuals from different pods, other surface characteristics of intermingling include rolling around at the surface and spyhopping. Commonly, the spyhops will involve pairs or even trios of whales emerging simultaneously. However, other types of acrobatics involving percussive splashing do not occur in intermingling. The surface activity of intermingling tends to be relaxed and splashless, especially during the early stages of execution. Usually after 20-40 min of intermingling, momentum mounts and individuals begin to wander out of the clumps and engage in increasingly noisy and percussive acrobatics. Almost always the increased activity results in a multi-pod pure play session.

Greeting ceremonies. Intermingling frequently follows multi-pod sleep/rest; it almost always immediately follows the meeting of two resident pods after they have been separated for a day or more. Under the latter circumstance the two pods will form two tight lines and approach each other head on. When the 2 groups are within 10-20 m of each other they stop motionless at the surface and hover, facing each other for 10-30 sec. Then the two groups submerge and swim toward each other. When they resurface they are in mixed tight swarms characteristic of intermingling (Fig. 10.8).

On two out of the seven occasions when pods were observed to come together after being apart for one or more days, the whales did not exhibit a greeting ceremony. On one of those occasions the two pods immediately engaged in pure play and on one other occasion began with active intermingling followed by pure play behavior. On the other five occasions the resident orca pods first engaged in a greeting ceremony before shifting into intermingling.

Although sample size for intermingling was too small for Chi-Square analysis, intermingling was followed most often by play behavior. This presumably occurred in

relation to the more active surface activity characteristic of the end of an intermingling session and, thus, automatically progressed into full-scale play behavior. However, on two occasions intermingling preceded foraging behavior and on another occasion was followed by multi-pod sleep/rest. Acoustic monitoring during intermingling revealed silence 30 percent of the time; which is the highest level of silence documented for any behavioral category other than sleep/rest.

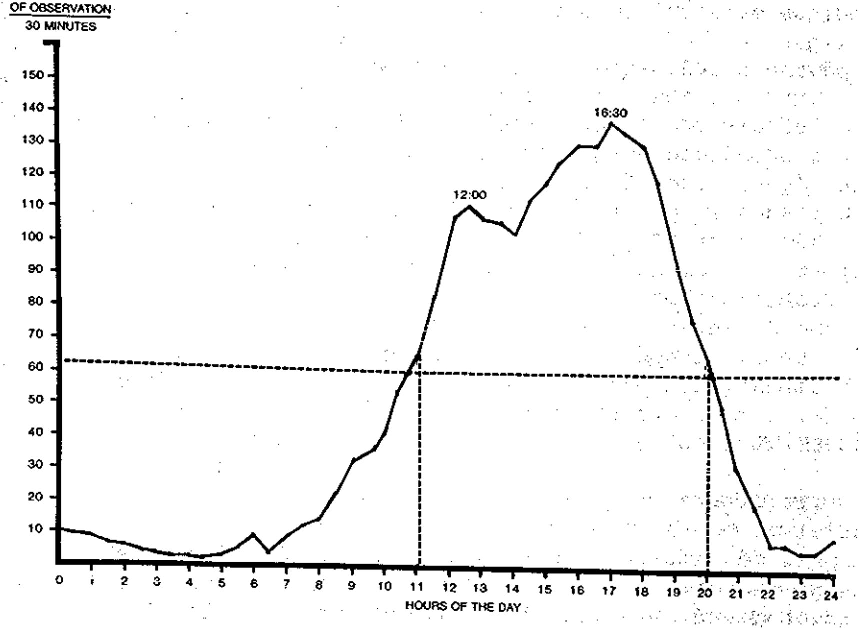


Fig. 10.9. A graph showing diurnal/nocturnal observational bias for behavioral data collection at 10 min intervals over the 24-hr circadian cycle.

Diurnal/Nocturnal Activity

The behavior of J-, K- and L-pods was observed at least three times every hour of the day. However, the bulk of the sampling occurred from 1100-2000 hr (Fig. 10.9). There was a minimum of 60 instances and a maximum of 140 instances of behavioral observation from 1100-2000 hr. The highest standard deviation (for the occurrence of a behavior over all 10 min time blocks) was 4.5 instances for travel. The standard deviations for all other behavioral categories fell within a range of 1.20-3.52 instances. This indicated relatively little variation in the distribution of activities among time blocks. When percentages were calculated for the number of times any one behavior was observed in a given 30 min interval, and then compared with the percentages yielded in the total time budget, the two did not differ by more than 10 percentage points (Fig. 10.10). This uniformity suggests that from 1100-2000 hr the behavior of the whales was unpredictable in relation to time of day. However, these findings must be considered preliminary and inconclusive in light of the sample bias in the data base and the lack of power in the statistical analysis.

