



Bottlenose dolphin mothers modify signature whistles in the presence of their own calves

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Human caregivers interacting with children typically modify their speech in ways that promote attention, bonding, and language acquisition. Although this “motherese,” or child-directed communication (CDC), occurs in a variety of human cultures, evidence among nonhuman species is very rare. We looked for its occurrence in a nonhuman mammalian species with long-term mother–offspring bonds that is capable of vocal production learning, the bottlenose dolphin (*Tursiops truncatus*). Dolphin signature whistles provide a unique opportunity to test for CDC in nonhuman animals, because we are able to quantify changes in the same vocalizations produced in the presence or absence of calves. We analyzed recordings made during brief catch-and-release events of wild bottlenose dolphins in waters near Sarasota Bay, Florida, United States, and found that females produced signature whistles with significantly higher maximum frequencies and wider frequency ranges when they were recorded with their own dependent calves vs. not with them. These differences align with the higher fundamental frequencies and wider pitch ranges seen in human CDC. Our results provide evidence in a nonhuman mammal for changes in the same vocalizations when produced in the presence vs. absence of offspring, and thus strongly support convergent evolution of motherese, or CDC, in bottlenose dolphins. CDC may function to enhance attention, bonding, and vocal learning in dolphin calves, as it does in human children. Our data add to the growing body of evidence that dolphins provide a powerful animal model for studying the evolution of vocal learning and language.

motherese | signature whistle | bottlenose dolphin | vocal learning | animal communication

Human mothers interacting with young offspring typically modify their speech in ways that are preferred by infants and children (1–6). Described as “motherese” or infant-directed speech, this phenomenon is present in many different cultures (2, 7–10). The term child-directed communication (CDC) has become a more common description of this phenomenon (11), as it has been found to occur with caregivers other than the mother (12), with children as well as infants (13, 14) and even as modifications to gestural languages (15, 16). In speech, CDC has a unique acoustic signature when compared to adult-directed speech that includes higher fundamental frequencies (pitch), wider pitch range, and shorter utterances (3–5, 8, 17, 18); these features are thought to support attention, bonding, and the process of language acquisition (3, 19–25).

Although CDC occurs in a variety of human cultures, evidence among nonhuman species is very limited. One example exists among avian species: Adult male zebra finches (*Taeniopygia guttata*) changed acoustic parameters of their song when singing in the presence of juveniles compared to when singing alone or to females (26). Adult squirrel monkeys (*Saimiri* sp.) and rhesus macaques (*Macaca mulatta*) used different vocalization types when communicating with young vs. older conspecifics (27, 28), but this is quite different from the more subtle changes associated with CDC in humans. Female greater sac-winged bats, *Saccopteryx bilineata*, produced pup-directed vocalizations that differed in timbre and peak frequency from adult-directed vocalizations; however, the structure of pup-directed vocalizations was also markedly different (29) and it remains unclear whether these differences represent the use of a different vocalization type rather than the more subtle changes within vocalization types characteristic of CDC in humans.

Since acoustic features of CDC are thought to promote learning and language acquisition in humans (3, 10, 19–25), we looked for its occurrence in another nonhuman species capable of vocal production learning (30, 31): the common bottlenose dolphin (*Tursiops truncatus*; hereafter referred to as “dolphin”). One feature of the dolphin communication system that makes it uniquely well suited for investigating motherese is that each individual produces a signature whistle (32, 33). These whistles are characterized by distinctive modulations in fundamental frequency, also known as the contour, that can be directly compared with speech intonation patterns (3). In addition, because dolphins produce signature whistles in many contexts, we can quantify subtle changes in the same vocalizations when

Significance

“Motherese” is a speech pattern that is nearly universal across cultures and languages in human caregivers interacting with children, but evidence among nonhuman species is sparse. Here, we report evidence for motherese in the bottlenose dolphin, a species that shows parallels to humans in their long-term mother–offspring bonds and lifelong vocal learning. Female bottlenose dolphins increase the maximum frequency and frequency range of the same vocalizations (signature whistles) when in the presence or absence of offspring, paralleling similar changes in human motherese. Our data provide an example of convergent evolution of motherese in a nonhuman mammal and support the hypothesis that motherese can facilitate vocal learning and bonding in nonhumans as well as humans.

