RESPIRATORY INTERVALS AND SWIMMING SPEED AS REMOTELY SENSED HEALTH METRICS IN FREE-RANGING KILLER WHALES (ORCINUS ORCA)

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Respiratory Intervals and Swimming Speed as Remotely Sensed Health Metrics in Free-Ranging Killer Whales (*Orcinus orca*)

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ABSTRACT: Respiratory rate (mean number of breaths per minute) and respiratory interval (mean time between breaths) can offer insight into a diving mammal's activity state, metabolic rate, behavior, and synchronization due to social cohesion. Also, respiratory rate can reflect an individual animal's health and has the potential to be an informative remotely assessed health metric for monitoring individual animal health in endangered whale species and populations such as southern resident killer whales (*Orcinus orca*). Using data collected from noninvasive, land-based theodolite tracking, we analyzed swimming speed and surfacing intervals (i.e., mean dive time or mean time between breaths) from 20,613 surfacings of 98 individuals from two populations of the fish-eating, resident killer whale ecotype, namely, one growing (northern resident) and one declining and endangered (southern resident) population. Focal animal sampling was used to measure behavior of individuals of known age and sex in various activity states. Our objective was to evaluate variability and generate normal ranges for respiratory intervals and swimming speeds for killer whales of the Northeast Pacific Ocean resident, fish-eating ecotype to identify baseline respiratory intervals. We found that median respiratory intervals for fish-eating killer whales were between 26 and 29 s for all activity states and that swimming speeds varied by activity state. Median swimming speeds were similar for foraging and traveling (1.6 and 1.7 m/s, respectively), but were significantly slower during resting (1.1 m/s) and social activity (1.3 m/s) states. Three southern resident killer whales in poor body condition (had body condition scores in the lowest 20th percentile of the population) swam at reduced speeds and had shorter median respiratory intervals than outwardly healthy whales of similar age and sex. Respiratory rates, respiratory intervals, and swimming speeds are valuable remotely sensed metrics of health for free-swimming killer whales, especially when combined with other metrics as is the standard in veterinary examinations.
Key words: Behavior, cetacean, health, orca, northern resident killer whale, respiratory interval, southern resident killer whale, swimming speed.

INTRODUCTION

Cetaceans have a series of physiologic, structural, mechanical, metabolic, neurologic, and hormonal adaptations that permit them to live as a diving mammal (Piscitelli et al. 2013; McHuron et al. 2022). Marine mammals, including cetaceans (whales, dolphins, and porpoises) and pinnipeds (seals, sea lions, fur seals, and walruses) differ from terrestrial mammals in that their respiratory cycle begins right at surfacing after a dive, with an explosive exhalation followed by a rapid inhale and submersion, often only spending seconds at the surface. Marine mammals have evolved several adaptations to allow them to minimize time spent at the surface and maximize time spent foraging at depth (Andrews et al. 2000). Breathing patterns in diving mammals may be quantified in terms of respiratory rate (number of breaths per minute), or respiratory interval, dive interval, or interbreath interval (mean duration between breaths, dives, or surfacings, respectively, in seconds). Although some species may take multiple breaths while resting (logging) at the surface (Isojunno et al. 2018), killer whales (*Orcinus orca*) typically take a single breath on each surfacing (McRae et al. 2024). Cetaceans are able to conduct deep, often prolonged dives while balancing retained air for echolocation, foraging, and buoyancy. In terrestrial mammals, respiratory rate is used as a gross indicator of pulmonary function and can provide data on metabolic state (Taylor et al. 1982). Based on these relationships, it has been expected that breathing frequency is tightly linked to energy requirements and may be used to assess or compare the metabolic cost of different activities (e.g., resting or swimming at the surface versus diving; Fahlman et al. 2016). Remotely observing the respiratory interval in diving mammals has the potential to be an informative metric for monitoring metabolic state, and potentially individual animal health, in highly endangered species and populations such as southern resident killer whales (NMFS 2007, COSEWIC 2008; Williams et al. 2024).

Respiratory interval is influenced by numerous factors that need to be taken into account when assessing its utility as a metric of health in wild cetaceans. It varies with swimming speed (positive correlation) in killer whales (Williams and Noren 2009), and studies of other cetaceans have shown that respiratory interval can be indicative of metabolic rate (Sumich 1983, 2001). An individual's activity state (e.g., foraging or resting versus travel) also will influence a cetacean's respiratory interval (Noren and Hauser 2016). In addition, in social animals such as killer whales, synchronization of behaviors and physiologic limits of conspecifics can alter an animal's dive and respiratory behaviors (Roos et al. 2016).

In addition to activity state, metabolic rate, behavior, and synchronization due to social cohesion, respiratory interval may reflect an individual animal's health. Pulmonary and cardiac function and acid-base balance may increase or decrease respiratory rate and change respiratory character (Malan et al. 1973). Counting the rate of respiration is therefore part of standard physical health examinations across taxa. Although odontocetes (toothed whales, dolphins, porpoises) have developed breath-holding capabilities distinct from nondiving mammals, the rate and quality of respirations are still a clinically useful metric for monitoring the health of killer whales in human care (Nollens et al. 2018).