Acoustic monitoring from the fixed hydrophone arrays at the Orca Survey research facility was much less biased than visual data. Aural monitoring by researchers often took place 24-hr a day, with the possible exception of from 0300-0600 hr in which very little data were collected. Percentages of instances where phonatory activity was recorded revealed 62 percent during daylight hours and 38 percent during darkness. This suggests that the activities of the whales were not obviously correlated with day/night cycles.

DISCUSSION

The behaviors observed in this study do show some consistent trends but the categories distinguished were not precise enough to be regarded as more than an initial attempt to describe the activity repertoire of this resident community of orca. The underlying complexity of social behavior in these killer whales will require more quantitative data both at the surface and underwater than was accomplished in this initial study. A multi-track video system and acoustic documentation mediated by a micro-processor would be desirable techniques to employ in a more thorough investigation. However, the basic behavioral characteristics delineated by this study do provide a framework within which to proceed with more detailed research.

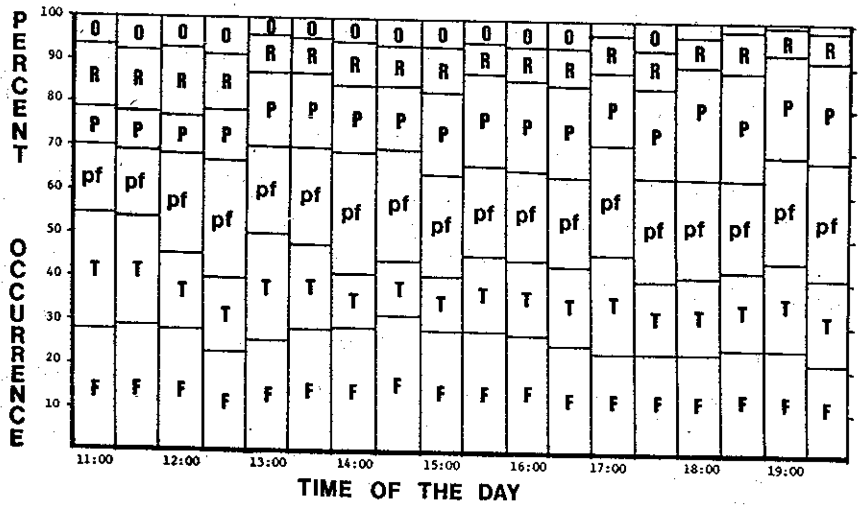


Fig. 10.10. A graph showing mean percent distribution of behavioral categories at 30 min intervals from a sample with a minimum of 60 observations between 1100 and 2000 hr. Note uniformity of percentages throughout all intervals.

For example, in preliminary Orca Survey investigations where observations in terms of the present behavioral categories were correlated with tides (Boran et al., 1981; F. Felleman, personal communication) changes in activity type and in directions of movement were associated with tide changes 61 percent of the time. There was also a small relationship among all behavioral categories and each of the six basic tidal variables. This suggests that the behaviors of these whales are dependent upon tidal environment but perhaps in a subtle and complex fashion that is not obviously apparent with the limited categories of surface behavior described here.

Where specific coastal and underwater geography have been correlated with behavior (Boran et al., 1981; see also Jacobsen, this volume; Jepson, 1981), distinct relationships have emerged even though every variable was also associated with every other to some extent. The environmental and behavioral categories that were highly correlated represent an important first step in understanding the way killer whales interact in specific ecological zones. In Boran et al. (1981) there were three contingent behavioral/geographic variables that were most salient: (a) feeding-related behaviors in the vicinity of underwater seamounts and shoreline banks; (b) play and percussive splashing in regions of heavy on-coming tidal rips and (c) travel behavior in areas spanning the distances between distinctive environmental features. These results suggest that more detailed investigations should yield important new insights into cetacean socioecology. To that end, the following behavioral model is presented as a research guide.

A Model of Orca Behavioral Adaptation

The basic configuration of behavioral categories depicted in Figure 10.11 represent a synthesis of the data where the relative size of each circle is consistent with the amount of time J-, K- and L-pods spent in each activity. The arrows indicate temporal relationships between categories. Dashed arrows are temporal relations that were above expectation, but not statistically significant ($p > 0.05$). Solid arrows indicate statistically significant relationships ($p < 0.05$). There were 72 possible temporal relations between the nine behavioral categories, of which 23 were above expectation and five were statistically significant (Table 10.2). Only 18 relationships (Fig. 10.11) that were above expectation are illustrated and six (three dashed and three solid arrows) of these indicate the statistically unanalyzable, but otherwise real relationships between intermingling and greeting ceremonies.

