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The function of multi-pod aggregations of fish-eating killer whales (*Orcinus orca*) in Kamchatka, Far East Russia

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Abstract In fish-eating North Pacific killer whales, large multi-pod aggregations of up to 100 animals often occur. These aggregations are thought to be reproductive gatherings where mating between members of different pods takes place. However, killer whales are social animals, and the role of these aggregations might also be establishing and maintaining social bonds between pods. Alternatively, it is also possible that multi-pod aggregations are in some way connected with foraging or searching for fish. In this study of killer whales in the western North Pacific, we describe multi-pod aggregations quantitatively and suggest their functional role in the life of fish-eating killer whales. We show that foraging is rare in multi-pod aggregations, whether inter-clan or intra-clan, and thus they are unlikely

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E. Hoyt Whale and Dolphin Conservation Society, North Berwick, Scotland, UK to play an important role in cooperative foraging. Socialising occurs more frequently in inter-clan rather than in intra-clan aggregations, which suggests the higher arousal level and possible mating during inter-clan aggregations. In summary, multi-pod aggregations of Kamchatka killer whales might be both reproductive assemblages and "clubs" of some kind in which whales gather to establish and maintain social bonds.

Keywords Killer whales · Orcinus orca · Social behaviour · Aggregations · Mating · Kamchatka

Introduction

There are three general factors that may lead to group living (Alexander 1974): (1) reduced predation risk either because of group defense or because of the "confusion effect" resulting from an inability of a predator to single out and attack individual prey in a group (Milinski 1977; Landeau and Terborgh 1986); (2) increased foraging success either because of cooperative hunting or with groups dependent upon scattered large supplies of food that individuals would be less likely to find on their own; (3) an extreme localisation of some resource, such as safe resting sites or suitable breeding sites.

Killer whales (*Orcinus orca*) have no natural predators (Baird 2002). Thus, it is unlikely that the reduction of predation risk plays a significant role in killer whale group living (Baird 2002), despite Baird and Dill's (1996) suggestion that large multi-pod groups in mammal-eating killer whales may function for the protection of calves from attacks by larger groups of fish-eating killer whales.

On the other hand, there is strong evidence for the importance of group hunting in their sociality stemming

from the fact that fish-eating and mammal-eating killer whales have a different mean group size (Baird and Dill 1996). These ecotypes were initially described in the nearshore waters of the temperate Northeast Pacific (Bigg et al. 1987) and were found recently in the Northwest Pacific (Burdin et al. 2004). Fish-eating and mammaleating killer whales represent sympatric non-mixing populations and differ in behaviour, group size, vocal activity, and genetics (Ford et al. 1998; Baird and Whitehead 2000; Burdin et al. 2004). The basic unit of the Northeast Pacific resident killer whale's social organisation is the "matriline", which consists of a living female and several generations of her offspring (Bigg et al. 1990). In fish-eating killer whales both sexes remain in the natal matriline for their entire lives. "Pods" were previously defined as matrilines observed together on 50% or more of observation days (Bigg et al. 1990). However, later association analyses have revealed considerable fluidity in the bonds among matrilines across years (Ford and Ellis 2002). Thus, "pod" is defined mostly acoustically as a group of whales that share a repertoire of discrete calls and have social bonds (Ford 1991). Ford (1991) referred to each set of pods that shared a number of discrete call types as a "clan".

In mammal-eating killer whales dispersion from the natal matriline often occurs (Baird and Whitehead 2000). Group size is usually smaller in mammal-eating killer whales because the energy intake rate per individual reaches a maximum in groups of three (e.g., when feeding primarily on harbour seals, *Phoca vitulina*), and declines for groups larger (or smaller) than three (Baird and Dill 1996). Group size may be related to the ability to detect prey, yet larger groups are also more likely to be detected by potential prey (Baird and Dill 1996).

Fish-eating killer whales benefit from large group size because they often feed on large schools of fish that can be chased and herded efficiently by a larger number of hunters (Ford et al. 1998). Also, large group sizes may enhance hunting success through the sharing of echolocation information over wide areas to locate patchily distributed fish schools (Barrett-Lennard et al. 1996). However, as group size increases, competition and interference will likely reduce the advantages of group membership (Giraldeau and Caraco 2000).

