Social organization of mammal-eating killer whales: group stability and dispersal patterns

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Abstract: The social organization of mammal-eating "transient" killer whales (*Orcinus orca*) was studied off southern Vancouver Island from 1985 through 1996. Strong and long-term associations exist between individual transients, so sets of individuals with consistently high association levels, termed pods, can be delineated. Pods consist of individuals of mixed ages and sexes, and typically contain an adult female and one or two offspring (averaging 2.4 individuals). The mother–offspring bond remains strong into adulthood for some male (and less often for female) offspring. Other males disperse from their maternal pod and appear to become "roving" males, spending some of their time alone, and occasionally associating with groups that contain potentially reproductive females. These males appear to have no strong or long-term relationships with any individuals, and adult male – adult male associations occur significantly less often than expected by chance. Females that disperse from their natal pod appear to be gregarious (having high average association rates) but socially mobile (having low maximum association rates). Differences in social organization from the sympatric fish-eating "resident" killer whales (where no dispersal of either sex occurs) likely relate to differences in foraging ecology. Transient killer whales maximize per capita energy intake by foraging in groups of three individuals, whereas no such relationship has been documented for resident killer whales.

Résumé : L'organisation sociale des Épaulards (*Orcinus orca*) consommateurs de mammifères « individus nomades » a été étudiée au large de Île de Vancouver de 1985 à 1996. Des liens étroits et continus se forment entre des individus nomades, si bien que des individus dont les liens sont particulièrement étroits et constants se regroupent en petites bandes reconnaissables. Ces bandes comptent des mâles et des femelles d'âges différents et se composent, typiquement, d'une femelle adulte et d'un ou deux rejetons (2,4 individus en moyenne). Le lien mère–petit reste fort jusqu'à l'âge adulte pour certains rejetons mâles et, plus rarement, pour certains rejetons femelles. Les autres mâles quittent la bande maternelle et semblent devenir des mâles « errants », passant une partie de leur temps seuls, et s'associant à l'occasion à des groupes qui contiennent potentiellement des femelles reproductrices. Ce mâles ne semblent pas entretenir de liens serrés et à long terme avec d'autres individus et les associations mâle adulte – mâle adulte se sont avérées significativement moins fréquentes que la fréquence aléatoire prévue. Les femelles qui quittent la bande natale semblent être grégaires (leurs taux moyens d'association sont élevés), mais socialement mobiles (à taux maximaux d'association faibles). Les différences d'organisation sociale entre ces épaulards et les épaulards piscivores « résidants » (dont ni les mâles, ni les femelles ne se dispersent) sont probablement attribuables à des différences dans l'écologie alimentaire. Les épaulards nomades maximisent leur consommation individuelle d'énergie en s'alimentant par groupes de trois, alors qu'une telle relation n'a pas été observée chez des individus résidants.

[Traduit par la Rédaction]

Introduction

Descriptions of a species' social structure or social organization typically arise from studies of interactions or associations between individuals (Hinde 1976; Whitehead 1997). Results of such studies cannot be applied uncritically to other populations of the same species without taking into account the degree of within- and between-population variability that may be present (e.g., Wrangham 1987; but see Di Fiore and Rendall 1994). Studies on more than one population of a species can be extremely valuable by documenting such variability and identifying the factors that may be responsible for it.

An unusual situation exists with killer whales (*Orcinus orca*) in the eastern North Pacific, where sympatric and apparently reproductively isolated and genetically differentiated forms appear to differ substantially in diet, behaviour, and social structure (Bigg et al. 1987; Baird and Stacey 1988; Baird et al. 1992; Ford et al. 1998; Hoelzel et al. 1998; Baird 2000). Case studies of these forms and investigation of the patterns of associations between individuals provide an important opportunity to investigate the relationship between mammalian social organizations and environmental factors. In this paper, we consider the terms social organization and social structure to be synonymous, both being used to describe the patterns and functions of associations between individuals (Whitehead 1997).

A long-term study of the social organization of one of these forms of killer whale has found natal "pod" philopatry of both sexes, a pattern not previously documented among mammals (Bigg et al. 1990; Baird 2000). Amos et al. (1993) suggested that both sexes of long-finned pilot whales (*Globicephala melas*) also exhibit natal pod philopatry,

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though the data presented are not conclusive (Connor 2000). A pod has been defined as a set of individuals that are seen more together than apart, that is, which associate with one another at least 50% of the time (Bigg et al. 1990). Stable pods of individuals associating along matrilines are quite large and average about 12 individuals, with a range from 3 to 50 individuals (Bigg et al. 1990). Individuals in these pods appear to feed primarily on fish (Ford et al. 1998). Based on their movement patterns, these individuals were originally termed “residents” (Bigg 1982); this term is still used even though it has subsequently been shown not to be particularly descriptive. The sympatric “transients” (although, again, the name is not particularly descriptive of movement patterns) feed primarily on marine mammals (Baird and Dill 1996). Although average pod size and many other aspects of behaviour and ecology differ between the so-called residents and transients, a quantitative examination of the social organization of transients has not been undertaken. The purpose of this study is to document and describe association patterns between individual transient killer whales in the inshore waters around southern Vancouver Island, British Columbia, and to relate differences in association patterns between resident and transient forms to ecological differences, thereby investigating the links between social organization and diet.