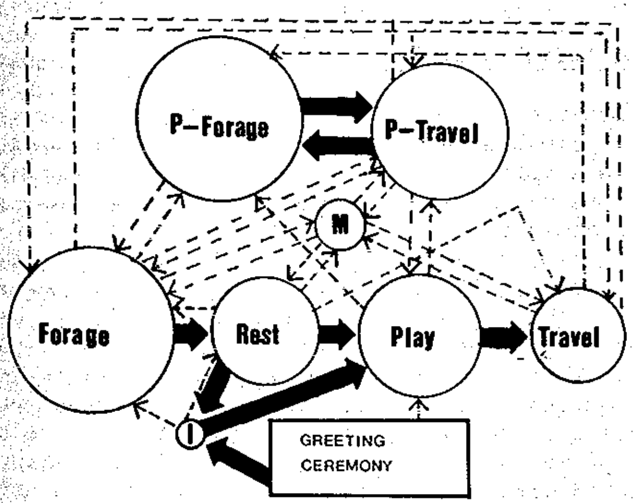


Fig. 10.11. A network model of the behaviors J-, K- and L-pods. Circle size indicates relative quantity of time devoted to the behavioral category, dashed arrows indicate one-way sequencing contingencies between behaviors that are above expectation, but below statistical sequencing contingencies between behaviors. (See text for further details.)

We see that the six prominent behavioral categories, comprising the majority of time, seem to form two separate groups in Figure 10.11. The group with the most components concern maintenance behaviors (food, sex and sleep). The other group appears to be arbitrarily separated from the first. It consists of an isolated cycle between two behaviors that are in reality difficult to observationally differentiate from each other when they occur for short durations (i.e., percussive-foraging contains intermittent percussive-travel as one of its components; see Fig. 10.5).

The basic sequence of forage, rest, play and travel corresponds functionally with the temporal arrangement one would be inclined to expect. In this respect foraging, which contains simultaneous milling and traveling as its components, is seen as a high energy behavior where the pod is actively working at making a living. Percussive-foraging and percussive-travel may be viewed similarly, but in terms of a much higher energy expenditure. Roughly half of the percussive splashing in these latter behaviors can be associated with cooperative herding. The other instances of splashing probably arise from play sessions and the constant antics of rambunctious calves. However, it is quite possible that adults use this boisterous calf splashing to their advantage in feeding. In a sense this could be considered a division of labor (i.e., a means of efficiently sharing food resources), where female-calf groups feed by herding and sparsely distributed peripheral adult males and females feed solitarily. Moreover, where pure milling by all individuals occurs we are possibly looking at a third and even more cooperative feeding strategy since during this latter behavior the density and variation of acoustic calls is the highest of all behavioral categories (Hoelzel and Osborne, this volume).

That sleep/rest should follow the work of active food searching and consumption logically makes sense from an energetic stand point, and this is precisely what appears to happen in these whales (Fig. 10.11). During sleep/rest the Greater Puget Sound resident pods are acoustically silent. In contrast, it appears that the northern resident pods on occasion emit a low volume high frequency whistle during sleep/rest (Ford and Fisher, 1982). This difference is consistent with the kind of behavioral variation that is evident in the different call vocabularies of these two socially isolated populations (Ford and Fisher, 1982; Hoelzel and Osborne, this volume). When the Greater Puget Sound resident pods emerge from the sleep/rest activity, social mechanisms for reactivating the group appear to be employed. The non-maintenance energy expenditure of play and/or intermingling and play follow statistically often ($p < 0.001$). Such play behaviors seem to activate the group and then give way to the necessity of traveling to a place where replenishment of food resources can be accomplished (Fig. 10.11).

This profile of forage, sleep/rest, play and travel seems to be the basic behavioral routine for a resident pod traveling alone. However, there are variations on this theme as represented by the dashed lines in Figure 10.11. The exact activity schedule the whales follow on any one occasion is far from predictable.

When more than one pod is present, definite variations occur in the basic sequence outlined above in connection with the intermingling ceremony. A primary prerequisite for intermingling is that more than one resident pod be present. Intermingling appears to facilitate social cohesiveness among resident pods. In Figure 10.11 it is shown that there were only two observed circumstances that resulted in intermingling. These conditions were when two pods met after separation of one or more days and when the resident whales emerged from a multi-pod sleep/rest session. In the situation of pods meeting, intermingling was nearly always preceded by a greeting ceremony. However, if a greeting ceremony did not occur, then a minimum of 20 min of intermingling transpired. Group play followed intermingling sessions about 70 percent of the time, although occasionally play was skipped and the whales immediately engaged in a maintenance behavior (note dashed lines in Fig. 10.11).

