

Social behavior increases in multipod aggregations of southern Alaska resident killer whales (*Orcinus orca*)

Daniel W. Olsen^{1,2}  | Craig O. Matkin¹ | Franz J. Mueter² | Shannon Atkinson² 

¹North Gulf Oceanic Society, Homer, Alaska

²University of Alaska Fairbanks-College of Fisheries and Ocean Sciences, Juneau, Alaska

Correspondence

Daniel W. Olsen, 3430 Main Street Suite B-1, Homer, AK 99603.

Email: waterdogdan@gmail.com

Abstract

Killer whales (*Orcinus orca*) are highly social and occasionally gather in large aggregations that reach 150 individuals. During 338 encounters with Southern Alaska resident killer whales, we collected 1,352 hr of behavioral data to assess the probability of various behaviors based on season, number of pods present, presence of rarely sighted pods, and number of mitochondrial DNA haplotypes present. A binomial generalized linear model was used to estimate the role of these factors in the probability of four behaviors, foraging, resting, socializing, and traveling. The presence of “rarely sighted” pods (sighted in <5% of encounters) significantly increased probability of social behavior, and significantly decreased probability of resting. The number of pods present also significantly increased probability of increased social behavior. The presence of rarely sighted pods and the number of pods present did not have a significant interaction. Ordinal day and number of mitochondrial DNA haplotypes appears to not have changed the probability of any behavior. Foraging remained the predominant behavior throughout all factors. The concurrent increase in social behavior and decrease in resting behavior with rarely sighted pods present implies an unusually high importance of social behavior in the lives of resident killer whales.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2020 The Authors. *Marine Mammal Science* published by Wiley Periodicals LLC on behalf of Society for Marine Mammalogy.

KEYWORDS

aggregation, Alaska, behavior, cetacean, distribution, killer whale, *Orcinus orca*, social

1 | INTRODUCTION

The resident killer whale (*Orcinus orca*) is a genetically distinct ecotype found only in the northern Pacific Ocean. This piscivorous resident ecotype (salmon specialist) is found sympatrically with transient (Bigg's, mammal specialist) and off-shore (shark specialist) ecotypes (Foote et al., 2016; Morin et al., 2010; Parsons et al., 2013). Multiple decades of research in Washington, British Columbia, and Alaska have shown that residents feed primarily on Pacific salmon, live consistently in natal groups, and make highly stereotyped group-specific calls (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990; Deecke, Ford, & Spong, 2000; Ford & Ellis, 2006; Ford et al., 2016; Saulitis, Matkin, Barrett-Lennard, Heise, & Ellis, 2000; Yurk, Barrett-Lennard, Ford, & Matkin, 2002). Regular seasonal movements and patterns of habitat use have been documented for the resident ecotype (Hauser, Logsdon, Holmes, VanBlaricom, & Osborne, 2007; Matkin, Matkin, Ellis, Saulitis, & McSweeney, 1997; Olsen, Matkin, Andrews, & Atkinson, 2018; Scheel, Matkin, & Saulitis, 2001).

Long-term photographic studies have consistently demonstrated that both male and female resident killer whales remain with their mother for the entirety of their lives, with outmigration being extremely rare (Bigg et al., 1990; Matkin, Ellis, Olesiuk, & Saulitis, 1999). Matriline is defined as stable groups whose members are direct descendants of a mother or grandmother. Pods are defined as groups of matriline that are photographed together in more than 50% of encounters (Bigg et al., 1990) and have similar repertoires of calls (Ford, 1989). The consistent nature of these related groupings facilitates the assessment of behavioral budgets within the context of social aggregations.

Resident killer whales are typically found in larger groups than transient killer whales, which could be a result of foraging strategies (Baird and Dill, 1996). For residents, typical pod size ranges from 5 to 40 whales (Bigg, Ellis, Ford, & Balcomb, 1987; Ford, Ellis, & Balcomb, 1996; Morton, 1990). A certain group size may aid in searching for schooling fish (Hoelzel, 1993); however, there could be an upper group size limit at which foraging efficiency begins to be compromised, as foraging has been observed less frequently during large multipod events (Filatova et al., 2009). Additionally, a negative correlation has been found with large groups and fast nondirectional (foraging) behavior (Hoelzel, 1993).

