



# The fitness consequences of human-wildlife interactions on foraging common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida

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## Abstract

Human-wildlife interactions (HI) are becoming more prevalent with increasing human population. These interactions could have important eco-evolutionary consequences that become apparent only after observing populations for multiple generations. Here, we analyzed 28 years (1993–2020) of data from the world's longest-running study of a wild dolphin population to assess the fitness consequences of HI on common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. We investigated how human-related foraging activities such as depredation, begging, and patrolling mediate reproductive output and reproductive success of conditioned (HI) and unconditioned (non-HI) females. The analysis of 84 females and their 286 calves born during 1993–2020 found a confluence of effects on individual fitness. Reproductive output of females engaging in moderate levels of human-related foraging was 94% greater than that of non-HI females. However, high frequencies of human-related foraging had a negative effect on female reproductive success by increasing the risk of calf death up to nine times when compared to non-HI females, resulting in 31% less calf survival. These findings provide evidence that human-wildlife interactions have considerable potential to catalyze population-level changes by altering individual

fitness, and demonstrate the value of comprehensive, long-term data to better understand the ecological and evolutionary implications of human-wildlife conflict.

#### KEYWORDS

behavior, fitness, foraging, hazard, human-wildlife conflict, Kaplan–Meier, reproductive success, survival, wildlife management

## 1 | INTRODUCTION

Human population growth is the best predictor of past mammalian extinctions (Andermann et al., 2020). Around 50% of worldwide decline in mammalian range since the 19th century is attributed to human causes (Ceballos & Ehrlich, 2002). Concomitant with population growth, anthropogenic destruction of wildlife habitat, and human encroachment into wild areas, human-wildlife interactions also have increased, often with negative consequences for wildlife (Hill et al., 2020; Konrad & Levine, 2021; Nyhus, 2016). Adverse human-wildlife interactions (HI)—also referred to as human-wildlife conflict—have been identified as being among the most critical threats to wildlife (Dickman, 2010). HI threats to wildlife are often perpetuated by deep-seated human bias due to social and cultural influence. Much of the negative bias is rooted in the association of HI with wildlife-induced losses to human capital and safety (Dickman, 2010; Konrad & Levine, 2021; Peterson et al., 2010; Treves & Santiago-Avila, 2020).

Adverse impacts to wildlife from human-wildlife conflicts can range from disturbance and inadvertent mortality and/or injury, to intentional killing or injury. In some instances, HI leads to retaliatory killing that has resulted in recent extinctions of wildlife populations, particularly large carnivores (Breitenmoser, 1998; Woodroffe et al., 2005). Large animals are more likely to interact with humans in their lifetime due to their long lifespan and have an increased probability of human encroachment into their natural range (Santini et al., 2019). Larger animals require larger ranges to succeed, and as human populations increase, available habitat is shrinking, subsequently forcing animals into increasing contact with humans (Santini et al., 2019). Therefore, human-wildlife interaction can be a serious risk to large, long-lived animals (Santini et al., 2019). The increase of HI experiences among wild populations may condition animals to human presence, exacerbating direct threats to both humans and animals (Dickman, 2010; Peterson et al., 2010). Still, many wildlife populations have shown resilience and adaptability to increased human influences (Bearzi et al., 2019; Montgomery et al., 2020). Some interactions with humans may be beneficial in the short-term but can lead to long-term negative fitness consequences.

Animals have shown their adaptability to coexisting with humans by changing key behaviors, particularly foraging (Bearzi et al., 2019). Most notably, many animals that live near humans seek alternate sources of food because anthropogenic food sources often provide easy and continuous access to abundant resources (Altmann & Alberts, 2003; Altmann & Muruthi, 1988; Bonizzoni et al., 2022; Chávez-Martínez et al., 2022;). These abundant resources alter time and energy budgets and allow animals more time to mate and tend to young (Birnie-Gauvin et al., 2017; Orams, 2002). However, higher rates of reproduction can reduce rates of infant survival by dividing maternal investment—critical for infant survival and development—among multiple dependent young born within a shorter time frame (Altmann & Alberts, 2003; Altmann & Muruthi, 1988). These trade-offs are common in response to increased human-wildlife interactions and have large potential for negative population-level consequences due to their strong influence on individual survival.

Direct (food provided by humans intentionally) and indirect (food acquired via human sources without human intent) provisioning by various fishing activities increases the potential for injury or death of marine mammals due to fishing gear entanglement, ingestion or hooking, and exposure to boat strikes (Adimey et al., 2014; Bonizzoni

et al., 2022; Byrd et al., 2014; Christiansen et al., 2016; Powell & Wells, 2011; Tulloch et al., 2020; Wells et al., 2008). Along with the indirect threats, foraging among and around human fishing activities also increases the risk of retaliatory killing by humans; of which directed violence represents the second most common reason for strandings of pinnipeds on the West Coast of the United States (Vail, 2016; Warlick et al., 2018). Despite these risks, human-related foraging activities (Table 1) of marine mammals are likely driven by the opportunity for a predictable food source that reduces energy expenditure associated with foraging (Birnie-Gauvin et al., 2017; Bonizzoni et al., 2014, 2022; Diaz Lopez, 2012). This is evidenced in many cases by the increased occurrence of human-wildlife interactions involving marine mammals during times of low prey abundance (Keledjian & Mesnick, 2013; Powell & Wells, 2011; Wilder et al., 2017). Additionally, the nutritional benefits of increased prey availability by HI-related foraging may influence individual reproduction and survival. For instance, calf survival of Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) to year 2 has been documented to increase when timing of birth corresponds with times of increased prey abundance (Bezamat et al., 2019), suggesting the high energy costs needed to nurse calves are offset by abundant resources. However, a study in Bunbury, Western Australia, found that provisioned female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) weaned half as many calves as nonprovisioned females (Senigaglia et al., 2019). Provisioned females weaned less because they often spend more time in shallow water, away from calves, reducing time for maternal investment; therefore, calves are less likely to learn the skills and have access to the resources they need to survive (Foroughirad & Mann, 2013; Mann et al., 2000). These studies provide evidence that direct provisioning programs may decrease reproductive success in the form of calf survival, despite females initially benefitting from increased resources. Moreover, studies show that decreasing provisioning increases calf survival presumably because females are forced to return to natural behaviors and hence, maternal investment (Foroughirad & Mann, 2013; Mann et al., 2000; Senigaglia et al., 2019).

