

# Ecological and social determinants of group size in *transient* killer whales

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Most analyses of the relationship between group size and food intake of social carnivores have shown a discrepancy between the group size that maximizes energy intake and that which is most frequently observed. Around southern Vancouver Island, British Columbia, killer whales of the so-called *transient* form forage in small groups, and appear to prey exclusively on marine mammals. Between 1986 and 1993, in approximately 434 h of observations on *transient* killer whales, we observed 138 attacks on five species of marine mammals. Harbor seals were most frequently attacked (130 occasions), and the observed average energy intake rate was more than sufficient for the whale's energetic needs. Energy intake varied with group size, with groups of three having the highest energy intake rate per individual. While groups of three were most frequently encountered, the group size experienced by an average individual in the population (i.e., typical group size) is larger than three. However, comparisons between observed and expected group sizes should utilize only groups engaged in the behavior of interest. The typical size of groups consisting only of adult and subadult whales that were engaged primarily in foraging activities confirms that these individuals are found in groups that are consistent with the maximization of energy intake hypothesis. Larger groups may form for (1) the occasional hunting of prey other than harbor seals, for which the optimal foraging group size is probably larger than three; and (2) the protection of calves and other social functions. *Key words*: dispersal, foraging, group hunting, harbor seals, killer whales, optimal group size, social structure. [*Behav Ecol* 7:408–416 (1996)]

Group hunting behavior has been recorded in numerous taxa (e.g., Bednarz, 1988; Estes and Goddard, 1967; Hector, 1986; Kruuk, 1972; Packer and Rutan, 1988; Pitcher et al., 1982). Schaller's (1972) seminal treatise has received the lion's share of attention, with numerous authors reexamining his data focusing on the energetic benefits of foraging in groups (Caraco and Wolf, 1975; Clark, 1987; Giraldeau and Gillis, 1988; Packer, 1986; Rodman, 1981). Caraco and Wolf (1975) noted that observed group sizes for lions matched the optimum for energy intake for small prey, but were larger than the optimum for large prey, and suggested that the lions may have been balancing energy intake with other determinants of fitness, such as preventing scavenging by other carnivores. Clark (1987) suggested that the group sizes of lions hunting large prey maximized survival, rather than energy intake, by reducing the variance in food intake. A further reanalysis by Giraldeau and Gillis (1988) indicated that the maximization of energy intake hypothesis might account for observed group sizes, but suggested that existing data precluded acceptance of either the energy maximizing or the survival maximizing hypotheses. These latter authors noted that the original presentation of Schaller's (1972) data did not take into account the variability associated with sexual dimorphism of body size, hunting efficiency, or genetic relatedness of hunting individuals. Despite the widespread interest in using Schaller's (1972) data to examine the question of an optimal foraging group size, numerous other problems exist with the presentation of the data which make them unacceptable for examining such a question (Packer et al., 1990). A subsequent field study by Packer et al. (1990) examined group size-specific foraging efficiency in lions, and concluded

that factors such as territorial defense and defense of cubs from infanticidal males are largely responsible for the observed group sizes.

Regardless, group hunting can have energetic benefits. An increase in foraging success could result from the synergistic effect of several individuals hunting together, either by increasing prey encounter and capture rates, or by decreasing the costs involved in the capture of large or difficult-to-handle prey. As with lions, most analyses of the relationship between group size and food intake for social carnivores have shown a discrepancy between the group size that is optimal for maximizing energy intake rate and that which most frequently occurs. Group sizes of social hunters are often larger than the predicted optima, possibly due to the benefits of increased vigilance and protection against predators and scavengers, improved use of information in the presence of scarce, patchily distributed resources, or the cooperative defense of territories or young (Clark and Mangel, 1986; Smith and Warburton, 1992).

In this study we examined the group hunting behavior of *transient* killer whales (*Orcinus orca*) around southern Vancouver Island, British Columbia. Research undertaken since the early 1970s has demonstrated the existence of two discrete forms of killer whales in that area, one that specializes on marine mammal prey (termed *transient*), and one that specializes on fish prey (termed *resident*) (Bigg et al., 1987). Our study has focused on the grouping patterns and group size-specific individual energy intake rates of *transient* killer whales to determine whether the observed frequency of occurrence of different size groups can be explained by the energy maximizing hypothesis. We also discuss our results in the context of other potential functions of grouping in this population.

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## STUDY ANIMAL

Intensive research has been undertaken on killer whales in British Columbia and in Washington State since the early 1970s. All individuals can be identified based on distinctive acquired and congenital characteristics of the dorsal fin and

saddle patch (Bigg et al., 1987). Early research identified the existence of the two forms of killer whale, originally termed *transients* and *residents* based on their site fidelity. Recent investigation has demonstrated that such names are not particularly descriptive of the movement patterns of the two forms. The *resident* form appears to be subdivided into two populations with partially overlapping ranges, one found generally from central and northern British Columbia to southeast Alaska (northern *residents*; Bigg et al., 1987; Dahlheim and Waite, 1992), and the other found in southern British Columbia and in Washington State (southern *residents*; Bigg et al., 1987). Individuals of the *transient* form are found throughout the ranges of both communities of *resident* whales. No form of territoriality, as may exist for *resident* communities, has been noted for *transient* individuals or groups. These *resident* and *transient* forms should not be confused with the territorial and nomadic or floater individuals seen in other social animals; the evidence suggests that the two forms are genetically isolated and may be incipient species (Baird et al., 1992). Such evidence includes differences in behavior, ecology, external morphology (Bain, 1989; Baird and Stacey, 1988; Bigg et al., 1987), and mitochondrial DNA (Hoelzel and Dover, 1991; Stevens et al., 1989).

