Occurrence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour, and prey handling

Robin W. Baird and Lawrence M. Dill

Abstract: We studied the occurrence and behaviour of so-called transient killer whales (*Orcinus orca*) around southern Vancouver Island from 1986 to 1993. Occurrence and behaviour varied seasonally and among pods; some pods foraged almost entirely in open water and were recorded in the study area throughout the year, while others spent much of their time foraging around pinniped haulouts and other nearshore sites, and used the study area primarily during the harbour seal (*Phoca vitulina*) weaning–postweaning period. Overall use of the area was greatest during that period, and energy intake at that time was significantly greater than at other times of the year, probably because of the high encounter rates and ease of capture of harbour seal pups. Multipod groups of transients were frequently observed, as has been reported for "residents," but associations were biased towards those between pods that exhibited similar foraging tactics. Despite the occurrence of transients and residents within several kilometres of each other on nine occasions, mixed groups were never observed and transients appeared to avoid residents. Combined with previous studies on behavioural, ecological, and morphological differences, such avoidance behaviour supports the supposition that these populations are reproductively isolated.

Résumé : Nous avons dénombré les Épaulards (*Orcinus orca*) dits itinérants et surveillé leur comportement le long de la côte sud de l'île de Vancouver de 1986 à 1993. La présence et le comportement des baleines variaient selon la saison et d'un banc à l'autre; certains bancs s'alimentaient presque exclusivement au large et restaient dans la région pendant toute l'année, alors que d'autres passaient une grande partie de leur temps à chercher leur nourriture près des rookeries de pinnipèdes ou autres endroits près de la côte et restaient dans la zone d'étude surtout durant la période de sevrage–post-sevrage du Phoque commun (*Phoca vitulina*). L'utilisation de cette zone était maximale au cours de cette période et la consommation d'énergie à ce moment était significativement plus grande qu'à d'autres moments de l'année, sans doute à cause de la probabilité élevée de rencontrer des petits Phoques communs et de la facilité à les capturer. Des groupes de plusieurs bancs d'épaulards itinérants ont été observés souvent, comme d'ailleurs les bancs d'épaulards « résidants » mentionnés dans la littérature, mais les associations contenaient surtout des baleines de différents bancs qui utilisaient les mêmes tactiques de recherche de nourriture. En dépit de la présence simultanée d'épaulards itinérants et d'épaulards résidants à plusieurs kilomètres les uns des autres en neuf occasions, des groupes mixtes n'ont jamais été observés et il semble que les épaulards itinérants évitent les épaulards résidants. Combinées aux résultats d'études antérieures sur les différences comportementales, écologiques et morphologiques, nos observations de ce comportement d'évitement confirment l'hypothèse selon laquelle ces populations sont isolées génétiquement. [Traduit par la Rédaction]

Introduction

Numerous studies have been undertaken on killer whales (*Orcinus orca*) in British Columbia and Washington State. Based on photodocumentation of individual association patterns and movements, research in the early 1970s identified three discrete associations of killer whale pods (i.e., long-term maternal groups) around Vancouver Island, each with a different home range (Bigg 1979). Pods in two of these associations had largely non-overlapping ranges that centred on northern and southern Vancouver Island, respectively, and were seen predictably in these areas over several years. Pods in the third association were seen throughout the home ranges of pods from the other two associations on a periodic basis, yet did not appear to interact with them. These differences in movement patterns led to the descriptive classification of pods in these associations as residential (later termed resident) or transient within a particular area (Bigg et al.

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1976[2]). As noted by Guinet (1990), more recent research has demonstrated that these terms are not particularly descriptive, but "resident" and "transient" have been retained here, owing to both their historical usage and the lack of adequate alternative designations.

Research over the past 20 years has focused on areas where the frequency of encounters with killer whales is highest, in Johnstone Strait off northeastern Vancouver Island and in Haro Strait, a transboundary area between southeastern Vancouver Island and the U.S. San Juan Islands. Concentrations of resident killer whales were found in both areas, and virtually all studies have focused on these populations, covering a diverse range of subjects, including foraging and feeding (Nichol 1990; Felleman et al. 1991), habitat use (Heimlich-Boran 1988), vocal traditions and acoustic behaviour (Hoelzel and Osborne 1986; Ford 1989, 1991), alloparental care (Waite 1988), life-history characteristics and population dynamics (Olesiuk et al. 1990), and social behaviour and social structure (Bigg et al. 1990; Jacobsen 1990; Rose 1992). Opportunistic encounters with transients in these areas added little to the understanding of their behaviour, yet cumulative information collected continued to imply that the transient individuals did not associate with the sympatric populations of residents. By the late 1980s, a combination of genetic and morphological data suggested that these populations might be reproductively isolated (Bigg et al. 1987; Baird and Stacey 1988*a*; Bain 1989; Hoelzel 1989; Stevens et al. 1989), which appears to have spurred more detailed investigation of the transient population (e.g., Baird and Stacey 1988*b*; Guinet 1990; Morton 1990; Baird et al. 1992; Baird 1994; Barrett-Lennard 1992).

Nevertheless, considerably less is known about the behaviour or ecology of transient killer whales. In this paper we report on a study of transients around southern Vancouver Island from 1986 through 1993. Behavioural data were collected during 434 h of observation, and predation on other marine mammals was observed on 136 occasions (Baird 1994). Here we present information on the occurrence and behaviour of transient killer whales, focusing on foraging and feeding behaviours and prey handling. While previous investigators have discussed age and sex differences in killer whale behaviour (e.g., Guinet 1991*a*; Jefferson et al. 1991), seasonal, individual, or pod-specific differences in occurrence and behaviour have received less attention. In this study we examine how occurrence and behaviour vary between seasons and among transient pods (i.e., long-term maternal groups).

Methods

Study area and other marine mammal populations

Data were collected over an area of approximately 3000 km^2 centred around the southern tip of Vancouver Island, British Columbia, Canada, and including the western San Juan Islands, Washington State, U.S.A. (Fig. 1). The study area is considered a "core area" for southern resident killer whales. Individuals from this population, which contains approximately 96 individuals (D. Ellifrit, personal communication), use the region on about 80% of the days during the summer months (R.W. Osborne, personal communication). Populations of several other species of marine mammals inhabit the study area (Osborne et al. 1988; Calambokidis and Baird 1994).

Five species of pinnipeds have been recorded; four of these are fairly common. Harbour seals (*Phoca vitulina*) are the most abundant marine mammal, with an estimated total year-round population of approximately 3000 (P. Olesiuk, personal communication). While harbour seals are found throughout the study area, concentrations occur primarily around sites where they haul out on shore. Such sites (referred to hereafter as haulouts) are used year-round for a variety of purposes, including resting, giving birth, and nursing young (see Watts 1991). Over 60 haulout sites are known within the study area, although most seals are found at a small number of major sites (12 sites have over 100 individuals, shown in Fig. 1; R.W. Baird, unpublished data; P. Olesiuk, personal communication). All but two of the major harbour seal haulouts and most of the minor haulouts within the study area have a rock substrate; the remainder have a sand or pebble substrate. Pupping occurs at all of the major sites and most of the minor sites from late June through early September (Bigg 1969). Unlike most other phocids, mothers and pups of this species regularly enter the water during the 3- to 6-week nursing period (Oftedal et al. 1987).

California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) are seen occasionally during summer, but are common within the study area from September through May, with a peak of approximately 1000 individuals in October and November. Only one major sea lion haulout is found within the region, at Race Rocks (Fig. 1). Northern elephant seals (*Mirounga angustirostris*) are seen regularly in the study area, both in open water and hauled out on shore, but no concentrations exist.