While we are beginning to understand the consequences of HI on dolphin populations, there is still a need to improve our understanding of the short- and long-term fitness consequences of HI. This is particularly true of those associated with indirect provisioning activities such as depredation, begging, and patrolling (Table 1). HI related activities are difficult to understand in the context of cetacean life history due to the long-lived and often highly mobile

**TABLE 1** Human interaction codes, activity, and description of activities associated with foraging as established by the Sarasota Dolphin Research Program. Referred to as human-related foraging activities.

HI code	Activity	Description
A	Patrolling	Dolphin milling (nondirectional movement) or travelling back and forth within 20 m of boats, lines, or pier.
B and C	Scavenging and Probable Scavenging	Observed or probable feeding by dolphins on bait or catch throwback not on angler's line, when angler did not intend to feed dolphin.
D and E	Depredation and Probable Depredation	Dolphin is confirmed or suspected of taking fish directly off a line.
F	Begging	Dolphin behavior(s) to elicit food from a person, such as bringing head out of water and/or opening mouth at surface. Typically, chin is out of water.
G and H	Provisioning and Attempted Provisioning	Dolphin intentionally being fed bait, catch, or other item(s) by humans. May be directly dropped into mouth or thrown toward dolphin. Includes humans trying to feed bait, catch, or other item(s) to dolphins when it is unclear if the dolphins took the item.
P	Fixed Gear Interactions	Repeated diving, milling, or probable feeding in close proximity to crab pots or other fishing gear. May or may not include direct physical contact with a trap and/or its associated line and float.

characteristics of cetacean species. The long-term resident community of common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida provides an unusually robust data set that allows it to serve as a model for marine mammal populations facing increasing human pressure (Wells, 2020). The ability to study and understand HI is especially critical due to social learning of cetacean species and the possibility of HI persistence (Wells, 2019), which could have cascading, population-level consequences globally.

We analyzed 28 years (1993–2020) of dolphin data to test for short- and long-term fitness consequences of HI activities in female bottlenose dolphins through their effects on calf production and survival. We asked (1) do human-related foraging activities increase reproductive output, and (2) do human-related foraging activities decrease reproductive success of female bottlenose dolphins? We hypothesized that while HI-related foraging may have positive, short-term fitness benefits, such as increased reproductive output, this foraging tactic may also have long-term fitness disadvantages in the form of reduced calf survival due to the increased risk of injury and death associated with these learned activities. The exploration of these questions will help us understand potential trade-offs of HI activities and may guide the development of data-driven targeted management regimes.

## 2 | METHODS

### 2.1 | Study area and dolphin community

The long-term resident Sarasota bottlenose dolphin community has been studied by the Sarasota Dolphin Research Program (SDRP) since 1970, making it the world's longest-running dolphin conservation research program (Wells, 2020). Approximately 160 resident bottlenose dolphins live in a multigenerational community in the waters between southern Tampa Bay and Venice Inlet, Florida (Figure 1; Tyson & Wells, 2016). Members of the dolphin community are considered inshore residents as they largely reside within Sarasota Bay and adjacent bay systems, and typically remain within 1 km of Gulf beaches (Wells, 2014). The sheltered, shallow habitat and year-round presence of identifiable resident dolphins provide the unique opportunity to closely study many aspects of wild dolphin biology and life history. This information is gathered through longitudinal monitoring of individuals using mark-recapture photographic identification (photo-ID) and periodic capture-and-release health assessments (Wells, 2014).

The Sarasota area is also home to a fast-growing human population that has more than tripled since 1970 and the number of registered boats has quadrupled during the same period (Christiansen et al., 2016; Wells, 2020). As a result, human-dolphin interactions have become more frequent and prominent, putting the dolphins and people of Sarasota at risk of harm (Christiansen et al., 2016). Human-dolphin interactions have become relatively common and by 2007, at least one act of HI behavior was reported on 26% of survey days (Powell & Wells, 2011). These interactions present substantial risk to the dolphin population by increasing the likelihood of injury or death to animals that engage in risky behaviors associated with human activities (e.g., begging, patrolling, and depredation; Table 1) (Christiansen et al., 2016). Additionally, evidence from this population suggests that wild dolphins' interest in humans is a learned behavior, with conditioning based on reinforcement with a food reward, and can be transmitted over generations (Christiansen et al., 2016; Powell & Wells, 2011; Wells, 2019). Generational conditioning of HI activities in the Sarasota dolphin population may also heighten the risks of these encounters.

### 2.2 | Data collection

Since 1970, SDRP has observed identifiable resident bottlenose dolphins in and around Sarasota Bay to document individual dolphin presence/absence, activities, social interactions, lineage, and reproduction. During 1993–2020, photo-ID efforts were standardized as year-round, monthly systematic surveys. These survey data were then used



**FIGURE 1** Map of the Sarasota Bay study area, which includes waters between southern Tampa Bay and Venice Inlet on the western coast of Florida.

to determine which females met the criteria of our analyses (i.e., resident females of reproductive age (>6 years old) with at least one known calf as of 1993).