Interestingly, although intermingling as described here does not appear to occur in the northern resident pods, a kind of greeting cermony does on occasion take place (J. Ford and J. Jacobsen, personal communications). Moreover, something similar to an intermingling session was observed in the context of a birth in the northern population (Jacobsen, this volume). We have never documented a birth in the southern population so we do not know if intermingling occurs in that context as well. However, in 1981 there were two behaviors akin to intermingling that were not included in the quantitative data analysis presented here. An unusual intermingling session with many components of a greeting ceremony was observed between J- and K-pods in the context of the illness and subsequent death of an adolesent male J15 (for a detailed description see Todd, 1981). It was preceded by multi-pod foraging and followed by separation of the two pods and subsequent single-pod foraging and travel. As can be seen from Figure 10.11 this represents a novel context for normal intermingling. Also in 1981, a new single-pod behavior was observed on three occasions that in some respects was similar to intermingling but did not involve rubbing and silent surface acrobatics. It consisted of the whole pod grouped tightly together with coordinated direction changes that sometimes alternated with respirations. The importance of these variations will remain for future studies to ascertain.

Cultural Variations

The continuity in surface formations and behavior described for the southern community of Puget Sound orca (J-, K- and L-pods), although important for comparative purposes, may be specific only to this resident community. The behavioral description given here should not be considered a typical model of orca surface behavior in temperate coastal fiords, and certainly not typical of orca surface behavior in more diverse habitats. Even within the fairly uniform habitat that surrounds the coastlines of Vancouver Island there are major variations in the patterns of surface behaviors among resident pod communities with different call vocabularies (Ford and Fisher, 1982; Jacobsen, 1980, this volume; Jepson, 1980) and especially between transients and resident pod communities (Balcomb et al., 1980; Bigg, 1982; Ford and Fisher, 1982; Osborne and Heimlich, 1981). These differences are evident not only in the phonatory call repertoires, but also in the budgeting of time devoted to basic maintenance behaviors like sleep/rest, and social rituals such as intermingling.

For example, from a preliminary sample of 100 hr of observation of the northern Vancouver Island resident community (A1-, A5- and B-pods; using the same behavioral coding described in this paper), significantly higher activity values have been found for sleep/rest and travel behaviors and significantly lower values for foraging, play and general percussive splashing activities (Osborne, 1981; M. Sidenstecker and J. Jacobsen, personal communications). This suggests that learned social traditions may play a major role in determining ecological adaptation among socially isolated populations (Bonner, 1980).

Resident orca communities consisting of a core pod (J-pod) and seasonally present peripheral pods (K- and L-pods) may have alternative feeding strategies even within the same pod community. During summer and fall, J-pod cooperatively feeds on salmon with the other pods and during the winter it feeds by itself occasionally splitting into age-sex class subgroups for differential exploitation of immature chinook salmon, herring and probably cod. On no occasion has J-pod been present during a marine mammal predation and on many occasions J-pod has been observed peacefully feeding in the immediate vicinity of other marine mammals (J. Heimlich-Boran, this volume).

The peripheral pods (K and L) likewise cooperatively feed on seasonal salmon runs but range further during off-season winter and spring months, spending most of their time along the unprotected outer coast away from the resident core area. K- and L-pods have rarely been behaviorally monitored in these peripheral regions (M. Bigg, G. Ellis, J. Ford, personal communications), but it is presumed they are feeding on wintering salmon, marine mammals and other abundant coastal resources. The two rare instances of documented marine mammal predation by resident whales have involved a subgroup of L-pod.

Transient pods show an even larger degree of variation in their behavioral repertoires. They range much further than resident pods, sometimes being observed only once and never returning (Bigg, 1982). The distribution of transients' ranges do overlap with resident home ranges; however, the transients tend to use routes that are out of the main thoroughfares of the resident pods. Many times the route of a transient pod suggests that the whales are lost or merely following coast lines (e.g., see Erickson, 1980). The more regularly occurring transients have been observed to feed annually on seasonal salmon runs specific to a certain river (i.e., O-pod and the August run at the Nooksack River in Bellingham Bay), scouring rocky shelves for cod and preying upon pinnipeds and cetaceans within the home ranges of resident communities (Balcomb et al., 1980; J. Heimlich-Boran, this volume). Some transient pods, who show annual patterns of a far ranging distribution, have seasonally been found traveling and foraging as multi-pod conglomerates (Bigg, 1982). This occasionally has taken place in the vicinity of northern resident pods, but did not result in any resident-transient interactions acoustically or otherwise (J. Ford, personal communication). In Greater Puget Sound, residents and transients have never been observed together. It appears that transients rarely phonate while in the core area of a resident community (Orca Survey observations and J. Ford, personal communication). Peculiarly, when acoustic calls of known transient pods have been documented at the Orca Survey Research Facility, it has always been at night.