Large multipod aggregations of resident killer whales are common and have exceeded 100 and 150 whales in British Columbia and Alaska, respectively (Bigg et al., 1987; current study). These large aggregations may occur for reinforcing social bonds between matriline and pods, mating purposes, and as opportunities for juveniles to learn social, mating, and reproductive skills (Filatova et al., 2009; Matkin et al., 1997). Vocal activity is typically very high in large aggregations (Ford, 1989). In Kamchatka, resident killer whales have been shown to engage in social behavior more frequently when multiple acoustic clans are present, and when multiple pods are present (Filatova et al., 2009).

There are two primary genetic mitochondrial DNA (mtDNA) haplotypes and a rare third one known to occur amongst resident killer whales (Parsons et al., 2013), which range in the Northern Pacific Ocean from Washington State to Alaska, Russia, and Japan. The Southern Resident (SR) mtDNA haplotype was first sampled among the southern resident killer whale population in Washington State/British Columbia, and the Northern Resident (NR) mtDNA haplotype was first sampled among the northern resident killer whale population in British Columbia (Barrett-Lennard, 2000). However, the SR mtDNA haplotype is found in resident killer whales across the North Pacific Ocean to Kamchatka, Russia, and the NR mtDNA haplotype is found as far west as Samalga Pass in the eastern Aleutian Islands (Parsons et al., 2013) and possibly Russia (Morin et al., 2010). From genetic studies of Southern Alaska residents, 65 individuals have the NR mtDNA haplotype, and 54 have the SR mtDNA haplotype (C.O.M., unpublished data). Although the population size for Southern Alaska residents is approximately 734 whales, the biopsy sampling was distributed through most pods, and therefore likely represents well over half of the population. A third resident mtDNA haplotype has only been documented once in the Aleutian Islands (Parsons et al., 2013), but has not been sampled in the Southern Alaska resident population. Microsatellite genotypes suggest weak separation between

Alaska residents with the NR mtDNA haplotype and the NR population in British Columbia, and stronger separation between the Alaska residents with the SR haplotype and the SR population in Washington State and British Columbia (Barrett-Lennard, 2000).

Social behavior and its function in resident killer whales is not well understood. Large aggregations may serve a complex purpose for this gregarious, cultural, long-lived species. Because it may occur at the expense of other important behaviors, such as foraging or resting, the function of nonforaging social behavior needs to be more closely examined. In this study, we test the hypothesis that Southern Alaska residents alter their behavior during aggregations that are large or when they contain rarely sighted pods.

2 | METHODS

Every year since 1984 and throughout this study (2006–2015), photo-identification based killer whale surveys were conducted in south-central Alaska (Figure 1). This region is characterized by long glacially carved fjords and a large sound with complex passageways and entrances. Surveys were conducted in the months of April through October from a 11 m research vessel as a part of a long-term photographic monitoring program. Each whale was assigned an alphanumeric label for identification, e.g., AB025, where the first letter represents Alaska, the second letter represents the pod, and the numeral represents the individual. In some cases, where after original naming, matriline within a pod were observed to then live together <50% of their time, they were split into separate pods. In these cases, the number of the matriarch was used as a part of the pod naming. For example, AB pod and AB025 pods are considered separate pods by definition, AB025 pod being named for the individual matriarch AB025.

The number of individuals present was estimated through photo identification, and was extrapolated to include all members of a given matriline (a mother/grandmother and all of her offspring) if at least one of the members of the