Methods

Background on study animal and study area

Individual transient killer whales can be recognized by using distinctive natural markings (Bigg 1982; Bigg et al. 1987), and studies of behaviour and ecology have typically relied on photo-identification of individual animals (e.g., Baird and Dill 1995, 1996). Detailed analyses of life-history characteristics have not been undertaken for transient killer whales, but some of the information available for the sympatric resident killer whales may be relevant to association patterns. At birth, expected longevity of resident killer whales is approximately 29 years for females and 17 years for males (Olesiuk et al. 1990). However, mortality is very high in the first 6 months of life and low thereafter; life expectancy for an individual that reaches sexual maturity, assuming a mean age of 15 years for both males and females (see below), is about 63 years of age for females and 36 years of age for males (Olesiuk et al. 1990). Mean female age at first birth is approximately 15 years (range 11–20 years), while average inter-birth interval is about 5 years (range 2–14 years) (Olesiuk et al. 1990; Ford et al. 1994; Baird 2000). Mean age at onset of sexual maturity for males, signified by an increase in the growth rate of the dorsal fin whose greater size at maturity is a secondary sexual characteristic, has been estimated at 15 years, with a range of 10 to about 17 years (Olesiuk et al. 1990). Physical maturity is estimated to be reached at about 21 years of age (Olesiuk et al. 1990).

This study was conducted around the southern tip of Vancouver Island, British Columbia, and in adjacent areas of Washington State. Transient killer whales were encountered over an area of about 3000 km^2. Transients were distinguishable from residents in a number of ways: based on observations of prey choice (i.e., feeding on marine mammals), associations with other known transients, and morphological appearance (cf. Bigg et al. 1987; Baird and Stacey 1988). The majority of animals documented in this study had previously been classified as transient killer whales by other investigators (Bigg et al. 1987; see also Dahlheim et al. 1997). A total of about 170 individually identified transient killer whales were recorded throughout British Columbia and Washington state between 1973 and 1996 (Ford et al. 1994) and new adult individuals are still occasionally documented (e.g., Baird and Dill 1995). The sample of transient killer whales from the current study contains 62 individuals, representing approximately 35% of the total identified population.

Field data collection

Details of the study have been previously presented (Baird and Dill 1995, 1996) and only those relevant to the examination of social structure are given here. Observations were made from small vessels (4–7 m). Whales were encountered on an opportunistic basis year-round, from 1984 through 1996. Transient killer whales were encountered on a total of 112 days. Most encounters were in the months of August through October (Baird and Dill 1995) and in the years 1987 through 1993; only six of the encounters were in the years 1984–1986 and 1994–1996, owing entirely to differences in effort. An extensive sighting network has developed in the area since the late 1980s; this comprises commercial whale-watching vessels, sports fishermen, dedicated land-based spotters, lighthouse keepers, and individuals who live along the waterfront. Because of this network, few killer whales (including lone individuals) that move through the study area in daylight hours in calm, clear weather are likely to be missed, particularly during the summer months and since 1990. Most (approximately 90%) of the encounters took place with good sighting conditions (< Beaufort 3), and encounters were distributed both near shore and offshore throughout the study area, thus we believe that there should be no strong bias for sighting larger groups.

Individuals in each encounter were identified photographically and (or) visually based on distinctive acquired and congenital characteristics of the dorsal fin and the saddle patch (a lightly pigmented area at the base of the dorsal fin; see Baird and Stacey 1988). In general, individuals were photoidentified rather than visually identified when groups were large (i.e., greater than 3 individuals), when particular individuals were seen for the first time in any particular year, and (or) when individuals did not have obviously distinctive characteristics. Visual identifications were usually relied upon only when a particular individual or small group of individuals was seen several days in a row and were distinctively marked. Following Bigg et al. (1987), an arbitrary alphanumeric code was used to designate each individual. Observations were made with eight-power binoculars and the naked eye. Individuals were considered associated if they were in the same group, a “group” being defined as all whales acting in a coordinated manner (e.g., all traveling in the same direction at the same speed, often surfacing within 5–10 s of each other) and within visual range of the observers (Baird and Dill 1996). Since many of the interactions between transient killer whales involved cooperative hunting, which is indicated by coordinated behaviour (Baird and Dill 1995, 1996), such a definition of group seems appropriate. Determination of group membership usually required continuous observation for 10 min or more. In most cases all group members were within a few hundred metres of each other. Only those encounters where all members of a group were identified were used in the analyses. This does not introduce bias, e.g., against large groups, since there were only a few encounters (n = 6) where not all individuals were identified and these were of various group sizes (mean = 4.5, range = 1–14). Encounters were of variable duration; in general, whales were followed for as long as possible and encounters were usually terminated when visual contact with the whales was lost, or when weather, daylight, or fuel considerations warranted termination.

Quantitative analyses

The relative maturity state (e.g., sexually or physically mature) of individuals was derived both from Bigg et al. (1987) and from sightings from this study, in both cases taking into account: relative body size at first sighting, the development of secondary sexual characteristics for males, the presence of individuals thought or known to be an offspring of a female, and (or) based on observations of the mother without an infant in the year or two prior to the first sighting of an infant. The sex of most individuals was determined through observations of dorsal fin size and changes in dorsal fin size throughout the study, as the dorsal fin is sexually dimorphic in adult killer whales, or, for young whales, through observations of the distinctive gender-specific pigmentation patterns in the genital area (Bigg et al. 1987). For both sex and maturity state, data from other researchers (e.g., Bigg et al. 1987; Ford and Ellis 1999; D. Ellifrit, personal communication) were used when informative.