In British Columbia (Northeast Pacific), groups of fisheating killer whales usually contained 3-39 individuals (mean = 10.6) (Morton 1990), but some multi-pod aggregations numbered more than 100 whales (Bigg et al. 1987). In Avacha Gulf, Kamchatka (Northwest Pacific), the reported group size was from 1 to 49 animals (mean = 9.56) (Tarasyan et al. 2005), although our recent observations show that aggregations of up to 100 animals sometimes occur (Ivkovich et al. 2007). Ford (1989) reported that multi-pod aggregations in fish-eating killer whales had extremely high levels of acoustic activity. Baird and Dill (1995) noted that social play behaviour increased with group size for mammal-eating killer whales and suggested that the increase in social play behaviour in large multi-pod groups may reflect increased mating opportunities. Matkin et al. (1997) suspected that killer whales form multi-pod aggregations for social and mating reasons. They noted that in these aggregations mature males were sometimes observed temporarily travelling apart from their natal pods closely following reproductive females from other pods, and social and sexual activity was frequently observed at these times (Matkin et al. 1997). However, the sexual activity in killer whales is not necessarily connected with mating; Rose (1992) described sexual interactions between adult male resident killer whales. Consequently, multi-pod aggregations may be not just reproductive assemblages, but they could function as "clubs" in which the whales gather to establish and maintain social bonds. It is also possible that multi-pod aggregations are in some way connected with foraging or searching for fish. In this study we describe multi-pod aggregations quantitatively and suggest their functional role in the life of fish-eating killer whales.

Methods

Data collection

Studies were conducted as part of the Far East Russia Orca Project (FEROP) in the central part of Avacha Gulf, Kamchatka peninsula, Russia (Northwest Pacific) (Fig. 1). We used the data from 2005 to 2007 field seasons for the analysis of the seasonality of multi-pod aggregations (Table 1). We used the data from 2006 to 2007 for the analysis of activity budgets in different types of aggregations, because the instantaneous sampling of activity type was performed only since 2006. We excluded eight encounters from 2006 to



Fig. 1 Map of the study area

2007 where activity type was not obvious during a substantial amount of time through the encounter. As a result, 52 encounters were included into the analysis of activity budgets in different types of aggregations.

We used a 4-m inflatable boat to approach the whales for observations, photography and underwater sound recordings. The photographic identification method (Bigg et al. 1983) was used for identifying individual killer whales and groups. A Canon EOS 1D digital camera and 100–400-mm lens were used for taking photographs. For photo-identification we approached the whales to a distance of 30–70 m when they were travelling, or moved the boat 200–300 m ahead of the animals and waited until they passed us.

In our observations we distinguished "groupings" and "aggregations" (Table 2). A "grouping" was defined as whales within three body lengths of each other moving together and displaying a similar type of activity. An "aggregation" was defined as all killer whale groupings moving together within visual range of the research boat. Each time we found a new aggregation of killer whales, we classified this as a new encounter.

Kamchatka fish-eating killer whales have pod-specific vocal dialects (Filatova et al. 2003). The repertoire of discrete calls—the vocal dialect—has been defined for most of the identified social units (for the definition of "unit" see Table 2). Discrete call classification is based on the existing catalogue (Filatova et al. 2004) with some additional call types found in groups rarely visiting the area.

We discern three major levels of acoustic relationship (Ford 1991) (see also Table 2):

- 1. If two different units share all the discrete calls in their repertoires, they belong to the same *acoustic pod*.
- 2. If two different units share not all but some discrete calls in their repertoires, they belong to different *acoustic pods*, but to the same *acoustic clan*.
- 3. If they share no calls, they belong to different *acoustic clans*.

Units from the same acoustic pod often travel separately, and we frequently met subgroups of pods rather than a whole pod. Thus, when we say that the particular pod was present in an aggregation, this means that at least one unit from this pod was identified.