Three ecotypes of killer whales co-occur in the northeastern Pacific Ocean: shark-eating offshore killer whales, mammal-eating transient (or Bigg's) killer whales, and northern and southern populations of salmon-eating resident killer whales (NRKWs and SRKWs, respectively; Ford et al. 1998; Dahlheim et al. 2008). The SRKW population is listed as Endangered both under the U.S. Endangered Species Act (NMFS 2007) and the Canadian Species at Risk Act (COSEWIC 2008). Initially, unsustainable live-capture fisheries for display in aquaria between 1962 and 1973 reduced the SRKW population size to a historic low (Bigg and Wolman 1975). Food availability, contaminants, and vessel disturbance have hindered recovery; currently, there are 74 individual SRKWs and the population is continuing to decline (Lacy et al. 2017; NMFS West Coast Region 2021; Center for Whale Research 2024; Nelson et al. 2024; Williams et al. 2024). Inbreeding and inbreeding depression are concerns for SRKW recovery (Kardos et al. 2023). In a small population, each individual contributes substantially more to the collective genetic makeup and population viability than in a larger demographic (Shaffer 1981). This applies particularly to the adult males in the SRKW population, because there is a lag between the ages of sexual and social maturity that results in most calves being sired by relatively few males (Ford et al. 2011). Inbreeding and the resulting decreases in genetic fitness have been likened to a threat amplifier (Brown et al. 2009; Keller and Waller 2002).

With such critically low population size, efforts to prevent the deaths of even one individual per year can make the difference between a declining and a stable or increasing population (Fujiwara and Caswell 2001; Lacy et al. 2017; Williams et al. 2024). Proactive interventions in support of conservation, such as health monitoring of individuals and providing veterinary intervention when possible, have resulted in positive population growth in mountain gorillas (*Gorilla beringei*; Robbins et al. 2011) and Hawaiian monk seals (*Monachus schauinslandi*; Harting et al. 2014). New analyses suggest that an occasional successful veterinary intervention to prevent mortality may be necessary to slow, stabilize, and ultimately reverse the SRKW decline (Williams et al. 2024). Tracking trends in the determinants of health of individual animals also can generate feedback on the overall efficacy of conservation measures and may lead to adaptive management or help to identify novel opportunities to prevent mortality in individuals of high conservation value.

We retrospectively analyzed swimming speed, behavioral state, and respiratory intervals of known individual killer whales from two populations of the resident, fish-eating ecotype—SRKWs and NRKWs—to identify baseline respiratory intervals and swimming speeds. Our goal was to evaluate variability and generate normal ranges for respiratory intervals for SRKWs of a given age and sex by activity state. We also conducted a preliminary exploration to assess whether "whales of concern" (i.e., whales that have been identified from aerial photogrammetry as having poor body condition; Stewart et al. 2021) had shorter respiratory intervals or slower swimming speeds than their putatively healthy counterparts of similar age and sex.

MATERIALS AND METHODS

Data from SRKWs were collected from three land-based sites along the west side of San Juan Island, Washington, USA, from 2003 to 2005 and in 2022. Data from NRKWs were collected from West Cracroft Island, Johnstone Strait, British Columbia, Canada, from 1995 to 1998 and in 2002 and 2004. The tracking teams consisted of a computer operator, a theodolite operator, and at least one observer recording scan sample data on whales, as outlined below. Protocols for both theodolite tracking and scan sampling were uniform across years and field teams to ensure that data were comparable.

In June 2022, Washington Department of Fish and Wildlife issued an emergency rule for vessels operating around vulnerable SRKWs (WDFW 2022). Analysis of drone imagery taken by colleagues identified whales with body condition scores in the lowest 20th percentile of the SRKW community (Fearnbach et al. 2018): J49 (juvenile male, 10 yr old), J56 (juvenile female, 3 yr old), and L110 (adult male, 15 yr old). A concerted effort was made to track these particularly vulnerable individuals when they were visible from shore during the 2022 field season.

Theodolite tracking of focal whales

Theodolite data were collected using a DT540 digital theodolite (Sokkia, Tokyo, Japan) connected to a laptop. Custom computer software (THEOPROG; available from DE Bain; Williams et al. 2002, 2009) was used to record horizontal and vertical angles measured by the theodolite from a stationary reference point to each focal whale. Several shoreline positions were collected to verify theodolite precision, and changes in tide height were taken into consideration. A focal whale was selected and identified by matching markings with photoidentification catalogs. In recent years, if a whale could not be identified in the field, digital photographs captured with a Canon EOS R camera (Canon, Melville, New York, USA) and a 600-mm lens were later reviewed to identify the focal whale. The computer operator recorded each surfacing of the focal whale, activity states (mainly resting, traveling, foraging, and socializing, as defined in Table 1), and descriptors such as relative location and morphology (i.e., shape of unique saddle patches and dorsal fin) as directed by the theodolite operator. Timestamps were recorded simultaneously with each breath (evidenced by the blow), followed by the focal whale's position. During each tracking session, hereafter referred to as a track, the theodolite operator recorded the time and position on successive breaths of the same focal whale, generally for a 15- to 30-min period. The number of surfacings in each track varied by focal whale. All members of the team assisted in locating and announcing focal whales transiting the field of view.