For *residents*, a matrilineal group comprising from one to four generations of individuals associates with one or more other matrilineal groups for long periods (i.e., greater than 20 years; Bigg et al., 1990). These long-term groupings have been termed "pods," and are defined as groups of individuals that are observed together at least 50% of the time, over a long period (Bigg et al., 1990). A *transient* pod appears to comprise a single matrilineal group with one to two generations (Baird RW, unpublished data). *Transient* pod size changes only through birth, death, or emigration; to date, no cases of long-term immigration of individuals into a pod have been recorded (individuals that emigrate from *transient* pods seem to form their own pod; Baird, 1994). Short-term associations between individuals from different pods occur for both *residents* and *transients*.

*Transients* in British Columbia have been recorded feeding on four of the five species of pinnipeds found there and five species of cetaceans (Jefferson et al., 1991). Foraging for marine mammals occurs in a wide variety of habitats, from harbor seal (*Phoca vitulina*) haul-out sites and other nearshore areas to open water. Killer whale behavior during foraging is extremely variable (Baird and Dill, 1995). Foraging behavior around seal haul-outs and nearshore areas is characterized by close following of the contours of the shoreline or circling of rocks that seals typically frequent. Spacing between individual whales and synchronization of surfacings in such situations (as well as during foraging in open water) are extremely variable, however. Prey can be captured while the individuals in a group are separated by less than one whale body length, or when separated by up to a kilometer or more. In both situations, individuals converge on the prey item once captured. Further information on *transient* killer whale foraging behavior can be found in Baird and Dill (1995).

## METHODS

### Study area and observational methods

Data were collected over an area of approximately 3000 km<sup>2</sup> centered around the southern tip of Vancouver Island, British Columbia, Canada, including the western San Juan Islands, Washington, USA.

We located whales through sightings reported by other researchers, whale watching charter operations, fishermen, lighthouse keepers, and the public, and by traversing the

study area by boat. Observations were made by one to four observers from one or two of several small vessels (to 8 m in length). Killer whales were encountered on an occasional basis year-round from 1986 through 1993. Approximately 434 h of behavioral observations were obtained in 100 encounters. Onset and termination of sampling sessions was ad lib (after Altmann, 1974); termination of sessions was usually when subject animals were lost or when forced by lighting, sea conditions, or fuel considerations. Behavioral data were voice recorded continuously throughout encounters using a micro-cassette recorder.

Subjects were visible during periods that generally lasted 1 to 2 min; intervals between surfacing periods typically ranged from 2 to 8 min. During surfacing periods individual whales usually surfaced three to six times. Since group size was typically small, and visible behaviors were usually interspersed with periods when whales were not visible, all visible behaviors of all individuals could be recorded simultaneously. A primary assumption of this sampling regime is that the activities visible at the surface are unbiased samples of below-water activities. We discuss the validity of this assumption later. Data recorded included date, time, location [either estimated in relation to known landmarks, triangulated using a handheld compass, or by a long-range navigation device (LORAN)], general behavioral state (foraging, feeding, traveling, resting, socializing), individual whales present, distance between individuals, and prey handling time (defined as the period from when prey was first seen in close association with a whale until no further remains of prey could be seen).

### Group composition and measures of grouping tendencies

Individual whales present in each encounter were identified visually and by using photographs, using the catalogs of Bigg et al. (1987) and Ellis (1987), and unpublished catalogs maintained at the Center for Whale Research (Friday Harbor, Washington), the Marine Mammal Research Group (Victoria, British Columbia), and the Pacific Biological Station (Nanaimo, British Columbia). For the purposes of this study a "group" was defined as all whales acting in a coordinated manner during the observation period and which were within visual range of the observers. All members of a killer whale group, regardless of age, were included in counts of group membership. No information is available to estimate precisely the age at which a calf becomes a fully functional member of a foraging group, but calves estimated to be younger than 1 year of age were present in only a small proportion of encounters (11%). Group size and composition changed both within and between encounters.