For analyses of the behaviour, we grouped the activities of killer whales into the following categories (based on Ford 1989; Barrett-Lennard et al. 1996):

Foraging: This category includes all occasions in which the whales were seen carrying fish in their mouths or when their behaviour featured intensive non-directional swimming, irregular diving patterns and varying swimming speeds with sudden changes in direction and short periods of high speed swimming just below the surface. *Travelling*: A pod is considered to be travelling when all of its members moved on the same course at the same speed, and there was no indication of feeding activity. *Resting*: When resting, all members of a pod joined together in a tight formation and either stayed in the

Year	Season	N days	N encounters	N pods			Encounter duration
				Single	Several	Multi	(min, mean \pm SD)
2005	June–July	16	16	6	5	5	253 ± 108
	August-September	17	19	2	13	4	278 ± 139
2006	June–July	18	21	7	11	3	161 ± 109
	August-September	14	18	6	8	4	260 ± 127
2007	July	7	8	3	2	3	197 ± 60
	August	12	13	4	7	2	241 ± 119
Total		84	95	28	46	21	

Table 1 Number of days, encounters with different numbers of pods and duration of encounters broken down by season and by year

Table 2 List of terms used in this paper for the description of social, spatial-temporal and acoustical associations of killer whales

Term	Type of association	Definition
Unit	Social	Individuals that form long-term stable associations and spend most of the time together
Pod	Acoustical	Whales that share a repertoire of discrete calls
Clan	Acoustical	Pods that share a number of discrete call types
Grouping	Spatial-temporal	Whales within three body lengths of each other moving together and displaying a similar type of activity
Aggregation	Spatial-temporal	Groupings moving together within visual range of the research boat

same place or moved slowly. Dives and surfacings became highly regular and coordinated.

Socialising: Socialising whales stayed grouped together or swam on a consistent course at 3–6 km/h and engaged in social interactions and aerial displays (e.g., breaching, flipper and fluke slapping, chases, rolling over each other and sexual interactions).

During the encounter, we noted the group activity type each 5 min using the method of instantaneous sampling (Lehner 1996). It was impossible to track the behaviour of each individual whale, so we noted the activity of the majority of whales. If there was no major activity type for all whales, the data were excluded from the analysis.

Study populations

Thirty-seven stable social units (for the definition of "unit" see Table 2) of fish-eating killer whales were distinguished based on statistical analysis of associations and direct observations in the Avacha Gulf area (Burdin et al. 2007). The ecological specialisation and social structure of all these whales appear similar to that of the Northeast Pacific fisheating ("resident") killer whales: they were seen feeding only on fish, and their travelling patterns, group size and lack of postnatal dispersion resemble those of the Northeast Pacific fish-eating killer whales (Burdin et al. 2004; Tarasvan et al. 2005; Ivkovich 2006). Besides this, some killer whales were found to have features similar to mammaleating ("transient") killer whales. They probably represent a separate population because they differed morphologically from fish-eating killer whales and did not intermix with them (Burdin et al. 2004; Ivkovich 2006). This study deals only with fish-eating killer whales, because the social structure and occurrence patterns of mammal-eating killer whales are different. Therefore, the data on mammal-eating groups were excluded from the analysis.

In the Avacha Gulf area there are at least three acoustic clans of fish-eating killer whales—Avacha clan, K19 clan and K20 clan (Filatova et al. 2006, 2007). Avacha clan, consisting of more than 250 whales in at least 12 pods, is the most common. There are also some rarely occurring groups with an indefinite status. In this study we regard them as separate clans because our limited recordings reveal no sounds shared with Avacha, K19 or K20 clans.

Data analysis

To define the number of pods in a multi-pod aggregation, we analysed how often we met aggregations of various numbers of pods and animals.

We analysed the occurrence of different aggregations throughout the field season (late June-early September)

using the chi-square test. For this, we divided the field season into two halves: (1) from the start of the field season till 31 July and (2) from 1 August till the end of the field season.

To analyse the frequencies of different activity types through different aggregations, we noted the group activity type every 5 min using the method of instantaneous sampling (Lehner 1996). These data were processed in two ways for further analysis:

- For the analysis of frequencies, we took ten regularly spaced samples from each encounter to avoid pseudoreplication. We compared the frequencies of occurrence of activity types during different aggregations using the chi-square test. We used the Yates chi-square test if there were only two types of events. We applied Bonferroni correction in all pairwise comparisons. To estimate the influence of two factors (the number of pods and number of clans) on the frequency of occurrence of different activity types, we performed a log-linear analysis.
- 2. To analyse the medium occurrence of activity types in different aggregation types, we calculated the number of samples of each activity for each encounter. The number of samples was not normally distributed and could not be adjusted to normal, so we used non-parametric methods to analyse this variable. We compared the number of samples of each activity in different aggregations using the Kruscall–Wallis H test. We performed post hoc pairwise comparisons using the Mann–Whitney *U* test. We applied Bonferroni correction in all pairwise comparisons.