Age was determined through field observation if the animal was born to a recognizable mother within the history of SDRP. In some cases, age was determined through examination of growth layer groups in teeth extracted at necropsy or under local anesthesia during brief catch-and-release health assessment efforts (Hohn et al., 1989; Wells, 2009). Similarly, sex was determined through direct field observation of genitals or through repeated observations of female with a dependent calf. Sex was also determined with examination of the genitals during health assessments or necropsy, as well as through genetic analyses of skin samples obtained through remote biopsy sampling (Sellas et al., 2005; Wells, 2009).

Calf birth and death dates were estimated from the sighting history of an individual or recovery of a carcass. Birth dates were estimated as the midpoint between the last date in which the mother was seen alone and the first date in which a calf was observed with the mother (Wells, 2000). Death dates were documented as the date in which a carcass was recovered. If a carcass was not recovered, death dates were documented as the first date in which a mother was seen without the calf following three confirmed sightings of the female without a calf. Three confirmed sightings without the calf ensure that it is presumed dead and not merely missed during a previous sighting. Lastly, separation dates were estimated as the most recent sighting date in which the rolling mean half-weight coefficient of association between mother and calf, calculated over a period of 1 year, was >0.5.

## 2.3 | HI classification

To compare reproductive output (number of calves) and success (calf survival to ages 1 and 4) between reproductive female dolphins that engaged in HI activities and those that did not, all dolphin females were initially sorted into one of two classes. HI classifications were determined using only sighting data collected during 1993–2020 due to the standardization of field techniques in 1993, ensuring equal probability of detection across animals. We assigned HI in a binary way rather than by each activity due to the opportunistic nature of observing HI directly and the low frequency of observation for individual activities (Table 1). Therefore, HI (conditioned) individuals were classified as those that had been confirmed engaging in any HI activities associated with foraging (Table 1) at any point between 1993 and 2020 (Christiansen et al., 2016; Donaldson et al., 2012; Wells, 2000), while non-HI (unconditioned) individuals were dolphins who had never been observed engaging in HI activities during 1993–2020. Furthermore, the percentage of sightings in which an individual was seen engaging in HI relative to their total number of sightings during 1993–2020 was very low, with percentages ranging from <0.1% to a maximum of 11.2%. Thus, HI individuals were later subdivided depending on the frequency of their HI behavior (see below).

To account for individual variation in the proportion of time engaged in HI behavior relative to total observed time, HI individuals were further subdivided into four quantiles of the probability function: 1%–25%, 26%–50%, 51%–75%, and 76%–100%. The quantiles were calculated based on the individual HI proportion data where the proportion of time an individual was observed engaging in HI was defined as: the number of sightings in which an individual was confirmed engaging in HI since first confirmed HI date, divided by total number of sightings since first confirmed HI date. The calculation of HI proportions was limited to the number of sightings following an individual's first confirmed HI occasion in the denominator, rather than the total number of sightings over their lifetime due to the low probability of observing HI directly and the likely underestimation of HI frequency. This allowed us to determine quantiles that were most representative of individual engagement in HI by relating the total number of sightings to a confirmed HI timeline. Proportion data were then subdivided into the four quantiles by fitting a beta distribution with the function *eqbeta()* from the R package “EnvStats” (v2.7.0; Millard, 2013). The beta distribution is commonly applied to describe probabilities or proportions (Bolker, 2008; Figure S1.1). Here, we used the beta to determine the appropriate quantile of each individual for the subsequent analyses of reproductive output and reproductive success.

## 2.4 | Reproductive output

To compare reproductive output between HI and non-HI individuals, we analyzed data of reproductive females and their known calves born from 1993 to 2020. Calves born to a female prior to 1993 were excluded from the analysis to remain temporally consistent with female HI classifications. Reproductive output was defined as the total number of calves born to a female over the course of her lifetime or to the end of the study period (2020), regardless of calf fate (van Daalen & Caswell, 2017). To test whether HI status was a predictor of female reproductive output, we modeled the number of calves born to an adult female as a function of HI category (i.e., non-HI, and four quantiles of HI), and the second degree polynomial effect of the number of observed reproductive years, using a generalized linear model with a Poisson distribution and a log link function in program R (Equation S1.1; R Core Team, 2020). A Poisson distribution was used as the count response data lacked significant overdispersion, making it more appropriate than a negative binomial ( $\theta = 162,817$ ) or quasi-Poisson. We further compared the goodness of fit of the Poisson and a quasi-poisson and found no clear difference between the fit ( $p = .99$ ; Figure S1.2, Table S1.2 in Appendix S1). We applied the functions *glm()* and *predict()* respectively from the R package “stats” (R Core Team, 2020) to fit the generalized linear model and determine the model predictions.

The number of observed reproductive years as of a mother's last observation was added as a controlling covariate in the model because calving intervals vary with maternal experience, as does reproductive success (Wells, 2000, 2003, 2014). For example, the successful calving rate in Sarasota increases until calf three and remains stable until about 25 years of age, when it begins to decline (Lacy et al., 2021). In addition, young mothers sometimes carry higher concentrations of persistent organic pollutants (POP), potentially reducing the survival of their early calves when these are transferred through lactation (Cockcroft et al., 1989; Genov et al., 2019; Wells et al., 2005). To control for changes in calving rate over a female's lifetime, the number of observed reproductive years was calculated for each female (year of last observation minus the birth year of their first observed calf since 1993). The number of observed reproductive years was used rather than age to include well-known females for which early reproductive histories were unknown, but whose subsequent life-history data were sufficiently complete to construct measures of reproduction relative to those with full histories (those tracked from birth). Additionally, exploratory analyses of full-history individuals with age as a covariate yielded no clear differences when compared to those using number of observed reproductive years. Due to the nonlinear relationship of maternal experience and reproductive output (Lacy et al., 2021; Wells, 2000, 2003, 2005, 2014) a polynomial effect of observed reproductive years was added in the models.