A "pod" was defined as the largest group of individuals that were observed together during at least 50% of the time those individuals were encountered, over a period of years (after Bigg et al., 1990). Pod composition was determined both from this study and from unpublished sighting records provided by the aforementioned organizations. Some pods were seen on only a few occasions and insufficient supplementary information was available to determine pod size accurately. These groups ( $n = 6$ ) were not included in calculations of pod size. Pods remained stable within each encounter, but could change between encounters via births, deaths, or emigration. The shortest interval between encounters when a change in pod size was recorded was 7 months. Each group, as defined above, comprised members from one or more pods. During an encounter with the whales one or more individuals from a pod occasionally separated and acted independently from other pod members. Such individuals temporarily spent time either alone or with members of a different pod. Thus, within a particular encounter, individuals from one pod could be

considered members of separate groups, as defined above. Accordingly, for any particular observation period, the group size could be smaller than the pod size, unless pod size was one. Such temporary separation of pod members was usually of short duration and individuals remained within a few kilometers of other pod members; the longest such period of separation of pod members recorded in this study was 112 min.

Overall measures of grouping tendencies were calculated both for groups and pods. Measures used to describe grouping tendencies include the modal (most frequently observed), mean, and "typical" sizes. As noted by Jarman (1974), mean group size may not accurately represent what individuals experience; because larger groups contain more individuals they must be proportionately weighted in any calculation of the group size experienced by the average individual. Jarman (1974) termed this the "typical" group size. It is calculated as

$$G = \frac{\sum_{i=1}^n x_i^2}{\sum_{i=1}^n x_i}$$

where  $x_i$  is the number of individuals in each of  $n$  groups. Typical group size was calculated using all observations of all groups. Thus, particular individuals and groups may have been counted more than once in determining typical group size. As the duration of observation periods varied, to avoid biasing the typical group size each observation period was weighted by its duration. This was achieved by multiplying  $x_i$  by the duration of the observation period in both the numerator and the denominator. In calculating typical pod size, each pod enters the equation only once, regardless of the number of times that pod may have been seen during the study. For pods whose size changed during the study ( $n = 5$ ), the sizes of the pods when last encountered were used in calculations of mean and typical pod size.

Gender was noted for most individuals, as previously determined by Bigg et al. (1987) or based on external morphology for adult males or pigmentation in the genital area for subadults. Gender could not be determined for some juveniles and for some adult female-size animals that had not previously been recorded in this study or elsewhere. Size (and thus approximate age of juveniles) was estimated by comparing the size relative to known adult whales using photographs and/or visual observations.

#### Prey captures and energy intake calculations

In 57% of the cases prey species was 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. For these latter cases prey species was determined using a combination of location (52% were at harbor seal colonies), observations of potential prey in the area prior to capture, prey handling time, behavior, and quantity of blood or blubber observed in the water.

Sharing of prey between individuals in a group, although difficult to observe since most prey handling occurred beneath the surface, was confirmed on many occasions. Guinet (1992) noted observations of killer whales in the Indian Ocean consuming prey away from their group, but no individuals obviously attempting to consume prey away from the rest of a group were observed in our study. For purposes of calculating energy intake rates, we assumed that each prey was

shared proportionately (according to relative energetic needs) among all individuals in a feeding group. In lions, feeding groups are often larger than the groups involved in hunting (Packer, 1986), but in our study killer whale hunting and feeding group sizes were not different.

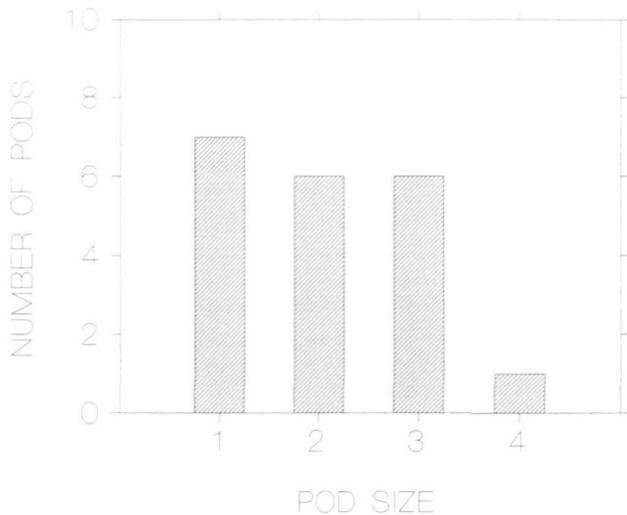
More than one prey was captured during some observation periods. Since prey handling can last up to several hours, distinguishing between consecutive prey captures can be problematic. The capture of a second or subsequent prey item was recorded when an intact prey was observed in a whale's mouth or at the surface after a prey item had been partially eaten or dismembered. In some cases, after a prey capture, it was clear that no whale in a group was carrying prey in its mouth. When whales were subsequently seen with prey, this was considered another prey capture if the whale's direction and speed of travel would have prevented retrieval of a dropped carcass. Behavioral information, such as sudden changes in speed or direction of travel, or distance between individuals, was also used to aid in discrimination of separate prey captures.