Four species of cetaceans, other than killer whales, are also found regularly in the study area. Dall's porpoise (*Phocoenoides dalli*) is the species most frequently encountered, being regularly seen in deeper (>50 m) areas, while harbour porpoises (*Phocoena phocoena*) are occasionally found in the area, usually in waters less than 100 m in depth. Minke whales (*Balaenoptera acutorostrata*) and gray whales (*Eschrichtius robustus*) are also seen within the region, but no interactions with killer whales have been observed locally (but see Jefferson et al. 1991).

Observational methods and analyses

Sightings of transient killer whales were reported by whale-watching vessels, lighthouse keepers, sport fishing charter operators, other research vessels, and members of the public. These records were used both to locate whales for encounters and to monitor seasonal occurrence.

Encounters were defined as periods of 15 min or greater in duration when all whales present in a group were identified and the distance between the whales and the observer was short enough for specific behavioural events to be recorded and behavioural states classified (see below). Observations were made by one to four observers from one or two of several small vessels (to 8 m). The onset and termi-

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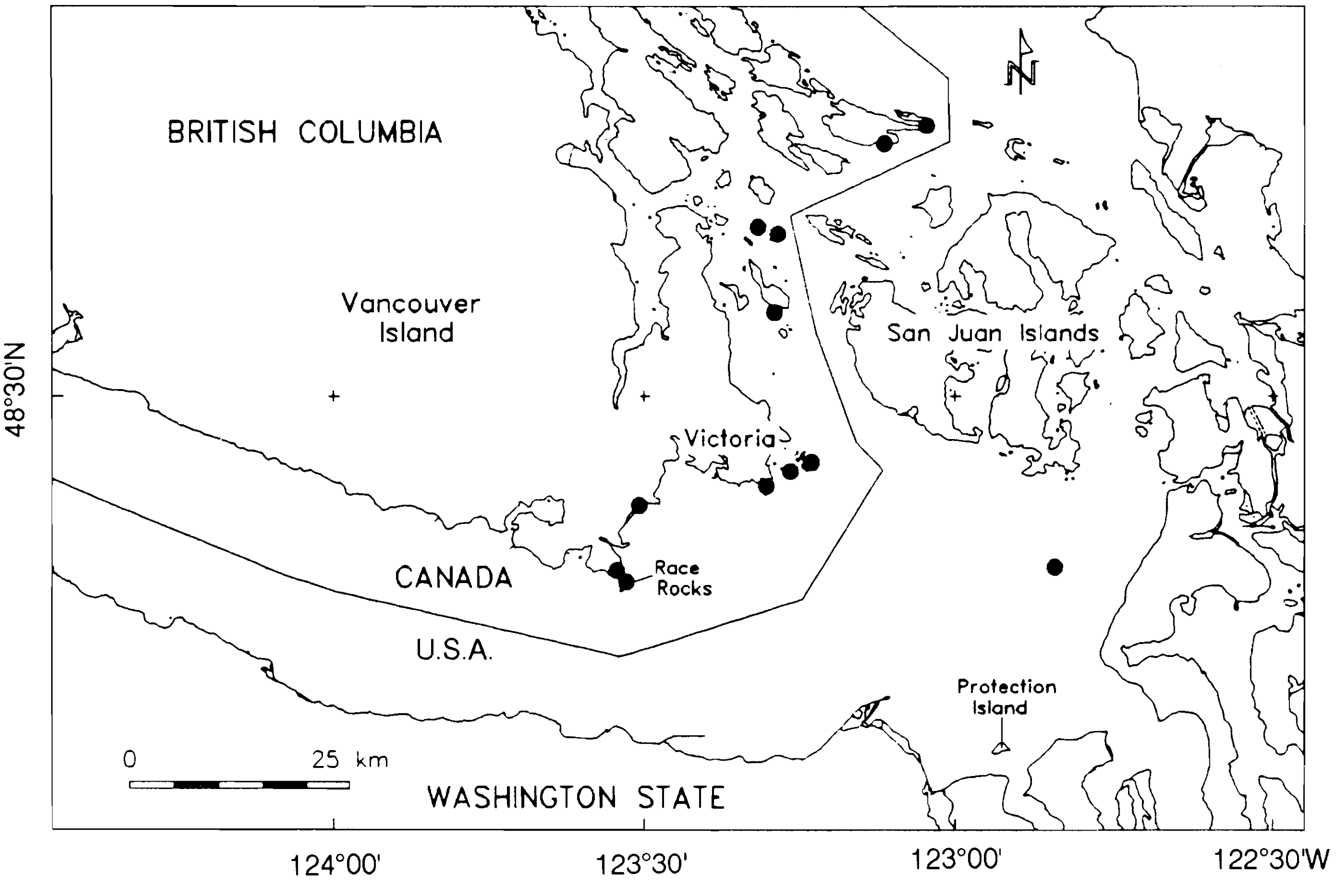
[2] M.A. Bigg, I.B. MacAskie, and G. Ellis. 1976. Abundance and movements of killer whales off eastern and southern Vancouver Island with comments on management. Unpublished report, Arctic Biological Station, Ste. Anne de Bellevue, Quebec.

Fig. 1. Map of the study area, showing the places mentioned in the text and locations of major harbour seal haulouts (●).



nation of encounters were ad libitum (after Altmann 1974); encounters ended for a variety of reasons (i.e., loss of contact with whales, approaching darkness, rough sea conditions, low fuel reserves). Data were voice-recorded continuously throughout encounters, using a microcassette recorder. Whales were visible at the water's surface during surfacing periods that generally lasted 1–2 min; intervals between surfacing periods typically ranged from 2 to 8 min. During surfacing periods individual whales usually surfaced 3–6 times. Because groups were typically small, all visible behaviours of all individuals could be recorded simultaneously (focal-group sampling, all occurrences of all behaviours; after Altmann 1974). Data recorded included date, time, location, direction of travel, identity of whales present, distance between and orientation of individuals, relative speed of travel, dive durations, synchronization of respirations between individuals in the group, and the occurrence of discrete behaviours (e.g., breach, spyhop, tail lob, prey capture; see Jacobsen 1986). This information was used to define the general behavioural state (Table 1). The occurrence of all other marine mammals visible at the surface or hauled out nearby was noted, including species, number, behaviour, and relative location. Sea state, other environmental conditions, and the number and type of nearby vessels were also recorded.

Periods during which group size and composition remained constant were considered single observation periods, and the time spent in each behavioural state was divided by the duration of the observation period to give the proportion of time spent in each behaviour. All proportion data were arcsine square root transformed before statistical analyses to normalize the data (Martin and Bateson 1988). To determine an overall behavioural budget, the time spent in different behaviours was summed over all observation periods and divided by the total time spent observing transients.