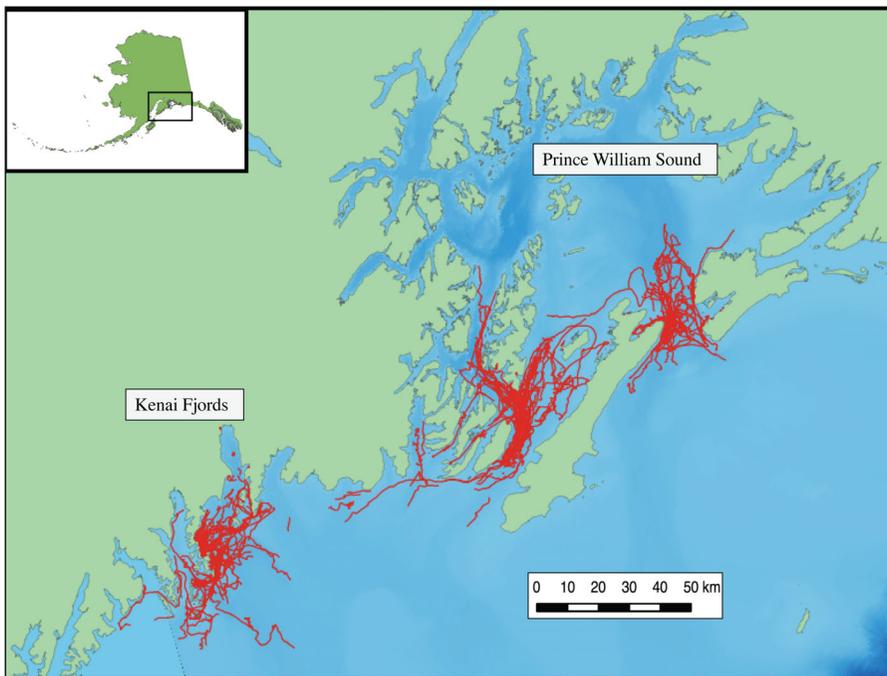


FIGURE 1 Prince William Sound and Kenai Fjords study area, with track lines of encounters with resident killer whales (*Orcinus orca*) from 2006 to 2015.

matriline was photographed and identified. This provides a conservative estimate, because all members of a matriline are together throughout their lives, but it is possible that entire matriline were missed through photographic identification during large aggregations.

Biopsy samples were taken from 1994 through the years of this study for 119 individual resident killer whales within the study area using the protocol established by Barrett-Lennard (2000) to determine mtDNA haplotype. Analysis of the mitochondrial DNA control region was used to determine whether a sampled individual belonged to the SR, NR, or a different mtDNA haplotype (Barrett-Lennard, 2000). Only the SR and NR mtDNA haplotypes have ever been encountered among resident killer whales in this region (southeast Alaska to the Alaska Peninsula). Several mtDNA haplotypes have been documented for transient killer whales (Parsons et al., 2013).

During the surveys between April and October, behavioral observations were collected from encounters during daylight hours, typically between 0700 and 2000. We used a "group follow" protocol (Altmann, 1974), and groups (aggregations) were defined as all individuals within visual range of the research vessel. Data were collected using "predominant group activity sampling," where the activity of the majority of the group is noted (Mann et al., 1999). Waypoints were collected on the survey vessel at the beginning of each encounter, and at each instance in which a change of behavior was noted. The time, location, and behavioral notes were noted in field documentation and stored as GIS shapefiles.

Behavioral category definitions were originally defined by Ford (1989), modified by Barrett-Lennard et al. (1996), Felleman et al. (1991), and Morton (1990). These categories were also used to describe behavioral differences between transient and resident killer whales in the current study area (Saulitis et al., 2000). They are as follows:

Socializing: Engaged in behaviors such as chasing, rolling, and aerial displays not related to feeding. Aerial displays included breaching, spy-hopping, and fluke- and flipper-slapping. Sexual behavior, indicated by erect penises, was also considered socializing. During socializing, vocal activity was high (Ford, 1989).

Foraging: Engaged in search for, pursuit of, capture, and consumption of prey. Fish foraging was indicated by echolocation clicks (Barrett-Lennard et al., 1996) and sporadic tight circling and lunging by individual whales (Ford, 1989; Hoelzel 1993). During fish foraging, the whales were widely dispersed, either singly or in small groups (Barrett-Lennard et al., 1996).

Traveling: Swimming in a line-abreast pattern in one or more groups, moving in a consistent direction at speeds of over 6 km/h (Barrett-Lennard et al., 1996). Individuals typically swam within a few body lengths of their neighbors.

Resting: Movement and breathing patterns closely synchronized and moving at speeds much slower than those of traveling whales (<4 km/hr) (Barrett-Lennard et al., 1996; Ford, 1989). Resting whales were commonly grouped in maternal units. Individuals typically surfaced within a single body length of their neighbors (Barrett-Lennard et al., 1996).