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produced by females in the presence vs. absence of their own calves. To our knowledge, such a study has not been conducted on the vocalizations of any nonhuman mammal, yet this paradigm is closely aligned with the definition of motherese in humans, where acoustic parameters of the same spoken words differ when directed toward offspring vs. adults (34).

Our study population was a resident community of bottlenose dolphins in and near Sarasota Bay, Florida, which has been the focus of a research program for more than 50 y (35, 36). This program includes brief catch-and-release health assessments, during which small numbers of dolphins (typically 1 to 4) were encircled together in a net. While each dolphin was being loosely held in the water or examined on the padded deck of a specialized boat, we were able to temporarily attach hydrophones with suction cups directly to each dolphin's melon (Fig. 1A). In this way, we obtained high-quality recordings of known individuals, which in this context are primarily composed of individually distinctive signature whistles (33, 37).

Dolphin offspring, called calves, remain with their mothers for on average 3 to 6 y in the Sarasota population (38). If a calf was associating with its mother at the time of capture, it was defined as dependent. We are confident that whistles produced by mothers in the presence of their dependent calves are directed toward their calves, rather than at other animals. During these catch-and-release events, mothers and their dependent calves are held close enough to hear each other and typically engage in near-continuous signature whistle exchanges (39, 40). Also, mothers and their dependent

calves were the only two animals present in the majority of recording sessions in this context (SI Appendix, Table S1).

Dolphins use their signature whistles for individual recognition and for maintaining contact with others (33, 41, 42). Signature whistle contours are typically remarkably stable over time, but parameters such as duration and absolute frequencies may vary to small degrees (43). We compared signature whistle parameters of the same adult female bottlenose dolphins recorded both with and without their dependent calves during brief catch-and-release events. If dolphins use motherese, we predicted that females would produce whistles with higher maximum frequencies, wider frequency bandwidths, and shorter durations of individual whistle components called loops (33) when recorded with vs. without their dependent calves; such differences would align with the higher fundamental frequencies, wider pitch ranges, and shorter utterances seen in human motherese.

Results

We recorded 19 adult female dolphins over 34 y (1984 to 2018) during health assessments when they were caught and released with their dependent calf (along with other individuals in seven cases, SI Appendix, Table S1), and during separate health assessments when they were caught either alone ($n = 4$) or with other dolphins but without a dependent calf ($n = 15$; SI Appendix, Table S1). For each individual included in this analysis, 20 whistles were analyzed