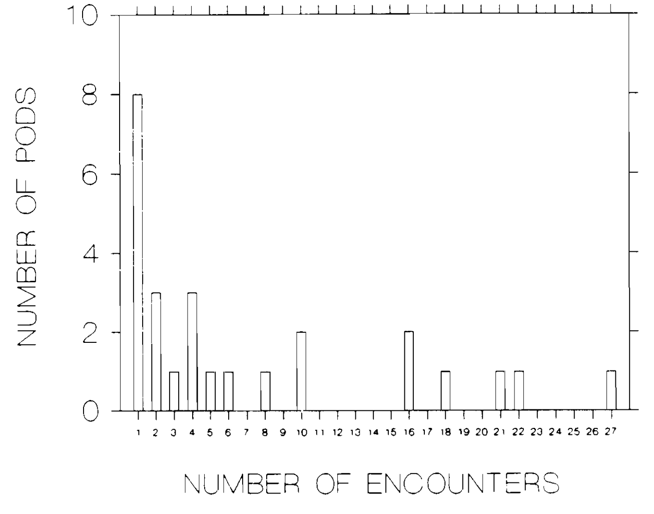
Individual whales present at each encounter were identified visually and (or) from photographs, using the catalogues of Bigg et al. (1987) and Ellis (1987) and unpublished catalogues maintained at the Center for Whale Research (Friday Harbor, Washington), the Marine Mammal Research Group (Victoria, B.C.), and the Pacific Biological Station (Nanaimo, B.C.). Pod designations use the alphanumeric (e.g., M1, Q3, Y1) system of Bigg et al. (1987), and pod membership and age of whales were determined using sightings from this study as well as sighting information provided by the above-mentioned organizations. For groups with extended sighting histories (i.e., greater than several years), the first sighting of a very small individual could be used to estimate the approximate year of birth, and for subadults, size relative to known-age or adult individuals could be used to estimate age.

Prey-handling time was defined as the period from when the whales first appeared to encounter a prey item until the last signs of prey were observed. This period could be broken down into the time from encounter with the prey to its death, and the time from death to complete consumption or abandonment of the prey carcass. In many cases it was not possible to determine accurately when the prey was killed, therefore there was a period during which the prey's status

Table 1. Behavioural categories used in this study.

Category	Description
Haulout foraging	Within 200 m of a harbour seal or sea lion haulout, not including short-duration (less than 30 s) passes by haulouts; synchronization of respirations variable; direction of travel variable
Nearshore foraging	Following contours of shoreline in and out of bays, around headlands
Offshore foraging	Respirations asynchronous; direction of travel not consistent (zigzagging); whales generally greater than five body lengths apart, in open water
Foraging – travel	Respirations synchronous; direction of travel consistent; whales generally less than five body lengths apart, in open water; prey occasionally caught during periods of this behaviour; otherwise indistinguishable from "travel"
Feeding	Prey or prey parts seen. Feeding was regarded as the period from when prey were first attacked to when the last remains of prey were consumed (cf. prey-handling time)
Resting	Respirations synchronous; direction of travel consistent; whales generally less than one body length apart, in open water or nearshore; usually no net motion relative to land or movement backwards in a current; occasional hanging motionless at surface, in open water
Fast travel	Respirations usually synchronous; direction of travel consistent, whales generally less than two body lengths apart; high speed, often porpoising partway out of the water
Travel	Respirations synchronous; direction of travel consistent; whales generally less than five body lengths apart; in open water; no prey captured during periods of this behaviour, otherwise indistinguishable from "foraging – travel"
Social – play	
All	Interactive movements between individuals, not associated with prey capture; all individuals in a group involved; includes percussive behaviour (e.g., tail lob) by lone individuals
Some	Interactive movements between individuals, not associated with prey capture; only some individuals in a group involved

Fig. 2. Frequency of encounters recorded for different pods.



(dead or alive) was unknown. For each prey capture various factors were recorded: time, whale group size, identity and age of individual whales involved, prey species, size, and caloric value (cf. Baird 1994), tidal height and direction (flood vs. ebb), time since sunrise or to sunset, and foraging type (Table 1) prior to the kill. Tide height and direction were determined using Canadian Tide and Current Tables published yearly by the Department of Fisheries and Oceans, and time since sunrise or to sunset were calculated from values presented in the Canadian Almanac and Directory.

In just over half the prey captures (57%), prey species could be determined by direct visual observations of prey, either in whales' mouths or at the surface amongst a group of whales, combined with observations of blood, blubber, or meat in the water. The remaining prey captures (43%) were detected without direct observations of intact prey and were based on observations of prey parts in whales' mouths or in the water. In these cases prey species identification was based on a combination of location, observations of potential prey in the area prior to capture, prey-handling time, behaviour, and quantity of blubber observed in the water. Per capita energy intake values, taking into account the size of prey and the size of killer whales in the hunting group, were calculated as described in Baird (1994). All seasonal comparisons were made between the harbour seal pupping – weaning – postweaning period (July through September) and the non-pupping – weaning period (October through June). Comparisons between pods were made using only those pods encountered on more than 10 occasions each.

Results

Transient killer whales were reported within the study area on 384 occasions from 1987 through 1993. Transients were encountered 99 times during this period, and an additional encounter from 1986 was also used in the analyses. Approximately 434 h of behavioural observations were recorded during these encounters. Changes in group size or composition during an encounter resulted in a total of 217 observation periods of constant group size and composition, ranging in duration from 15 min to 9 h 11 min. Group size ranged from 1 to 15 individuals, but the most frequently recorded group size was 3 (see Baird 1994). During the 100 encounters, a total of 62 different individuals from 26 separate pods were recorded. Not all pods were seen with equal frequency (Fig. 2). Several pods were regularly resighted throughout the study, both within and between years. Others were seen only occa-

Table 2. Summary of seasonal differences in occurrence and behaviour of transients.

	Harbour seal pupping–weaning–postweaning period (July–September)	Non-weaning–postweaning period (October–June)	Statistical significance
Occurrence	Relatively high	Relatively low	—
Average food intake[a] (kcal · kg^{-1} · day^{-1})	76.8	33.4	$p = 0.005$
Percentage of time spent foraging	49.61	47.93	ns
Percentage of time spent in haulout foraging	7.16	1.68	$p < 0.001$
Percentage of time spent in nearshore foraging	12.91	3.08	$p = 0.002$
Percentage of time spent in social–play behaviour	4.73	2.15	ns
Mean group size	3.96	4.39	ns
Number of pods present	Most	Primarily non-haulout foragers	—
Average prey-handling time (min)	42.0	20.8	$p = 0.003$

[a] Calculated as presented in Baird (1994).

Fig. 3. Cumulative numbers of pods encountered during the study. While many pods were resighted both within and between years, new pods were regularly encountered throughout the study.

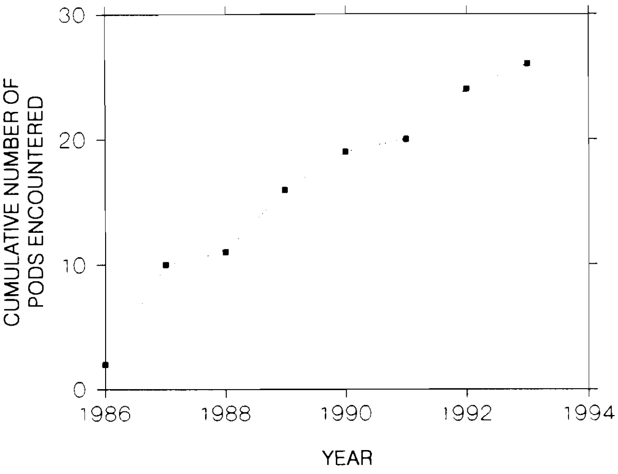
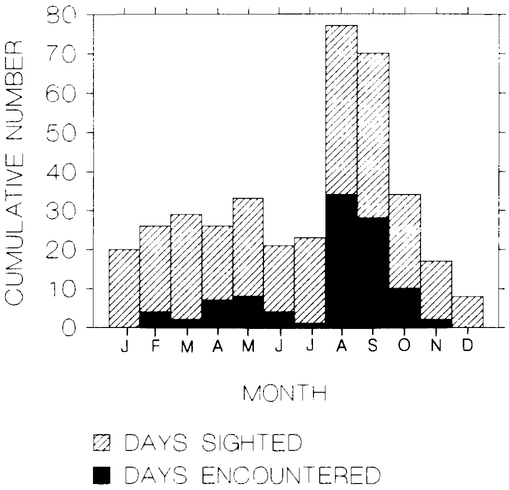


Fig. 4. Seasonal distribution of transient killer whale sightings and encounters between January and December. Sighting effort between October and April was low, therefore the decrease in records during this period does not necessarily reflect a decrease in the number of transient killer whales in the study area.



sionally and new pods were recorded within the study area each year (Fig. 3), suggesting that the total number of transients that use the region is much greater than 62. Most of the pods (23 of 26) had been previously sighted elsewhere, but 3 were documented for the first time in this study.