Intact prey could usually (79%) be categorized as adult, juvenile, or pup/calf. Average weights and caloric values of different size prey were estimated from published values (Deutsch et al., 1990; Leatherwood and Reeves, 1983; Olesiuk, 1993; Olesiuk and Bigg, 1988). Within a species, body composition varies regionally, seasonally, and with age, sex, and reproductive condition (Bowen et al., 1992; Pitcher, 1986; St. Aubin et al., 1978). Because body composition has not been examined in our study area for any of the prey species, and we were generally unable to assess factors such as sex, reproductive condition, or age accurately, we assumed that all prey consisted of 30% blubber, 60% proteinaceous tissue, and 10% indigestible matter. These estimates are intermediate for body composition values of harbor seals reported from southeast Alaska and several locales in the North Atlantic (Bowen et al., 1992; Markussen et al., 1992; Pitcher, 1986; St. Aubin et al., 1978).

Killer whale groups of equal size but composed of individuals of different age/sex categories differ in their total energetic needs. To standardize energetic values for groups of different age/sex composition, we calculated energy intake rates relative to an adult female-size animal. Individuals were classified into four categories: adult males, adult females/subadult males, juveniles, and calves. Energetic needs relative to an adult female-size animal, based on food consumption of captive killer whales at the Vancouver Public Aquarium and at Sealand of the Pacific, Victoria (unpublished data), were chosen to be 1.4 for adult males, 1.0 for adult females/subadult males, 0.5 for juveniles, and 1.0 for calves less than 1 year of age. The latter value was due to an observation of a doubling of food intake for lactating adult female killer whales in captivity (Vancouver Public Aquarium, unpublished data). We discuss the resiliency of our conclusions to changes in these values later.

We used an estimate of 4000 kg for adult female-size killer whales (Kriete, 1995). To calculate average energy intake rates for different size groups and for the population as a whole, we thus assumed adult males weighed 5600 kg, juveniles weighed 2000 kg, and calves less than 1 year of age weighed the same as an adult female, based on relative food intake (above).

Each block of time during which group size and composition remained constant was considered a single observation period. The energy intake rate (kcal/kg/day) for each period was calculated using the caloric content of the prey captured (taking into account their number, species, and estimated size), the combined energy requirements of the whales in the group, and the duration of the observation period. Energy



**Figure 1**  
Number of pods of each size observed during the study. For the five pods whose size changed during the study, the pod size when last encountered is used.

intake rates (kcal/kg/day) during observation periods that were less than 1 h in duration were significantly higher than for longer observation periods (Mann-Whitney U test,  $p < .001$ ). When comparing only periods greater than 1 h in duration, in 1 h blocks, no such difference in energy intake rate was found (Kruskal-Wallis one-way ANOVA,  $p = .781$ ). Thus, for statistical analyses, only observation periods greater than 59 min, for groups for which there were three or more such observation periods, were used.

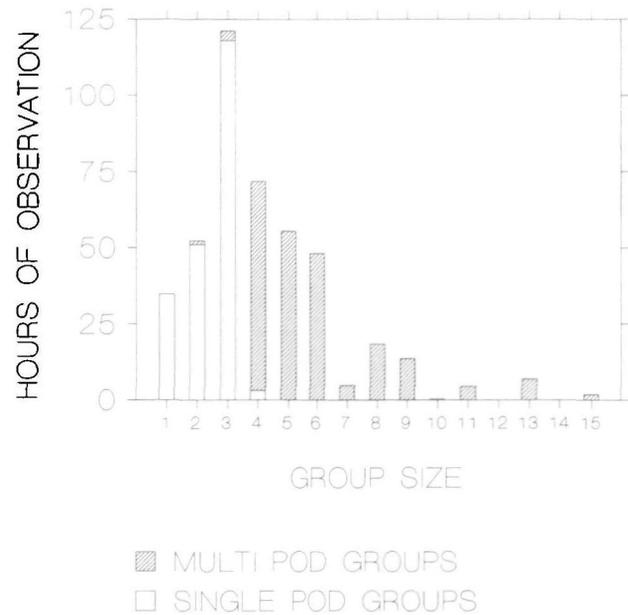
To determine whether observed prey captures accounted for the animals' energetic needs, an average energy intake rate was also calculated. This took into account all observations of all group sizes (including short-duration encounters; i.e., those less than 59 min in length) and the caloric value for all prey captured during the study. The group size (in adult female energetic equivalents) was multiplied by the duration for each observation period, resulting in a measure equivalent to the observation time of a single adult female-size whale (e.g., four adult females observed for 6 h equals 24 observation hours). These values were summed over all observation periods, producing a measure of the number of days of observations (in adult female equivalents). The summed caloric value of consumed prey was then divided by this value and by 4000 (the weight of an adult female) to produce the average energy intake rate (kcal/kg/day).

## RESULTS

### Group composition and measures of grouping tendencies

Killer whale group sizes ranged from 1 to 15 individuals. Group size and/or composition changed occasionally during some encounters, or groups were lost for short periods, resulting in 217 periods of constant group composition. These periods ranged in duration from 3 min to 9 h 11 min. During the 100 encounters in this study, 62 different individuals from 26 separate pods were recorded.