## 2.5 | Reproductive success

To assess the effect of HI status on calf survival, we analyzed all calves born during 1993–2020. This time frame was again selected due to the standardization of survey techniques in 1993, and to meet the model assumption of equal probability of detection (Kaplan & Meier, 1958). In this analysis, reproductive success of resident adult females was quantified at two key stages: (1) as the number of calves that survived from birth to year 1, and (2) as the number of calves that survived from year 1 to year 4 throughout the lifetime of the mother (Wells, 2000). A female was assumed to be reproductively successful if her calf survived to each of these stages due to the high rate of mortality and disappearance during these vulnerable years (Lacy et al., 2021). The later stage of years 1–4 was chosen because Sarasota residents typically separate from their mothers 3–6 years following their birth, with average separation at slightly more than 4 years old (Wells, 2014).

To quantify reproductive success, the Kaplan–Meier method was used to calculate survival probabilities of calves at each stage (Kaplan & Meier, 1958). We estimated stage-specific survival as the number of surviving

individuals divided by the number of total individuals alive and uncensored. The Kaplan–Meier method assumes that all animals are independent and at equal, constant risk of death and detection at all time periods, regardless of censorship (Kaplan & Meier, 1958; Powell & Gale, 2015). To meet these assumptions only calves that were born after year-round systematic photo-ID surveys were implemented (1993–2020) were included, giving each individual the same probability of being sighted. Additionally, all calves of the same HI quantile are assumed to have access to the same resources and threats and are therefore assumed to have equal probability of survival.

In Kaplan–Meier survival analysis, individuals without observed failure times (i.e., known dates of death) are considered “censored” at the time of their last known sighting, meaning they will be excluded from the subsequent time intervals (Kaplan & Meier, 1958). However, because survival estimates are broken into intervals, censored individuals can still provide partial information that is relevant to estimates of individual survival up until the time of censorship (Turkson et al., 2021). In this analysis, all calves of unknown fates (no documented date of death) in the first year were assumed dead due to the high rate of failure at this life stage; in these cases, observed failure time was considered the date of their last sighting (Lacy et al., 2021). For the interval of years 1–4, calf fate is less predictable, therefore, individuals of unknown fates were censored at the time of their last sighting. Other censored individuals include those who were unable to complete the time interval in question due to the limitations of the study period (e.g., animals were unable to reach year 1 or year 4 by 2020). Lastly, those that were known to have survived from birth to year 1 and from year 1 to year 4 were right censored (date of death was considered to be the end of the interval).

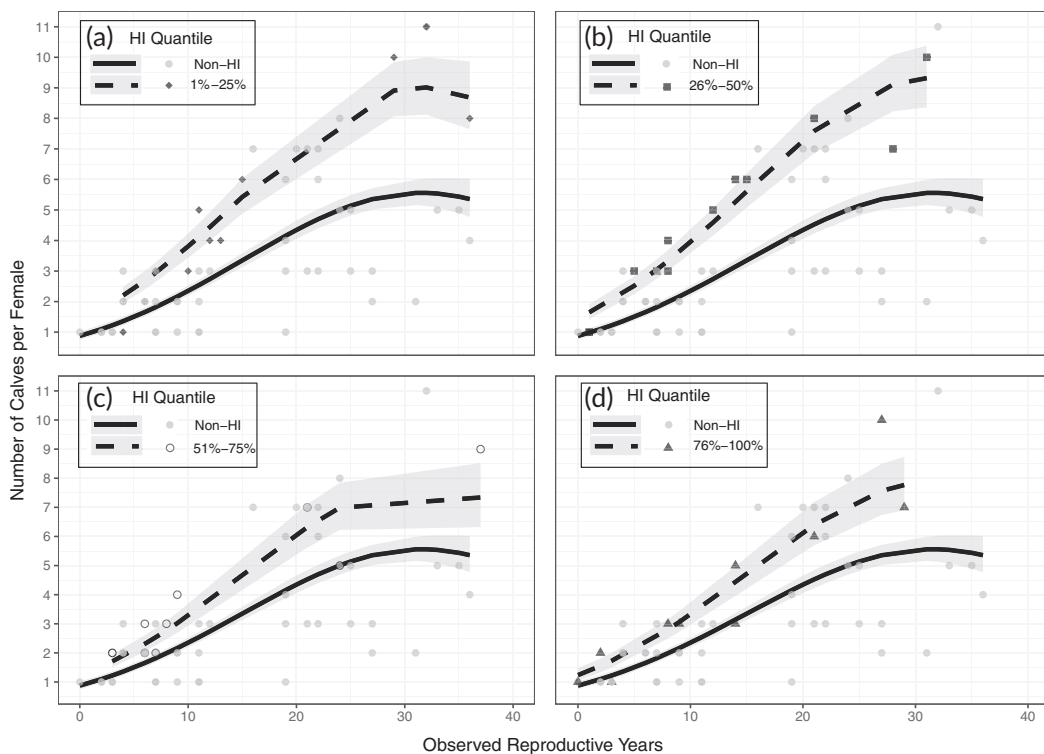
The influence of covariates on the risk of instantaneous death associated with each HI quantile was tested using the Cox Proportion Hazards Model (Cox, 1972). The covariate of interest was the assigned HI quantile of the mother for each calf. The Cox Proportion Hazard Model builds on the assumptions of the Kaplan–Meier method including individual homogeneity of threats with the key addition that the hazard ratio does not depend on time (Bewick et al., 2004; Cox, 1972). Our analysis assumed that due to their residency in Sarasota Bay and common maternal HI quantile, threats are equal across individuals. The risk of each HI quantile on calf survival was assessed by comparing the cumulative hazard and hazard ratio for HI and non-HI individuals, where the baseline hazard was calf survival of the non-HI category. The hazard ratio was interpreted as 1 being no change from the baseline hazard, <1 as a reduction in hazard, and >1 as an increase in hazard (Bewick et al., 2004). To perform the survival analysis and create the Cox hazard model we applied the functions *survfit()* and *coxph()* respectively from the R package, “survminer” (v0.4.9; Kassambara et al., 2021). For both analyses, a *p*-value of <.05 was used to establish statistical significance. We also conducted a power analysis to test the likelihood of detecting an effect of HI on calf survival from birth to year 1 and from years 1–4 (see Appendix S2).