Seasonal occurrence

The seasonal distribution of sighting records and encounters is shown in Fig. 4. Transient killer whales were recorded in the study area in all months of the year, with a peak in both sighting records and encounters in August and September. There were no encounters with transients during December or January, owing to weather constraints. Sighting effort is high from May through September; thus, the large number of records in August and September compared with May through July implies an increase in use of the area by transients during that period. The average individual energy-intake rate was also significantly higher in July–September than during the remainder of the year (Table 2; Mann–Whitney *U* test, $p = 0.005$).

Pod-specific differences in seasonal occurrence were found. Considering the 6 pods seen on more than 10 occasions each, 3 (Q3, T3, Y1) were seen almost entirely (63 of 70 encounters) during the harbour seal pupping–weaning–postweaning period (hereafter referred to as the seal pupping period), while 3 others (M1, O4, O20) were encountered both during the pupping period (21 of 50 encounters) and at other times throughout the year (29 encounters). Taking all pods into account (including those seen on 10 or fewer occa-

Fig. 5. The proportions of time that pods were seen during the pupping non-pupping periods; some were seen primarily during the pupping period (right-hand side), while others were seen primarily during the non-pupping period (left-hand side).

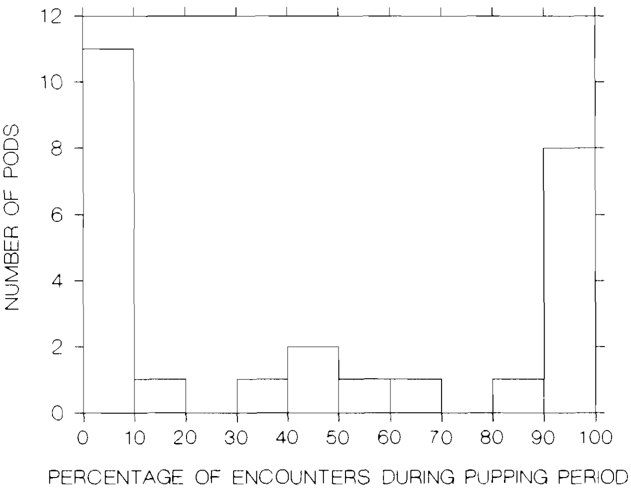


Table 3. Behavioural budget of transient killer whales based on 434 h of behaviour observations (see Table 1 for a description of behaviour categories).

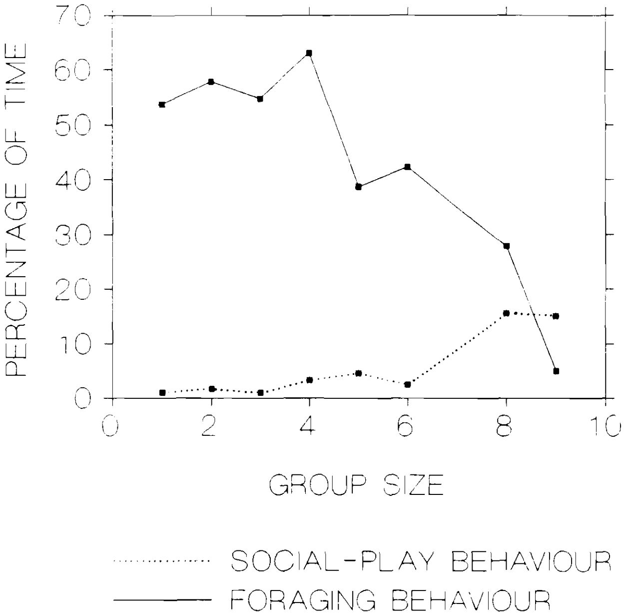
Behaviour	Percentage of time for each category	Percentage of time for each subcategory
Foraging	63.13	
Haulout foraging		5.15
Nearshore foraging		9.31
Offshore foraging		24.92
Foraging−travel		9.60
Feeding		14.15
Fast travel	0.30	
Travel	31.07	
Rest	1.72	
Social−play	3.78	
All		1.79
Some		1.99
Total	100	

sions) also indicates that some pods appear to use the area preferentially during the seal pupping period, while others are seen primarily in the non-pupping period (Fig. 5).

Foraging patterns

Foraging behaviours (including feeding) occupied approximately 63% of the total observation time (Table 3). Behaviour during foraging is extremely variable: as noted in Table 1, foraging can be divided into several subcategories based on location (seal haulouts, other nearshore areas, open water), spacing between individuals, synchronization of respirations, and directionality of travel. Foraging around seal haulouts and other nearshore areas typically involves close following of the contours of the shoreline or circling of rocks or small islets. The distance between individuals is variable during foraging, ranging from less than one body length (~3−8 m) to over a kilometre. The pattern of alignment of individuals in a foraging group, in terms of travelling abreast, staggered, or clumped, is also variable.

Fig. 6. Variation in foraging and social−play behaviour with group size. Only group sizes with more than three observation periods (group sizes 1−9, not including 7) are shown.



The percentage of time spent foraging decreased with increasing group size (Fig. 6; weighted regression on transformed percentages, $r^2 = 0.68$, df = 227, $p < 0.001$). Foraging type varied seasonally; significantly more time was spent foraging in haulout and nearshore areas during the harbour seal pupping period than during the rest of the year (Table 2; Mann−Whitney U test, $p < 0.001$ and $p = 0.002$ for haulout and nearshore areas, respectively). While the proportion of time spent foraging did not differ significantly among pods (Kruskal−Wallis one-way ANOVA, $p = 0.82$; $n = 6$ pods), the occurrence of different foraging types did differ among pods (Kruskal−Wallis one-way ANOVA, $p = 0.02$). Some pods (M1, O4, O20) spent virtually no time (i.e., <2%) foraging in haulout or nearshore areas, while others (Q3, T3, Y1) spent between 25−50% of their time engaged in these types of foraging. Those pods that generally did not forage in nearshore areas spent more time engaged in offshore foraging (Table 4).

Feeding behaviour

As a behavioural state, feeding was defined as the period from when a prey item was first encountered until consumption was completed. Just less than 15% of the whales' time was engaged in feeding behaviour (Table 3). In many cases, feeding behaviours overlapped with other behaviours, i.e., feeding did not prevent the whales from engaging in other behaviours. For example, portions of a prey item could be carried for extended periods while foraging continued or the whales engaged in travel or social−play behaviour.

We observed 138 prey attacks, 136 of which were successful (Baird 1994); thus, all but 2 of the prey attacks were included in the feeding category. The vast majority of prey killed (130/136) were or were suspected to be harbour seals (see Baird 1994); the remaining prey included three harbour

Fig. 7. Frequency distribution of prey-handling times.