Data were analyzed using SOCPROC 1.0, a program developed in MATLAB 5.1 (The Mathworks, Inc., Natick, Mass., U.S.A.) by H.W. for analyzing social structure. Group membership was noted every 10 min and individuals were considered associated if they were in the same group. This resulted in a total of 2730 samples of group composition. Since whales were tracked for as long as possible and encounters primarily ended because of external circumstances (e.g., weather conditions, time of day) rather than conditions related to group size or composition, such subsampling of group membership should not introduce any bias into our analyses. Two main types of analysis were undertaken: (*i*) involving production, analysis, and display of an association matrix and (*ii*) the examination of temporal trends in association through the computation and display of lagged association rates.

To estimate the proportion of time each pair spent associating, a simple-ratio index of association (Cairns and Schwager 1987) was used to produce a symmetric association matrix (not shown). The simple-ratio index is probably the most appropriate index when association is defined by presence in the same group (Ginsberg and Young 1992). To reduce inaccuracies and biases associated with small sample sizes, for most analyses and presentations of data only those individuals observed for 30 or more hours were used. This limited the analyses to 22 individuals that were seen on a number of different days (mean = 18 days, SD = 14.1 days, range = 8–30 days) in several different years (mean = 6 years, SD = 2.8 years, range = 3–9 years), and for which gender was known. The association matrix was displayed in two ways. (1) By an average-linkage cluster analysis showing the average level of association between hierarchically formed clusters. Individuals are arranged on the *y* axis with the strength of associations presented on the *x* axis. (2) By a sociogram, where points representing the individuals are arranged around a circle and the thickness of lines between the points indicates the strength of their relationship.

To test for sex differences in patterns of association, the mean and maximum association index was calculated for each combination of interactions between and within the sexes (e.g., female–female, male–male, female–male) for all adult (i.e., physically or sexually mature) individuals seen for 30 or more hours. The mean association index is an estimate of the probability that a randomly chosen member of class *X* was associated with a randomly chosen member of class *Y* during any sampling period, thus the estimates are insensitive to the different numbers of males and females in the population. The maximum association index between classes *X* and *Y* is the average of the largest association index between each member of class *X* and any member of class *Y*. To test the null hypothesis that associations between and within gender classes are similar, associations between gender classes were permuted 1000 times so that random association matrices were constructed and distribution of association indexes by gender combination from the real data were compared with those from the permuted data sets (Schnell et al. 1985). The mean and maximum association values and typical group size (cf. Jarman 1974; Baird and Dill 1996) for each individual were also calculated.

Temporal trends in association were examined by plotting the changes in average association rate with time lag, termed the lagged association rate (Whitehead 1995; Whitehead and Dufault 1998). This is an estimate of the probability that if two animals are associating at some time they will also be associated after various time lags. All individuals were used for these analyses regardless of the number of times sighted, as restricting the data set to frequently observed individuals is likely to positively bias the lagged association rates. Analyses were undertaken on individuals of all ages, as well as only on adult and subadult (those estimated to be >10 years old based on relative body size or known year of birth) whales.

Although not used in any of our quantitative analyses, in interpretations of the strength and duration of associations we refer to unpublished information on associations between some individual transients from sightings in the 1970s and 1980s (provided by M.A. Bigg).

Results

Association analyses: and strength and longevity of associations

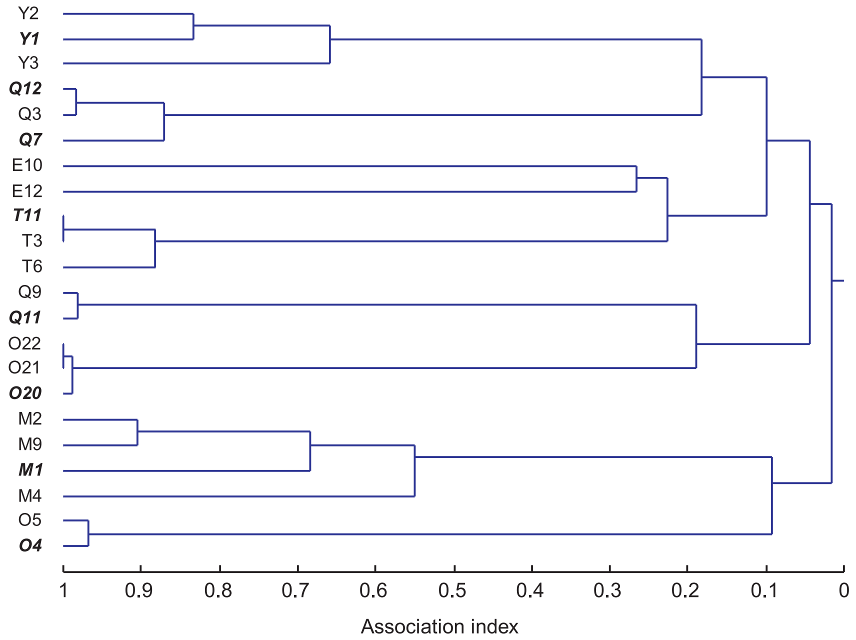
A dendrogram produced from an average-linkage cluster analysis shows that some associations are extremely strong, with those individuals spending between 90 and 100% of their time together (Fig. 1). Applying the 50% association rule that Bigg et al. (1990) used with resident killer whales, nine pods were documented. The alphanumeric code of one pod member was arbitrarily used as a designation code for the entire pod (after Bigg et al. 1987). Sex, maturity stage (when first documented), mother (when known), association values, and the pod-membership designation for each of these 22 individuals are presented in Table 1.