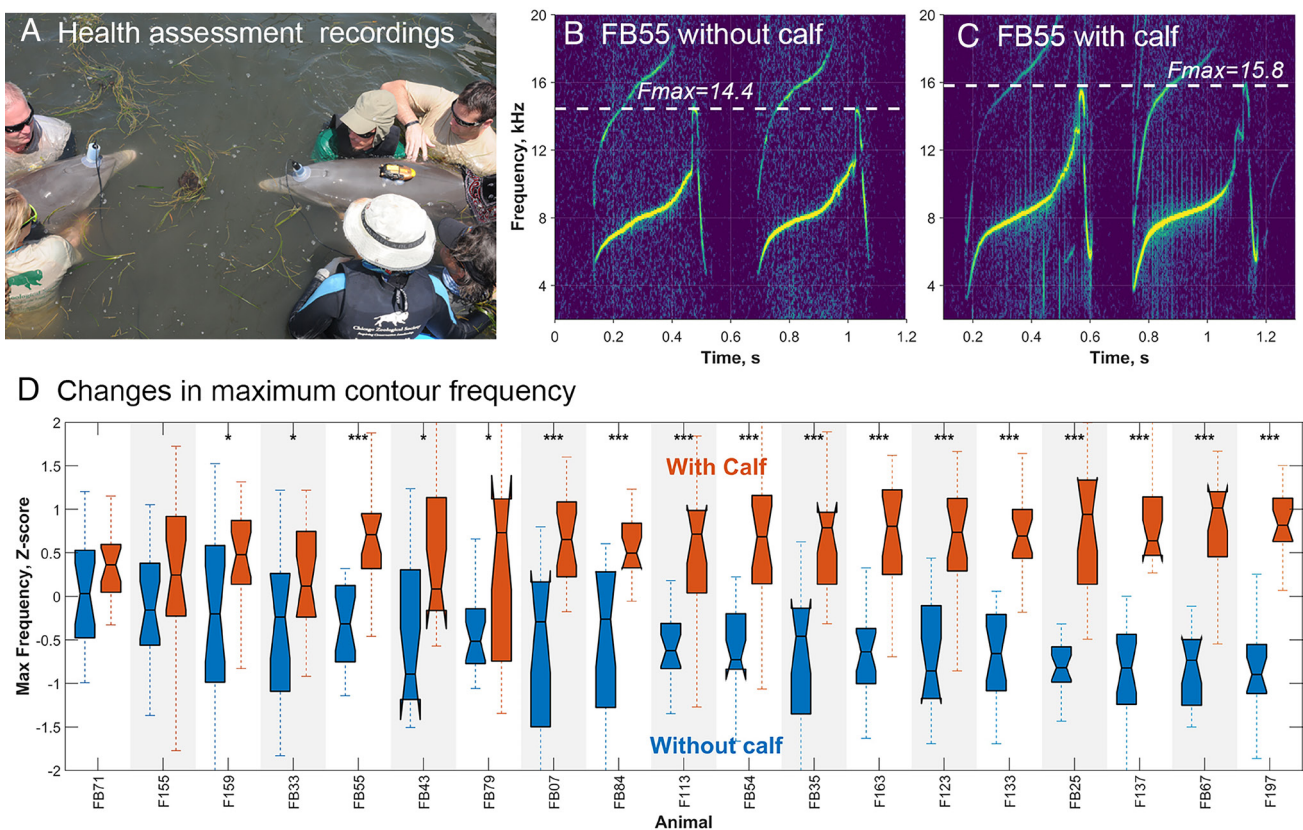


Fig. 1. Motherese in bottlenose dolphin signature whistles: (A) Bottlenose dolphin mother-calf pair being recorded with suction-cup hydrophones directly on the melon (forehead) during health assessments in Sarasota Bay, Florida. Comparison of maximum frequency of signature whistles (each with 2 loops) of FB55 when (B) she was not with a calf, and (C) when she was with a dependent calf. (D) Changes in maximum contour frequency across 19 adult females with (red) or without (blue) dependent calves. For each individual, maximum frequency was Z-transformed (subtract mean, divide by SD) to correct for differences in maximum frequency across individuals, and individuals were sorted by effect size. An overall LME model was significant ($F_{(1, 55, 758)} = 325.13, P < 0.001$), and for each individual, statistical significance (Kruskal-Wallis test on max frequency) is indicated as $* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$. Photograph taken by Chicago Zoological Society's Sarasota Dolphin Research Program under National Oceanic and Atmospheric Administration/National Marine Fisheries Service Scientific Research Permit No. 15543.

