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NOTE

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Dive and movement behavior of a humpback whale competitive group and a multiday association between a primary escort and female in Hawai‘i

E. Elizabeth Henderson[1] | Mark Deakos[2] | Dan Engelhaupt[3]

[1]WARP Lab, Environmental Readiness Division, NIWC Pacific, San Diego, California

[2]HDR, Wailuku, Hawaii

[3]HDR, Virginia Beach, Virginia

Correspondence
E. Elizabeth Henderson, Naval Information Warfare Center, 53560 Hull Street, San Diego, CA 92152-5001.
Email: ehenders@spawar.navy.mil

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Humpback whale competitive group behavior on breeding grounds was first described in the early 1980s (Baker & Herman, 1984; Mobley & Herman, 1985; Tyack & Whitehead, 1982), and has been found to be consistent across breeding grounds and ocean basins. When an adult female, with or without a calf, is temporarily accompanied by two or more males, often with surface activity and characterized by male–male aggression, this is considered a competitive group (e.g., Clapham et al., 1992). The dominant male, considered the primary escort, maintains a position in close proximity to the female (sometimes referred to as the nuclear animal), staying between her and one or more secondary escorts. Some secondary escorts may challenge the primary escort in an attempt to displace him; these challenges can last from 30 s to over 10 min (Tyack & Whitehead, 1982), and occasionally result in a successful displacement of the primary escort. For the duration of a competitive group, new males may join while other males may leave the group. In general, males join and leave the group alone but on occasion will affiliate or disaffiliate as a pair or group of three, leading some to suggest possible cooperation in attempts to displace the primary escort (Clapham et al., 1992; Darling et al., 2006; Felix & Novillo, 2015). Males with the highest level of testosterone have been shown to hold the primary escort position (Mingramm et al., 2020), suggesting more elevated testosterone levels in secondary escorts may be necessary to displace the primary defending male. Primary escorts also tend to be the largest or second-largest male within their individual competitive group (Spitz et al., 2002).

This paper describes a unique situation in which four of the seven members of a competitive group were tagged with Wildlife Computers SPLASH10 F-333 tags and their dive behavior was recorded for a large portion of the encounter. In addition, the primary escort and nuclear animal (referred to as the female from here on) remained together for at least 4 days before the tag on the female stopped transmitting. The location, movement behavior, and dive behavior of these two whales were highly correlated. The events of the competitive pod encounter are detailed herein, with a focus on the dive behavior of the four tagged whales, along with a description of the movement and dive behavior of the primary escort and female during their 4-day association.

Vessel-based satellite tagging and photo-identification were conducted March 21–26, 2019, in waters off Kaua'i and Ni'ihau, the northwestern-most islands of the main Hawaiian Islands. Nonsystematic surveys were conducted using a 6.7 m rigid-hulled inflatable boat. Sighting data for each encountered humpback whale group was recorded on an iPad using the app COMPASS (Richlen et al., 2017) in addition to handwritten data sheets. In addition to date, time, and location, sighting data included the group size, group behavior, and individual photo-identifications of the tail fluke, right and left dorsal fins when possible, and the social role of each individual. Photographs were taken using one of three digital SLR cameras (Canon 50D, 7D, or 7D Mark II) with a 100–400 mm zoom lens.

Satellite-monitored, location-dive tags (Wildlife Computers SPLASH10 F-333) in the Low-Impact Minimally Percutaneous External electronics Tag (LIMPET) configuration were used. Tags were attached to or near the whale's dorsal fin with two 6.8 cm sterilized surgical-grade titanium subdermal darts with six backward-facing petals and deployed with a DanInject JM25 pneumatic projector (DanInject ApS, Børkop, Denmark). Tags were programmed to transmit 18 hr per day (based on satellites availability in the area) with up to 750 transmissions per day. The tag's series function was used to record depth every 75 s to extend battery life. It should be noted that a sampling interval of 75 s can create less accurate maximum depth and durations as a result. Data gaps were expected due to multiple factors affecting message transmittal and reception. Track positions were estimated using the Argos Data Collection and Location System with a Kalman filtering algorithm, and further screened using the Douglas-Argos Filter version 8.50 (Douglas et al., 2012) available in Movebank (https://www.movebank.org/). Additional manual filtering was conducted to remove erroneous locations appearing on land. All locations were utilized for analysis regardless of location class (other than class Z; classes are based on estimated error and number of messages received), unless they were removed during the filtering process.