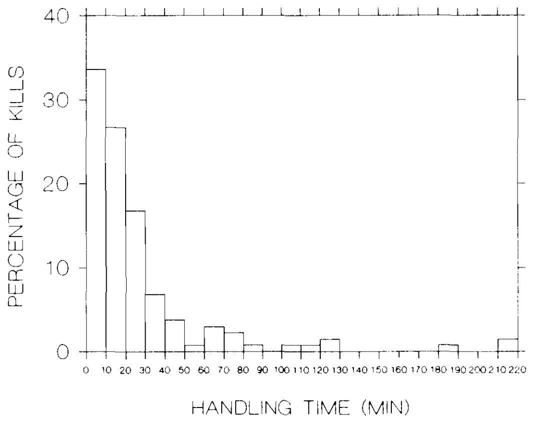
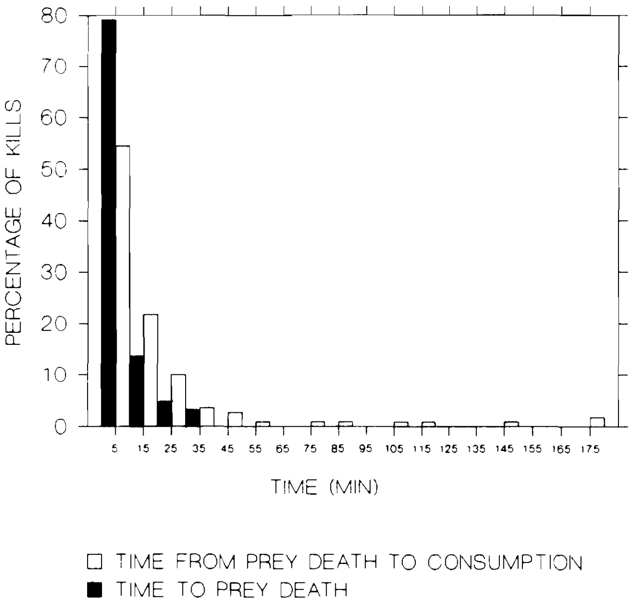


Table 4. Behavioural budgets for transient pods that regularly forage in nearshore areas (Q3, T3, Y1) and those that do not (M1, O4, O20) when only a single pod was present.

	Percentage of time for each category and subcategory	
Behaviour	Nearshore foragers	Non-nearshore foragers
Foraging	87.54	67.35
Haulout	10.23	0
Nearshore	25.41	1.56
Offshore	18.80	46.84
Foraging−travel	12.87	7.34
Feeding	20.23	11.61
Fast travel	0	0
Travel	10.03	31.38
Rest	2.21	0
Social−play	0.22	1.27
All	0.15	0.06
Some	0.07	1.21
Total	100	100
Number of hours	68.6	90.9

Fig. 8. Frequency distribution of prey-handling times, divided into the two components: the time from when the prey is encountered until it is killed (T_K) and the time from the death of the prey until it is completely consumed (T_E).



porpoises, two sea lions (exact species identification was not possible), and an adult male elephant seal. As the estimated average energy intake rate more than surpassed the predicted energy needs of killer whales (Baird 1994), we suspect that the observed prey attacks must account for the vast majority of prey actually attacked during the observation periods (i.e., the observers likely missed very few attacks).

When a prey item was first captured by a member of a foraging group, all whales in the group typically converged, sometimes from distances of up to a kilometre. Prey were seen in whales' mouths during 93 of the 136 observed kills (68%). Multiple whales in a group carrying all or part of a prey item during a particular kill, which suggested prey sharing, were observed for 51% of these kills. Active prey division or transfer was also observed on 15 occasions, involving two whales ripping a seal apart, or one whale dropping a prey item and a second whale recovering it. On several occasions two whales were seen approaching each other slowly head on, one carrying a seal. Both whales then grasped the seal and backed away from each other, pulling it apart. On several other occasions, two whales were seen swimming side by side, one carrying a seal. The second individual grasped one end of the seal and the two individuals then moved their heads apart, pulling the seal in two.

Cooperation and (or) division of labour between individuals was apparent in many prey attacks. During one attack on a Dall's porpoise by a group of three killer whales, two whales alternately engaged the porpoise in a high-speed chase. In several cases when harbour seals appeared to hide in underwater rock crevices or caves, whales appeared to coordinate time below water so that at least one whale was always underwater, preventing the seals from escaping. During several harbour seal attacks in which the time from encounter with the prey to its death, T_K, was prolonged, an adult male in a group appeared not to be directly involved in attacking the prey. In these cases, while a group of females or subadults made passes by the seal, striking it with their tail or pectoral flippers, adult males occasionally appeared to prolong their dive times, possibly to stay beneath the seal and prevent its escape.

Prey-handling time was extremely variable, ranging from less than 2 min to over 3 h (Fig. 7). Taking into account prey ranging in size from harbour seal pups (ca. 10 kg) to an adult male elephant seal (ca. 1700 kg), handling time increased significantly with prey size (regression, $r^2 = 0.47$, df = 44, $p < 0.001$). However, this effect was largely due to the influence of the single elephant seal kill observed; without this observation, no effect of prey size on handling time was apparent (regression, $r^2 = 0.05$, df = 43, $p = 0.13$). For harbour seals, both T_K and the time from the death of the prey to complete consumption or abandonment of the carcass, T_E, were variable, ranging from less than 1 min to 38 and 178 min, respectively (Fig. 8). Regressions of total handling time, T_K and T_E, against killer whale group size, the age of the youngest and second-youngest whales in the group, tide height, tide direction (ebb vs. flood), sea state, and time since sunrise or to sunset were not significant. Unfortunately, observation periods were not long enough to be able to estimate the whales' hunger state. No significant differences in handling time existed between pods, but there was a seasonal difference (Mann–Whitney *U* test, $p = 0.003$), with a longer average handling time during the non-pupping–weaning period (Table 2).

Social–play behaviour

Social–play behaviours included body contact and (or) interactive movements between individuals (e.g., chasing, one whale rolling over top of another), as well as percussive and other behaviours (e.g., breaching, spyhopping, tail lobbing, flipper slapping, penile extrusion). While frequently occurring in conjunction with feeding, social–play behaviour of this type also occurred independently of other behaviours for 3.78% of the observation time. When it occurred independently, we termed this "pure" social–play behaviour. The percentage of time engaged in pure social–play behaviour increased with group size (Fig. 6; weighted regression on transformed percentages, $r^2 = 0.49$, df = 227, $p < 0.001$), and was twice as high during the seal pupping period (4.73 vs. 2.15% during the non-pupping period; Table 2), although this difference was not significant (Mann–Whitney *U* test).

Multipod associations and interactions with resident killer whales

Resident killer whales were reported and observed much more frequently within the study area than were transients (R.W. Baird, unpublished data). While multipod associations of transients were regularly observed during this study (Baird 1994), residents and transients were never observed travelling together, even though the two types of whale were recorded within several kilometres of each other on nine occasions. On four occasions, when the two types were not on intersecting courses, no obvious changes in the travel patterns of transient killer whales were observed. On five occasions where residents and transients were on intersecting courses, the transients changed their direction of travel, effectively avoiding contact with the residents. No change in the direction of travel of resident groups was observed when they were in proximity to transients.

Virtually all transient pods observed in the study have been seen associating with one or more other transient pods, either in this study or elsewhere. However, associations between transient pods were nonrandom. Pods that foraged primarily in open water (M1, O4, O20) were more likely to be found associating with each other than with pods that regularly foraged at seal haulouts and other nearshore areas (Q3, T3, Y1) and vice versa (21 of 26 multipod associations involving at least 2 of these pods were between pods with similar foraging habitat preferences). Such patterns were not due to a lack of opportunity for associations between pods that foraged in different ways. Those that foraged in nearshore areas also spent up to or over 40% of their time (Table 4) in offshore areas. Thus, there was the potential for interactions between pods that foraged in these different areas.