Differences in the values of the terminal association node (the node designating the weakest association within the pod) for individuals within a particular pod can be related to several factors (Table 1): birth of an individual subsequent to its mother's first sighting (M9 born after M2's first sighting, T6 born after T3's first sighting), dispersal of an individual from a pod subsequent to its first sighting (M4, which left pod M1 in 1991 and then rejoined in 1993), or possible death or dispersal of an individual prior to the last sighting of its pod (Y2, Y3, M1, Q7; all of which have not been seen by researchers in either British Columbia, Alaska, or Washington for several years). For all cases where all individuals in a pod were known to be alive at both the first and last sighting of the pod (pods O20, Q9, O4), the association between pod members was between 0.9 and 1.0 (Fig. 1).

Associations between individuals in different pods can be seen in a sociogram (Fig. 2). Associations between different pods or individuals are clearly not random, based on the relative absence and asymmetry of linkages through the axes of the circle.

The mean and maximum association levels for each sex and between different sex classifications of adults are shown in Table 2. Most association levels (e.g., female–female and female–male associations) are similar; the only exceptions are the associations between males. For both mean and maximum levels, adult male – adult male associations appear substantially weaker than other combinations (Table 2). Results of temporal analyses (Figs. 3 and 4) suggest that male–male associations decrease with time at greater rates than for any other combination. A permutation test showed significant differences in association rates between adult male – adult male pairs and other sex combinations (permutation test, $p = 0.03$). Female–male associations for adults and subadults also

Fig. 1. Dendrogram from cluster analysis of individuals observed for 30 or more hours. The 0.5 level was chosen in the designation of "pods" (cf. Bigg et al. 1990). Males are shown in boldface italic type.



appear to decrease at a higher rate than female–female associations or associations between all individuals (Fig. 4), which are quite stable with time over the time periods being investigated in this study (approximately 3 years).

Adult males

Grouping characteristics of all adult males documented in this study (including those seen for less than 30 h) are presented in Table 3, including the typical group size recorded for each individual and the number of constant companions (individuals estimated to spend more than 50% of their time with the male, determined using an average-linkage cluster analysis of all individuals in the study). Additional information compiled by M.A. Bigg is also presented for some of the males to supplement the small sample sizes in this study. Six males were members of mixed-sex permanent pods throughout all or much of the study; five others appeared to have no constant companions and were generally found in smaller groups (Table 3).

Discussion

An examination of social organization based primarily on presence within a group assumes that the number and type of behavioural interactions between any particular pair within a group are similar for each pair (Whitehead and Dufault 1998). To help address this assumption in this study, information on the behavioural context of interactions (from Baird and Dill 1995, 1996) has been included in interpretations of observed association patterns.

Pod composition, structure, and dynamics

Individual transient killer whales show clear preferences for association with certain other individuals (Figs. 1 and 2). As with the resident killer whales studied by Bigg et al. (1990), some of these associations are extremely strong, with individuals spending virtually all of their time together over a period of years (Fig. 1; Table 1). Using Bigg et al.'s (1990) definition of all individuals that spend 50% or more of their time together being considered a single pod, transient killer whales clearly can be classified into discrete pods (Fig. 1). As noted, this definition simply means those individuals that are seen more together than apart are considered a single pod. While somewhat arbitrary, only three nodes in Fig. 1 are close to the 50% point, thus changing this value would have little impact on our interpretations of the data. As well, all three cases where the nodes are close to the 0.5 cutoff appear to be due to either dispersal (M4) or the presumed death (Y3, M1) of an individual in the pod. Pod membership determined in this study by using only those individuals seen for 30 or more hours closely matches that reported from a qualitative assessment of association patterns of these same individuals by Bigg et al. (1987). One difference in pod membership between these two studies (pod T3) results from a larger number of encounters and more hours of observation available for that pod in this study. Such differences suggest that pod designation for transient killer whales should only be made for animals seen a number of times both within and between years.

Pods are of mixed sex and age and frequently contain both an adult female and an adult male (Table 1). Plots of lagged association rates (Fig. 3) show that most interactions (e.g., between males and females or between all individuals) are of long duration. At least one of the pairs of whales associating in this study (O4, O5; association index 0.97) was also recorded together a number of times by M.A. Bigg (unpublished data) from 1975 (when O4 was a subadult male) through to the first sighting in this study in 1984, as well as almost every year in the present study, and again in 1997 and 1998 (R.W. Baird, unpublished data).

Based on observations of births of individuals into a pod and on the enduring associations of known mothers and

Table 1. Characteristics of the 22 most frequently encountered individuals.