Results

Number of pods in a multi-pod aggregation

We found that most often we encountered single pods, and less often, in decreasing order, aggregations of two, three and four pods (Fig. 2). Aggregations of five pods, however, were encountered more frequently than four pods. On this basis we decided to consider the aggregation of five or more pods to be "multi-pod". We refer below to aggregations of two to four pods as "several".

Occurrence of multi-pod aggregations throughout the field season

We compared the frequency of occurrence of single, several and multi-pod aggregations between the first and second halves of the field season using the chi-square test. There were no significant differences in the frequency of



Fig. 2 Histogram showing number of encounters with different numbers of pods

Table 3 The frequency of occurrence of different activity types in single, several and multi-pod aggregations

	Travelling	Foraging	Resting	Socialising	Total
Single	93	40	42	5	180
Several	129	49	36	36	250
Multi	57	4	16	13	90
Total	279	93	94	54	520

occurrence between the first and the second halves of the field season ($\chi^2 = 0.70$, df = 2, P = 0.706). There were no significant differences in the frequency of occurrence of different aggregations between the years 2005, 2006 and 2007 ($\chi^2 = 1.162$, df = 4, P = 0.884).

Frequency of occurrence of different activity types in aggregations with different numbers of pods and clans

The frequency of occurrence of different activity types in single, several and multi-pod aggregations (Table 3) differed significantly ($\chi^2 = 33.26$, df = 6, P < 0.001). The percentages of activity types in single, several and multi-pod aggregations are shown in Fig. 3a.

To find out which differences contributed more to the overall significance, we performed pairwise comparisons of aggregation types and calculated residual (observed minus expected) frequencies for each activity type (Table 4). The differences for all pairwise comparisons were highly significant (single vs. several pod aggregations: $\chi^2 = 19.78$, df = 3, P < 0.001; single vs. multi-pod: $\chi^2 = 26.22$, df = 3, P < 0.001; several vs. multi-pod: $\chi^2 = 11.91$, df = 3, P < 0.01). The lowest absolute values of residuals had travelling and foraging in the single versus several pod comparison; resting in the single versus multi-pod comparison (Table 4). The highest





Fig. 3 Frequency of the occurrence of activity types in aggregations with different numbers of **a** pods, **b** pods and clans

Table 4 Residual (observed minus expected) frequency of each activity type in pairwise comparisons of aggregation types ("several" means two to four pods; "multi" is five pods or more)

	Type of activity				
	Travelling	Foraging	Resting	Socialising	
Single vs. several	0.70	-2.74	-9.35	12.16	
Single vs. multi	-7.00	10.67	3.33	-7.00	
Several vs. multi	-7.76	10.03	-2.24	-0.03	

absolute values of residuals had socialising in the single versus several pod comparison; foraging in the single versus multi-pod comparison and in the several versus multi-pod comparison.

We also compared the frequencies of occurrence of different activity types in aggregations including one acoustic clan versus aggregations with more than one clan. The difference was highly significant ($\chi^2 = 32.66$, df = 3, P < 0.001).

Log-linear analysis of a three-way cross-tabulation table showed the interaction of all three variables: (1) number of pods, (2) number of clans and (3) type of activity (best model 321: $\chi^2 = 0.0000$, df = 0, P = 1.0000; see Table 5).