Discussion

Seasonal occurrence

Sighting and encounter records showed a clear peak in the presence of transient killer whales in the study area during August and September, which represent the latter two-thirds of the harbour seal pupping–weaning–postweaning period (Fig. 4). The average per capita energy intake rate during the seal pupping–weaning period is significantly greater than during the remainder of the year (Table 2), implying that transients may preferentially use the study area during this period because of the increase in prey availability, as has been suggested for other areas (Condy et al. 1978; Lopez and Lopez 1985; Guinet 1991*b*). The relatively small number of sightings and encounters in the first month of this 3-month period (July) implies that it may be the harbour seal weaning and postweaning periods that result in the greatest increase in prey availability, rather than pupping per se. Because the timing of pupping varies along the British Columbia coast (Bigg 1969), it is possible that during July, transients may be spending most of their time in other areas where pupping has occurred earlier.

If this research had been land-based (as were the other studies mentioned), a seasonal peak in occurrence would have been even more pronounced than is apparent in this study, owing to the seasonal differences in use of nearshore areas. However, because these differences in habitat use were largely pod-specific, to conclude that transients utilize the area more during the pupping period is not strictly accurate. Rather, some groups of transients appear to use the area regularly year-round, while others (which appear to specialize in foraging around pinniped haulouts and other nearshore areas) seem to use the area preferentially during the weaning–postweaning period (Fig. 5).

Such conclusions, and others we draw below, hinge upon our assumption that the presence of our research vessel and other recreational or commercial vessels around the whales had little or no effect on their occurrence or behaviour within the study area. Recreational and commercial vessel traffic in the study area is greatest during the seal pupping–weaning period. Increased use of the area by transient killer whales during August and September suggests that their broad-scale use of the study area may not be greatly affected by the presence of vessel traffic. Similarly, Osborne (1991) noted that southern resident killer whales appear to have increased their use of Haro Strait in recent years despite an increase in the amount of commercial whale-watching traffic, suggesting that the increase in vessel traffic has not resulted in broad-scale shifts in their habitat use. Little information is available on the potential short-term impacts of vessels on killer whale behaviour or spatial patterns. Kruse (1991) claimed that northern resident killer whales increased their speed in the presence of boats, but her conclusions were not supported by the data presented (Duffus and Dearden 1992). Evidence collected during a study in progress in Haro Strait on interactions between boats and killer whales suggests that resident killer whales do not change their behaviour in the presence of boats (R. Otis, personal communication; see Phillips and Baird 1993). In the case of transients, Baird (1994) noted that the observed food intake was approximately twice the animals' predicted energy needs, suggesting that at least in terms of prey capture, transients were not greatly affected by the presence of the research boat. For all these reasons, we believe that the occurrence and behaviour of transients in this study were not greatly affected by our presence.

Behavioural budgets

Comparisons with previous studies that present behavioural budgets for transient killer whales are problematic for several reasons. Other researchers have focused on acoustical recordings (e.g., Morton 1990; Barrett-Lennard 1992; Saulitis 1993) or have used observational methods developed for behavioural observations of resident killer whales (e.g., Felleman et al. 1991). In both cases the distances between the observer and the whales are so great that they preclude recording the majority of prey captures (cf. Baird 1994). Thus, observations of feeding appear to have been underrepresented in their samples, and behaviours often associated with feeding, such as social–play behaviours, might have been interpreted in a purely social context. As well, previous behavioural budgets have generally not included feeding as a discrete behaviour, lumping it with other foraging behaviours. Sample sizes have also been small, resulting in biased representations of actual behaviour (e.g., no social behaviour, Felleman et al. 1991; Barrett-Lennard 1992; no resting behaviour, Morton 1990).

Seasonal and pod-specific differences in occurrence and behaviour (summarized in Tables 2 and 4), corresponding to differences in prey availability and foraging tactics, also affect comparisons between studies. Taking into account differences in study design and behaviour categories, no obvious differences in the amount of time spent foraging were apparent between this study and previous work; to be noticed, however, such differences would have to be extreme, all things considered.

Foraging patterns

Less than 1% of the study area falls within 200 m of a harbour seal haulout, yet 12.4% of the total time during which transients were observed foraging was spent in these areas and 35% of the seal kills occurred there. Prolonged foraging at a haulout often resulted in multiple kills, particularly during the harbour seal pupping period. Adult and subadult harbour seals were frequently observed to move into shallow water or to haul out on shore after becoming aware of the presence of foraging transients, so prey capture probably becomes more difficult during prolonged foraging at haulouts. However, haulout foraging occurred more often during the harbour seal pupping and weaning period (Table 2), and inexperienced individuals (i.e., pups) seemed less likely to haulout in the presence of foraging transients (personal observations).

Transients were not seen intentionally stranding to capture hauled-out seals, as is regularly observed elsewhere (e.g., Lopez and Lopez 1985; Guinet 1991*a*; Hoelzel 1991). One such event has been noted locally, however, on a pebble beach at Protection Island (P. Gearin, personal communication; see Fig. 1 for the location). Such behaviour is probably infrequent for this population of transients, for several reasons. Sites where intentional killer whale stranding occurs elsewhere appear to comprise steeply sloping pebble substrates, and such sites are only rarely used by harbour seals in our study area. Intentional stranding to obtain prey also carries a risk of mortality (Guinet 1991*a*), and such behaviour should occur only when the benefits outweigh the costs. In the area around southern Vancouver Island prey abundance and food intake rates are so high (Baird 1994) that such behaviour may not be worth engaging in. Intentional stranding as a prey-capture technique also appears to be a learned behaviour, requiring extensive practice and training (Guinet 1991*a*); as such its value as a hunting technique likely increases with use, and its use may not be profitable on only an occasional basis.

Sixty-five percent of the observed kills occurred away from seal haulouts. There are several possible explanations for the occurrence of such a large proportion of kills occurring in non-haulout areas. One possibility is that the whales "trapline," i.e., they forage extensively at a haulout before moving to another, occasionally capturing prey in between, as suggested by Barrett-Lennard (1992). Data on travel routes collected in this study (R.W. Baird, unpublished data) do not support such a conclusion, however, because the routes of whales leaving haulouts vary considerably, with whales switching to any one of the other foraging types. Fast travel was observed rarely (Table 3), and never between haulouts. Another possibility is that foraging offshore may allow capture of prey other than harbour seals. All the kills Saulitis (1993) observed while watching killer whales foraging in open water were of Dall's porpoise, while all marine mammals killed near shore were harbour seals. While both the Dall's porpoise attacks and two of the three harbour porpoise kills in this study were in open water, the large number of harbour seal kills offshore (55) implies that foraging offshore in the area around southern Vancouver Island does not function solely to allow predation on other species of marine mammals. Rather, such observations seem to be best explained by the pod-specific differences in foraging patterns noted above.

Feeding behaviour

Prey sharing was difficult to observe, requiring positioning of the research vessel in front of or beside whales carrying prey, at distances less than 5 m. Handling time during many prey captures was very short, and much of the prey handling occurred far beneath the surface, with only blood or bits of blubber seen; thus, in many cases it would not have been possible to observe sharing of prey even if it occurred. Guinet (1992) observed a killer whale in the Indian Ocean consuming prey away from its group, but no such observations were made in this study. Although multiple whales in a group were documented carrying prey for only 35% of the kills, we believe that division of a single prey item between individuals in a hunting group occurred more frequently.