Scan sample data collection

Fine-scale, theodolite tracking of the behavior of focal individual whales was complemented by coarse-scale, scan sampling of activity states of the entire group of whales. Scan sampling data collection was conducted by two observers, with one observer focused on boats and the other observer focused solely on whale behavior (Altmann 1974). This whale scan sampler recorded group size, sex, activity state (Table 1), degree of dispersion among group members, and any notable surface-active behaviors such as breaching, tail lobbing, or spy hopping. Although the whale scan sampler observed the behavior of the group continuously, instantaneous sampling was used to

TABLE 1. Definitions of resident killer whale (*Orcinus orca*) activity states (Lusseau et al. 2009) used for defining behavior during scan sampling conducted in British Columbia, Canada, on northern resident killer whales and in Washington, USA, on southern resident killer whales.

Activity state and subcategory	Definition
Rest	Characterized by prolonged surfacing in contrast to the rolling motion typically observed during travel
1	Deep rest, hanging, logging: whales progress through the water, although they may not make forward progress over the ground
2	Resting travel, slow travel: whales progress through the water, although they may not make forward progress over the ground
Travel	Characterized by a rolling motion at the surface, progress through the water, and membership in a subgroup >4 individuals
3	Moderate travel, medium travel: travel in which whales do not porpoise
4	Fast travel: travel that includes porpoising
Forage	Characterized by progress through the water by lone individuals or while a member of a subgroup of 4 or fewer individuals
5	Dispersed travel: foraging in a directional manner
6	Milling, feeding, pursuit of prey: foraging involving changes in direction
Social	Interaction with other whales, or other species in a nonpredator-prey context
7	Tactile interactions: socializing that involves touching another whale, such as petting or nudging
8	Display: socializing that does not involve touching, but may include behaviors such as spy hops, tail slaps, and breaches

record the group's activity state every 5 min while whales were in view of the study site.

Data analysis

Angles measured by the theodolite were converted into decimal degrees of latitude and longitude during postprocessing by using modules in the software THEOPROG (Williams et al. 2002, 2009). Timestamps and locational data were used to estimate the swimming speed of whales between successive fixes and as a mean for the duration of each tracking session. Killer whales exchange one breath rapidly (exhale then inhale) at every surfacing (McRae et al. 2024), except during rare bouts in which a whale "logs" or rests at the surface for an extended period; the exhale (blow) is clearly visible (Fig. 1). No bouts of logging activity were included in these analyses. Therefore, respiratory intervals were defined as the mean time (seconds) elapsed between adjacent surfacings. We conducted *t*-tests in R Studio to detect any significant difference in mean swimming speeds and respiratory intervals between populations (R Core Team 2023). The 2022 SRKW data were subsetted to look for differences in swimming speeds and respiratory intervals between whales in relatively good body condition and whales of concern. Boxplots were used to visualize patterns in focal whale data (swimming speeds and respiratory intervals) and activity state. An inspection of boxplot notch placement, showing the 95% confidence interval around the median, enabled inference of how median values differ across activity states.

RESULTS

In total, 235 NRKW and 186 SRKW tracks of 98 unique individuals (43 NRKW, 55 SRKW) collected during 1995–2022 were available for determining respiratory intervals in postprocessing. The mean swimming speed and respiratory interval did not differ between populations ($P>0.05$ for both, Welch's *t*-test), so data from NRKWs and SRKWs were pooled. For both SRKWs and NRKWs, males represented the majority of focal whales (82% of NRKWs and 56% of SRKWs). The combined dataset included 22,209 surfacings. Biologically

FIGURE 1. A group of killer whales surfaces to exhale, with the exhalation (blow) clearly visible. (Photo: Ryan Tidman for Oceans Initiative.)

implausible swimming speeds (i.e., those >12.5 m/s; Williams 2018), dive times >10 min, and fixes of focal whales of unknown age or sex were removed. These cutoffs were chosen to slightly exceed maxima reported in previous studies (Williams and Noren 2009; McRae et al. 2024), because the larger sample size in the current study increased the possibility of capturing rare events. Our final analysis used 20,613 respiratory intervals from surfacings from 98 identified individuals of known age and sex in known activity states, of which 15,647 were adult males, 4,966 were adult females, 783 were juveniles, and 212 were calves.

Swimming speeds varied by activity state (Table 2 and Figs. 2 and 3). Median swimming speeds were similar for behaviors associated with foraging and traveling (1.6 and 1.7 m/s, respectively), but were significantly different from those of resting (1.1 m/s) and social activity (1.3 m/s; Fig. 2) states. Swimming speeds were fairly uniform across ages and sex, although the majority of data were based on tracks of mature individuals (>12 yr old; Fig. 4). Respiratory intervals were recorded between 3 and 586 s. Median respiratory intervals ranged from 26 to 29 s for all activity states (Figs. 3 and 5).