Five pods changed size during the study, either through a birth ( $n = 3$ ), death, or emigration of an individual. One emigration was positively documented in this study, but no deaths could be confirmed. In two cases pod size remained constant after a birth, as one individual disappeared from each pod. Exact times of the deaths or emigrations of the



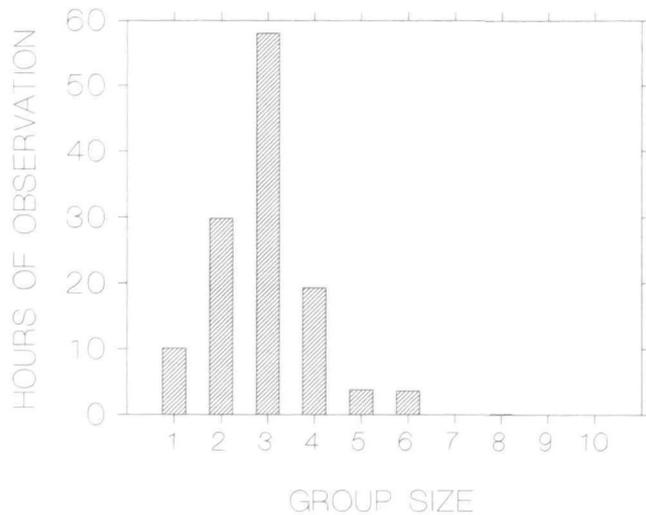
**Figure 2**  
Total hours of observations for each group size. All encounters, regardless of duration, are included. For all but one observation, groups larger than three individuals were temporary associations of two or more pods.

latter individuals are not known. For the 20 pods for which size was available (Baird, 1994; Figure 1), mean size was 2.05 individuals. Maximum pod size was 4 individuals, and typical pod size was 2.46 individuals.

The amount of time groups of different sizes were observed is shown in Figure 2. Groups larger than three individuals were almost always temporary associations of two or more pods. Conversely, groups of three individuals virtually never contained members of more than one pod, implying that pods containing one or two individuals do not join to form foraging coalitions of three individuals. The modal group size observed was 3 individuals, the mean group size was 4.21 individuals, and the typical group size was 5.62 individuals.

Large groups contain a disproportionate number of calves and juveniles (less than 6 years of age). The ratio of calves to noncalf individuals in a group increases significantly with group size (regression,  $p = .001$ ,  $r^2 = .896$ ; group sizes 2–9, not including 7). Such an increase was not due to higher productivity in larger groups since these were temporary associations of several pods. Longitudinal information on two pods (T3 and M1) encountered both before and for more than 3 years after the birth of a new calf in each, also support the conclusion that larger groups have a disproportionate number of young whales. In these cases, the typical group sizes when the calves were less than 2 years of age (12.28 and 8.31 individuals, respectively) were substantially greater than the average size of groups before the births and after the calves were more than 2 years of age (5.34 and 5.08 individuals, respectively), due to increased association with other groups.

Because groups with relatively large numbers of calves and juveniles may exist for reasons other than foraging (see Discussion), we calculated typical group size using only groups composed of adult and subadult whales (>5 years of age) that were engaged in foraging and feeding activities at least 85% of the time; typical size of such groups was 3.29 individuals (Figure 3).



**Figure 3**  
The total hours of observation for groups consisting only of adult and subadult whales engaged primarily in foraging and feeding activities.

#### Prey capture and energy intake

In total, 136 of 138 recorded attacks on marine mammals were successful (Table 1). Only 3 of 20 seabirds attacked were eaten, and thus are not considered further in these analyses [see Stacey et al. (1990) for further details]. No predation of fish was observed. During the three known captures of large prey (elephant seal and sea lions), handling times were extended (mean = 138 min) and large quantities of blubber were observed at the water surface. Similarly, handling time during the three harbor porpoise kills was prolonged (mean = 66 min), and all porpoise attacks involved high-speed chases where prey were clearly visible at the surface. During known harbor seal captures ( $n = 71$ ), handling times were shorter (mean = 28 min) and only small quantities of blubber were observed in the water. During unidentified marine mammal kills (which were classified as harbor seals), behavior did not include high-speed chases and only small quantities of blubber were observed. The handling time during these kills averaged 20 min. The beginning of these kills (i.e., when the prey was captured) was usually not noted by the observer; thus the handling time recorded was truncated. There were no significant differences between handling times for known harbor seals of different sizes (Kruskal-Wallis one-way ANOVA,  $p = .412$ ). Thus there is no evidence to indicate that the size frequency of unknown kills (classified as harbor seals) differed from the size frequency of known harbor seal kills.