## 3 | RESULTS

### 3.1 | Reproductive output

During 1993–2020, 137 resident females of reproductive age (>6 years old), or with at least one known calf were sighted 52,388 times collectively. Of these resident females, 84 individuals (40 non-HI, 44 HI) collectively had 286 calves with known birth years as of 1993. HI quantiles 1%–25%, 26%–50%, 51%–75%, and 76%–100% consisted of 11, 12, 11, and 10 females respectively. Overall, participation in HI activities at all frequencies increased reproductive output when compared to non-HI females. At low (1%–25%) to moderate (26%–50%) frequencies, females had on average  $1.78 \pm 0.31$  SE ( $z = 3.29$ ,  $p = .001$ ; Figure 2A, Table S1.1) and  $1.94 \pm 0.33$  SE ( $z = 3.96$ ,  $p < .001$ ; Figure 2B, Table S1.1) times more calves than non-HI individuals. While females who



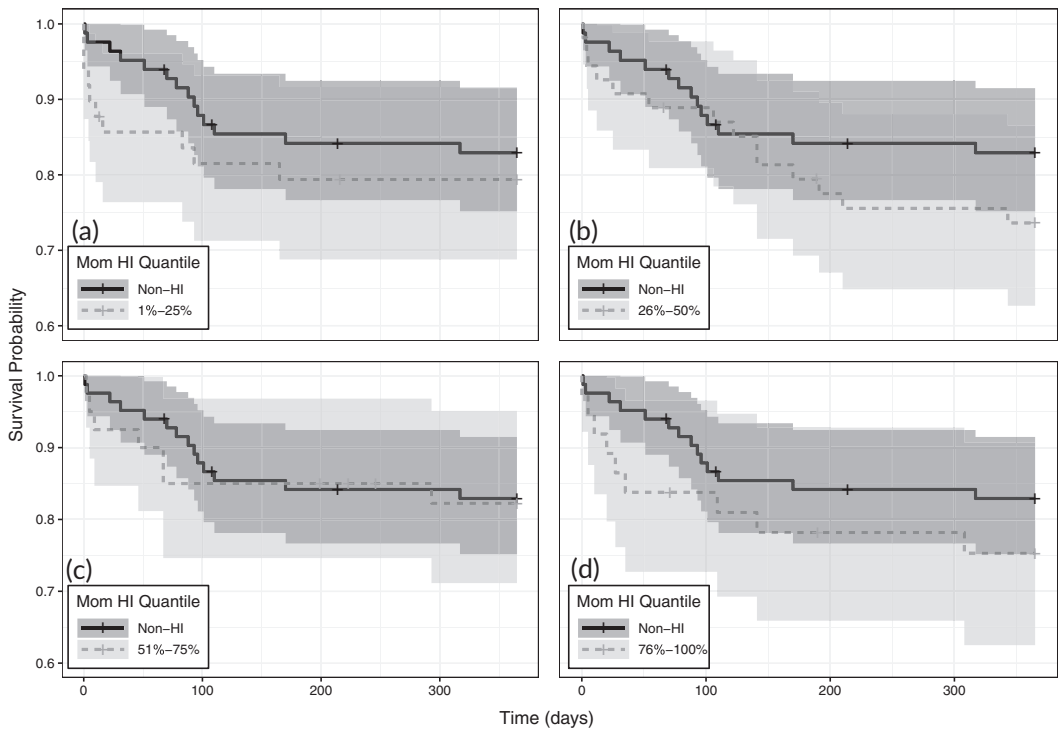


**FIGURE 2** Number of calves born to females of each HI quantile as compared to non-HI females as a function of observed reproductive years. Observed reproductive years were calculated as the difference between each female’s last year of observation and her first observed year of reproduction. Solid lines and dots represent the predicted and raw values of non-HI females, respectively, with 95% confidence intervals derived from the GLM (Table S1.1; Equation S1.1). Dashed lines represent the predicted values, paired with the raw values represented by diamonds, squares, open circles, and triangles for each HI quantile respectively.

engaged in HI activities at high frequencies (51%–75% and 76%–100%) increased their reproductive output by  $1.60 \pm 0.30$  SE ( $z = 2.51, p = .012$ ; Figure 2C, Table S1.1) and  $1.62 \pm 0.31$  SE ( $z = 2.57, p = .010$ ; Figure 2D, Table S1.1), respectively, when compared to non-HI individuals (effect sizes are reported in Table S1.3). Thus, also revealing a difference in reproductive output when comparing frequency of HI activities, where low to moderate frequencies yield up to 34% more young than high frequencies. As expected, the model predicted that reproductive output increases nonlinearly in a concave down fashion with maternal experience ( $z = 4.64, p < .001$ ;  $z = -3.2, p = .001$  for the linear and polynomial term, respectively). This model explained a large portion of the variability in the data ( $R^2 = 0.76$ ; Table S1.1).