Figure 3b shows the percentages of activity types in single, several and multi-pod aggregations including one acoustic clan versus several and multi-pod aggregations with more than one clan. Socialising rates in several and

 Table 5 Results of testing different models with log-linear analysis

Model to be tested	Max likelihood χ^2	df	Р	
21	252.60	18	< 0.001	
31	332.83	12	< 0.001	
32	196.53	16	< 0.001	
21, 32	31.99	12	0.001	
31, 32	86.17	8	< 0.001	
31, 21	21.84	9	0.009	
31, 21, 32	2.84	6	0.828	
321	0.00	0	1.000	

Variables in the model: (1) number of pods; (2) number of clans; (3) type of activity

multi-pod aggregations within clan categories were similar (several vs. multi-pod in one clan: $\chi^2 = 0.29$, df = 1, P = 0.591; several vs. multi-pod in more than one clan: $\chi^2 = 0.55$, df = 1, P = 0.458), but socialising rates in several and multi-pod aggregations including one acoustic clan versus several and multi-pod aggregations with more than one clan were significantly different (several + multi in one clan vs. several + multi in more than one clan: $\chi^2 = 14.41$, df = 1, P < 0.001).

Foraging rates differed significantly across aggregation categories (single vs. several vs. multi-pod: $\chi^2 = 13.88$, df = 2, P < 0.001). In pairwise comparisons, foraging rates differed significantly between several and multi-pod aggregations ($\chi^2 = 11.55$, df = 1, P < 0.01) and between single and multi-pod aggregations ($\chi^2 = 13.90$, df = 1, P < 0.001). Foraging rates did not differ significantly between single and several-pod aggregations ($\chi^2 = 0.44$, df = 1, P = 0.508). In the comparison between aggregations with different clan numbers, the foraging rate did not differ in several and multi-pod aggregations including one acoustic clan versus several and multi-pod aggregations with more than one clan (several + multi in one clan vs. several + multi in more than one clan: $\chi^2 = 2.00$, df = 1, P = 0.158).

The medium occurrence of each activity in aggregations with different numbers of pods and clans

The number of samples of socialising per encounter differed significantly across single versus several versus multi-pod aggregations (Kruscall–Wallis *H* test, N = 52: H = 7.70; P = 0.021). Other activity types did not differ significantly across single versus several versus multi-pod aggregations (Kruscall–Wallis *H* test, N = 52: travelling H = 1.17; P = 0.56; foraging: H = 5.08; P = 0.079; resting: H = 2.55; P = 0.279) (Fig. 4). In pairwise comparisons, the number of samples of socialising differed significantly across single (N = 18) versus several



Fig. 4 Amount of time spent in four activity types in aggregations with different numbers of pods. *Rectangles* give the median number of calls, *boxes* show the percentiles (25–75%), and *whiskers* give the non-outlier range. *Horizontal line* shows the statistically significant difference

(N = 25) aggregations (Mann–Whitney with Bonferroni correction, U = 131.0, P = 0.025) and did not differ significantly across single (N = 18) versus multi (N = 9) (U = 46.0, P = 0.077) and across several (N = 25) versus multi (N = 9) (U = 110.0, P = 0.918).

For comparison of encounters with one clan versus more than one clan, we excluded encounters with a single pod, because there were no encounters with a single pod and more than one clan. Thus, we compared the number of samples of each activity during the presence of several and multi-pods from one clan (N = 25) and from more than one clan (N = 9). The Mann–Whitney U test showed significant differences in the number of samples of socialising in the presence of one versus more than one clan (U = 50.5, P = 0.011). Differences in the number of samples of other activity types were non-significant (travelling U = 76.0, P = 0.152; foraging U = 108.0, P = 0.854; resting U = 79.0, P = 0.161) (Fig. 5).

Discussion

Occurrence of multi-pod aggregations throughout the field season

We found no significant differences in the occurrence of multi-pod aggregations by year and throughout the field season (late June–early September). Our results agree with those from observations of multi-pod aggregations in Southeastern Alaska (Matkin et al. 1997), which take place mostly in July and August. Hoelzel (1993) reported that in Washington State and southern British Columbia, multipod sightings were considerably more common in August– September than in May–July, which may reflect local



Fig. 5 Amount of time spent in four activity types in aggregations with different numbers of clans. *Rectangles* give the median number of calls, *boxes* show the percentiles (25–75%), and *whiskers* give the non-outlier range. *Horizontal line* shows the statistically significant difference

differences in killer whale behaviour. Matkin et al. (1997) suggest that successful matings in Southeastern Alaska take place in July–August based on an estimated gestation period of 17 months (Walker et al. 1988) and the presence of calves when their observations began in mid-April. In Kamchatka, calves were already born when our field season began, except one case in 2006 when a calf was definitely born in August. We can say nothing about the frequency of occurrence of multi-pod aggregations outside of our field season; we know, however, that such aggregations can take place in May (personal communication from local fish inspector).