Individual ID	Sex	Mothers[a]	First year seen in this study	Maturity stage when first seen	Last year seen in this study	Number of days observed in this study	Number of 10-min samples used in this study	Mean level of association	Maximum level of association	Pod ID
E12	F	—	1989	Physically mature	1993	8	225	0.10	0.27	E12
E10	F	—	1987	Sexually mature	1991	10	251	0.10	0.32	E10
M1	M	M2?	1987	Physically mature	1992	11	340	0.10	0.73	M1
M2	F	—	1987	Physically mature	1993	16	429	0.13	0.90	M1
M4	F	M2	1987	Immature	1993	14	330	0.09	0.60	M1
M9	F	M2	1989	Newborn	1993	14	394	0.12	0.90	M1
O4	M	O5?	1984	Physically mature	1996	18	392	0.09	0.97	O4
O5	F	—	1984	Physically mature	1996	18	395	0.09	0.97	O4
O20	M	O21?	1989	Physically mature	1993	21	576	0.15	0.99	O21
O21	F	—	1989	Physically mature	1993	22	570	0.15	1.0	O21
O22	F	O21?	1989	Sexually mature	1993	21	570	0.15	1.0	O21
Q3	F	—	1986	Physically mature	1992	20	393	0.13	0.98	Q3
Q7	M	Q3	1986	Immature	1990	19	366	0.13	0.88	Q3
Q12	M	Q3	1986	Juvenile	1992	20	398	0.13	0.98	Q3
Q9	F	—	1987	Physically mature	1996	13	315	0.09	0.98	Q9
Q11	M	Q9	1987	Juvenile	1996	13	321	0.09	0.98	Q9
T3	F	—	1987	Physically mature	1996	22	548	0.16	1.0	T3
T6	F	T3	1988	Newborn	1996	18	484	0.15	0.88	T3
T11	M	T3?	1987	Immature	1996	22	548	0.16	1.0	T3
Y1	M	Y2?	1986	Physically mature	1995	30	599	0.14	0.83	Y1
Y2	F	—	1986	Physically mature	1993	28	567	0.14	0.83	Y1
Y3	F	Y2	1987	Sexually mature	1989	22	434	0.12	0.72	Y1

Note: See the text for features used to determine sex and estimate maturity state. Individual identifications and pod designations were given arbitrarily and have no implications regarding associations between pods (following Bigg et al. 1987).

[a] Question mark denotes a “tentative” identification.

Fig. 2. Sociogram of individuals observed for 30 or more hours. The key shows thickness for three values; lines linking individuals vary with the precise level of association. Strong (>0.5) linkages along the perimeter of the circle represent clear association in "pods," as with resident killer whales. Males are shown in boldface italic type.

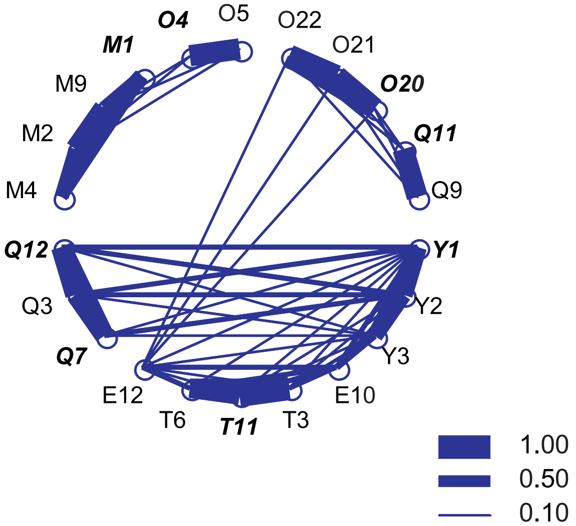


Table 2. Distribution of associations for adult (>15 years old) individuals observed for 30 or more hours between and within gender classes.

Relationships between	Mean association (SD)	Maximum association (SD)
F–All	0.09 (0.03)	0.50 (0.31)
M–All	0.09 (0.05)	0.73 (0.34)
F–F	0.08 (0.03)	0.27 (0.09)
F–M	0.11 (0.07)	0.46 (0.34)
M–F	0.11 (0.07)	0.73 (0.34)
M–M	0.03 (0.01)	0.06 (0.02)
All–All	0.09 (0.03)	0.57 (0.33)

Note: For the relationships between class *X* and *Y* (written "*X*–*Y*"), the mean association is the probability that a randomly chosen member of class *X* was associated with a randomly chosen member of class *Y* during any sampling period; the maximum association is the average of the largest association index between each member of class *Y* and any member of class *X*. F, female; M, male.

offspring (Table 1), transient killer whale pods appear to be generally comprised of an adult female and one or two of her offspring. While for the adult males in the study it is not known if their close associate when present is definitely their mother, there are several lines of evidence other than those already mentioned that support this supposition. If the long-term adult male – adult female associations were for breeding purposes, we would expect that at least some of the pods that contain these adult males would have had one or more offspring during the course of the study, assuming that the average interbirth interval of about 5 years found for resident killer whales is similar for transients (Olesiuk et al. 1990). Of the four pods that contained an adult male at the beginning of the study (Table 1), a birth was only recorded in one (pod M1). There is no evidence that the matriarchs in the other three pods have given birth over a 10-year period (one female, O5, has not been documented to give birth since she was first seen as an adult in 1975; M.A. Bigg, unpublished data). Also, there were no cases where an adult or subadult of either sex permanently joined another pod, suggesting that the adult female – subadult male bonds documented for some pods (e.g., pod T3) are at least sometimes retained into adulthood.