### 3.2 | Reproductive success

The model for reproductive success included all calves born to resident females with known birth dates from 1993 to 2020. This included 263 of the 286 calves born to 78 of the 84 resident females from the reproductive output analysis (6 females had 23 calves without confirmed birthdates and were therefore excluded). The number of calves born to non-HI females and females of each HI quantile, 1%–25%, 26%–50%, 51%–75%, and 76%–100% consisted

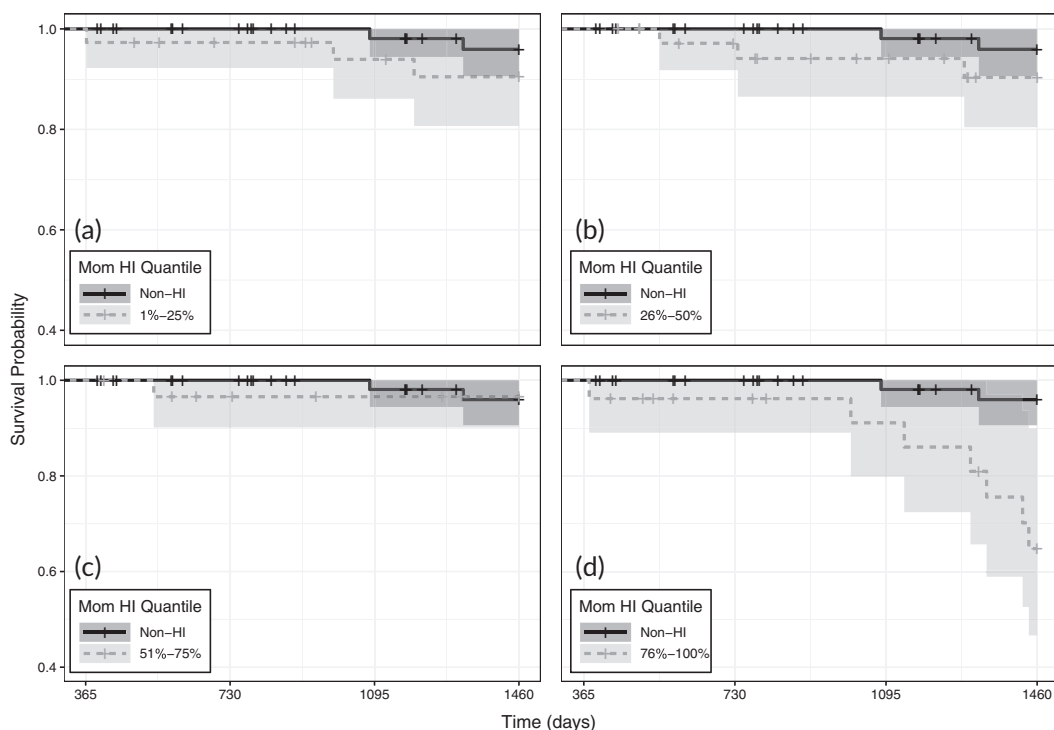


**FIGURE 3** Kaplan–Meier survival probability of calves from birth to year 1 born to each HI quantile assigned to the mother. Solid, darker lines represent non-HI calf survival rate. Dashed, lighter lines represent each HI quantile. Tick marks represent censored individuals who do not have observed failure times, are included in survival estimates up until the interval in which they are censored, then excluded from the following intervals. 95% confidence intervals are bounded by the respective shade.

of 83, 49, 54, 40, and 37 individuals, respectively. Of the calves included 57 (16 non-HI, 41 HI) did not survive year 1 and an additional 43 (17 non-HI, 26 HI) did not survive to year 4. Furthermore, due to the time constraint of the analysis ending in 2020, 10 calves were unable to reach age 1 (age <1 as of 2020) and 28 were unable to reach age 4 (age <4 as of 2020). Therefore, the sample size consisted of 263 calves for birth to year 1 and 196 calves for year 1 to year 4, with 125 calves surviving both intervals.

Results of the Kaplan–Meier analysis showed no clear statistical differences in survival probability across HI quantiles from birth to year 1 ( $S_{\text{Non-HI}} = 0.83 \pm 0.04 \text{ SE}$ ;

$S_{1\%-25\%} = 0.79 \pm 0.06 \text{ SE}$ ;  $S_{26\%-50\%} = 0.74 \pm 0.06 \text{ SE}$ ;  $S_{51\%-75\%} = 0.82 \pm 0.06 \text{ SE}$ ;  $S_{76\%-100\%} = 0.75 \pm 0.07 \text{ SE}$ ; Figure 3, Table S1.4). Similarly, there were no clear statistical differences in survival between calves born to females of non-HI and the 1%–25%, 26%–50%, and 51%–75% HI categories from year 1 to year 4 ( $S_{\text{Non-HI}} = 0.96 \pm 0.03 \text{ SE}$ ;  $S_{1\%-25\%} = 0.91 \pm 0.05 \text{ SE}$ ;  $S_{26\%-50\%} = 0.90 \pm 0.05 \text{ SE}$ ;  $S_{51\%-75\%} = 0.97 \pm 0.03 \text{ SE}$ ; Figure 4A–C, Table S1.5). Calculation of the hazard ratio (Figure S5, Table S1.6) using the Cox Proportion Hazard model also showed no clear statistical difference across the first three HI quantiles when compared to the baseline hazard (non-HI). However, the model did predict a significant difference in survival between the non-HI category and the 76%–100% HI category ( $S_{76\%-100\%} = 0.65 \pm 0.11 \text{ SE}$ ; Figure 4D, Table S1.5). Moreover, calves born to mothers in the 76%–100% were over nine times more likely to die than those born to naturally foraging mothers ( $HR = 9.95$ ;  $p = .004$ ; Figure 5, Table S1.6). The Cox proportion hazard model explained a small amount of the variability in the data at both intervals (Figure 5, Table S1.6).