In the 2022 SRKW season, 18 individual whales were monitored during 21 tracking sessions. The focal individuals in three of these tracks were previously identified as whales of concern (J49, J56, and L110). Although these tracks represent a small portion of the 2022 data, the fine-scale behavioral data collected from these three whales with low body condition scores suggest that focal whales in poor body condition swam at slower speeds and had shorter respiratory intervals than other, putatively healthy SRKWs (Figs. 6 and 7). No observations of resting or social activity were noted in the three whales of concern (Fig. 7).

DISCUSSION

Our findings suggest that remote monitoring of swimming speed and respiratory intervals can

TABLE 2. Summary of resident killer whale (*Orcinus orca*) swimming speeds and respiratory intervals by activity state for complete dataset, including northern resident and southern resident killer whales observed in British Columbia, Canada, and Washington, USA, respectively. This represents data from 98 individual focal whales collected across 421 tracks.

	Mean swimming speed[a]	Median swimming speed	Minimum swimming speed	Maximum swimming speed	Mean respiratory interval[b]	Median respiratory interval	Minimum respiratory interval	Maximum respiratory interval
Rest	1.7	1.1	0.0	12.3	51.0	28.0	3.0	561.0
Travel	2.2	1.7	0.0	12.5	44.0	29.0	3.0	586.0
Forage	2.2	1.6	0.0	12.5	45.4	26.0	4.0	585.0
Social	1.3	1.3	0.0	11.8	46.2	26.0	6.0	521.0

[a] Swimming speeds in meters per second.
[b] Respiratory intervals in seconds.

be used reliably to evaluate free-ranging killer whales. Using noninvasive methods, we showed that mean and median swimming speeds for resident ecotype killer whales were fairly consistent across ages and sexes, even though the majority of data were collected from mature whales. Similar metrics have been measured using animal-borne tags (McRae et al. 2024), but land-based theodolite tracking obviates the need to follow a tagged whale with a research vessel that might alter the behavior of the focal whale (Williams et al. 2002). Emerging photogrammetry studies may allow simultaneous tracking of multiple individuals within the group (Lo et al. 2022). The mean respiration rates are remarkably similar to those reported recently from a telemetry study (McRae et al. 2024), which lends confidence in recommending the use of these swimming speeds and respiratory intervals as normal baseline values for members of this population.

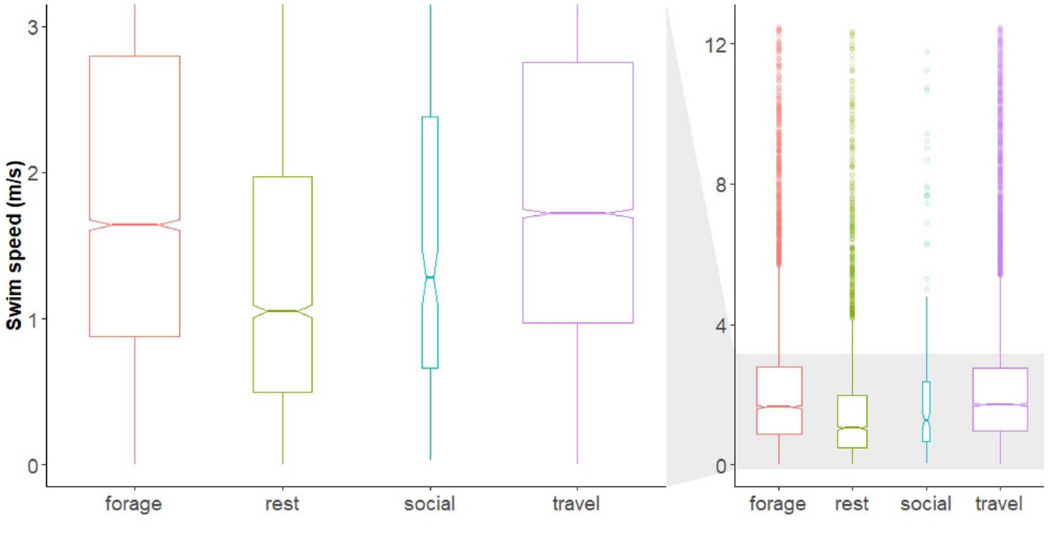

FIGURE 2. Resident killer whale (*Orcinus orca*) swimming speeds (meters per second) for each activity state recorded in British Columbia, Canada, and in Washington, USA. The mid lines represent medians, boxes are first and third quartiles, and vertical lines are 95% confidence intervals. The left panel is zoomed in to focus on differences in medians for each activity state. Notches that do not overlap suggest that the medians are significantly different. Box width is proportional to sample size. Outliers are denoted by circles in the right panel. This represents data from 98 individual focal whales collected across 421 tracks.