Milling and beach rubbing, which accounted for <1% of all observations, were not included in the analysis.

We defined "rarely sighted" pods as those that were seen in <5% of all multipod encounters, and twelve pods satisfied this definition. Fifteen pods were seen in 5% or more of encounters and were considered "frequently sighted" (Table S1).

A binomial generalized linear model (GLM) was fit using the `glm` function in R (Faraway, 2005) to estimate the probability of a given behavior based on the following factors: number of pods present, presence of rarely sighted pods, ordinal day, and estimated number of mtDNA haplotypes present. Two sets of models were fitted: one in which the observations were weighted by the duration of each behavioral event, and one where observations were not weighted, thus giving equal weight to each behavioral period. Weights were set to half of the duration of each behavioral event (in hours), which is approximately equivalent to subsampling every 2 hr. A full model was constructed that included all factors and their pairwise interactions, and a stepwise procedure was used in combination with Akaike information criterion (AIC) scores to identify the AIC-best submodel. The probability of each of the four behaviors was estimated separately using GLMs with a binomial response consisting of 1 if the behavior occurred in a given period and 0 otherwise.

3 | RESULTS

Total aggregation size ranged from 6 to 150 whales, and from 1 to 10 pods. The median number of individuals for all encounters was 15, the median number of individuals for the multipod aggregations was 28. The median number of

pods was two for all encounters, and three for multipod aggregations. On seven different days, over 100 estimated individuals were present, and on three of these days over 100 were individually photographed and identified. The two largest events (150 and 142 individuals) each continued at over 100 animals for 2–3 consecutive days. Large

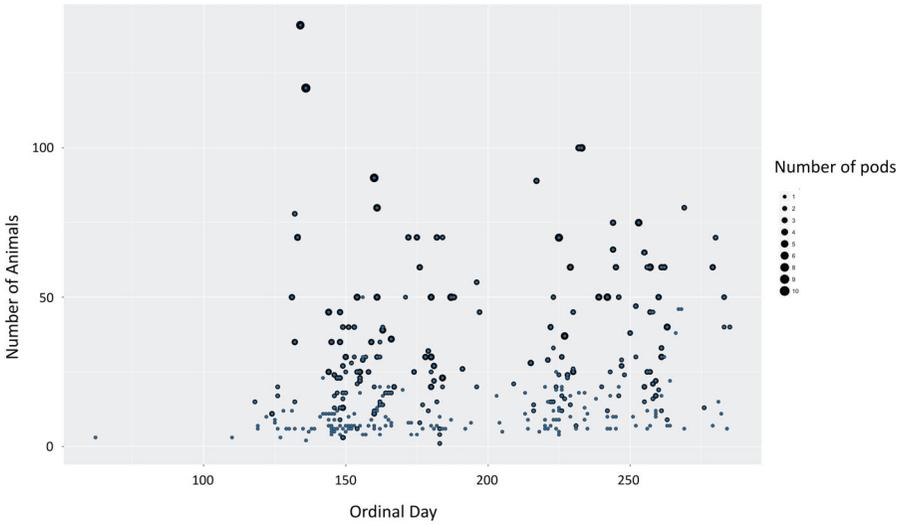


FIGURE 2 Number of whales (estimated) and pods present during encounters throughout the field season for all years, 2006–2015. Gap in data near day 200 is reflective of lower survey effort. Note: Figure includes single-pod encounters, which were not included in the analysis.