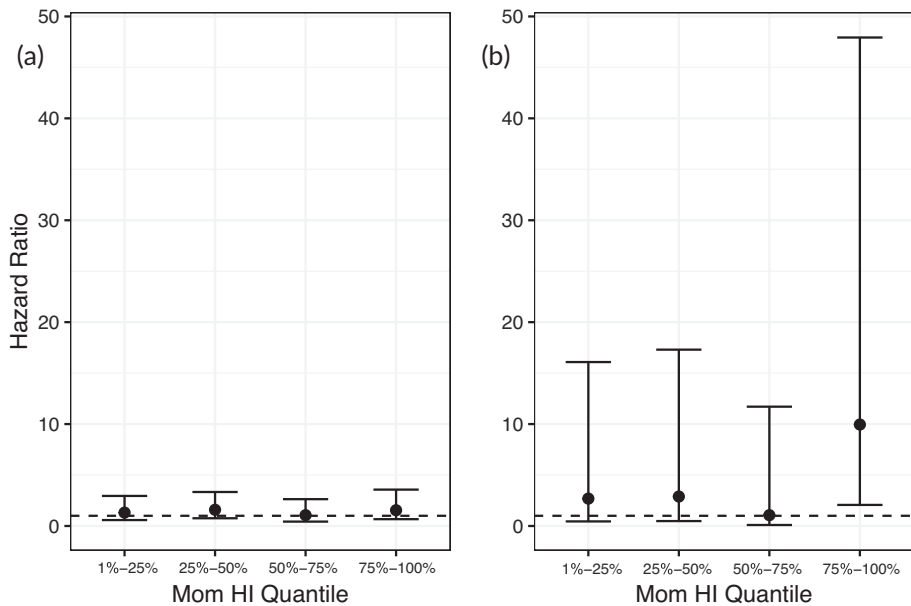


**FIGURE 4** Kaplan–Meier survival probability of calves from year 1 to year 4 born to each HI quantile assigned to the mother. Solid, darker lines represent non-HI calf survival rate. Dashed, lighter lines represent each HI quantile. Tick marks represent censored individuals who do not have observed failure times, are included in survival estimates up until the interval in which they are censored, then excluded from the following intervals. 95% confidence intervals are bounded by the respective shade.

## DISCUSSION

This study analyzed some of the most detailed long-term monitoring data available for wild dolphins to quantify the influence of HI-related foraging activities on individual fitness of reproductive females. We hypothesized that engaging in HI activities may have a positive short-term benefit for reproductive output, but that these activities would have negative long-term consequences on calf survival. The results of this study support our hypothesis that HI engagement has mixed effects on individual fitness and provide additional insights regarding frequency of engagement. We found that engaging in HI activities does increase individual reproductive output, particularly at lower frequencies of HI. At low to moderate frequencies of HI engagement, reproductive output increases by up to 94%, while individuals that participated in HI activities at high frequencies increased reproductive output to a lesser extent (~60%). In terms of reproductive success, we found that calf survival from years 1–4 of those born to females exhibiting the highest frequency of HI (76%–100%) is 31% less than that of non-HI calves, and that these calves are nine times more likely to die. Our results suggest that engaging in HI related foraging has mixed consequences, where HI engagement can be beneficial to short-term individual fitness in the form of reproductive output but is offset at least from years 1–4 by increased calf loss. However, it should be noted that the high variability and low observation frequencies of HI make it difficult for us to make conclusions about these groups with a high level of confidence. Therefore, these reported findings reflect the most conservative measures of our analyses and may not fully represent the influence of HI foraging on individual fitness.

A fitness advantage in the form of increased reproductive output may be partially explained by human-related foraging strategies reducing nutritional demands by providing increased quantity or quality of food (Diaz Lopez, 2012) and



**FIGURE 5** Hazard ratio (HR) of calves from birth to year 1 (panel A) and year 1–4 (panel B) born to each HI quantile assigned to the mother relative to the non-HI category as calculated by the Cox proportion hazard model with 95% confidence intervals. Hazard measures the instantaneous risk of death. The dashed line represents a hazard ratio of 1. HR = 1 represents the baseline hazard (non-HI), HR > 1 represents an increase in hazard, and HR < 1 represents a decrease in hazard.

reduced energy expenditure when foraging (Birnie-Gauvin et al., 2017). The nutritional and energetic benefits of HI-related foraging may allow animals that participate in these activities to maintain body condition, which in turn allows them to spend more time and energy mating and providing maternal care (Castrillon & Bengtson Nash, 2020).

Increased time for maternal care may then allow HI females to raise and wean independent young faster than non-HI females. For instance, reduced time spent foraging by HI females can then be spent increasing the opportunities for calves to learn the skills needed for independence, potentially preparing calves for independence more quickly than non-HI females. Overall, HI females provided less maternal investment (average 1,570 days  $\pm$  563 days SD) compared to the non-HI females (average 1,730 days  $\pm$  819 days SD); however, this difference was not statistically significant due to high individual variability of separation to independence. A trend of increased reproductive output for females that engage in HI is consistent with a study of killer whales (*Orcinus orca*) that reported a 4% increase in calving probability in animals that engage in HI-related foraging as compared to those that do not (Tixier et al., 2015). To our knowledge, this is the only additional study to correlate increased reproductive output of marine mammals with the suite of HI-related foraging activities considered here (see Table 1). Our findings suggest that engaging in infrequent HI activities yields benefits in terms of individual fitness, while engaging in more frequent HI activities increases risks. Therefore, the subsequent fate of these calves is an important consideration when interpreting these results.

The results of this study suggest that HI foraging can influence individual survival, especially when considering the later calf years. This is further supported by other studies of multiple taxa documenting the negative effects of direct provisioning on reproductive success and calf survival (Foroughirad & Mann, 2013; Mann et al., 2000; Senigaglia et al., 2019). However, the high variability of our survival models stresses that the risk associated with engaging in human-related foraging activities only represents one factor in the overall survival of Sarasota dolphins.

We suggest three nonmutually exclusive hypotheses to explain the observed survival variability: (1) dependent calves may be less likely to engage in HI activities than juveniles and adults; (2) individual HI activities may have fundamentally

different fitness consequences (some positive and some negative) or magnitude; and (3) true estimates of calf survival may be masked by environmental stochasticity that is unaccounted for (e.g., red tide, prey abundance).