Plots of lagged association rates for both transient killer whales of all ages (Fig. 3) and just for adults and subadults (Fig. 4) show that associations are quite stable. However, there are some sex and age-related differences in patterns and longevity of associations. That the probability of two males being associated decreases with time and with increasing age (Figs. 3 and 4), and that there are several lone males in the population (Table 3), reflects dispersal of some males from maternal pods and indicates that adult males rarely associate with each other. Such dispersal appears to be a social dispersal (Isbell and Van Vuren 1996). Whether these dispersing individuals exhibit locational philopatry is unclear, although in the one documented case of male dispersal (see below), the male was resighted within its original range. The relative decline in female–male and male–male associations with time (Fig. 4) may also reflect in part the higher mortality rates of males.

Based on the long-term bonds between males and females and the observations that at least some of these males are the offspring of the female that they associate closely with (Table 1), male offspring appear to have two options, either remaining closely associated with their mother their entire lives or dispersing. Why do some males disperse? In the one documented case of male dispersal (Bigg et al. 1987), the male left its maternal pod around the age of 7, near the time when its mother (M2) gave birth to another offspring (M4), potentially increasing the pod size from three to four individuals. The pod already contained one adult male (M1), which was thought to be the brother of the dispersing individual. Baird and Dill (1996) demonstrated that per capita energy intake rates for transient killer whales reaches a maxima for groups of three individuals and declines for larger (or smaller) groups. Such an optimal foraging group size likely exists because of trade-offs in detection abilities between transient killer whales and their potential prey; as group size increases, the ability to detect prey increases, yet larger groups are also more likely to be detected by potential prey (Baird and Dill 1996). Baird (2000) suggested that dispersal likely occurs whenever pod size surpasses the energy-maximizing optimum of three individuals. He also suggested that the first-born male should be more likely to remain philopatric, since there is an energetic cost associated with dispersal and the first-born male, being larger, would be able to retain its position in the pod (Baird 2000).

Female–female association levels are generally lower than those for female–male associations, both for adults and subadults (Fig. 4; Table 2) and for all ages (Fig. 3). There is some evidence to suggest that female offspring disperse at some point close to the time when they become sexually mature. The one documented case of a female (M4) dispersing from its maternal pod (pod M1) occurred when the female was about 12 years of age and was within 2 years after the birth of a third offspring into her pod, thus bringing the pod size above three individuals (see relatively low

Fig. 3. Plots of lagged association rates for a number of different types of associations between all individuals of all ages. The lagged association rate effectively shows the probability of association at time $T + t$ if two individuals were associated at time T. A different moving average was chosen for each type of association to smooth lines. Jackknife standard error bars are shown on three lines. Lagged association rates between females and males (F–M) are high and relatively stable. Lagged association rates between all individuals (All) are high and relatively stable, though lower than those seen between males and females (see also Table 2). Lagged association rates between males (M–M) drop off dramatically with time. Lagged association rates between females (F–F) are relatively stable over time. The expected lagged association rates of all individuals ("random") if individuals had a random chance of associating are low and relatively constant.