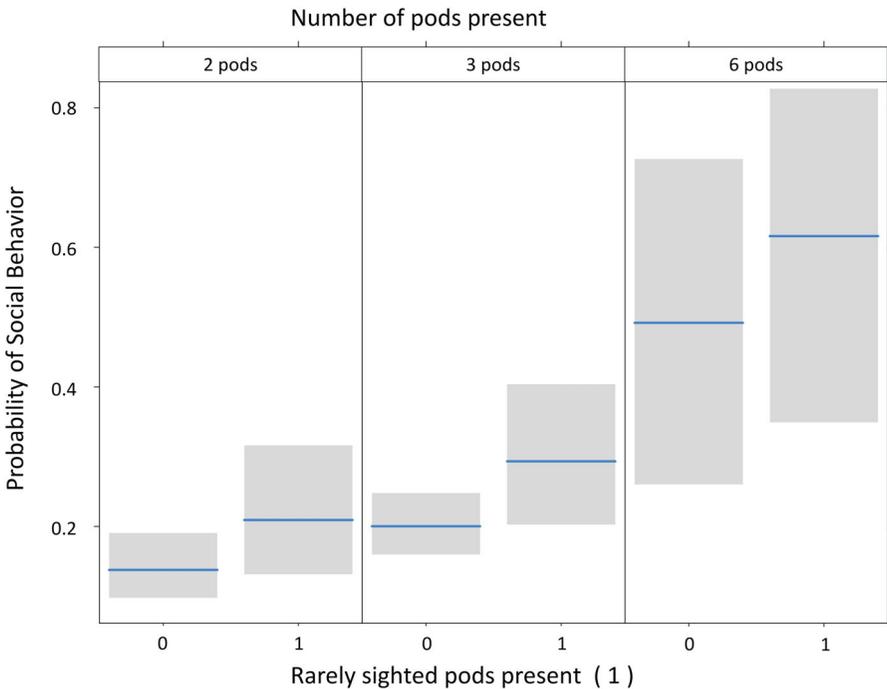


FIGURE 3 Probability of social behavior by number of pods and rarely sighted pods (interaction not significant), resulting from best-fit binomial GLM $Social \sim numberPods + rarelySightedPres + ordinalDay + numHapPres$.

aggregations of 80 individuals or more occurred in all months between May and October (Figure 2). As of 2015, the minimum estimate of cataloged individuals based on all pods documented in this region since 1984 was 734 resident killer whales from 33 pods. During the ten years of this study, 27 of these pods were encountered.

We collected 1,352 (901.7 multipod) hours of behavioral observations during 338 (178 multipod) encounters in the months of April to October, between 2006 and 2015. Percentage of time spent in the four behaviors during all encounters was social (14.7%), forage (41.8%), rest (28.9%), and travel (14.5%). Mean duration for all behaviors was 1.56 hr ($SD = 1.21$), median 1.23 hr.

For all behaviors, we began with a model that included number of pods, rarely sighted pods, number of mtDNA haplotypes present, ordinal day, and all interactions:

$$\text{response} \sim (\text{numberPods} + \text{rarelySightedPresent} + \text{numberHapPres} + \text{ordinalDay})^2.$$

This model was then run through a stepwise procedure using comparison of Akaike information criterion (AIC) scores to find the most parsimonious model for each behavior.

Probability of social behavior was significantly greater when rarely sighted pods (sighted in <5% of total encounters) were present, and significantly greater with an increase in number of pods present (Figure 3, Table 1). The interaction between these variables was not significant, and both factors were significant when run in models alone. The probability of resting behavior decreased significantly when rarely sighted pods were present (Figure 4, Table 2).

Probability of foraging was shown to be significantly less with increased number of pods and with rarely sighted pods present, but these two factors also had a significant interaction with each other, and neither factor was

TABLE 1 Results from best-fit binomial GLM for social behavior.

	Estimate	SE	z value	Pr (> z)
(Intercept)	-3.5441	1.0249	-3.458	0.000544***
numberPods	0.8232	0.3286	2.505	0.012231*
rarelySightedPresent	0.5058	0.2424	2.087	0.036905*
numHapPres	0.8075	0.5942	1.359	0.174141
numberPods : numHapPres	-0.3727	0.1772	-2.103	0.035492*

Note. Significance codes: 0 "****" 0.001 "***" 0.01 "**" 0.05 "." 0.1 " " 1.

