BEHAVIORAL AND RESPIRATORY SYNCHRONIZATION QUANTIFIED

IN A PAIR OF CAPTIVE KILLER WHALES

Roger D. Ray, Milo L. Carlson, Mark A. Carlson, Timothy M. Carlson and James D. Upson

Department of Psychology
Rollins College
Winter Park, Florida

INTRODUCTION

Members of social species must on occasion synchronize their activities with individuals of their own kind. Christensen (1978) reported wild killer whales diving and surfacing synchronously as they fled from observers attempting to tag individuals. Jacobsen (this volume) argues that the extent of synchrony in movements or respiration among wild killer whales is an indication of the affinity among individuals. He suggests that coordinated respiration and swimming is a major characteristic of social subgroups within a pod and cites as examples of synchronous activities, group shifts in foraging direction (accompanied by increased vocalizations), diving, and mother-calf interactions. Jacobsen proposes two levels of respiratory coordination for orca. The movements of maternal subgroups appear to exhibit a greater degree of concordance than the movements of the whole group or pod.

Methods for quantifying and analyzing such coordinated patterns in social dynamics must be sensitive to both individual behavioral systemics and group systemics. Methods for an integrated temporal, spatial and sequential analysis of individual systemics of captive
killer whales were reported previously (Ray et al., 1977). Comparable techniques to analyze group dynamics remain to be detailed. This, especially as it applies to the understanding of a male and female pair of captive killer whales, was the first of several interrelated objectives of the present chapter. A second aim was to offer a description of diurnal variations extant in the temporal synchronization of the pair's behaviors.

Our previous work focused chiefly upon a single captive killer whale in isolation. Of particular interest were the sequential and temporal organization we found in respiration and functionally defined behaviors. The results suggested that certain macro-behavioral categories of captive orca may be described by ultradian and circadian rhythms concerned with the frequency, average duration, and total time spent in those activities per hour. In contrast, diurnal rhythmicity in respiration seems to be primarily a function of time spent engaging in specific behavioral activities which have their own signature respiration rate.

Behavioral specificity of maintenance activities such as respiration and autonomic levels of emotion and alertness is not that uncommon (c.f., Obrist, 1981). For example, if Free-Swimming vs. Surface-Floating activities of a captive killer whale were considered, one would most likely find unique patterns of respiration and vocalization within each category of behavior, as well as finding that the length of each behavioral bout varied with time of day. It might also be expected that the frequency of such bouts would vary independently from their duration. Perhaps even more importantly, perturbations or disruptions in these regular patterns of activity would most likely occur as a result of particular social and/or environmental conditions.

For instance, Morton et al. (this volume) report a strong correlation between specific behavioral and vocalization patterns. They were successful in ascertaining the general emotionality of a female killer whale by determining the behavioral and contextual specificity of vocal patterns. Their opportunistic observations of a female orca who experienced a stillbirth and the subsequent removal of the dead calf from the holding tank provided an unambiguous context for
analysis. Especially germane to the present study was Morton et al.'s observation that social loss resulted in a marked increase in Submerged-Floating behavior and heightened arousal expressed repeatedly as a particular vocalization pattern. Such behaviors could have been regarded simply as lethargy in that little overt movement occurred, but by knowing both the contextual setting and the behavioral correlates, a social interpretation was more reasonable.

During the execution of the present study, we also had an unplanned opportunity for acquiring observational data under circumstances somewhat analogous to those reported by Morton et al. Our subjects were a male and female orca who had been housed continuously in a single tank since 1970. Therefore, the social dynamics of this dyad were highly stable. Soon after completion of our primary observational series, the male became ill and died within a short period of time. Two weeks following his death we were able to undertake additional observations of the surviving female. The results from this subsequent series served as the final objective of the present report.

To summarize, Ray et al. (1977) studied circadian and ultradian rhythms in respiration, behavioral activities and spatial usage by an individual captive orca. The present study applied a similar methodology that includes an extension of social-synchrony measurements to the analysis of two captive killer whales housed together. This chapter focuses first upon a partial replication of the previous results. It then evaluates the social dynamics of a dyad in terms of possible circadian cycles of social synchrony. Lastly, it reports an assessment of the female two weeks after the death of her male companion.