The analysis conducted on the resulting location and dive data is described in detail in Henderson et al. (in press), but is briefly summarized here. The filtered locations were fitted with a correlated random walk to smooth the fitted track and interpolate the positions every hour using the package *crawl* (McClintock & Michelot, 2018) in the statistical computing program R (R Core Team, 2019). In order to capture the movement behavior of the whales, a discrete-time Hidden Markov Model (HMM) was developed based on step length (distance between interpolated positions) and turning angle between interpolated hourly locations using the package *momentuHMM* (McClintock & Michelot, 2018). A gamma distribution was used to fit the step length and a wrapped Cauchy distribution was used to fit the turning angle data for three behavioral states: (1) Area-Restricted Search (ARS), which typically indicates milling or foraging but may also be indicative of social behavior; (2) an intermediate behavior; and (3) directed travel. The intermediate state represents a transition between ARS and travel, as there were few instances when the whales switched directly between those states and therefore seems to be an intentional behavior (i.e., rather than "indeterminant" as this state is sometimes referred to). This was the dominant behavior in nearshore waters. The intermediate state was also observed as the whales approached or moved away from islands and seamounts. The Viterbi algorithm (a dynamic programming algorithm) was used to compute the most likely sequence of those three underlying states for each track (Zucchini et al., 2016). In addition, the hour of day and a binary factor indicating whether animals were greater than 50 km from shore (following Palacios et al., 2019, this was determined to be the distance at which animals began transitioning from breeding to migratory behavior) were included as covariates in the state transition probabilities to provide further information on where and when behavior transitioned between states. Dive behavior was analyzed using the package *diveMove* (Luque, 2007), which determines the number of dives and dive depths (median, mean, and maximum), and identifies: (1) the start of the descent, (2) the end of the descent and start of bottom time, (3) end of bottom time and start of the ascent, and (4) total dive duration. Note that since dive time series data are only recorded every 75 s, these values are not exact, and only represent the phase of the dive at each 75 s interval.

The competitive group was first encountered off the northeast side of Kaua'i at 10:08 HST on March 25, 2019, cued by surface active behavior. The initial group size estimate, confirmed by photo-identification, was four animals—the female (initially assumed based on her position of nuclear animal in the competitive group and her behavior, and later confirmed via resighting information in HappyWhale, see below), primary escort, and two secondary escorts (sex of these three escorts was confirmed with underwater photographs). At 10:29 and 10:34 two additional secondary escorts were photo-identified, and another was photographed at 10:47, bringing the total group size to seven animals. The female was tagged on her second surfacing at 10:12 (Tag 173791, hereafter referred to as FE1), and the primary escort was tagged shortly thereafter at 10:28 (Tag 179028, hereafter referred to as PE2) on his third surfacing of the encounter. As we attempted to take photographs of every animal at each surfacing, the dive and surface intervals can be identified from the photo-id record. However, some surface intervals could have been missed and we cannot be certain we captured all individuals when there were multiple animals at the surface (e.g., if all animals surfaced every time the female surface).

During the first hour of the encounter, the group was moving slowly north (Figure 1). Surfacing intervals of the group lasted 2–8 min (mean 3.3 min), with four surfacings of single individuals that lasted only 1–2 min. Between these surface periods, the dives of the group lasted 4–13 min (mean 7.1 min). Other than one extended surfacing period by most of the group from 10:56 to 11:03, when PE2 was at the surface repeatedly but FE1 was in a long 11 min deep dive, the dive patterns of PE2 and FE1 were closely matched (Figure 2). FE1 had 5 dives to maximum depths of 36–65 m, with dive times of 8.8–18.8 min (although the dive pattern in Figure 2 indicates that FE1 at least started surfacing with PE1 during that long 18.8 min dive interval; it is possible the tag may have missed her actual surfacing), and the four associated dives of PE2 were similar to those of FE1 although somewhat shorter, with depths of 41–61 m and dive times of 6.3–11.3 min. The correlation between their dive depths in each 75 s bin was 86%.

At 11:25 one of the original secondary escorts was tagged (Tag 179030, hereafter referred to as SE3). Around this time the group changed heading slightly to a northwest direction, and the group behavior changed. The last sighting of one of the smaller secondary escorts was at 11:20. At 11:23 and 11:31 PE2 and FE1 surfaced together in