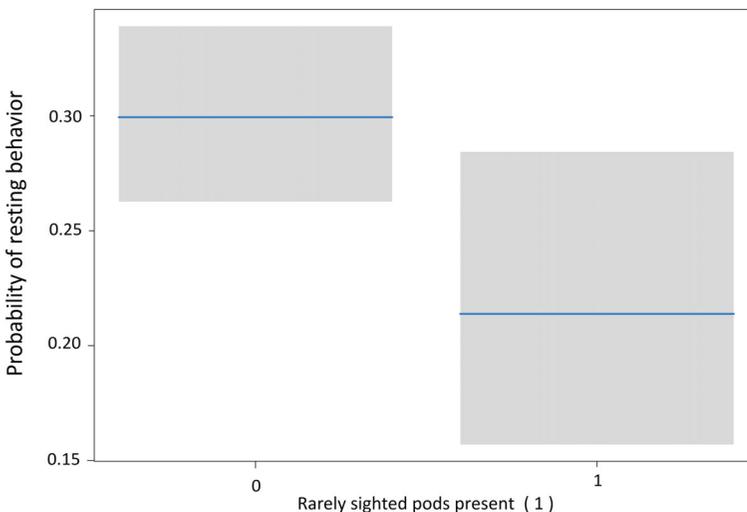


FIGURE 4 Probability of resting behavior by number of pods and rarely sighted pods, resulting from best-fit binomial GLM $\text{Rest} \sim \text{numberPods} + \text{rarelySightedPres} + \text{ordinalDay} + \text{numHapPres}$.

TABLE 2 Results from best-fit binomial GLM for resting behavior.

	Estimate	SE	z value	Pr (> z)
(Intercept)	1.10	0.90	1.23	0.22016
rarelySightedPresent1	-1.34	0.53	-2.53	0.01134*

Note: Significance codes: 0 "****" 0.001 "***" 0.01 "**" 0.05 "." 0.1 " " 1.

TABLE 3 Results from best-fit binomial GLM for foraging behavior.

	Estimate	SE	z value	Pr (> z)
(Intercept)	1.10	0.90	1.23	0.22016
numberPods	-0.59	0.25	-2.36	0.01807*
rarelySightedPresent1	-1.34	0.53	-2.53	0.01134*
jday	-0.01	0.00	-1.48	0.14023
numHapPres	0.29	0.19	1.50	0.13426
numberPods : rarelySightedPresent1	0.35	0.12	2.82	0.00474**
numberPods : jday	0.00	0.00	1.42	0.15506

Note: Significance codes: 0 "****" 0.001 "***" 0.01 "**" 0.05 "." 0.1 " " 1.

significant when alone in a model (Table 3). Probability of traveling was not significantly different by any of the covariates. Neither the ordinal day nor the number of mtDNA haplotypes present (one vs. two) had a significant difference in probability of any behavior.

Models were also run without weighting, irrespective of behavior duration, to effectively test simply the instances of observed behavior changes as individual occurrences. In these cases, social behavior still significantly increased with the presence of rarely sighted pods. Other behaviors showed no significant changes with the unweighted model.

4 | DISCUSSION

In this study, the presence of rarely sighted pods of resident killer whales resulted in increased social behavior and decreased resting behavior during multipod aggregations. Social behavior also increased with increased number of pods present. This is not the first study to find increased social behavior during multipod aggregations at the expense of other important behaviors (Filatova et al., 2009), and illustrates the importance of social behavior for these whales.

The function of large multipod aggregations is not fully understood for resident killer whales. Mating, the establishment of long-term bonds, and foraging events are all possibilities. While large aggregations of herring-consuming whales in Norway may occur due to abundant food source (Similä and Ugarte, 1993), herring appears to be unimportant for resident killer whales in the NE Pacific (Ford et al., 1998, 2016; Saulitis et al., 2000). Cooperative foraging has not been described in long-term studies of resident killer whales in Alaska or Canada (Ford et al., 1998; Saulitis et al., 2000). Most prey sharing described in British Columbia has occurred within matriline and pods (Wright, Stredulinsky, Ellis, & Ford, 2016). Among Russian residents and Southern Residents, foraging behavior has been shown to be less frequent with larger aggregations (Filatova et al., 2009; Hoelzel, 1993). In the current study, foraging remained the predominant activity through all iterations, although the probability of foraging was less during large aggregations. It may be possible that abundant prey allows for large aggregations, but is not the causal factor for them.