Almost 15% of the whales' time was spent feeding, but other behaviours often occurred after a prey animal had been killed but before it had been completely consumed. Whales often engaged in social–play behaviours after a kill. Because transient killer whales appear to hunt by stealth (Morton 1990; Baird 1994; Baird et al. 1992; Barrett-Lennard 1992; Saulitis 1993), and social–play behaviours are characterized by frequent body contact between individuals and extensive percussive behaviour (such as breaches, spyhops, tail lobs, and cartwheels), engaging in social–play behaviour during foraging periods may reduce foraging success. Once a prey item has already been captured, social–play behaviour can be exhibited without the consequent negative impact on future short-term foraging success.

The time spent feeding on a prey item varied from less than 2 min to over 3 h (Fig. 7). Such variability in prey handling time is typically ignored in studies of foraging theory (Stephens and Krebs 1986), prompting us to investigate factors possibly responsible for it. That handling time should increase with prey size or in response to prey defenses seems intuitively obvious (see Werner 1974; Forbes 1989). However, excluding the single elephant seal caught (which weighed much more than the whales could possibly have consumed), there was no relationship between handling time and prey mass (for prey ranging from 10 to 300 kg). Similarly, there is no significant relationship between handling time, T_K and T_E, and the defensive abilities of the prey. For harbour seals, both T_K and T_E could be very short (i.e., less than 1 min each). The required minimum T_K value appears to be greater (i.e., >1 min) only for prey that are more difficult to capture or dangerous, such as Dall's porpoises or sea lions, respectively, while the minimum value for T_E is likely only increased for very large prey (i.e., close to or exceeding the maximum stomach capacity of killer whales), such as adult sea lions and elephant seals.

Another factor that might affect handling time is whale group size (although it is difficult to predict whether handling would be prolonged in larger groups because of conflicts over prey allocation or reduced because of a greater number of whales consuming prey of a particular size). However, there was no relationship between whale group size and handling time. Similarly, handling time was not related to environmental factors such as tide height, tide direction (ebb vs. flood), or time since sunrise or to sunset. Thus, for harbour seals, handling prey for longer than about 2 min appears to be an unnecessary allocation of time, assuming that prey handling has no function other than as the direct outcome of killing and consuming prey. Prolonged prey handling was often characterized by behaviours typical of social–play behaviour. Play behaviour frequently decreases with increasing age, being a presumed function of learning in young animals (Fagen 1981; Harcourt 1991*a*). We suspected that prolonged prey handling by killer whales might thus serve the function of allowing young to learn prey-handling techniques, and we tested this hypothesis, but found no significant relationship between the age of the youngest or second-youngest whale in a group and the duration of prey handling, or T_K. The function of extended prey handling for transients thus remains unclear.

Social–play behaviour

Based on a sample of approximately 43 h of behaviour observations, Felleman et al. (1991) reported that percussive behaviour in transient killer whales is only regularly exhibited during predation. However, transients in this study engaged in social–play behaviours, not associated with prey captures, for 3.78% of their time, and this typically involved percussive behaviour. The frequency of such social–play behaviour varied both among group sizes (Fig. 6) and between seasons (Table 2). As the small groups seen most frequently usually comprise related individuals (Bigg et al. 1987; Baird 1994), the increase in social–play behaviour with group size may reflect increased mating opportunities or opportunities to learn courtship or mating skills in larger, multipod groups (Baird 1994), as has been suggested for resident killer whales (Rose 1991).

While the average group size was similar between the seal pupping period and the rest of the year (mean of 3.96 and 4.39 individuals, respectively), social–play behaviour was more than twice as frequent during the seal pupping period. The decrease in social–play behaviour during the non-pupping period may be related to the lower food intake during those months (Table 2). Potential prey may be alerted by the percussive activity characteristic of killer whale social–play behaviour, and harbour seals may be more difficult to catch during the winter months; as the pups age they likely gain experience in detecting killer whales and assessing the associated danger. Thus, the costs associated with social–play behaviour (i.e., alerting prey) may be greater during the non-pupping period (cf. Harcourt 1991*b*). Alternatively, play behaviour may decrease because of increased hunger levels during the non-pupping period, a trend seen in a variety of organisms (Fagen 1981).

Multipod associations and interactions with residents

Associations between pods of killer whales that inhabit a particular area are not random. Variability in association patterns has been noted within a resident community (Bigg et al. 1990), and has also been used to delineate sympatric populations (Bigg 1979). In this research, resident killer whales were observed more frequently than transients, and while multipod associations were observed for both transients and residents, the two forms were never seen associating with one another. Morton (1990) described three interactions between transients and residents; in all cases the transients appeared to avoid the residents, and in one instance the residents also changed their direction of travel, apparently to avoid the transients. In this study, transients appeared to avoid residents whenever the two forms were on intersecting courses. Because transient killer whales are usually silent, while residents vocalize frequently (Morton 1990), it is more likely that transients will detect resident killer whales while remaining undetected themselves. A recent observation by G. Ellis (personal communication) provides some functional basis for avoidance of residents by transients: a group of southern resident killer whales appeared to attack and chase a group of transients off Nanaimo, British Columbia. Combined with the morphological, genetic, ecological, and behavioural differences noted in previous studies (summarized in Baird 1994), such observations of avoidance and possible aggression between the two forms supports the supposition that transient and resident populations are reproductively isolated.

Variability in association patterns within the transient population was also apparent. As noted in Baird (1994), pods containing young whales were found disproportionately often in association with other pods, and pod-specific differences in association patterns were also observed in this study. The ability to discriminate between pods in terms of foraging tactics and seasonal patterns of habitat use has provided a possible functional explanation for these pod-specific association patterns for transients: pods preferentially associate with others with similar foraging specializations. As with Baird et al.'s (1992) argument as to why transients should not associate with residents, preferentially travelling with hunters with similar foraging abilities may be advantageous to an organism that benefits from cooperatively hunting in small groups (Baird 1994; see also Ritchie 1991; Trowbridge 1991). Intraspecific variability in foraging techniques, possibly corresponding to differential association patterns, has also been observed in other cetaceans (e.g., humpback whales, *Megaptera novaeangliae*; Weinrich 1991).

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References

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, **49**: 227–265.

Bain, D.E. 1989. An evaluation of evolutionary processes: studies of natural selection, dispersal, and cultural evolution in killer whales (*Orcinus orca*). Ph.D. thesis, University of California, Santa Cruz.

Baird, R.W. 1994. Foraging behaviour and ecology of *transient* killer whales (*Orcinus orca*). Ph.D. thesis, Simon Fraser University, Burnaby, B.C.

Baird, R.W., and Stacey, P.J. 1988*a*. Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State. Can. J. Zool. **66**: 2582–2585.

Baird, R.W., and Stacey, P.J. 1988*b*. Foraging and feeding behavior of transient killer whales. Whalewatcher, **22**(1): 11–15.

Baird, R.W., Abrams, P.A., and Dill, L.M. 1992. Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. Oecologia, **89**: 125–132.

Barrett-Lennard, L. 1992. Echolocation in wild killer whales (*Orcinus orca*). M.Sc. thesis, University of British Columbia, Vancouver.

Bigg, M.A. 1969. Clines in the pupping season of the harbour seal, *Phoca vitulina*. J. Fish. Res. Board Can. **26**: 449–455.