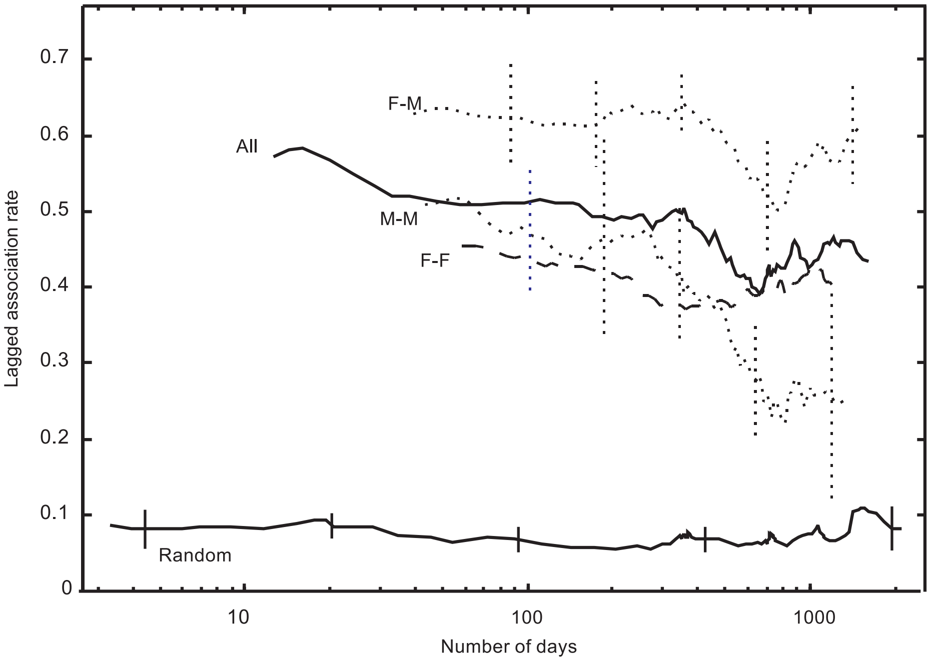
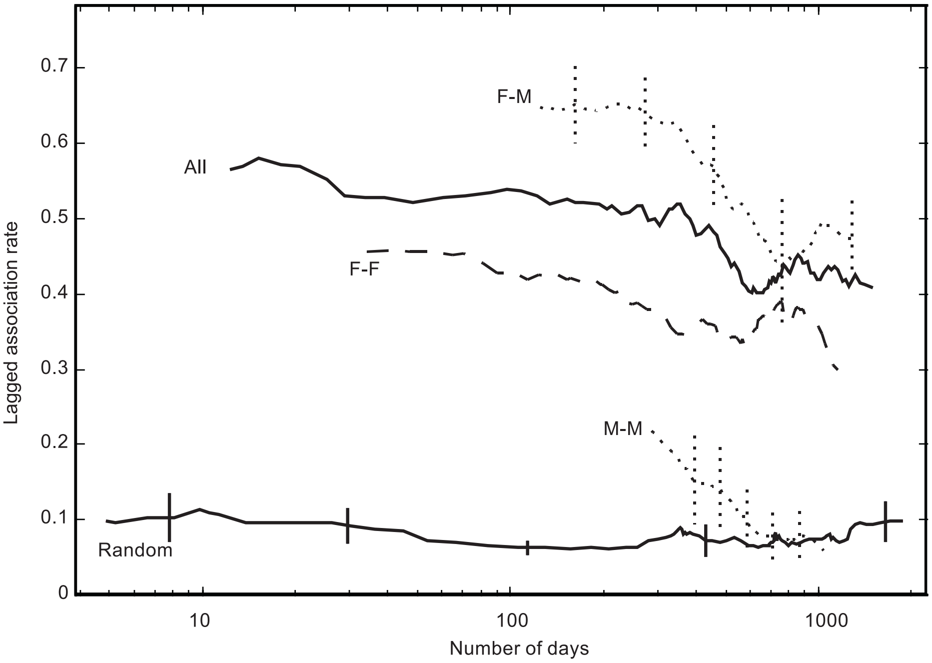


Fig. 4. Lagged association rates for interactions between adults and subadults (> 10 years of age) only. Lines shown are the same as in Fig. 3. Note the male–male associations (M–M) fall to random levels within 2 to 3 years, reflecting the lack of enduring associations between adult males.



association levels between M4 and other pod M1 members in Fig. 1). This female appeared to rejoin its mother 2 years later after the disappearance of one of its putative siblings (M1) and was unaccompanied by any offspring. This observation suggests that females that are unable to reproduce successfully may return to join their natal pod. There is one

Table 3. Grouping characteristics for individual adult males, excluding one male that became an adult partway through the study (T11).

Individual	Typical group size[a]	No. of constant companions[b]	Sample size[c]	No. of days[d]	Percentage of days[e]
O20	4.72	2	34	10	0
M1	4.37	3	19	24	0
Y1	4.15	2	74	15	6.7
N3	4.00	3	1	—	—
AO1	3.65	2	10	—	—
O4	3.19	1	21	32	9.4
T2	3.32	0	2	—	—
P1	2.12	0	5	14	57.1
F1	1.0	0	3	14	78.5
V1	1.0	0	4	—	—
X10	1.0	0	1	—	—

[a] Calculated as per Jarman (1974).

[b] Number of individuals of either sex and all ages associating at the 50% level (see Fig. 1).

[c] Number of groups in which each individual is seen.

[d] Number of days documented by the late M.A. Bigg between 1974 and 1986. These data are included to supplement the small sample sizes of certain individuals (P1, F1) to support the trend in grouping tendencies of roving males. Data are only shown for those individuals in Bigg's data set that had multiple records (>2).

[e] Percentage of days that individuals were recorded alone by M.A. Bigg (see note *d*). It should be noted that the information from Bigg's data set came from multiple sources and efforts were not always made to photograph every individual present. Other individuals may have been present but not positively photographed on some of the days when individuals were recorded alone.

pod (O2) recorded in this study and documented by Bigg et al. (1987) that contains only two adult females, neither of which has been known to give birth since they were first seen in the 1970s (M.A. Bigg, unpublished data). It is possible that this adult female – adult female pod may have formed in the same way, although other explanations (e.g., that the two females are not a mother–daughter pair) are also possible.

Interactions between individuals from different pods

No females were documented traveling alone in this study. It appears that upon dispersal from her maternal pod, a female is rarely alone but instead associates with a number of different groups, which appear to always contain an adult male, for relatively short periods of time (e.g., days, weeks, or perhaps months). Examples of this can be seen in the relatively high mean and relatively low maximum association values for two adult females (E10, E12; Table 1), which reflect frequent but short-term associations with other individuals. Pods that allow adult females to join suffer an energetic cost if group size increases beyond three individuals (Baird and Dill 1996), thus acceptance of such females likely occurs because of some benefit like increased mating opportunities for the adult male in the pod.