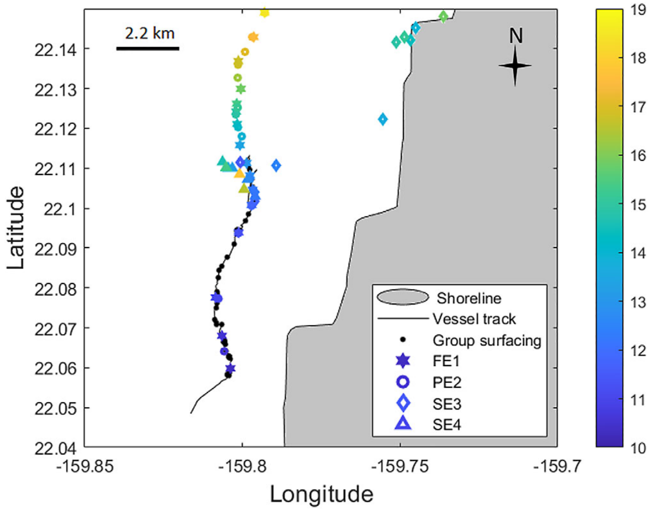

FIGURE 1 Vessel track (black line) and surfacing locations (black dots) of competitive pod on March 25, 2020. The FASTLOC GPS tag locations are also given for each animal from the time each animal was tagged through 19:00, with the local time indicated by the color bar. This figure shows the excellent correlation between tag GPS positions and the true sighting locations, as well as an indication of the movement behavior of the group during the competitive pod and the timing and movement of disaffiliating escorts. The pair continued along the same path, while SE3 moved close inshore to Kaua'i (the gray shape outlined in black), and SE4 remained in the area before eventually turning south.

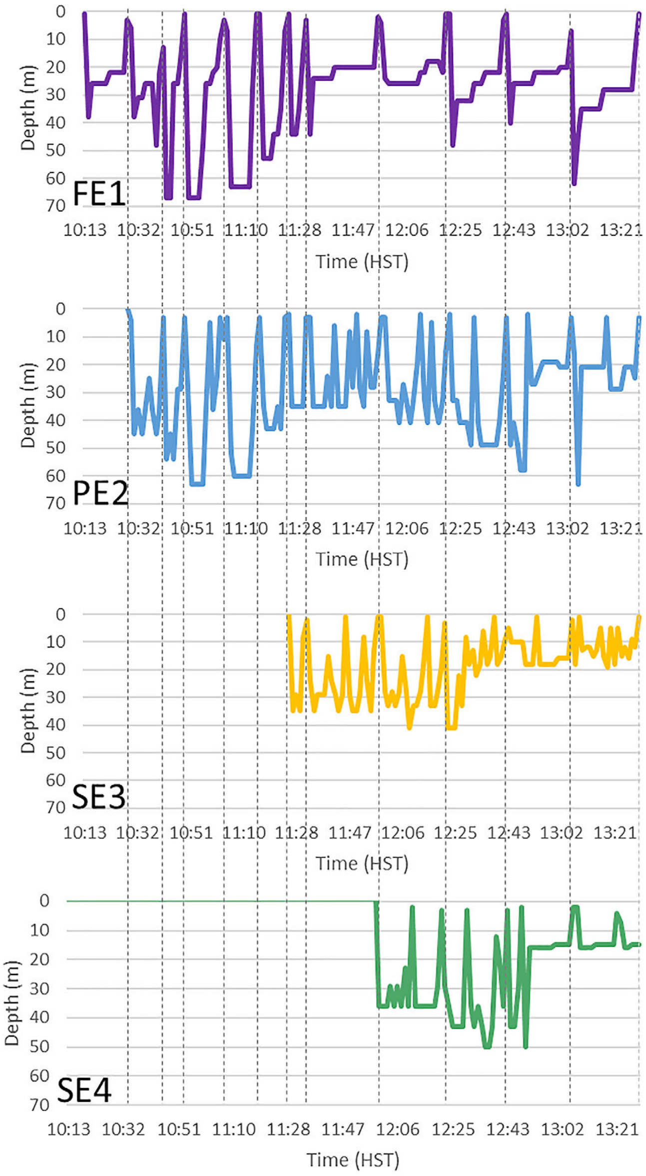

FIGURE 2 Dive record for each of the four animals tagged in the competitive pod on March 25, 2019. The top plot is FE1 in purple, the second plot is PE2 in blue, the third plot is SE3 in yellow, and the bottom plot is SE4 in green. The dive behavior of PE2 correlates with FE1 for the first hour, with SE3 for the next 45 min (~11:30–12:15), and then SE4 in the last hour (~12:15–13:20). The light gray lines indicate each surfacing of FE1; PE2 surfaces with FE1 every time, but also surfaces with the challenging secondary escorts during the periods when their dive behavior is correlated. Note that all three males surfaced every time the female surfaced until they had disaffiliated.

close proximity; after that followed a series of short 1–2 min surfacings by either a single secondary escort or a secondary escort and PE2, with PE2 apparently chasing any secondary escorts that may have been challenging. Although not recorded comprehensively, some surface-active behaviors were noted, including trumpeting, head lunges, and linear bubble trails. At the end of this series of short surfacing periods by the males, the whole remaining group surfaced for 5 min, while PE2 continued to focus on the challengers. From this point to the end of the group encounter, FE1's dives became somewhat stereotyped, with an initial deep descent to about 42 m, then a longer plateau at about 25–30 m, and the dive durations become longer, lasting from 21.3–45 min (Figure 2). These longer dive durations indicate that FE1 was likely stationary at this point. In fact, the whole remaining group stopped traveling and most of the remaining observed activity happened around the largely stationary female.