Social behavior and its function are not fully understood in resident killer whales. It has been suggested that long lasting bonds may be important for residents in Kamchatka (Filatova et al., 2009). It is also possible that social behavior is linked to outbreeding opportunities, although this has not been shown definitively. Sexual behaviors have been noted during periods of social behavior in British Columbia (Ford, 1989). While inbreeding has been shown to occur among the SR community (Ford et al., 2011), the authors acknowledged that all instances were performed by just one individual, and that there was also evidence of inbreeding avoidance. Mating has previously been shown in British Columbia and Southern Alaska to occur between pods that are acoustically distinct (Barrett-Lennard, 2000). In Kamchatka, increase of social behavior has also been demonstrated when acoustically distinct clans are found together (Filatova et al., 2009). For the transient killer whale ecotype in British Columbia, social behavior also increases when more than seven whales are present, suggesting that larger aggregations may be important for outbreeding (Baird and Dill, 1995). While seasonality has been suspected as a covariate for resident social and mating activity in other regions (Hoelzel, 1993), our findings do not show significant differences in any behavior by ordinal day within the field season, and aggregations of more than 80 whales occurred in all months between May and October.

The presence of rarely sighted pods was chosen as a parameter to investigate the role of interactions with pods that spend less time in the region than others. It is generally suspected and supported by satellite telemetry that the core use areas for many of these rarely sighted pods are relatively distant from the current study area. The rarely sighted AF5, AF22, and AG pods, whose primary range is Southeast Alaska, have been shown to make trips of 1,000–1,300 km to Prince William Sound and Kodiak (Matkin et al., 1997; Olsen et al., 2018). The frequently sighted AE pod, by contrast, has a very limited range of only about 200 km (Olsen et al., 2018). This extreme range difference could possibly be explained by either foraging, social, or reproductive behavior. However, trips by the AF5, AF22, and AG pods often occur during seasons in which salmon is generally abundant in their core range, making such a long trip unnecessary for the purpose of foraging (Matkin et al., 1997). It is conceivable that certain pods may travel long distances for outbreeding opportunities. The purpose of these long-distance movements warrants further investigation.

During encounters, not all matriline from a given pod were photo-identified. However, the analysis was run at the pod-level because we considered a pod to reflect one cultural unit, regardless if all matriline were present. As an example, if only one matriline of a pod were present, then presumably the calls from that pod would still be represented (Ford, 1989). It is possible that different matriline from one pod could have a differing impact on the behavior of a multipod aggregation, but we would not anticipate this, nor did we attempt to measure this impact. Furthermore, a matriline-level analysis could be inappropriate for this study when considering that certain pods such as the AJ pod have many matriline that share calls and habits, and often travel together.

In conclusion, this study presents evidence that multi-pod aggregations that contain rarely sighted pods and larger numbers of pods are accompanied by increased social behavior at the expense of resting behavior. The function of social behavior and large multipod aggregations for resident killer whales remains poorly understood. However, social behavior seems to play an important role in either reproduction, social bonding, or both. As an intelligent long-lived social species, these dynamics are likely complex. Further study is needed to define the role and function of social behavior more clearly in Southern Alaska resident killer whales, and its relationship to reproduction.

ACKNOWLEDGMENTS

The research described in this paper was supported by the Exxon Valdez Oil Spill Trustee Council. However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. This research was conducted under National Marine Fisheries Service permit #15616.