METHODS

Animal Subjects

The subjects in this experiment were a captively housed pair of killer whales (Orcinus orca). The tank was also shared by a pair of performance-trained dolphins (Lagenorhynchus obliquidens). The 15-yr old male orca, Hugo, weighed 4,500 kg, measured 6.8 m in length and had lived in Wometco's Miami Seauarium since 1968. The 12-yr old female, Tokitae (nicknamed Toki), weighed 2,835 kg,
measured 5.92 m in length and had lived in the oceanarium since 1970. Hugo expired in late February, 1980. Both whales were maintained in a single circular tank 24.4 m by 18.3 m in size, and 6.7 m deep. The tank held 1,900,000 l of sea water with an average temperature of 17.2°C. The sea water was kept fresh by continuous circulation between the captivity tank and Miami's Biscayne Bay.

**Observation Procedures**

Ninety-six hours of continuous observations were recorded from January 15-18, 1980. Approximately 2 weeks after Hugo's death, another 48 hr of continuous observations were conducted on the surviving female.

Observations were documented on paper, by video tape and with audio recordings in conjunction with a digital clock used to determine visually, to the nearest second, the time of initiation of each tabulated behavior. Audio recordings were used during peak times of activity to ensure data accuracy.

For ease of audio record transcription, male/female experimenters (with obvious voice distinctions) were matched to the subjects' sex. Observers were located on the uppermost seats in the stadium which surrounds the holding tank. This position provided an approximate 30 degree vantage point to the tank from a height of 10 m. Together with the behavioral activities which were operationally defined by previous research (Ray et al., 1977), the observers also recorded the respiration of each orca as discrete events across time. The behavioral categories used included Surface-Floating, Submerged-Floating, Free-Swimming, Head-Bobbing, and Spyhopping.

**Behavioral Definitions**

**Surface-Floating.** This behavior is characterized by the animal floating, with virtually no lateral motion, at the water's surface. The blowhole is totally out of the water and the fluke is hanging in a relatively relaxed or slightly undulating position. In this behavioral
configuration, the animal rarely relocates spatially unless a strong current exists to carry it from place to place.

Submerged-Floating. This category is somewhat similar to Surface-Floating. It involves virtually no spatial relocation and the body remains nearly without motion. However, in this activity the animal is totally submerged and is typically found lying on the bottom of the tank or at some specific, fixed locale such as an interconnecting gate or observation window.

Free-Swimming. This behavior is a broadly defined activity consisting of many different movements and body configurations, both at the surface and submerged. Typically, Free-Swimming results in spatial relocation as it is executed, but may involve in-place rubbing or even social or sexual contact.

Spyhopping and Bobbing. Spyhopping is a relatively well-known behavior of orca in the wild (Jacobsen, this volume), in which the animal's rostrum is raised fully out of the water, usually to at least the level of the eyes. It is this characteristic of nearly complete verticality plus the eyes brought above the water's surface that gives the behavior its name. However, during this activity the animal will often Bob its head under the water's surface, very much like a fishing cork might bob when fish are nibbling at one's bait. It was assumed that when the rostrum went completely under the surface, the Bobbing component of this category was initiated. Also when the rostrum reappeared for at least a continuous two second period, the Bobbing behavior was regarded as terminated.

An exhaustive list of behavioral categories was used in data collection. At no time did a behavior occur that was not within one of these categories. Moreover, all behaviors were recorded in their actual sequence.

Analysis Procedures

Recorded data were computer analyzed to develop measures of (a) breath frequency; (b) behavioral category frequency, mean duration, and total duration; and (c) the sequential probabilities of behavioral change for both
individuals. Each whale's individual data, previously stored within separate computer files, were merged by temporal criteria to form paired behaviors describing the behavioral activity of the dyad. Similar to the individual data, the data were analyzed to determine "paired-behavior" frequency (from which lag/lead latencies could subsequently be determined by sequential paired-category comparisons), duration, total time in that activity, and the sequential organization of paired-behavior changes. Throughout this study, the subjects participated in four public performances daily, each lasting approximately 30 min. The shows were scheduled at 2 hr intervals beginning at 1130 hr and ending at 1730 hr. During the shows, only respiration events were recorded. A behavioral category Show was created for the duration of each performance.