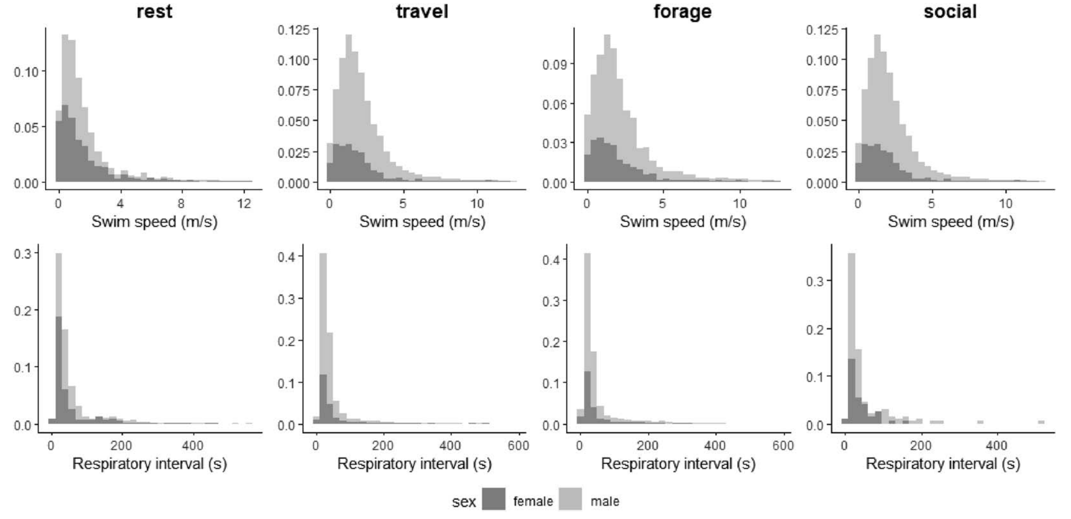

FIGURE 3. Resident killer whale (*Orcinus orca*) swimming speeds (meters per second; top row) and respiratory intervals (seconds; bottom row) observed in British Columbia, Canada, and Washington, USA. This represents data from 98 individual focal whales collected across 421 tracks.

Although the sample size from "whales of concern" was small, the preliminary data suggest that the three southern resident killer whales observed in poor body condition had both slower swimming speeds (Fig. 6) and shorter respiratory intervals (Fig. 7) than whales presenting with normal body condition. We propose to test this hypothesis statistically as additional data from future compromised SRKW become available, but recognize that low statistical power may always be an issue when studying a population as small as SRKW (Nelson et al. 2024).

Although males and females may partition their ecological niches for foraging, no doubt due to differing diving capabilities and possibly to reduce within-matriline competition for prey, these whales live their entire lives in their natal units (Beerman et al. 2016). The fastest individuals in a matriline may slow down to avoid taxing the slowest members of the matriline (Beerman et al. 2016). As body condition worsens in marine mammals, animals tend to become negatively buoyant, causing them to reduce their rates of ascent, descent, and swimming speeds (Richard et al. 2014). In killer whales, there is some evidence that mothers with calves swimming in echelon formation slow down to swim at a cruising speed that matches the calf's physiological constraints, despite increased energetic cost to the mother (Williams and Noren 2009). Epimeletic (caregiving) behavior near distressed conspecifics has been observed in many odontocete cetaceans (Connor and Norris 1982) and is not limited to cow-calf pairs. One member of the SRKW community spent 17 d with the corpse of her dead calf, and her labored swimming required to push the calf was obvious even to casual observation (King 2019). Pod members stayed with the grieving mother despite her slower swim speed at times, which suggests that slower swimming speeds of a pod might indicate a compromised status of one or more of its members.

Although testing with a larger sample size is needed, the current study is consistent with the hypothesis that animals in poor body condition will display slower swimming speeds than that individual would have when it was healthy. Swimming speeds need to be viewed in the context of age, sex, and activity state, and not just body condition or health alone. In our study, socializing and resting whales had the slowest median swimming speeds: they were significantly different from the median speeds for traveling or foraging activities. Resting whales had the longest mean respiratory intervals, whereas