From 11:27 to 12:15, the dive behavior of PE2 shifted from being correlated to the dive behavior of FE1 to being correlated with the behavior of SE3 (Figure 2); this may indicate that SE3 was challenging PE2 for his position and PE2 was focused on blocking him. During this time frame, their dive depths were correlated at 61%, while the dives between PE2 and FE1 dropped to a correlation of only 27%. Herman et al. (2007) also noted that primary escorts seemed to both closely track the female and chase off challengers. Note that even while the dive behavior of PE2 is more correlated with SE3 during this time, both males still surface at the same time as the female. The last sighting of SE3 was at 12:14 and was observed being chased by PE2. As evidenced in Figure 1, SE3 immediately left the group and moved away to the east along the north side of Kaua'i. The final sightings of the remaining two secondary escorts also occurred during this period, at 12:15 and 12:21; they may have been chased away by PE1 as well. Interestingly, although SE3 followed a similar path along the northern side of Kaua'i to PE2 and FE1 after the cessation of the competitive pod (Figure 3), SE3 actually ended up being 1–3 hr behind the pair, and so must have stopped moving or traveled very slowly after his initial move away from the group.

At 11:57 the other secondary escort from the initial group of four whales was tagged (Tag 179029, hereafter referred to as SE4). After SE3 disaffiliated, the focus of PE2 seems to shift to SE4 as a new challenger, as from 12:15 to 13:20 the dive behavior of PE2 becomes highly correlated (91%) with SE4 (Figure 2). SE4 was last observed at 12:43, again being chased by PE2 on its second to last sighting. However, note that the dive behavior of PE2 and SE4 is still correlated through 13:20 even though the animal was not visually sighted again, and that both PE2 and SE4 surfaced at 13:02 at the same time as the female. Therefore, although we did not see SE4 again after 12:43, he likely did not actually disaffiliate until 13:20, when his dives become out of sync with both PE2 and FE1. Based on the tag record, SE4 remained in the area before moving back south and eventually traveled west to Ni'ihau (Figure 4).

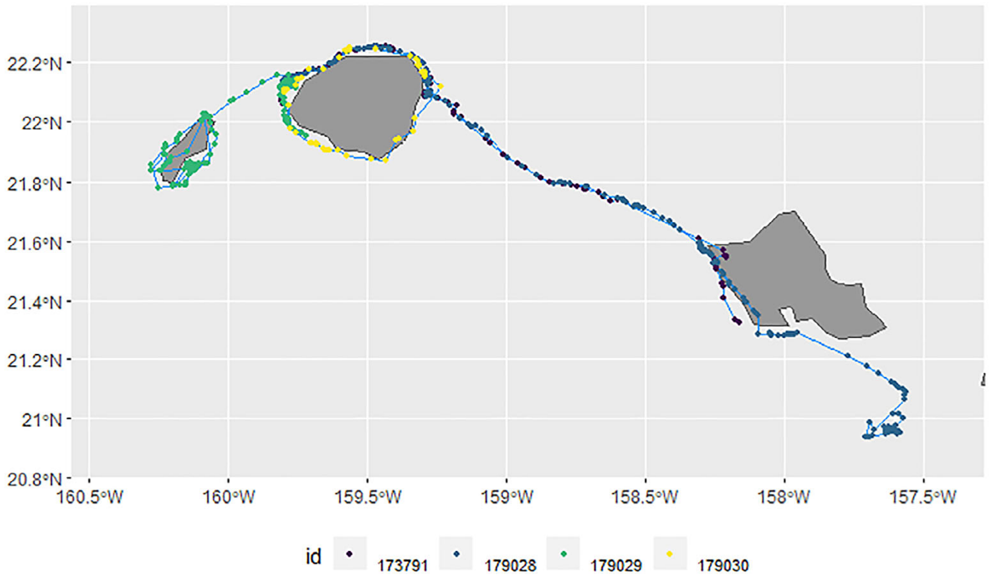

FIGURE 3 Argos satellite and Fastloc GPS location tracks of the four tagged humpback whales. FE1 is in purple, PE2 is in blue, SE3 is in yellow, and SE4 is in green.