RESULTS

Respiratory Rhythms

Figure 9.1 illustrates total breaths per hour across successive 1-hour intervals for both daily recordings and an average day in three distinct observational episodes. First, to indicate the temporal stability of respiratory rhythms, some of the respiration data for this same pair of orca reported in the Ray et al. (1977) study (i.e., 1976 data) are provided. Secondly, the data from the 96-hr observation period for each whale (social condition) of the present study (1980 data) are represented. Finally, the subsequent 48 hr of observation of the isolate female (Toki-solo) are depicted. The consistent highs and lows in respiration rates which occurred once every 24 hr demonstrate clear circadian rhythmicity. The peak spectral frequency for essentially every day analyzed was a frequency of 24 hr. Thus, peak breath rates occurred during daylight hours (open sections of the figure), while the lowest breath rates occurred during night hours (dark-banded sections).

Breath rates for each whale are somewhat lower in 1980 when compared to the 1976 data. In the earlier study, Hugo was demonstrating peak respiration rates of 100-110 breaths/hr; Toki's rates were 90-100 breaths/hr. However, in the present study the average-day peaks were
70-80 breaths/hr. Further, Hugo's overall rates at this time were lower than Toki's, whereas they were previously comparable to Toki's. Hugo's peak respiration rates declined systematically from the first day of observation to the last day.

Fig. 9.1. Total number of breaths per hour across successive 1-hr intervals for both "average day" (top) and daily recordings from three distinct observational periods: (bottom) May, 1976; January, 1980 (social); and February, 1980 (Toki-solo).

The most comparable respiration rates for the two subjects in both studies were during the late evening and early morning hours when rates were at their minimum levels. Moreover, after Hugo's death Toki's respiration levels were much higher during peak levels in the afternoon than in the preceding 96-hr observational
period. It is apparent from the average-day plots that her respiratory rates were elevated throughout the afternoon, but returned to normal lows during the night. These data will be discussed further when social synchronization is considered.

**Fig. 9.2.** "Average-day" curves for Hugo and Toki repeated across two consecutive days and depicting: hourly frequency of initiation, hourly mean duration, and hourly total time accumulated in seconds for each of the five macro-behavioral states.
Behavioral Rhythms

Figure 9.2 illustrates the average frequency of each of the five behavioral activities, along with their mean and total duration in seconds per hour. These curves depict calculated averages for each specific hour across the four days (i.e., "average day" data). They are then repeated once to better illustrate the rhythmicity inherent in the data.

Aside from the obvious circadian variations, the most notable aspect about these curves is the degree of correspondence between the two subjects. Only the lower frequency and longer daytime duration of Hugo's Free-Swimming activity varied appreciably from Toki's activity. This difference is reflected in the somewhat greater amount of Hugo's time per hour spent in swimming activity during the daylight hours as compared to Toki who, in turn, spent slightly more time in Submerged-Floating in the post-dawn hours.

Figure 9.3 illustrates the same data (social condition) as above for Toki, except that they are now superimposed upon her average-day's data under the alone condition. In view of Morton et al.'s (this volume) observation of increased Submerged-Floating, one of the more interesting aspects of Figure 9.3 concerns that behavior. In the solitary period following Hugo's death, a marked increase in the frequency, duration and total time spent in Submerged-Floating by Toki appeared. However, little or no change occurred in the circadian rhythmicity of Submerged-Floating behavior, which is obviously very stable. Also, when Toki increased her total time in Submerged-Floating she increased her Swimming and decreased her Surface-Floating activities. Swimming actually increased at two different times: first, in the late afternoon, slightly shifted in phase from the increased Submerged-Floating; and second, in the late night-time hours which compensated for the simultaneous decrease in Surface-Floating.
Fig. 9.3. "Average-day" curves for Toki under social circumstances and while alone (Toki-solo) repeated across two consecutive days and depicting: hourly frequency of initiation, hourly mean duration, and hourly total time accumulated in seconds for each of the five macro-behavioral states.

Thus, compared to the social situation, Toki's solitary behavior is depicted by (a) her spending far less time Surface-Floating (a behavior associated with sleep patterns during the night), and (b) spending significantly more time either in active Free-Swimming (especially at night) or engaging in the relatively inactive behavior of lying on the tank bottom during the day.
Behavioral Velocity

Behavioral velocity reflects the total number of behavioral activity changes occurring within successive time periods. Figure 9.4 illustrates this measure for successive 3-hr periods across all conditions. The maximum frequency of behavioral changes occurred during the day, with much slower rates of change evident at night.