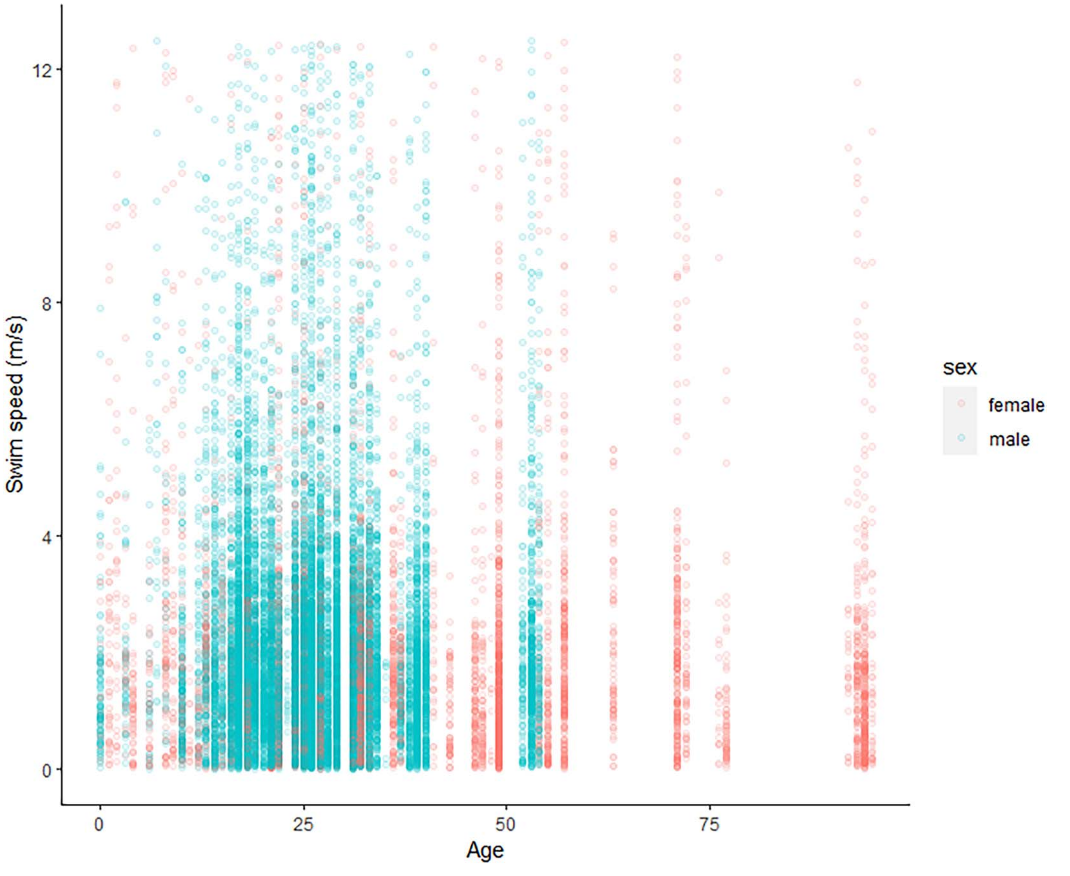

FIGURE 4. Resident killer whale (*Orcinus orca*) swimming speeds (meters per second) by age observed in British Columbia, Canada, and Washington, USA. This represents data from 98 individual focal whales collected across 421 tracks.

socializing, traveling, and foraging whales had similar mean respiratory intervals.

Intraspecific variability is expected to be lower than the cumulative variability in SRKW individuals combined; however, there still may be added value in developing baseline respiratory intervals for specific age and or sex classes, or more ideally, baseline data for each of the 74 individual animals in the endangered SRKW population. We expect that using repeated respiratory interval data from the same individual would provide a narrower baseline range and could therefore be a more sensitive indicator of health for that individual. This also is an important avenue for future study.

In managed care, frequency of respirations is typically counted as the number of respirations during a fixed time period, such as over the course of 5 or 15 min (Nollens et al. 2018). Deviations from the known baseline respiratory intervals can then be interpreted by the attending veterinarian. Wild whales cannot always be reliably observed for this period, although most of our tracking sessions exceeded 20 min. A boat-based observer with a narrower field of view may have a shorter period to count surfacings and breaths before the whale is lost to the observer. Therefore, for the purposes of collecting respiratory frequency data, we chose to measure the respiratory interval (in seconds) observed while the whales were within the field of view of land-based observers instead of counting the number of respirations over a predetermined time period. Respiratory intervals