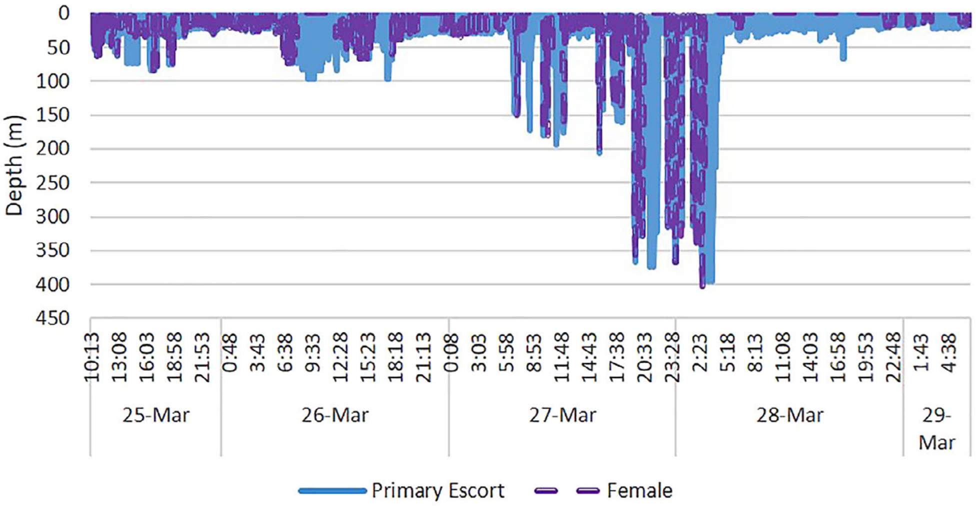

FIGURE 4 Full dive record of the primary escort (in blue) and female (overlaid in purple). Other than the period during the competitive pod at the beginning of the record, and periods when there were no dive data for the female, the dives of both animals match closely in depth and duration.

Fluke photographs of FE1, FE2, SE4, SE3, and one other secondary escort were all matched in HappyWhale, an online repository of humpback whale fluke photographs with an automated fluke photograph matching algorithm (https://happywhale.com; Cheeseman et al., 2022). This has provided some insight into the observation histories of these individuals on both the Hawaiian breeding grounds and some feeding grounds. The resighting history of FE1 extends back to 2005 where she was first photographed in the Prince William Sound area of the Alaskan feeding grounds by the North Gulf Oceanic Society during the Structure of Populations, Levels of Abundance and Status of Humpback Whales (SPLASH) effort (Olga von Ziegsar, personal communication, August 10, 2021). Winged Whale Research also resighted FE1 in the area in 2010 and 2011 (Olga von Ziegsar, personal communication, August 10, 2021). In 2009, FE1 was photographed by Gulf Watch Alaska in the same area (Jan Straley, personal communication, August 15, 2021). FE1 was also photographed off Maui in 2005 by Whale Trust as part of a pair; DNA from a skin sample was also collected at this time, which confirmed the whale is female (Jones 2010; Meagan Jones, personal communication, July 29, 2021). Interestingly, FE1 and PE2 were sighted together at 14:00 on March 30, 2019, off Honolulu, Oahu by Atlantis Cruises; this is a full 29 hr after FE1's tag stopped transmitting, and confirms the two animals remained together for an additional day (or at least remained close enough to be resighted together). The only other resight information for PE2 was off Maui on March 9, 2020 (Magic Merman; Derek Brown, personal communication, August 5, 2021).

SE3 has been observed by the Pacific Whale Foundation off Maui in 2013, 2018, and 2020 (Jens Currie, personal communication, August 3, 2021). SE4 was first observed off Maui in 1998, also by the Pacific Whale Foundation (Jens Currie, personal communication, August 3, 2021), and was observed in Gambier Bay in the southeast Alaska feeding grounds by Alaska Sea Adventures (Dennis Rogers, personal communication, July 28, 2021) on August 30, 2019, 5 months after being tagged in this effort. Finally, one of the untagged secondary escorts was photographed in 2006 off Socorro Island by the Universidad Nacional Autónoma de México (UNAM), also as part of the SPLASH effort (Jeff Jacobson, personal communication, August 2, 2021).