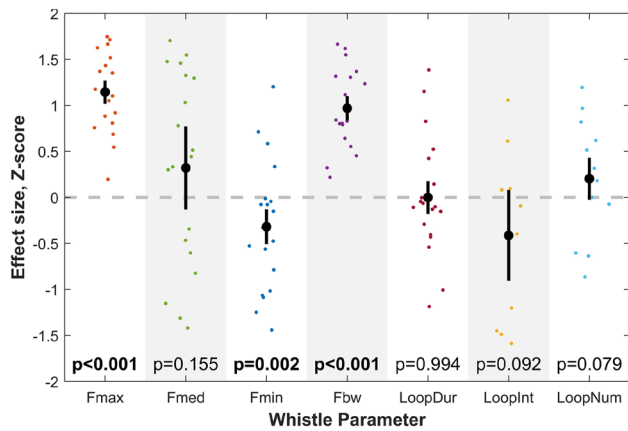


Fig. 2. Changes in signature whistle contour parameters in the presence of calf: Each acoustic variable was z-transformed for each individual and then fitted with a mixed-effects model including dependent calf presence as a fixed effect and individual ID as a random effect on both intercept and slope. Colored points show mean change in acoustic parameter for each female, and black circles and solid black lines, respectively, show estimated mean change and 95% CIs from a mixed-effects model. Fmax = maximum (95%) frequency; Fmed = median frequency; Fmin = minimum (5%) frequency; Fbw = frequency bandwidth (90%); LoopDur = duration of discrete whistle segments (loops); LoopInt = interval between loops in whistles with multiple disconnected loops; and LoopNum = total number of whistle loops.

from each context (with and without their calf) using a linear mixed-effects model (LME) framework.

Individual female dolphins recorded with their dependent calves produced signature whistles with significantly higher maximum frequencies than those of the same females recorded without calves (LME: $F_{(1, 55, 758)} = 325.13$, $P < 0.001$, Fig. 1 B–D, and *SI Appendix, Table S1*). The mean change in maximum contour frequency was 2.4 ± 0.39 kHz (95% CI 1.6 to 3.2 kHz) or 1.14 ± 0.06 (95% CI 1.01 to 1.27) SD. We found no effect of female age on these results (LME: $F_{(1, 155, 74)} = 0.0068$, $P = 0.934$), nor of calf age (LME: $F_{(1, 97, 118)} = 0.12499$, $P = 0.724$), when including these variables as additional fixed effects, and the significant difference in maximum frequency persisted even when the analysis was conducted only on the four females that were younger when caught with a dependent calf than when caught without a calf (LME: $F_{(1, 9, 81)} = 43.822$, $P < 0.001$). In fact, every mother showed an increase in frequency when in the presence of her calf, and even when tested individually, all but two increased significantly, regardless of age (Kruskal–Wallis test on maximum frequency; see Fig. 1D). (See *SI Appendix, Supporting Text* describing additional tests related to age.)

Apart from maximum frequency, female dolphins showed a significant decrease in minimum contour frequency (LME: $F_{(1, 36, 267)} = 11.77$, $P = 0.0015$, Fig. 2) and a significant increase in contour frequency range, or 90% bandwidth (LME: $F_{(1, 62, 409)} = 219.25$, $P < 0.001$, Fig. 2) when with their dependent calves. Females did not show significant changes in either median contour frequency (LME: $F_{(1, 18, 677)} = 2.196$, $P = 0.155$), loop duration (LME: $F_{(1, 41, 03)} < 0.001$, $P = 0.994$), interloop interval (LME: $F_{(1, 10, 145)} = 3.46$, $P = 0.09$), or total number of whistle loops (LME: $F_{(1, 25, 599)} = 3.336$, $P = 0.079$). Number of whistle loops also did not change when focusing exclusively on individuals that produced multiloop whistles (10 individuals: LME: $F_{(1, 19, 525)} = 1.3804$, $P = 0.25$) (the other nine dolphins produced whistles without repeated loops; ref. 33).

Discussion

Our results demonstrate motherese, or child (calf)–directed communication, in bottlenose dolphins. Females produced signature whistles with significantly higher maximum frequencies and

slightly lower minimum frequencies, resulting in a greater frequency range (bandwidth) when they were with their dependent calves than when they were alone or with unrelated dolphins, mirroring similar patterns seen in human CDC (3, 4). Dolphins, although obviously phylogenetically very different from humans, share traits such as a long period of dependence during which mothers and offspring maintain vocal contact, using the same vocalizations as when communicating with adults. In addition, like humans, they show high social and vocal complexity and extensive social and vocal learning (38, 44). Thus, the putative functions of CDC in promoting bonding and vocal learning in humans appear highly relevant to dolphin behavior and social structure.