Power spectral analysis of the average-day plots of the social situation revealed a marked 24-hr periodicity for both animals. However, Hugo's data also contained an equally prominent 12-hr cycle and attest to his mid-day dip in behavioral velocity. While Toki's circadian respiration cycle was highly correlated with circadian variations in her behavioral velocity, Hugo's respiration peaked at the very time that his behavioral velocity reached a mid-day low. Thus, Hugo's data illustrate a diurnal desynchronization in respiration and behavioral velocity. There was a third, but relatively low power, 2-hr oscillation in Hugo's behavioral velocity data.

Toki's behavioral velocity was about 60-70 percent elevated in peak levels during the solitary condition which followed Hugo's death. In addition, a marked 2-hr periodicity became apparent in her average-day power spectra, reflecting a relatively high frequency temporal variation in velocity. While the circadian pattern remained, Toki developed an oscillation frequency unique to her, but reminiscent of Hugo's data in the 96-hr period. While recognizing the tentativeness of such speculations, this mimicry might signify an emotional response by Toki to Hugo's rapidly deteriorating health and subsequent death. If so, some diagnostic utility of these measures might be indicated.

Behavioral Syntax Patterns

Individual kinematics. Kinematic flow charts are a means of diagramming behavioral sequences. Such diagrams may be used to reveal information about individuals as well as social dyads. Figure 9.5A presents individual kinematic diagrams of Hugo and Toki's 48-51 hr (0000 hr to 0300 hr) data. The beginning behavior in each diagram was the most frequently initiated behavior during the period illustrated. The larger the arrow, the greater
Fig. 9.4. Total number of macro-behavioral state changes (behavioral kinetic velocity) averaged within each hour (average-day plots) and occurring within each successive 3-hr block across all days and observation periods (Toki-Hugo social and Toki-solo).

the probability that a given sequence of behaviors was likely to occur. These data were selected as representative of night-time behavioral patterns and indicate very little variability (i.e., very few alternate "paths" of behavioral change). For both subjects the most frequent sequence involved changing from Submerged-Floating to Surface-Floating and subsequently back to Submerged-Floating.
Figure 9.5B presents kinematic diagrams for both whales' 60-63 hr (1200 hr to 1500 hr) and are

**TOKI:**

![Diagram A]

**HUGO:**

![Diagram B]

**Fig. 9.5.** Kinematic flow diagrams depicting the sequential organization of behavior for Toki and Hugo during (A) the 48-51 hr (0000 hr to 0300 hr) and (B) the 60-63 hr (1200 hr to 1500 hr) of the social observation periods. Widths of connecting arrows are proportional to the probability of each sequential pairing.
representative of daytime data. A much more variable and complex patterning of behaviors is evident, particularly in Toki's kinematics. The most consistent behavioral sequence in Toki's P.M. kinematics was the Swim/Surface-Float/Swim combination. In Hugo's P.M. kinematics, the Swim/Surface-Float/Submerged-Float dominated, with the next prominent sequence being the Swim/Submerged-Float/Float combination.

Toki's changing syntactic organization for an average day, broken into successive 3-hr segments, was also considered. In the social situation her most dominant behavior was Surface-Floating, which tended to be followed by Submerged-Floating and then Surface-Floating. This sequence was similar to her individual profile (see Fig. 9.5A). However, the same successive 3-hr analysis for data collected during Toki's solitary condition revealed the appearance of Submerged-Floating as the most dominant behavioral activity for almost every 3-hr block of the day. Also, some of the sequences were changed; Submerged-Floating was often followed by Bobbing and, subsequently, Submerged-Floating. This was a very atypical sequence in the 96-hr social situation but was quite typical of the subsequent 48-hr solitary condition.

After the death of Hugo, Toki would briefly surface to catch a breath, then would return to the bottom to continue her long bouts of Submerged-Floating. Before the loss of Hugo, she usually remained at the surface for prolonged periods, breathing successively while floating there. Thus, both an organizational change in behavior as well as a temporal-budgeting change occurred after Hugo was gone.