The tag was placed lower on the dorsal area of FE1 than PE2, which we believe resulted in more periods of missing data where the Argos uplink could not be completed. While the animals were in range of the mote antennas on Kaua'i and Oahu, both had frequent Fastloc GPS location updates, but FE1 had several 2–4 hr periods of missing dive data throughout her tag record, and is missing almost a day of location and dive data while the animals transited over deep water to Oahu (Figures 3 and 4). However, from the end of the observed competitive pod through 6:58 on March 29, 4 days later, the dive depths of FE1 and PE2 were correlated at 97% (Figure 4) during periods when there are data for both animals. There are periods across the 4 days when the dive behavior becomes asynchronized, with substantially different dive patterns, although the male still surfaces every time the female surfaces (e.g., top plot, Figure 5). These could represent periods when this pair was part of another competitive group, as this asynchronous dive behavior was observed in the initial competitive group (see movement behavior below as well). However, these could also just be periods where the male is circling at the surface and then returning to the female (e.g., Jones, 2010). There are also periods where the dives become highly synchronized (middle and bottom plots, Figure 5), particularly when the animals are traveling across the channel between Kaua'i and Oahu (see below).

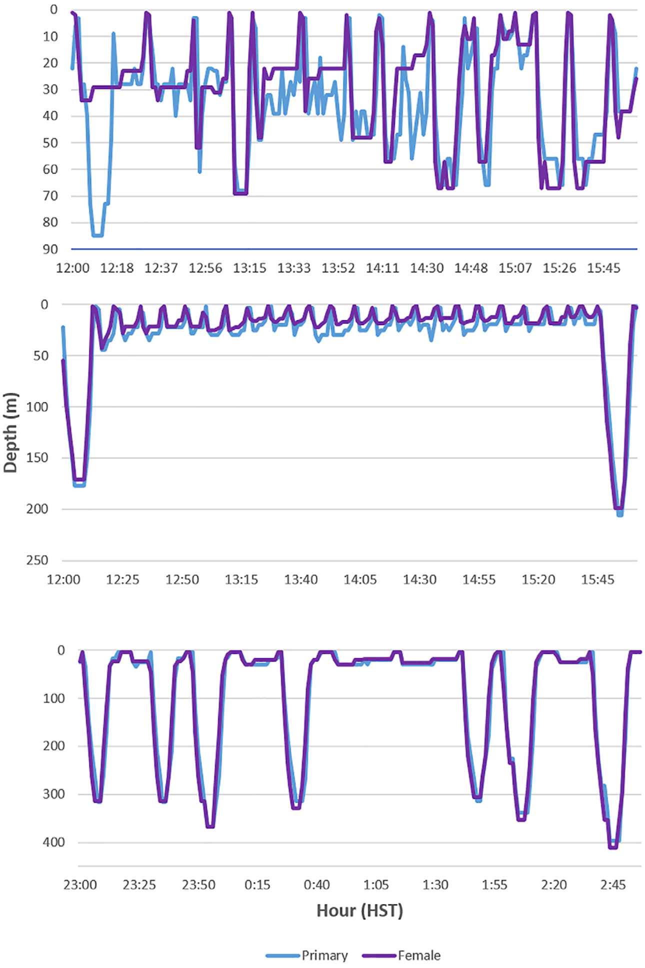

FIGURE 5 Dive behavior comparison for the female and primary escort for portions of the 4-day period the animals spent together. The top plot spans the period from 12:00 to 16:00 on 26 March; the whales begin this period in ARS and then transition to the intermediary behavior state around 14:00. The middle plot spans the period from 12:00 to 16:00 on March 27; here the dive behavior is more similar between both animals, although the male consistently dives deeper and with more movement at depth than the female. The bottom plot spans the period March 27 23:00 to March 28 3:00; these deep dives occur as the animals transited between islands and were highly synchronized. In both the middle and bottom plots, the whales were in directed travel and had moved into the channel between Kaua'i and Oahu; however, the middle plot takes place during the middle of the day while the bottom plot takes place at night. Note than in all these examples, the male always surfaces with the female.

Through the entire shared dive record, there are only 16 times the female surfaced without the male, with the male 8 m or deeper when she was at the surface. However, in all of these cases the male appears to be surfacing with the female, but the surface interval may have been missed by the 75 s binning. On the other hand, there were 35 times that the male surfaced while the female clearly remained at depth, seven of which occurred during the observed competitive group. Another six surfacings by the male without the female occurred in the second period of ARS, and at least two more occurred during the last period of ARS near Kauai, although the female's dive record was not complete at that time. This supports the idea that the female probably never surfaces alone but is always accompanied by her escorting males, while the males may surface without the female, especially when expending more energy during competition, requiring more frequent replenishment of oxygen reserves.