The most extreme variations in behavioral repertoire have been documented in lone males; V2 is a good example. He was first systematically observed in 1977 by M. Bigg (personal communication) traveling with a female and a calf. During an encounter with him in 1979 he was alone and had been publicly reported wallowing in kelp beds off the southern shore of Discovery Island outside Victoria, British Columbia. Boaters were concerned that he was in distress. He was encountered in the same spot about 18 hr after the first public sighting. He was alternately undulating in the kelp and cruising along the shallow bottom as though feeding on rock cod. After two hours of this activity he then hovered inside a small underwater canyon. Here he slowly and methodically swam against the 2-kn tide rip maintaining the same position with highly repetitious respirations (in minutes: 3.0 - 0.2 - 0.3 - 3.0 - ...). From then on he surfaced in the same spot without alteration and we assumed he must have gone into sleep/rest. Observations ceased after one hour and the next day he was sighted heading north up the eastern shore of Vancouver Island. That was the last time V2 was sighted.

Another lone male designated F1 was observed from 1974-1976 and then disappeared until 1981 when he was encountered traveling with a transient pod at the north end of Vancouver Island (M. Bigg, personal communication). The fate of these lone whales and their reproductive and social origins are unknown, though future data on call dialects should prove fruitful in this regard (Ford and Fisher, 1982). In the resident communities no immigrations, emmigrations or ostracisms have been documented. However, transient pods with differing call repertoires have been encountered traveling together (Bigg, 1982; Ford and Fisher, 1982) and may represent antecedent groups of lone individuals and nuclear family units that are sporadically encountered (M. Bigg, personal communication). In many respects the transients could be considered nomadic and more ecologically dependent upon non-resident inter-pod interactions. In contrast, the resident communities are comparatively sedentary, socially isolated and composed of larger and more stable populations. However, within resident communities there occasionally are changes in the membership of resident pods through the shifting of sub-pod units (usually composed of three to seven individuals and containing one adult male). This shifting of sub-pod units within a resident community has been documented between K- and L-pods (Balcomb et al., 1980, 1982; S. Heimlich-Boran, this volume). Also within this resident community some individuals seem to alternate between pod units (e.g., L19, a male; L20 and L15, a male and female pair).

The strange association of L20 (male) and L15 (female) deserves mention. Though both have been observed by M. Bigg (personal communication) traveling with L-pod since 1974, in the past four years they have never been seen apart from each other and are usually no closer than 3-4 km from the nearest group of other resident whales. In 1981 their isolation became even more extreme, to the point that they spent periods of days by themselves.

This high degree of variation in activities of transient pods and resident communities suggests that the adaptive behavioral and ecological repertoire of orca are quite flexible, even within the confines of a uniform habitat and a population of little over 300 individuals. In terms of what is known about the cerebral morphology of the orca brain (Jerison, 1978; Morgane, 1978; Osborne and Sundsten, 1981; Ridgway, 1980) it is no surprise that they exhibit such behavioral variations (Bonner, 1980). Thus, it is improbable that any one model will suffice for depicting the activity repertoire of these large-brained social predators. However, such modeling should facilitate our understanding of the data at hand and indicate the challenges in research ahead.

POSTSCRIPT

In the time since this chapter was prepared, behavioral data collection using this system has continued on the resident pods and has been expanded to include comparative observations on the transient pods of this region. Initial observations on the differences between resident and transient pods presented in this chapter are supported by this subsequent research (Osborne, Felleman and J. Heimlich-Boran, unpublished report to Cascadia Research Collective, 1985). This longitudinal data base was in excess of 1,400 hr in 1984 and will continue to be expanded.

Additionally, this behavioral data base has been successfully applied to studies of killer whale predation by F. Felleman as part of his thesis research at the University of Washington, studies of habitat use in J. Heimlich-Boran's thesis research through Moss Landing Marine Laboratory and San Jose State University, and S. Heimlich-Boran's thesis research on social structure also through Moss Landing Marine Laboratory and San Jose State University. All of these studies were conducted under the auspices of The Whale Museum, Moclips Cetological Society.

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