**Individual syntax variability.** The kinematic diagrams (Fig. 9.5) illustrate the stability of behavioral sequences across time. This phenomenon can be easily quantified by counting the number of connecting arrows (i.e., possible paths) in each kinematic analysis. This measure is termed the "syntactic pattern variability index." Figure 9.6 represents such an index computed for each successive 3-hr segment across all observation periods for both subjects. It indicates a clear circadian rhythm in syntactic variability, with very few sequential patterns occurring during the night and several complex patterns occurring during the day. It is important to
note that, while these variations parallel the velocity measures reported earlier, the two measures are theoretically independent of one another. The rate of change from one behavior to another in no way limits the variety of behavioral patterns and vice versa.

In the last day of the 96-hr observational period, both animals markedly reduced the number of different behavioral patterns. No similar change was found for the velocity measure (Fig. 9.4). The first signs of Hugo’s advancing illness became apparent to most observers that day, including trainers (who had, in fact, complained a day or so earlier about qualitative shifts in Hugo’s show performances).

Fig. 9.6. Number of different syntactic patterns of behavioral sequences during each successive 3-hr block across all days and observation periods. Toki-Hugo social (left); and Toki-solo (right) two weeks after the death of Hugo.
Social Analysis

Group kinematics. Up to this point, each whale has been considered a separate behavioral system and the analysis to date has been treated accordingly. When the data of each whale are merged according to temporal correspondence, unique "paired" behavioral activities are apparent. Figure 9.7A illustrates these paired behavior states in kinematic form for the period of 48-51 hr (morning). The behavioral sequence with the greatest frequency of occurrence was the one in which Toki maintained a Surface-floating behavior while Hugo submerged for a short time and then resurfaced. Figure 9.7B is a kinematic diagram of paired-behavioral states in the period of 60-63 hr (afternoon). It may be compared to the much less variable pattern of the dyad in Figure 9.7A (morning). Clearly, the afternoon reveals a much more complex pattern of social behaviors.

These variations in paired-behavior syntax are best illustrated by the variability index (Fig. 9.8) calculated across successive time periods, as previously discussed for individual subjects. Similar to the individual indices, the pair show a marked circadian rhythm in the consistency of behavioral activities, with much greater variability occurring during the day.
Fig. 9.7. Kinematic flow diagrams depicting the sequential organization of dyadic, or "paired," behaviors (i.e., behaviors defined by temporal pairing of the behaviors of each animal one to the other) during (A) the 48-51 hr (0000 hr to 0300 hr) and (B) the 60-63 hr (1200 hr to 1500 hr) period in social circumstances. Widths of connecting arrows are proportional to the probability of each sequential pairing.
Fig. 9.8. Number of different syntactic patterns of dyadic, or "paired," behavioral sequences during each successive 3-hr block across all four days of social observations.
Social synchronization. Using paired-behavioral analysis, it is possible not only to indicate the probability of changing from one behavior to another, but also which whale initiated the change. Thus far our analysis has not considered lead or lag times (i.e., the interval of time from the initiation of a behavior by one organism to the initiation of the same behavior by the other organism). In doing so, the duration of each behavior in its appropriate sequence of occurrence must be considered. The duration of "unlike" behaviors which follow "like" behaviors, and are subsequently followed themselves by "like" behaviors (i.e., a "like/unlike/like" behavioral sequence), indicates which animal is initiating the sequence. If the other animal subsequently changes its behavior to match the newly initiated behavior, an instance of imitative behavior has occurred.

A computer program was utilized to determine all possible occurrences of social initiation-imitation, and to sort these into two distinct categories. The first category was defined by "unlike" behaviors having a duration of 7 sec or less, interceding between initiation and imitation. All such occurrences were considered to be instances of "socially synchronized," or truly imitative behaviors. The other category was defined by durations above 7 sec and was considered to represent socially desynchronized activities, even though the pair eventually may have engaged in the same, or "like," behaviors.

Figure 9.9 shows the percentage of all paired-behavioral changes which were regarded as socially synchronized. Peak periods of social synchrony were evident during night hours when individual measures of respiration, behavioral velocity, and complexity of behavioral sequences were lowest.