Although we had predicted shorter loop durations in dolphin CDC, we did not find any significant change in this parameter. Temporal features may not be selected for as qualities of CDC in signature whistles because not all dolphins produce multiloop whistles, and thus this feature would not be consistent across whistle types. Approximately 25% of dolphins in Sarasota produce whistles without repeated loops (33).

We considered whether age of the mother or calf could have impacted our results, but did not find any effect of age on our measured whistle parameters. This likely reflects that the overall contour shape that encodes identity information (45) is in most cases highly stable (33), enabling dolphins to recognize and remember conspecifics by their signature whistle over many years (46).

Another possible confounding variable is experience with the catch-and-release process. Esch et al. (47) studied effects of prior catch-and-release experience on whistle production in the same population of dolphins in Sarasota, under the assumption that animals more experienced with the process would be less stressed by it. Their main finding was that whistle rate and number of whistle loops increased with stress. They also reported higher maximum frequencies in whistles of females with vs. without their dependent calves, a similar result to ours but based on a smaller sample size of females ($n = 8$), and concluded that previous catch-and-release experience was unlikely to have played a role. Females both with and without dependent calves had similar levels of experience (mean catch-and-release number with dependent calves in Esch et al.'s (47) data set was 7.1 and in ours was 6.3; without a dependent calf, the values were 6.3 and 4.6, respectively). Also, only 4 of 38 analyzed recording sessions in our study were made during a female's first experience with a catch-and-release event (all females without calves). (See *SI Appendix, Supporting Text* for discussion of potential impacts of these four recording sessions.)

It is also possible that experiencing the catch-and-release process with a dependent calf is inherently more stressful than without a calf, regardless of age or capture experience. However, if this were the case, we would expect females with dependent calves to show more of the vocal correlates of stress reported by Esch et al. (47) (increases in whistle rate and loop number) than females without calves. However, Esch et al. (47) did not find that these parameters differed for females with and without dependent calves; we similarly did not find significant differences in loop number (Fig. 2; whistle rate was not included in our study). Thus, comparison of whistles recorded from females with dependent calves to the same females recorded without calves did not show the significant changes in vocal production that were attributed to stress in other members of the same dolphin population.

We also considered whether presence or absence of other dolphins in the recording sessions where females were without dependent calves might have influenced our results. Females were alone in only 4 of 19 sessions (*SI Appendix, Table S1*), and the frequency differences in these cases (mean = 2,705 Hz) were not

significantly different from those when females were recorded with other dolphins (mean = 2,296 Hz; Mann–Whitney $U = 22$, $P = 0.45$; *SI Appendix, Table S1*). Another way of looking at this is to compare whistles produced by a female with her calf to whistles of the same female with other conspecifics (all individuals except FB07, FB33, FB54, and F123). This analysis still results in a highly significant difference in maximum frequency (LME: $F_{(1,38,407)} = 238.47$, $P < 0.001$), clearly indicating that the observed increase in maximum frequency occurs only when females are with their calves, and not with other conspecifics. Thus, we concluded that whether a female was in the presence of other dolphins or not (other than her dependent calf) was not a factor that influenced our results.

The median age of calves in our sample was 2 y, which is well within the range of ages for which CDC occurs in humans [and dolphin lifespans are also comparable to those of humans (35)]. However, several were older (*SI Appendix, Table S1*), paralleling findings of CDC in older human children (13, 14). Although calves typically develop their own signature whistles in the first few months of life (48), other vocalizations that may be context specific, such as nonsignature whistles or burst-pulse sounds, may take longer to learn. In addition, CDC may have functions in addition to vocal learning, such as the promotion of long-term social bonds, as has been suggested for humans (3, 49). Dopamine in the medial amygdala of humans has recently been found to mediate mother–infant behavioral synchronization and bonding (50). In juvenile zebra finches, social tutoring increased the activity of noradrenergic and dopaminergic midbrain neurons (26). If CDC stimulates similar neural activity in mammals, this suggests a neural pathway whereby motherese could promote social bonding. This idea is supported by the finding that signature whistle exchanges promote bonding in bottlenose dolphin male alliances (51), thus emphasizing the link between acoustic interactions and social bonding in these animals.