Possible functions of multi-pod aggregations

Large aggregations of cooperatively foraging oceanic dolphins have been observed in all oceans of the world (Würsig 1986). Cooperative fish herding has been described for Norwegian herring-eating killer whales (Similä and Ugarte 1993; Simon et al. 2006), but their typical foraging group size was only 10–20 animals (Domenici et al. 2000). In the nearshore waters of the temperate Northeast Pacific, fish-eating killer whales feed mostly on salmon (Saulitis et al. 2000, Ford and Ellis 2006), and behavioural observations suggest that they may benefit from cooperative food searching, but not necessarily from cooperative food capture (Hoelzel 1993). Hoelzel (1993) reported that the number of foraging events in killer whale subgroups diminished with increasing group size.

In our study, foraging activity was observed most often during encounters with subgroups of pods and single pods, followed by aggregations of several pods. In the larger multi-pod aggregations, foraging rarely occurred. Thus, it is unlikely that multi-pod aggregations play an important role in cooperative prey searching and foraging. It is interesting to note that foraging occurred with equal frequency in "several pod" aggregations irrespective of the number of clans and was infrequent in multi-pod aggregations of either one or two or more clans. It seems likely that a great assemblage of killer whales in one place reduces the success of individual foraging because competition and interference lower the advantages of abundance coming from the increased ability to detect and herd fish.

Socialising was rare during single-pod encounters, but occurred with equal frequency in several and multi-pod aggregations. However, socialising occurred much more frequently in aggregations that involved members of two or more clans than in intra-clan several and multi-pod aggregations.

Mating within acoustic clans appears to be rare in the Canadian Northern resident community, comprised of three clans (Barrett-Lennard 2000). However, Barrett-Lennard (2000) found no preferences for inter- or intra-clan mating in two clans from the Southeast Alaska resident community, and intra-clan mating appears to be the rule in the Southern resident community (Southern British Columbia-Washington waters), comprised of a single acoustic clan. Thus, mating preferences vary greatly between communities. However, the higher socialising rate in the inter-clan aggregations of Kamchatka killer whales suggests the higher arousal level in these aggregations compared to intra-clan aggregations. The increased mating activity may be the reason for the higher arousal level, though alternative explanations cannot be ruled out. Genetic studies to show paternity are necessary to reveal the mating patterns of Kamchatka killer whales.

Nevertheless, mating might not be the only function of multi-pod aggregations. We suggest that such aggregations also play the role of "clubs" in which the whales gather to establish and maintain social bonds. Killer whales are longlived animals with low birth rates; they live in relatively small communities (up to several hundred animals) (Baird 2001; Matkin et al. 1999) and likely recognise other members of their community. Members of different pods often travel and forage together, and this suggests that between-pod social bonds are also important for them. In social carnivores, intra-group interactions before feeding are important to alert individuals and prepare the group for hunting activities (Creel and Creel 1995; Estes and Goddard 1967). In Delphinidae, foraging aggregations of animals from different social groups (pods, families, alliances) are common (Würsig and Würsig 1980; Hoelzel 1994). Because they hunt together, dolphins need to maintain social bonds. Bottlenose dolphins living in fission-fusion societies recognise a large number of individuals and have complex short- and long-term relationships with individuals participating in two to three levels of shifting alliances (Connor 2007). Dolphins maintain social bonds with different affiliative behaviours such as petting, contact swimming (Connor et al. 2006a), synchronous surfacing (Connor et al. 2006b) and flipper rubbing (Sakai et al. 2006), which are similar to killer whale behaviours during socialising. Intra-clan socialising in several and multi-pod aggregations of killer whales occurs more frequently than in single-pod encounters, which suggests that it could be used to maintain inter-pod social bonds.