Males that disperse appear to spend part of their time alone. We term these individuals "roving" males, not because they are known to move more geographically but because they appear to have no strong or enduring associations with any other individuals (similar to the females E10 and E12 noted above). While our sample sizes are small for these individuals, unpublished sighting data on several of these same individuals collected by M.A. Bigg (Table 3) also support this trend, and there is also possibly a weak bias against sighting lone individuals (see Methods). When roving males associated with groups of other individuals, these groups have always contained at least one adult female without any nursing offspring (assuming offspring are weaned around 3 years of age), and such associations were for relatively short (e.g., hours, days, or weeks) periods (e.g., adult male P1 was seen with pod Q3 on three occasions in 1988 but not before or since). There were no observations of roving males associating together nor of roving males associating with lone individuals temporarily (i.e., for minutes or hours) separated from their pod. There has been only one observation of two roving males in close proximity to each other, both of which were alone at the time. Both individuals were heading towards each other, when one began a series of four highly percussive behaviours (cartwheels) within several hundred metres of the other. The whales passed within 50–100 m of each other but continued moving in opposite directions (R.W. Baird, personal observations). That roving adult males do not associate, despite the energetic benefits that would accrue from cooperative hunting (Baird and Dill 1996), suggests that there must be some cost in pairing. This is in striking contrast to bottlenose dolphins (*Tursiops* sp.), where long-term associations exist between pairs or trios of adult males (Smolker et al. 1992); such associations appear to allow males to sequester females (Connor et al. 1992). It is interesting to note that a long-term adult male – adult male pair has been documented for killer whales elsewhere. Hoelzel (1991) noted such a pair of two adult males off Punta Norte, Argentina. These individuals were closely related genetically (Hoelzel 1991) and were regularly seen cooperatively hunting southern sea lions (*Otaria flavescens*) through intentional stranding. Such foraging tactics differ greatly from those used for hunting seals (*Phoca vitulina*) around southern Vancouver Island (Baird and Dill 1995).

Individuals from different pods interact frequently (Fig. 2). When in relatively small groups (e.g., up to six individuals) behaviour in such multipod groups is predominantly foraging; larger groups, however, spend greater and greater proportions of time engaged in social interactions (Baird and Dill 1995).

Comparisons with "resident" killer whales

This study has provided the first quantitative examination of association patterns in the transient form of killer whale off the Pacific coast of North America. The pattern of female-biased social dispersal (Isbell and Van Vuren 1996) and at least partial male social philopatry appears to be unique among cetaceans and is unusual among mammals in general (Greenwood 1980; Clutton-Brock 1989). Quantitative comparisons with resident killer whale association patterns are not possible because data on groupings were measured differently, with residents considered together if they were in the same photographic frame (Bigg et al. 1990). However, there is an immediately obvious difference in social structure from sympatric resident killer whales, where no dispersal of either sex from maternal pods occurs (Bigg et al. 1990). As noted above, dispersal from transient pods probably occurs because of the increased costs in terms of reduced energetic intake associated with foraging in large groups (Baird and Dill 1996). So why would resident killer whales remain philopatric? For resident killer whales, unlike transient killer whales, no clear relationship between group size and food intake has been documented (though cf. Hoelzel 1993). In general, resident killer whales are thought to feed on schooling fish (Ford et al. 1998), and while resident killer whales travel in larger groups than transient killer whales, they rarely share prey and one whale feeding does not appear to reduce the chances of another whale in the group catching prey (unlike transients; see Baird et al. 1992). Other potential costs of remaining philopatric are also likely low (see Connor 2000). Since killer whale pods frequently associate, mating can occur between pods, thus eliminating the potential cost of inbreeding. This also seems to be the case with transient killer whales, since there is a strong increase in the amount of social and sexual behaviour when several pods are together (Baird and Dill 1995).

What are the implications of the observed social structure of transient killer whales for the apparent isolation between resident and transient killer whales? Baird et al. (1992) suggested that the two forms of killer whale are in the process of speciating, that is, they are incipient species. Given the benefits for transient killer whales hunting in small groups and the dispersal from maternal groups that results, and considering that foraging groups appear to be primarily of related individuals, it is not surprising that mammal-eating transients and fish-eating residents do not appear to associate. As Baird et al. (1992) state, this social isolation between the two foraging specialists sets the stage for reproductive isolation, which appears to be the case today (Hoelzel et al. 1998; Baird 2000).

Despite the occurrence of dispersal of transient killer whales from their natal pods, there is one obvious similarity in association patterns between resident and transient killer whales. Associations between individual transient killer whales are both strong (Figs. 1 and 2) and enduring (Figs. 3 and 4), just like associations between resident killer whales (Bigg et al. 1990). Using the terminology of Bigg et al. (1990), these long-term groups can clearly be considered pods, but transient pods are composed of only a single matriline, while resident pods may contain from 1 to 11 matrilines (Bigg et al. 1990). Another difference in association patterns between resident and transient killer whales is the relative infrequence and long-term instability of interactions between adult male transient killer whales (Table 2; Fig. 4). Rose (1991) described a number of types of interactions between adult male resident killer whales, and Harms (1997) argues that after the age of 21, male resident killer whales show increased levels of social contacts of all types. Both situations are in striking contrast to the patterns seen with transient killer whales, and again it seems likely that such social differences might be related to these underlying ecological differences (cf. Wrangham 1987), with social organization adapting to optimize the intake of energy from food, whether it be fish or mammals.

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