Bigg, M.A. 1979. Interaction between pods of killer whales off British Columbia and Washington. *In* Abstracts of the Third Biennial Conference on the Biology of Marine Mammals, Seattle, Wash., October 7–11, 1979. p. 3. [Abstr.]

Bigg, M.A., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. 1987. Killer whales—a study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo, B.C.

Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B., and Balcomb, K.C. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whaling Comm. Spec. Issue No. 12. pp. 383–405.

Calambokidis, J., and Baird, R.W. 1994. Status of marine mammals in the Strait of Georgia, Puget Sound and the Juan de Fuca Strait and potential human impacts. Can. Tech. Rep. Fish. Aquat. Sci. No. 1948. pp. 282–300.

Condy, P.R., van Aarde, R.J., and Bester, M.N. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca*, at Marion Island. J. Zool. (1965–1984), **184**: 449–464.

Duffus, D.A., and Dearden, P. 1992. Whales, science and protected area management in British Columbia, Canada. George Wright Forum, **9**(3–4): 79–87.

Ellis, G.M. 1987. Killer whales of Prince William Sound and southeast Alaska—a catalogue of individuals photoidentified, 1976–1986. Hubbs Marine Research Center Tech. Rep. No. 87-200.

Fagen, R. 1981. Animal play behavior. Oxford University Press, New York.

Felleman, F.L., Heimlich-Boran, J.R., and Osborne, R.W. 1991. The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *In* Dolphin societies—discoveries and puzzles. *Edited by* K. Pryor and K.S. Norris. University of California Press, Berkeley. pp. 113–147.

Forbes, L.S. 1989. Prey defences and predator handling behaviour: the dangerous prey hypothesis. Oikos, **55**: 155–158.

Ford, J.K.B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Can. J. Zool. **67**: 727–745.

Ford, J.K.B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. **69**: 1454–1483.

Guinet, C. 1990. Sympatrie des deux catégories d'orques dans le Détroit de Johnstone, Colombie Britannique. Rev. Ecol. Terre Vie, **45**: 25–34.

Guinet, C. 1991*a*. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). Can. J. Zool. **69**: 2712–2716.

Guinet, C. 1991*b*. L'orque (*Orcinus orca*) autour de l'archipel Crozet—comparaison avec d'autres localités. Rev. Ecol. Terre Vie, **46**: 321–337.

Guinet, C. 1992. Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. Can. J. Zool. **70**: 1656–1667.

Harcourt, R. 1991*a*. The development of play in the South American fur seal. Ethology, **88**: 191–202.

Harcourt, R. 1991*b*. Survivorship costs of play in the South American fur seal. Anim. Behav. **42**: 509–511.

Heimlich-Boran, J.R. 1988. Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. Can. J. Zool. **66**: 565–578.

Hoelzel, A.R. 1989. Behavioural ecology and population genetics of the killer whale. Ph.D. dissertation, University of Cambridge, Cambridge.

Hoelzel, A.R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina; food sharing, provisioning and foraging strategy. Behav. Ecol. Sociobiol. **29**: 197–204.

Hoelzel, A.R., and Osborne, R.W. 1986. Killer whale call characteristics: implications for cooperative foraging strategies. *In* Behavioral biology of killer whales. *Edited by* B.C. Kirkevold and J.S. Lockard. Alan R. Liss, Inc., New York. pp. 373–403.

Jacobsen, J.K. 1986. The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia. *In* Behavioral biology of killer whales. *Edited by* B.C. Kirkevold and J.S. Lockard. Alan R. Liss, Inc., New York. pp. 135–185.

Jacobsen, J.K. 1990. Associations and social behaviors among killer whales (*Orcinus orca*) in the Johnstone Strait, British Columbia, 1979–1986. M.A. thesis, Humboldt State University, Arcata, Calif.

Jefferson, T.A., Stacey, P.J., and Baird, R.W. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Rev. **21**: 151–180.

Kruse, S. 1991. The interactions between killer whales and boats in Johnstone Strait, B.C. *In* Dolphin societies—discoveries and puzzles. *Edited by* K. Pryor and K.S. Norris. University of California Press, Berkeley. pp. 149–159.

Lopez, J.C., and Lopez, D. 1985. Killer whales (*Orcinus orca*) of Patagonia and their behavior of intentional stranding while hunting nearshore. J. Mammal. **66**: 181–183.

Martin, P., and Bateson, P. 1988. Measuring behaviour, an introductory guide. Cambridge University Press, Cambridge.

Morton, A.B. 1990. A quantitative comparison of the behaviour of resident and transient forms of the killer whale off the central British Columbia coast. Rep. Int. Whaling Comm. Spec. Issue No. 12. pp. 245–248.

Nichol, L.M. 1990. Seasonal movements and foraging behaviour of resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. M.Sc. thesis, University of British Columbia, Vancouver.

Oftedal, O.T., Boness, D.J., and Tedman, R.A. 1987. The behavior, physiology, and anatomy of lactation in the Pinnipedia. Curr. Mammal. **1**: 175–245.

Olesiuk, P.F., Bigg, M.A., and Ellis, G.M. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep. Int. Whaling Comm. Spec. Issue No. 12. pp. 209–243.

Osborne, R.W. 1991. Trends in killer whale movements, vessel traffic, and whale watching in Haro Strait. *In* Proceedings of Puget Sound Research '91, Seattle, Wash., January 4–5, 1991. *Edited by* T.W. Ransom. Puget Sound Water Quality Authority, Olympia, Wash. pp. 672–688.

Osborne, R., Calambokidis, J., and Dorsey, E.M. 1988. A guide to marine mammals of Greater Puget Sound. Island Publishers, Anacortes, Wash.

Phillips, N.E., and Baird, R.W. 1993. Are killer whales harassed by boats? Victoria Nat. **50**(3): 10–11.

Ritchie, M.E. 1991. Inheritance of optimal foraging behaviour in Columbian ground squirrels. Evol. Ecol. **5**: 146–159.

Rose, N.A. 1991. All-male groups in killer whale, *Orcinus orca*: fights or fun? *In* Abstracts of the Ninth Biennial Conference on the Biology of Marine Mammals, Chicago, Ill., December 5–9, 1991. Society for Marine Mammalogy, Chicago. p. 59. [Abstr.]

Rose, N.A. 1992. The social dynamics of male killer whales, *Orcinus orca*, in Johnstone Strait, British Columbia. Ph.D. dissertation, University of California, Santa Cruz.

Saulitis, E.L. 1993. The behavior and vocalizations of the "AT" group of killer whales (*Orcinus orca*) in Prince William Sound, Alaska. M.Sc. thesis, University of Alaska, Fairbanks.

Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

Stevens, T.A., Duffield, D.A., Asper, E.D., Hewlett, K.G., Bolz, A., Gage, L.J., and Bossart, G.D. 1989. Preliminary findings of restriction fragment differences in mitochondrial DNA among killer whales (*Orcinus orca*). Can. J. Zool. **67**: 2592–2595.

Trowbridge, C.D. 1991. Diet specialization limits herbivorous sea slug's capacity to switch among food species. Ecology, **72**: 1880–1888.

Waite, J.M. 1988. Alloparental care in killer whales (*Orcinus orca*). M.S. thesis, University of California, Santa Cruz.

Watts, P. 1991. Hauling out behaviour of the harbour seal (*Phoca vitulina richardsi*), with particular attention to thermal constraints. Ph.D. thesis, University of British Columbia, Vancouver.

Weinrich, M.T. 1991. Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. Can. J. Zool. **69**: 3012–3018.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. **31**: 1531–1536.