In summary, multi-pod aggregations among Kamchatka killer whales appear to be a manifold phenomenon. They might be both the reproductive assemblages and the kind of "clubs" where whales gather to establish and maintain social bonds. The lower arousal level in intra-clan aggregations compared to inter-clan meetings is likely to be responsible for the reduced frequency of socialising, which could be because mating apparently occurs more often between clans than within clans.

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References

- Alexander RD (1974) The evolution of social behaviour. Annu Rev Ecol Syst 5:325–383
- Baird RW (2001) Status of killer whales in Canada. Can Field Nat 115:676–701
- Baird RW (2002) Killer whales of the world: natural history and conservation. Voyageur Press, Stillwater
- Baird RW, Dill LM (1995) Occurence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour, and prey handling. Can J Zool 73:1300–1311
- Baird RW, Dill LM (1996) Ecological and social determinants of group size in transient killer whales. Behav Ecol 7:408–416
- Baird RW, Whitehead H (2000) Social organization of mammaleating killer whales: group stability and dispersal patterns. Can J Zool 78:2096–2105
- Barrett-Lennard LG, Ford JKB, Heise K (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim Behav 51:553–565
- Barrett-Lennard LG (2000) Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. PhD thesis, University of British Columbia, Vancouver
- Bigg MA, MacAskie I, Ellis G (1983) Photo-identification of individual killer whales. Whalewatcher 17:3–5
- Bigg MA, Ellis GM, Ford JKB, Balcomb KC (1987) Killer whales—a study of their identification, genealogy and natural history in British Columbia and Washington State. Phantom Press, Nanaimo

- Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep Int Whale Comm Spec Issue 12:383–405
- Burdin AM, Hoyt E, Sato H, Filatova OA, Tarasyan KK (2004) Resident and transient-type killer whales, *Orcinus orca*, in southeast Kamchatka, Russia. IWC Scientific Committee (SC/ 56/SM15)
- Burdin AM, Hoyt E, Filatova OA, Ivkovich TV, Tarasyan KK, Sato H (2007) Status of killer whales (*Orcinus orca*) in Eastern Kamchatka (Russian Far East) based on photo-identification and acoustic studies. Preliminary results. IWC Scientific Committee (SC/59/SM4)
- Connor RC (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Philos Trans R Soc B 362:587–602. doi:10.1098/ rstb.2006.1997
- Connor RC, Mann J, Watson-Capps J (2006a) A sex-specific affiliative contact behavior in Indian Ocean bottlenose dolphins, *Tursiops* sp. Ethology 112:631–638. doi:10.1111/j.1439-0310. 2006.01203.x
- Connor RC, Smolker RA, Bejder L (2006b) Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins (*Tursiops aduncus*). Anim Behav 72:1371–1378. doi: 10.1016/j.anbehav.2006.03.014
- Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Anim Behav 50(5):1325– 1339
- Domenici P, Batty RS, Simila T, Ogam E (2000) Killer Whales (Orcinus orca) feeding on schooling herring (Clupea harengus) using underwater tail-slaps: kinematic analyses of field observations. J Exp Biol 203:283–294
- Estes RD, Goddard J (1967) Prey selection and hunting behavior of the African wild dog. J Wildl Manage 31(1):52–70. doi: 10.2307/3798360
- Filatova OA, Burdin AM, Hoyt E, Sato H (2003) Vocal dialects in killer whales of eastern Kamchatka peninsula, Russia. In: Proceedings of 15th Biennial conference, Society of Marine Mammalogy, Greensboro, NC, USA, p 51
- Filatova OA, Burdin AM, Hoyt E, Sato H (2004) A catalogue of discrete calls of resident killer whales (*Orcinus orca*) from the Avacha Gulf of Kamchatka peninsula. Zoologicheskyi J (J Zool) 83:1169–1180 (in Russian with English abstract)
- Filatova OA, Burdin AM, Hoyt E (2006) Estimating the status and population structure of killer whales (*Orcinus orca*) from Avacha Gulf, Kamchatka using vocal dialects. In: Proceedings of the 4th biennial conference marine mammals of Holarctic, St. Petersburg, Russia, pp 538–540
- Filatova OA, Fedutin ID, Burdin AM, Hoyt E (2007) The structure of the discrete call repertoire of killer whales *Orcinus orca* from Southeast Kamchatka. Bioacoustics 16(3):261–280
- Ford JKB (1989) Acoustic behavior of resident killer whales (*Orcinus* orca) off Vancouver Island, British Columbia. Can J Zool 67:727–745
- Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483
- Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb KC (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can J Zool 76:1456–1471
- Ford JKB, Ellis GM (2002) Reassessing the social organization of resident killer whales in British Columbia. In: Proc of the 4th international orca symposium and workshop, pp 72–74