The mean dive duration for FE1 was 12.8 ± 8.6 min, while the mean dive duration for PE2 was 13.5 ± 8.0 min. The mean dive depth for FE1 was 47.4 ± 74.0 m, with the deepest dive descending to 412 m. The mean dive depth for PE2 was 47.3 ± 66.6 m, with the deepest dive extending to 396 m. These deep dives occurred as the animals transited between the islands and had the most synchronous behavior across the dive records for both animals (bottom plot, Figure 5). These are similar depths to what was found for previously tagged humpback whales in Hawai‘i that moved offshore into deep water (Henderson et al. 2019, in press), but are deeper than previously reported dives for humpback whales in Hawai‘i. Previous deep dive records were to 176 m (Baird et al., 2000) and 298 m (Herman et al., 2007), although in both studies the dive depths may have been constrained by the water depth. Derville et al. (2020) also reported a deep dive record of 616 m for a humpback whale in the South Pacific off New Caledonia.

In addition to their dive behavior, the movement behavior of the dyad remained similar throughout the duration of their association (Figure 6). The interpolated locations (based on the combined Argos and GPS records) between March 25 at 13:00 (the end of the competitive pod) through March 29 at 9:00 were correlated. The correlation coefficient between the behavioral states at each 1 hr interpolated location of the two animals was 0.82, indicating a high degree of

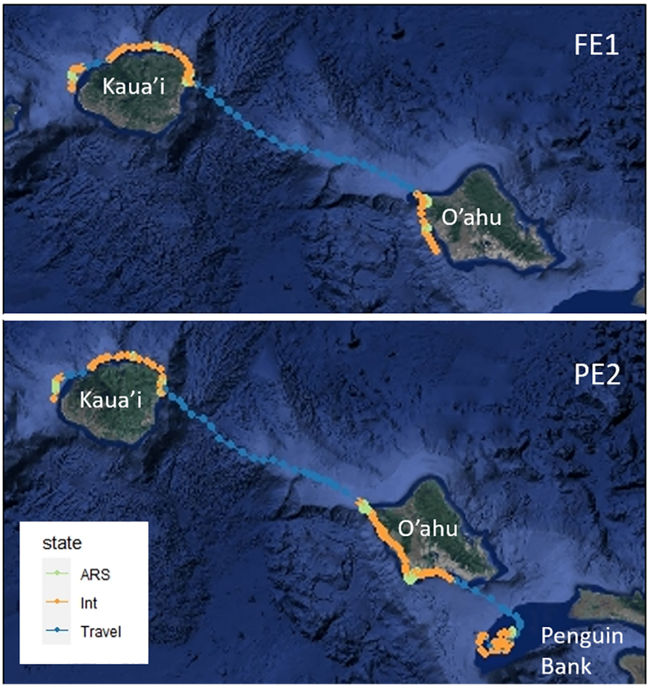

FIGURE 6 Hourly interpolated track positions for the female (FE1; 173791) and primary escort (PE2; 179028) color-coded by their behavioral state as determined by Hidden Markov Models.

correspondence. Their behavioral states varied in a coordinated manner (Figure 6), with alternating periods of ARS and intermediate behavior co-occurring between FE1 and PE2 as they moved around Kauaʻi, and then they switched to directed travel as they headed towards Oahu. The track movement behavior for FE1 and PE2 indicates three periods of ARS while the whales were close to Kauaʻi. The first of these was during our initial encounter with the competitive group. The second of these is plotted in Figure 5 (top plot); the whales are both in ARS at the start of the plot, when the dives are largely uncoordinated, and then transition into the intermediate state around 14:00 when the dives begin to synchronize again. That period of ARS could also be indicative of another association with a competitive group. Unfortunately, the dive data for FE1 are missing for part of the third period of ARS at Kauaʻi, and during the period of ARS when the whales reach Oahu (Figure 6), so it is difficult to compare the dive data at those times to determine whether the dive behavior became similarly asynchronous during ARS. However, during both the first period of ARS, starting with the observed competitive group, and the third period of ARS before the dyad moved offshore of Kauaʻi that lasted about 3 hr, FE1 conducted several long dives while PE2 surfaced repeatedly. This increase in dive frequency by PE2 while still synchronizing with FE1's surfacings could suggest that PE2 was once again engaging with one or more challengers, although this is only speculative. These periods of ARS may indicate that the dyad became part of a competitive group and the female was escorted by multiple males across multiple days, and should be investigated further in future tagging efforts. Jones (2010) reported a female without a calf in Maui seen 17 days apart and escorted by competing males on both occasions, although could not confirm that the male and female were together consecutively over that period. Further observations of the surface behavior of tagged animals will be needed to fully identify dive patterns of competitive pods as compared to dyads.