ORCID

Daniel W. Olsen  <https://orcid.org/0000-0003-4284-8598>

Shannon Atkinson  <https://orcid.org/0000-0003-1536-9209>

REFERENCES

- Altmann, J. N. (1974). Observational study of behavior: Sampling methods. *Behavior*, 49(3–4), 227–266.
- Baird, R. W., & Dill, L. M. (1995). Occurrence and behavior of transient killer whales: Seasonal and pod specific variability, foraging behavior, and prey handling. *Canadian Journal of Zoology*, 73, 1300–1311.
- Baird, R. W., & Dill, L. M. (1996). Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology*, 7, 408–416.
- Barrett-Lennard, L. G. (2000). *Population structure and mating patterns of killer whales (Orcinus orca) as revealed by DNA analysis* (Doctoral dissertation). University of British Columbia, Vancouver, Canada.
- Barrett-Lennard, L., Ford, J. K. B., & Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, 51, 553–565.
- Bigg, M. A., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1987). *Killer whales - a study in their identification, genealogy, and natural history in British Columbia and Washington State*. Nanaimo, BC: Phantom.
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, 12, 383–405.
- Deecke, V. B., Ford, J. K., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, 60, 629–638.
- Faraway, J. J. (2005). *Extending the linear model with R: Generalized linear, mixed effects and nonparametric regression models*. Boca Raton, FL: CRC Press.
- Felleman, F. L., Heimlich-Boran, J. R., & Osborne, R. W. (1991). The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. In K. W. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 113–148). Berkeley, CA: University of California Press.
- Filatova, O., Fedutin, I. D., Ivkovich, T. V., Nagaylik, M. M., Burdin, A. M., & Hoyt, E. (2009). The function of multi-pod aggregations of fish-eating killer whales (*Orcinus orca*) in Kamchatka, Far East Russia. *Journal of Ethology*, 27, 333–341.
- Foote, A. D., Vijay, N., Ávila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., ... Robertson, K. M. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nature Communications*, 7(1), 1–12.
- Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, 67, 727–745.
- Ford, J. K. B., & Ellis, G. M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series*, 316, 185–199.
- Ford, J. K. B., Ellis, G. M., & Balcomb, K. C. (1996). *Killer whales: The natural history and genealogy of Orcinus orca in British Columbia and Washington*. Vancouver, Canada: University of British Columbia Press.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb, K. C., III. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 76, 1456–1471.
- Ford, M. J., Hanson, M. B., Hempelmann, J. A., Ayres, K. L., Emmons, C. K., Schorr, G. S., ... Balcomb-Bartok, K. (2011). Inferred paternity and male reproductive success in a killer whale (*Orcinus orca*) population. *Journal of Heredity*, 102, 537–553.
- Ford, M. J., Hempelmann, J. A., Hanson, M. B., Ayres, K. L., Baird, R. W., Emmons, C. K., ... Park, L. K. (2016). Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. *PLoS ONE*, 11(1), e0144956.
- Hauser, D. D., Logsdon, M. G., Holmes, E. E., VanBlaricom, G. R., & Osborne, R. W. (2007). Summer distribution patterns of southern resident killer whales *Orcinus orca*: Core areas and spatial segregation of social groups. *Marine Ecology Progress Series*, 351, 301–310.
- Hoelzel, A. R. (1993). Foraging behaviour and social group dynamics in Puget Sound killer whales. *Animal Behaviour*, 45, 581–591.
- Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, 15, 102–122.
- Matkin, C. O., Ellis, G. M., Olesiuk, P., & Saulitis, E. (1999). Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound. *Fisheries Bulletin*, 97, 900–919.
- Matkin, C. O., Matkin, D. R., Ellis, G. M., Saulitis, E., & McSweeney, D. (1997). Movements of resident killer whales in South-eastern Alaska and Prince William Sound, Alaska. *Marine Mammal Science*, 13, 469–475.
- Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., ... Bouffard, P. (2010). Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research*, 20, 908–916.
- 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. Report of the International Whaling Commission, Special Issue 12, 245–248.
- Olsen, D. W., Matkin, C. O., Andrews, R. D., & Atkinson, S. (2018). Seasonal and pod-specific differences in core use areas by resident killer whales in the Northern Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, 147, 196–202.

- Parsons, K. M., Durban, J. W., Burdin, A. M., Burkanov, V. N., Pitman, R. L., Barlow, J., ... Wade, P. R. (2013). Geographic patterns of genetic differentiation among killer whales in the northern North Pacific. *Journal of Heredity*, *104*, 737–754.
- Saulitis, E., Matkin, C. O., Barrett-Lennard, L. G., Heise, K., & Ellis, G. M. (2000). Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, *16*, 94–109.
- Scheel, D., Matkin, C. O., & Saulitis, E. (2001). Distribution of killer whale pods in Prince William Sound, Alaska 1984–1996. *Marine Mammal Science*, *17*, 555–569.
- Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, *71*, 1494–1499.
- Wright, B. M., Stredulinsky, E. H., Ellis, G. M., & Ford, J. K. B. (2016). Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*. *Animal Behaviour*, *115*, 81–95.
- Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, *63*, 1103–1119.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Olsen DW, Matkin CO, Mueter FJ, Atkinson S. Social behavior increases in multipod aggregations of southern Alaska resident killer whales (*Orcinus orca*). *Mar Mam Sci*. 2020;1–10. <https://doi.org/10.1111/mms.12715>