Relative prey age (and thus size) was determined for the sea lion and elephant seal kills (all adults), 2 of the 3 harbor porpoise kills (juveniles), and 57 of the harbor seal kills (34 pups, 12 adults, and 11 juveniles). The average weights for the age/size class of each species attacked were used in energetic calculations. For harbor seal prey whose size could not be determined, the caloric value was estimated from the above ratio of known prey. To be conservative, for the two sea lion kills observed we used weights of California sea lions, the smaller of the two potential species. It was not possible to note accurately the proportion of each prey eaten, but Rice (1968) provides evidence that entire animals, including the skull and skeleton, are eaten by killer whales at least some of the time. Remains larger than 1% of the estimated body size of the prey were observed on only four occasions, and all occurred when prey abundance and vulnerability was highest (during the har-

**Table 1**  
Attack success and whale group sizes for different prey types

Prey type	Number of attacks	Number of successful attacks	Average number of whales (range)
Harbor seal ( <i>Phoca vitulina</i> )	130	130	3.84 (1–11)
Harbor porpoise ( <i>Phocoena phocoena</i> )	3	3	3
Dall's porpoise ( <i>Phocoenoides dalli</i> )	2	0	3
Elephant seal ( <i>Mirounga angustirostris</i> )	1	1	3
Sea lion (species not determined)	2	2	6 (4–8)

bor seal pupping and weaning period). It is likely that portions of the prey that are not eaten do not always float to the surface and are thus not visible to the observer, so for the purposes of energetic calculations we assumed that 90% of each harbor seal, harbor porpoise, and sea lion was eaten. We assumed that only 17% of the adult male elephant seal was eaten, based on the size and number of whales present and their stomach capacities (cf. Hoyt, 1990). Average energy intake, calculated for all observations of all group sizes, was approximately 62 kcal/kg/day.

As noted above, only group sizes for which there were three or more observation periods lasting more than 59 min each were used for statistical analyses. One hundred and thirty-one observation periods, on group sizes from one to nine (not including groups of seven), fit this criterion. During these periods (totalling 373.5 h) a total of 112 marine mammal kills was observed. Summary statistics for these observations are presented in Table 2.

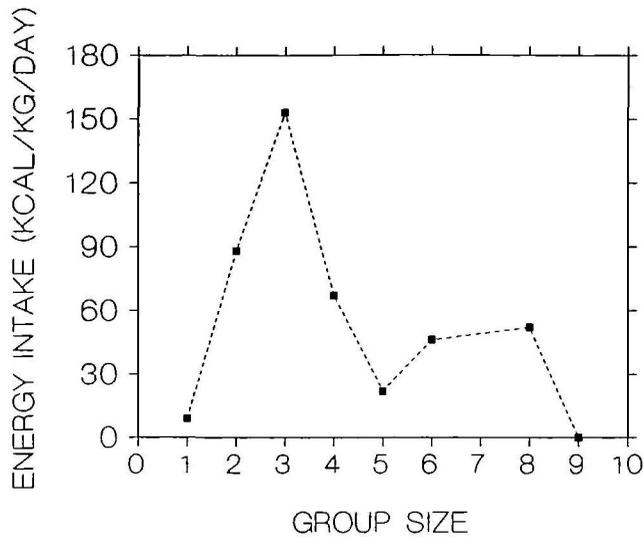
Energy intake (kcal/kg/day) for group sizes ranging from one to nine individuals is shown in Figure 4. Energy intake rate depends on group size (Kruskal-Wallis one-way ANOVA,  $p < .001$ ), due to a higher energy intake rate for individuals in groups of three (Mann-Whitney  $U$  test,  $p < 0.001$ ; group size of three versus all others combined). The lower energy intake rate for small groups was not due to these groups utilizing different hunting areas (Baird RW, unpublished data).

Repeat observations were made on some groups. Figure 5 shows the number of observation periods used in statistical analyses for each unique combination of individuals. The ma-

**Table 2**  
Group size versus energetic intake

Group size	Number of observation periods	Average energy intake in kcal/kg/day (SD)	Number of kills	Duration (h)
1	10	9 (29)	2	31.9
2	12	88 (173)	12	41.6
3	33	153 (144)	53	111.4
4	19	67 (75)	15	65.8
5	14	22 (36)	9	51.6
6	12	46 (51)	18	42.4
8	5	52 (60)	3	15.6
9	4	0 (—)	0	13.2

Only group sizes for which there are at least three observation periods, each longer than 59 min in duration, are included.



**Figure 4**  
Daily energy intake for each group size, expressed as mean consumption rate (kcal/kg/day).

majority of observation periods (71%) used in statistical analyses were for groups observed for four or less periods each. To test whether repeat observations on particular groups may have biased our results, we compared energy intake rates between several groups (of constant composition) seen repeatedly during the study. For five different groups seen repeatedly (each of three individuals), no significant differences were found in the average energy intake rate (Kruskal-Wallis one-way ANOVA,  $p = .138$ ).