The animals transitioned into directed travel as they moved away from Kauaʻi and into the deeper Kaieiewaho Channel (Figure 6). The middle and bottom plots in Figure 5 are both snapshots of dive data during directed travel; the dives in the middle plot occurred during the afternoon, while the dives in the bottom plot occurred overnight. The increase in deeper dives at night in offshore waters has been observed previously for humpback whales in Hawaiʻi (Henderson et al. 2018, in press). Deep, oscillating dives during travel may provide similar benefits seen for other species such as thermoregulation, inspecting the water column for chemical cues, electromagnetic information for navigation (especially as these repeated deep dives occur at night), or energy efficiency during bouts of travel (Klimley et al., 2002; Williams et al., 2000). Alternatively, the whales could be opportunistically foraging on the rising scattering layer, as is known to occur with pelagic odontocetes (e.g., Abecassis et al., 2015; Copeland et al., 2019).

This is the first record of a confirmed multiday association between a male and female humpback whale on the breeding grounds. Previous observations had found primary escorts to remain with females on the order of hours up to two or three consecutive days before being displaced by another male (Baker & Herman, 1981; Darling & Bérubé, 2001; Mobley & Herman, 1985; Tyack & Whitehead, 1982). Jones (2010) reported a male–female pair sighted together after 28 hr and a male escort sighted with the same mother repeatedly over a 3-day period. While Baker and Herman (1984) observed the same escort with a female and yearling over 2 days, it could not be confirmed that the animals remained associated for that whole period. Similarly, Pack et al. (2002) also reported an escort observed with the same mother over a period of 3 days, although they could not verify that the male remained associated with the female for the entire duration.

Craig et al. (2002) hypothesized that males may display mate choice by remaining with females with high conception probability for longer durations and expending more energy defending their position. They posited that allocating energy on females with high probabilities of conception is a better use of resources than indiscriminate competition. This was supported by the findings of Mingramm et al. (2020), where females without calves found in competitive pods had higher levels of estradiol, indicating ovulation, than females found alone or with a calf. Mingramm et al. (2020) also hypothesized that the duration of an association between a male and female may be an indication of the female's reproductive status (ovarian condition). If that is true, then the minimum 4-day association found between PE2 and FE1 in this case may indicate a high level of estradiol and receptivity in the female. PE2 may be displaying mate-guarding behavior as hypothesized by Mobley and Herman (1985), either waiting until FE1 is receptive and willing to mate, or having already mated and ensuring his sperm have time to fertilize while guarding against other males mating with her. Herman et al. (2007) tagged humpback whales with video cameras and posited that primary escorts may be demonstrating their fitness to the female during competitive pods. Some benefit may be conferred to the female as well by staying with a single dominant male for a long duration, either as protection from other males or as an indication of his high testosterone levels and potential good reproductive status. She may also have been waiting until the pair reached an area with a greater concentration of adult males (e.g., Penguin Bank; Figure 6), to evaluate before choosing to mate; however, the longer she delays she also runs the risk that PE2 may choose a different reproductively available female, leaving her to mate with a less fit male.

Multiple combined modes of observation, including passive acoustic monitoring, tagging, visual observations, and biopsy sampling, can lead to greater insights into animal behavior than a single method. This has proven successful with many behavioral response studies, in which cetaceans have been tagged and observed visually and acoustically while sonar and other sounds are played (e.g., Dunlop et al., 2017; Miller et al. 2012, Southall et al., 2016, Wensveen et al., 2019). These combined modes of observation would be invaluable to baseline behavior studies as well in providing insight into the interpretation of tag data. For example, ARS behavior in mysticetes is commonly associated with foraging, but in the case of humpback whales on breeding grounds where foraging is thought not to occur, it may instead be indicative of interactions in a competitive pod as has been hypothesized herein. Alternatively, it could be indicative of resting behavior as was determined by Weinstein et al. (2018). Additional visual or unmanned aerial vehicle observation of tagged animals could help inform such inferences, leading to a better analysis of future tag data. Similarly, multiple lines of evidence support the hypothesis that both males and female humpback whales are contributing to the selection of mates on the breeding grounds, including visual observations, Crittercam footage, long-term data, and hormone data (e.g., Craig et al., 2002; Herman et al., 2007; Mingramm et al., 2020). If these modes were combined in a single study, further insights would be gained into this theory.

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AUTHOR CONTRIBUTIONS

E. Elizabeth Henderson: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; visualization. **Mark H. Deakos:** Data curation; investigation; methodology; resources. **Dan Engelhaupt:** Data curation; investigation; methodology; resources.

ORCID

E. Elizabeth Henderson https://orcid.org/0000-0002-3212-1080

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