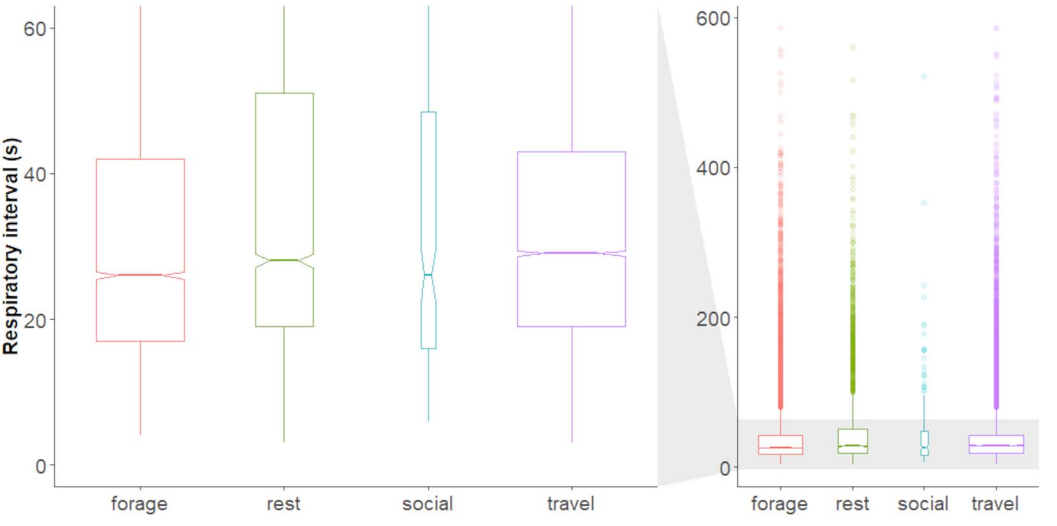

FIGURE 5. Resident killer whale (*Orcinus orca*) respiratory interval (seconds) for each activity state observed in British Columbia, Canada, and Washington, USA. The mid lines represent medians, boxes are first and third quartiles, and vertical lines are 95% confidence intervals. The left panel is zoomed in to focus on differences in medians for each activity state. Notches that do not overlap suggest that the medians are significantly different. Box width is proportional to sample size. Outliers are denoted by circles in the right panel. This represents data from 98 individual focal whales collected across 421 tracks.

and respiratory rate are in effect the reciprocal of one another. When respiratory effort increases, the respiratory rate increases and the respiratory interval decreases. If it became necessary to use these metrics to monitor health of a free-ranging killer whale, we see value in coordinating tracking activities between land-based and boat-based observers, to benefit from the land-based observer's wide field of view and the boat-based observer's close inspection of the whale's condition.

Wildlife health is an important and challenging consideration in conservation management of endangered species or populations (Deem et al. 2001). Determining health status in wild animals is difficult, but particularly important in small, endangered populations where infectious and noninfectious disease may directly influence population decline or lack of recovery. Importantly, the health of wildlife can be viewed more broadly as a cumulative effect involving multiple factors that extend beyond simply disease and pathogens (Wittrock et al. 2019). These multiple factors are referred to as determinants of health, and they comprise biological, social, and habitat influences on individual animals' health. As such, the health of wildlife reflects the health of the ecosystem on which they rely, and the health of high trophic species can serve as an indicator for the ecosystems that they inhabit. For SRKWs, information regarding both disease (narrower definition of health) and determinants of health (broader definition of health) are needed for recovery planning, development or improvement of recovery policy, and guiding research and for promoting protective actions across the determinants of health categories. With small cetaceans, these health data are collected using traditional veterinary, hands-on, physical examinations during short-term captures and restraint in shallow nearshore areas as part of health assessment initiatives (Barratclough et al. 2019). Because of the size, weight, and strength of killer whales, the physical environment that they inhabit, and considerations for human and animal safety, capture and restraint are not an option for routine health assessments. Wild killer whales also cannot be conditioned using positive reward systems to participate in health examinations as is done with killer whales in human care. Understanding