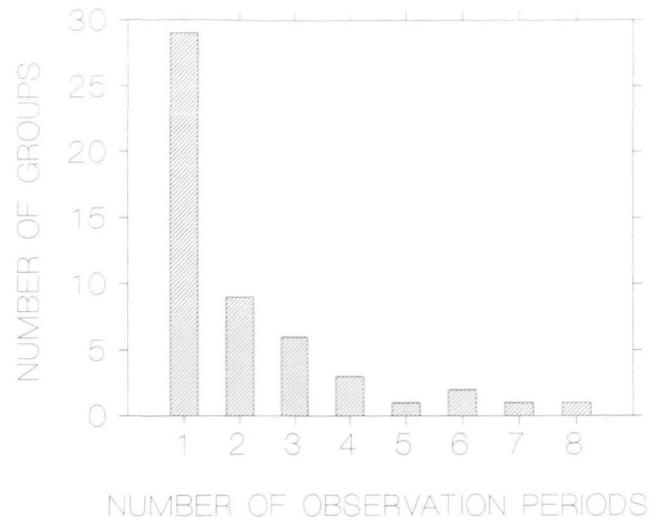
## DISCUSSION

### Energy intake and prey capture

As in most behavioral studies on cetaceans, we assumed that activities visible at the surface are representative of activities beneath the surface. While such an assumption may not always be valid, the observed average energy intake rate gives some support to its validity here. The estimated average energy intake rate of about 62 kcal/kg/day, while based on several assumptions regarding the size and proportion of prey eaten, is still substantially greater than the predicted energetic needs of the animals. Using breathing rates and physiological measurements of captive whales and swimming velocities of free-ranging animals Kriete (1995) calculated energetic requirements of 30–35 kcal/kg/day for free-ranging adult animals. We thus believe that the observed prey intake must account for the vast majority of prey actually captured during the observation periods.

This study's estimate of energy intake rate for killer whales based on observed prey captures is unique. Energy intake estimates in other studies of marine mammals have usually been based on captive animals or examination of stomach contents from wild animals. Both methods have numerous biases that limit their value for estimating energy intake of free-ranging animals. One other study discussed food intake of wild killer whales, but only presented data on weight of prey captured as a proportion of estimated whale body weights (Hoelzel, 1991).

There are several possible reasons why the average energy intake rate estimate from our study is substantially higher than the energetic requirements estimated by Kriete (1995). One possibility is that our observations are biased toward actively



**Figure 5**  
Frequency distribution of the number of observation periods for each group of a unique composition, showing only those used in statistical analyses. For example, 29 unique groups were recorded only once, 8 unique groups were recorded twice, and so on.

foraging groups. However, Baird and Dill (1995) present a time budget for *transients* in this area and note that they do not seem to spend a disproportionate amount of time foraging compared to *transients* in other areas (Barrett-Lennard, 1992; Morton, 1990). Observations of prey capture are less frequent in these other studies, but this may be due in part to biases in observational methods (Baird and Dill, 1995). On the other hand, harbor seal abundance in our study area is approximately four times higher than for the coast of British Columbia as a whole (Olesiuk PF, personal communication); thus killer whales would be expected to catch more prey here. In fact, they may increase their energy intake in this area to compensate for decreased prey abundances in other areas of the coast (cf. Katz, 1974).

Another possible reason for our high estimate of energy intake is that food intake may be lower at night than during the day. Limited evidence from a radio-tracking study implies that behaviors at night are generally similar to those during the day (Erickson, 1978), but this possibility warrants further study. Similarly, if our assumption about the proportion of each prey consumed (90%) is too high, our estimate of an average energy intake rate would be inflated. Inaccuracies in our estimates of the relative energetic needs of different size/age individuals could also affect our estimate for the average energy intake, although no information is available to suggest whether this would increase or decrease our average estimate.

The energy maximizing group size for *transient* killer whales hunting harbor seals is three individuals (Figure 4). The biases discussed above would also affect group size-specific energy intake rates. Changes in the proportion of each prey consumed, the body composition of prey, or the amount of prey caught at night should not affect our conclusions, however, as these biases should apply equally for different size groups. If the age/sex composition of groups varies with group size, our energy intake estimates could be affected, as the values we chose for relative food intake for males and females of different ages could be biased. To examine what effect changes in our estimates of the relative energetic needs of different size/age individuals would have, we calculated group size-specific energy intake rates using six alternate values (as well as combinations of these values) for different age/size classes. The alternate values chosen generally increased

the range of potential differences in energetic needs of individuals of different ages or sexes. Compared to the energetic requirements of an adult female, these values were 1.5 and 1.6 for adult males, 0.7 and 0.8 for juveniles, and 0.7 and 0.8 for calves less than 1 year of age. Each analysis indicated that individuals in groups of three had significantly (all  $p$ 's < .001) higher energy intake rates than individuals in other group sizes. Thus, our basic conclusion regarding an energy maximizing group size appears to be robust to changes in our assumptions regarding the proportion of prey consumed, the body composition of prey, the amount of prey caught at night, or the relative energetic needs of different size or age individuals.

The peak in energy intake for groups of three may occur because of a trade-off in detection abilities between killer whales and their potential prey. As killer whale group size increases their ability to detect prey (cf. Pitcher et al., 1982) and the prey encounter rate should increase. The proportion of prey captured when encountered probably also increases with group size, since larger groups are able to cooperate in chasing prey (Baird and Dill, 1995). Conversely, larger groups of killer whales should be easier for prey to detect (cf. Bertram, 1978; Goss-Custard, 1976), and marine mammals may have a variety of options to avoid predation once they have detected a potential predator. Pinnipeds may haul out to avoid capture if they are close to a haul-out site, or in open water they may dive deeply or remain motionless at the surface to avoid being detected (cf. Thomas et al., 1987). Similarly, porpoises may either flee or reduce movement in an attempt to avoid being detected. Even when seals are detected by hunting *transients*, they may occasionally be able to escape, albeit temporarily, into underwater hiding sites. While individual killer whales in a group may alternate spending time at the bottom waiting for a hiding seal to run out of air (Baird and Dill, 1995), a lone whale would have to leave the seal unguarded in a hiding site to return to the surface for air.