For instance, Powell and Wells (2011) reported that 24 individuals were observed engaged in HI activities in 2007, but only 4% of these interactions were observed to be performed by a calf. Due to the dependence of calves on lactation for the first 1–2 years of life, HI may be less likely to impact calf survival because young calves are less likely to be motivated by human sources of food. Dependence on lactation for young calves may also explain the lack of significance from birth to year 1. Here we found that the effect of HI on survival is more prominent during the later calf years, suggesting that the effect of HI on survival is likely higher postseparation, which this study does not explore. However, we again stress that these results are based on our most conservative measure of HI frequency and are likely largely underestimated.

Additionally, in this study, we used a binary method to classify HI and non-HI individuals due to low observation frequencies of each HI. However, it is likely that different HI activities impact survival in different ways or at different magnitudes, accounting, in part, for the variability in our results. Both ingestion of and entanglement in fishing gear have been reported to have a high probability of mortality (Wells et al., 2008), but some HI activities may be more likely to result in injury vs. death. For example, hook and line depredation and scavenging may be more likely to result in ingestion of gear, whereas patrolling or interacting with a crab pot presents risk of external entanglement (Wells et al., 2008). Moreover, due to the visibility of external entanglement, entangled animals are more likely to be detected and are better suited for human intervention, improving long-term survival (McHugh et al., 2021). Although preliminary analyses suggest there may be differences in survival among HI activities, low observation frequencies do not allow for robust statistical inference (Appendix S3).

Lastly, our survival models do not account for environmental variation, which may explain the high variability and unclear differences in survival of the less-frequent HI categories. Harmful algae bloom (i.e., *Karenia brevis* red tide) events are an important consideration for Sarasota, where an estimated 31% of weeks during 2003–2019 were within a red tide bloom span (McCabe et al., 2021). HI individuals may be better adapted to these times of environmental stress than non-HI individuals. For instance, following peak illegal fishing periods, in which prey availability has been depleted, depredating killer whales have shown higher survival and demographic growth rates than those that do not (Tixier et al., 2017), suggesting that during times of lower prey abundance, depredation strategies are a beneficial tactic. If HI individuals are better at adapting to stressful events such as red tide, it is possible that the true estimate of calf survival is partially masked. Moreover, this study does not consider an individual's broader social environment which is known to influence both participation in and persistence of HI activities via generational conditioning (Christiansen et al., 2016; Senigaglia et al., 2022). While the broader social connections may be less likely to influence calf survival during the early stages of life, these connections should be considered when assessing the influence of HI at later stages of life – particularly following separation.

The long-term data of SDRP have shown that HI activities can persist through at least four generations through social learning (Wells, 2019). The importance of generational conditioning as a management concern is underscored by a 40-year-old female resident of Sarasota, known as Vespa. Vespa falls into the 76%–100% HI quantile and has been observed with 10 calves during the study period, while engaging in HI activities such as patrolling, scavenging, and provisioning (based on fig. 15.3 by Byrskov & McHugh in Wells, 2019). Vespa passed her HI behavior on to seven calves, three of which have had human-related injuries, and two died after injury. The three unconditioned calves were unlikely to have survived long enough to be involved in HI, as they did not survive the first year of life (Wells, 2019). Three of Vespa's calves were alive as of 2020, and two have been observed with calves of their own. One calf, known as Scooter, has been documented with five calves, three of which have been seen engaging in HI, and of those three, one has been observed with a human-related injury (Wells, 2019). Similar to Vespa, Scooter's unconditioned calves did not survive the first year of life. Moreover, only one of Scooter's calves had reproduced as of 2020, and that calf has also adopted HI activities (Wells, 2019). The case of Vespa makes it clear that HI mothers will pass on conditioned behaviors, and calves that survive to reproduction will likely continue to engage in HI foraging despite the potential for negative consequences on survival. We also see that the fates of calves born to HI mothers are highly variable and represent a spectrum of the effects HI has on calves (Wells, 2019). To counter these threats, understanding the influence of human interaction through long-term study should play a critical role in conservation management globally.

Despite the high variability of this study, our analyses provide key insights into the consequences of human interaction on the life history of the Sarasota dolphin community, representing a key step in further developing conservation strategies. This is especially true because engaging in HI foraging activities is transmitted via social learning in marine mammals (Bonizzoni et al., 2022; Christiansen et al., 2016; Donaldson et al., 2012; Powell & Wells, 2011; Wells, 2003, 2019) and has the dangerous potential to give rise to generations that are more likely to engage in risky foraging activities. These activities then bring individuals closer to boats and fishers (Bonizzoni et al., 2022; Foroughirad & Mann, 2013; Senigaglia et al., 2019) and increase the likelihood of injury and death from fishing gear, boat strikes, and even retaliatory killing. Therefore, the rise and persistence of individuals that engage in HI activities should be a particularly important consideration for management due to increased HI-related losses later in life, which in turn, may have population-level consequences (Christiansen et al., 2016; Vail, 2016). Thus, our results highlight the importance of long-term, comprehensive research that provides critical data for the conservation of wild populations, especially marine mammals. As human population continues to increase and encroach on wild areas, a clear understanding of how individual life-history is influenced by anthropogenic threats is becoming essential to conservation management. With the continuation of long-term studies, we are beginning to understand how wild populations are adapting to human pressures, and with that knowledge, we can hope to improve the coexistence of humans and wildlife.

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**Kylee M DiMaggio:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Miguel A Acevedo:** Formal analysis; investigation; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing. **Katherine A McHugh:** Conceptualization; data curation; funding acquisition; investigation; methodology; resources; supervision; writing – original draft; writing – review and editing. **Krystan A. Wilkinson:** Investigation; methodology; supervision; writing – original draft; writing – review and editing. **Jason B Allen:** Data curation; resources; writing – original draft; writing – review and editing. **Randall Wells:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

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## SUPPORTING INFORMATION

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

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