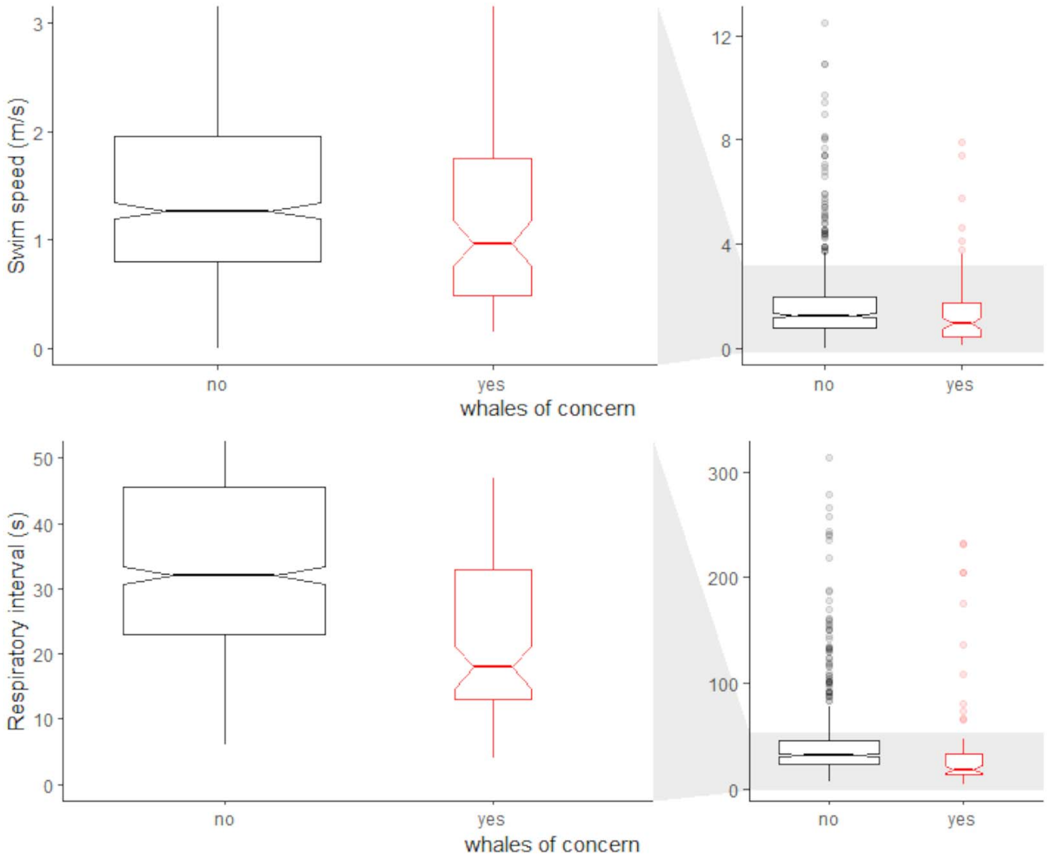

FIGURE 6. Southern resident killer whale (*Orcinus orca*; SRKW) swimming speeds (meters per second) and respiratory interval (seconds) recorded during the 2022 season across 21 tracks in Washington, USA. The left panel is zoomed in to focus on differences. The three whales with low body condition scores are displayed on the right of each panel. Data from other SRKWs (n=15) in comparatively better body condition are displayed on the left. The mid lines represent medians, boxes are first and third quartiles, and vertical lines are 95% confidence intervals. Box width is proportional to sample size within each comparison plot. Outliers are denoted by circles.

what respiratory intervals tell us about individual animal health in the wild is an extension of what has been done in captive care. Swimming speed is not used in evaluating health in captive animals, but as shown herein, it has promise in identifying either pods containing an individual animal of concern or even individual animals that are consistently lagging behind the group. Developing these tools for evaluating health is part of a larger effort to develop, test, and validate multiple remotely sensed health metrics for evaluating health in free-ranging killer whales. Identifying animals of concern, however, is just the first step in conservation medicine. Recent modeling (Williams et al. 2024) suggests that in addition to addressing primary threats of food availability, vessel disturbance, and contaminants, saving this unique population will require not only diagnosis but also treatment of sick animals, making treatment delivery an additional research and development need.

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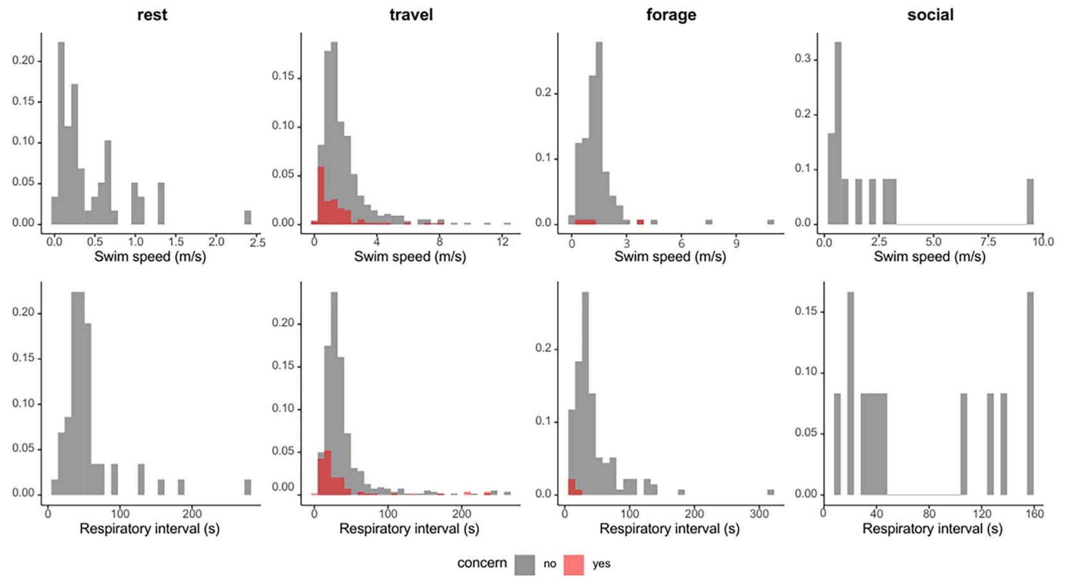

FIGURE 7. Southern resident killer whale (*Orcinus orca*; SRKW) swimming speeds (meters per second; top row) and respiratory intervals (seconds; bottom row) recorded during the 2022 season across 21 tracks in Washington, USA. Data from the three tracks of whales of concern are in red. Data from the other 15 SRKWs in comparatively better body condition are displayed in pale gray.

Washington, USA (2003–2005, 2022). Theodolite tracking was made possible by grants from BC Parks, National Marine Fisheries Service, Vancouver Fraser Port Authority Enhancing Cetacean Habitat and Observation Program, and Washington Department of Fish and Wildlife. Additional funding for processing, data analysis, manuscript writing, and page charges was provided by the SeaDoc Society, a program of the Karen C. Drayer Wildlife Health Center, University of California–Davis School of Veterinary Medicine. Oceans Initiative's Healthy Whales Initiative is supported by Arthur L. & Elaine V. Johnson Foundation and the Regina Bauer Frankenberg Foundation. We thank two anonymous reviewers and the editor, Debra Bourne, for their careful review and helpful suggestions.

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