### Grouping patterns

Having demonstrated that there is a group size that maximizes energy intake, the next step is to compare this to observed *transient* killer whale group sizes. Three individuals is the group size most frequently observed, both in terms of number of encounters and duration of observation time, but the typical group size is much larger (5.61 individuals). However, several potential biases in our data collection lead us to believe this value is inflated. First, large groups are easier to spot than small groups, thus biasing the typical group size value upward, and second, groups were occasionally lost during data collection and such groups were always of four or fewer individuals. We believe the modal group size would not be similarly affected by these biases, due to the clear peak in observations of groups of three and to the relatively small impact on detectability of a small increase in group size from two to three individuals (Baird RW, personal observation).

Giraldeau and Gillis (1988) noted that comparisons between predicted and observed group sizes should be limited to groups engaged in the behavior of interest. Two lines of evidence (see Results) suggest that large groups contain a disproportionate number of calf and juvenile whales, and groups containing young whales may not be appropriate for comparison with the energy maximizing group size. For comparisons of the observed group sizes with the predicted group size, we thus excluded groups containing calves and juveniles less than 6 years of age. In addition, we utilized only observation periods during which whales were engaged in foraging or feeding activities for at least 85% of their time. The typical size of groups composed of adults and subadults primarily engaged

in foraging and feeding was 3.29 individuals, a value more similar to that predicted by the energy maximizing hypothesis.

In theory, minimizing the risk of an energy shortfall could also be important in terms of determining in which group sizes *transients* spend their time. However, the energetic stores of killer whales should be large enough to buffer short-term variation in energy intake, and a proper analysis of risk minimization would require knowledge of the variance in energy intake over weeks or possibly months, a logistical impossibility at the present time.

### Functions of large multipod groups

One possible function of large groups is for the occasional hunting of prey for which the optimal foraging group size is larger than three. An increase in prey size may allow additional individuals to feed from a kill without increasing competition, but it appears that large prey size per se is not a factor that drives larger foraging groups (cf. Earle, 1987; Guinet, 1991). Kills of two large (adult male) elephant seals involved only small groups (this article; Samaras and Leatherwood, 1974). Large groups may be more important for increasing the success rates for prey that are difficult to capture, such as Dall's porpoise, and/or whose capture entails risk of injury, such as sea lions. Indeed, the mean group size noted for the two instances where sea lions were captured (6.0) was higher than the mean observed for harbor seal captures (3.84; Table 1). Both the unsuccessful attacks of Dall's porpoise were by small groups of killer whales (three individuals), while two successful Dall's porpoise attacks observed locally were by larger groups (four and eight individuals; Claridge D, Walters EL, personal communications).

A second possibility is that social functions of large groups may be important. In our study, the frequency of social behavior increased with group size; groups of from one to seven individuals generally spend less than 5% of their time in social activities, whereas groups larger than seven individuals generally spend more than 15% of their time in such activities (Baird and Dill, 1995). The occasional formation of larger groups may thus function to provide opportunities for mating, alloparental care, and/or learning courtship or mating skills (cf. Haenel, 1986; Rose, 1991; Waite, 1988). As noted above, *transient* killer whale calves and juveniles are disproportionately common in large groups. G. M. Ellis (personal communication) recently observed a group of 14 southern *resident* killer whales attack and chase a group of 3 *transients* off Nanaimo, British Columbia. It is possible that the disproportionate presence of calves and juveniles in larger groups of *transients* functions to protect these more vulnerable individuals from attacks by *residents* (cf. Packer et al., 1990). Bigg et al. (1990) suggested that the absence of dispersal of *resident* killer whales might arise from a particularly strong requirement for reliable and familiar associates for hunting or maintaining territorial boundaries, or from a unique breeding structure. Similarly, the formation of large groups of *transients* might function to familiarize young whales with other individuals in the population. Such familiarization may be important for future associations between individuals, particularly to facilitate the cooperative hunting of dangerous prey such as sea lions or gray whales (*Eschrichtius robustus*).

### Pod size and dispersal

Pod size of *resident* killer whales ranges from 3 to over 50 individuals (Bigg et al., 1987), and no dispersal appears to occur from *resident* pods (Bigg et al., 1990). The largest pod size of *transients* recorded in this study was four individuals, and dispersal clearly occurs. While dispersal has only been

definitely observed twice, once in this study and once by other researchers (Bigg et al., 1987), the presence of numerous lone males is proof of its occurrence. We suggest that dispersal of individuals from *transient* pods likely occurs due to the energetic benefits of foraging in small groups. Which individuals disperse, and at which age and/or reproductive state, is discussed elsewhere (Baird, 1994, in press).

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