Figure 9.10 demonstrates the percentage of Toki-initiated socially synchronized behavior for each 3-hr time block across the entire observation period. Six of the 32 time blocks indicate a 50 percent probability of Toki-initiated change and eight other blocks fell within the 40-60 percent probability range. These were at chance level, thus reflecting no systematic social dominance in initiating behavioral change. However, the remaining 18 3-hr observation blocks clearly indicated initiated
behavioral changes by one whale or the other. Furthermore, 67 percent of those blocks revealed Toki to be the leader. Moreover, two-thirds of those Toki-initiated paired-behavioral changes occurred during the night (Figs. 9.9 and 9.10) when the greatest degree of social synchronization was evinced. Hugo had only one night-time instance of initiated behavior which occurred just after sunset on the last day of observations.

**Fig. 9.9.** Number of dyadic, or "paired," behavior changes which were socially initiated ("synchronized") divided by the total number of dyadic, or "paired," behavioral change for each successive 3-hr block across all four days of social observation.
This social synchrony of follow-the-leader was negatively correlated with the complexity and velocity of behavioral sequences. When behavior complexity was low, socially synchronized behavioral changes were high, and conversely. It was during night hours when behavioral velocities (see Fig. 9.4) and respiration rates (see Fig. 9.1) were at their lowest.

DISCUSSION

The intent of this paper was threefold. The first of these was to assess the robustness of our previous results (Ray et al., 1977) indicating circadian rhythms in the behavior and respiration of individual captive orca. The individual data in the present study showed a very strong correspondence with data from the 1977 study, even in view of the fact that most of the earlier work included an

![Graph]

**Fig. 9.10.** Number of dyadic, or "paired," behavior changes which were socially initiated ("synchronized") by Toki leading and Hugo lagging divided by all socially initiated ("synchronized") behaviors, regardless of who led the change in pattern. Plots are for each successive 3-hr block across all four days of social observations.
additional killer whale in a different oceanarium.

A second aim was to extend our systems-analysis approach to social phenomena. The present results suggest that such an extension provides meaningful data. The pair's social synchronization was clearly described in terms of a circadian rhythm. Moreover, findings that the female initiated most of the behavior subsequently imitated by the male, and that such initiations-imitations also showed circadian oscillations are unique contributions to the social literature on orca, if not to marine mammals more generally.

As noted earlier, Jacobsen (this volume) cites several circumstances in which social synchrony occurs among wild killer whales. A major focus of interest for him is the social consequences of coordinated respiration. Jacobsen proposes respiratory synchrony as a major indicator of social organization and affinity. Although we have just begun to analyze our respiratory data, it is already apparent that respiratory synchrony exists almost exclusively when behavioral state synchrony is occurring. Further, from our preliminary analyses of these instances when no one initiator was evident in synchronized behavioral changes (i.e., each whale participated 50 percent of the time), there is the indication that the whales were actively alternating the lead. For example, Toki would change from Submerged-Floating to Surface-Floating, followed by Hugo who would, in turn, change back to Submerged-Floating, followed by Toki. Such periodicities of behavioral states suggest the fruitfulness of similar quantification in the wild. There is an obvious need for convergent efforts between captive and non-captive research in this regard.

A third, rather fortuitous objective was also served by the present study. Our data suggest characteristic changes in the activity of an orca which might have diagnostic utility in captivity, signaling that an animal is experiencing stress or highly emotional reactions. If such information could be obtained before a point of risk to the animal, intervention might prevent an undesirable outcome. To this end, it might be useful to develop a behavioral profile to which short-term samples of the critical parameters could be compared. Implementation of diagnostic and care programs could follow.
Certainly, the activity pattern which emerged for Toki subsequent to Hugo's death is not unlike bereavement. Considering both the respiration and behavioral velocity data, we obtained a profile of Toki in the solitary condition, consisting of hyperkinetic activity at times and lethargy at other times (i.e., the Submerged-Floating). This oscillating regimen was in marked contrast to Hugo's hypokinetic behavior of slowed velocity and respiration. If Toki's hyperkinesis had continued, with its disrupted sleep pattern (i.e., swimming increased at night), health problems might have developed. Although short-term stress and emotionality induced by social loss seemed measurable by the observation techniques utilized in this study, the breadth of this approach, most assuredly, awaits future research efforts.

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REFERENCES