- Ford JKB, Ellis GM (2006) Selective foraging by fish-eating killer whales (*Orcinus orca*) in British Columbia. Mar Ecol Prog Ser 316:185–199
- Giraldeau L-A, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton
- Hoelzel AR (1993) Foraging behavior and social group dynamics in Puget Sound killer whales. Anim Behav 45:581–591
- Hoelzel AR (1994) Genetics and ecology of whales and dolphins. Annu Rev Ecol Syst 25:377–399. doi:10.1146/annurev.es.25. 110194.002113
- Ivkovich TV (2006) Population structure of killer whales (Orcinus orca) in Avacha Gulf. M.Sc. thesis, St. Petersburg State University, Russia
- Ivkovich TV, Burdin AM, Sato H, Hoyt E (2007) Towards an understanding of the population structure of the killer whales (*Orcinus orca*) of Avacha gulf (Kamchatka, Russia, Northwest Pacific). In: 21st Conference of the European cetacean society, San Sebastián, Spain
- Landeau L, Terborgh J (1986) Oddity and the "confusion effect" in predation. Anim Behav 34:146-153
- Lehner PN (1996) Handbook of ethological methods. Cambridge University Press, London
- Matkin CO, Matkin DR, Ellis GM, Saulitis E, McSweeney D (1997) Movements of resident killer whales in southeastern Alaska and Prince William Sound, Alaska. Mar Mamm Sci 13:469–475. doi: 10.1111/j.1748-7692.1997.tb00653.x
- Matkin CO, Ellis G, Olesiuk P, Saulitis E (1999) Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska. Fish Bull 97:900–919
- Milinski M (1977) Do all members of a swarm suffer the same predation? Z Tierpsychol 45:373–388
- Morton AB (1990) A quantitative comparison of the behaviour of resident and transient forms of the killer whale off the central

British Columbia coast. Rep Int Whale Comm Spec Issue 12:245–250

- Rose NA (1992) The social dynamics of male killer whales, *Orcinus orca*, in Johnstone Strait, British Columbia. PhD thesis, University of California, Santa Cruz
- Sakai M, Hishii T, Takeda S, Kohshima S (2006) Flipper rubbing behaviors in wild bottlenose dolphins (*Turiops aduncus*). Mar Mamm Sci 22:966–978. doi:10.1111/j.1748-7692.2006.00082.x
- Saulitis E, Matkin CO, Barrett-Lennard LG, Heise K, Ellis G (2000) Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Mar Mamm Sci 16:94–109
- Similä T, Ugarte F (1993) Surface and underwater observation of cooperatively feeding killer whales in Northern Norway. Can J Zool 71:1494–1499
- Simon M, Ugarte F, Wahlberg M, Miller LA (2006) Icelandic killer whales Orcinus orca use a pulsed call suitable for manipulating the schooling behaviour of herring Clupea harengus. Bioacoustics 16:57–74
- Tarasyan KK, Filatova OA, Burdin AM, Hoyt E, Sato H (2005) Keys for the status of killer whales in Eastern Kamchatka, Russia: foraging ecology and acoustic behaviour. Biosph Conserv 6:73–83
- Walker LA, Cornell L, Dahl KD, Czekala NM, Dargen CM, Joseph B, Hsueh AJW, Lasley BL (1988) Urinary concentrations of ovarian steroid hormone metabolites and bioactive foliclestimulating hormone in killer whales (*Orcinus orca*) during ovarian cycles and pregnancy. Biol Reprod 39:1013–1020
- Würsig B (1986) Delphinid foraging strategies. In: Schusterman RJ (ed) Dolphin cognition and behavior: a comparative approach. Lawrence Erlbaum, Hillsdale, pp 347–359
- Würsig B, Würsig M (1980) Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the south Atlantic. Fish Bull 77:871–890