The subtle differences we observed in mothers' signature whistles may have an additional communicative function related to the large and fluid social networks of female bottlenose dolphins (38, 52, 53). Given their frequent interactions with conspecifics, subtle changes in signature whistles may help females target their calves as recipients, or conversely help calves identify calls meant for them; such functions could facilitate maintenance of mother–calf contact. Although signature whistle copying can function in contacting a specific individual (54) such copies are used rarely, presumably to maintain the integrity of signature whistles as individual identifiers (40). The subtle changes characteristic of CDC could help to maintain continual, close contact between a mother and calf that frequently encounter and socialize with other conspecifics.

We should emphasize, however, that we currently do not know either the mechanistic driver(s) or function(s) of CDC in bottlenose dolphins. For example, acoustic differences could arise as a consequence of physiological changes associated with lactation and/or parental behavior. Functions could range from those outlined in previous paragraphs (vocal learning, promotion of social bonds, targeting of recipients, or facilitation of caller identity), or could be nonexistent, if the observed acoustic changes are simply by-products without adaptive value. We also are unable to determine whether dolphins are as flexible in their use of CDC as humans, who are able to modulate their vocal production on a moment-to-moment basis, depending on their audience. Further research is needed on this aspect, as well as to elucidate whether CDC is in fact preferred by calves, as it is by human infants (over adult-directed speech). Although the latter finding would still not increase our understanding of the mechanistic basis, it would

nonetheless suggest that dolphins have evolved to capitalize on this preference and/or on the occurrence of CDC.

Songbirds have long been viewed as the primary animal model for the evolution of vocal learning and human speech (ref. 55; reviewed in ref. 56), but it is clear that bottlenose dolphins have also convergently evolved many similarities to human communication, including lifelong vocal learning (44), referential communication through imitation of signature whistles (54, 57), and long-term social memory (46). Signature whistles are the closest analog to human names that have been found in nonhuman animals, representing individuals across modalities (58). Adding to this list of similarities, our study found that dolphins modify their signature whistles in ways that parallel CDC in humans. Given that dolphins and humans also share strong, prolonged mother–offspring bonds and complex social structures (38, 59), dolphins appear to be potent animal models for studies of language evolution, especially if, as speculated by Schick et al. (25), “...CDC in hominins arose to support the acquisition of highly culturally variable acoustic and structural features of language.”

In summary, we conclude that our results demonstrate motherese, or child (calf)–directed communication, in dolphins, providing evidence in a nonhuman mammal for modification of the same vocalizations when in the presence or absence of offspring. This phenomenon is closer to what is observed in human motherese than what has been described for nonhuman animals other than zebra finches (26). Given that dolphins have a flexible communication system enabled by vocal production learning (30, 44), features shared with the vocal production system of humans, it seems likely that motherese may convergently function to enhance attention, bonding, and vocal learning in bottlenose dolphin calves, as it does in humans. Our data add to the growing body of evidence that dolphins provide a powerful animal model for studying the evolution of vocal learning and language.

Materials and Methods

This study was carried out using data from the resident bottlenose dolphin community in Sarasota Bay, Florida (33, 35, 60). Since 1984, we have been recording dolphins during brief catch-and-release sessions, in which we placed suction-cup hydrophones directly on the dolphin melon, enabling us to identify which dolphin was making a sound (Fig. 1A). Mothers and calves frequently exchange whistles back and forth in this context (39). More detail about field methods for catch-and-release and acoustic recordings can be found in studies by Wells et al. (60) and Sayigh et al. (33). Over the past 38 y, we have built the Sarasota Dolphin Whistle Database (33) from these recordings. Recording media included cassette tapes prior to 1990, VHS tapes from 1990 to 2005, and digital recordings from 2006 onward. Analog recordings were digitized into wav files prior to analysis, and files were analyzed with Raven Pro 1.6. (K. Lisa Yang Center for Conservation Bioacoustics, Cornell, NY, USA). Spectrograms of signature whistles were visually classified by identifying the most commonly produced whistle contour in a given recording session (61); signature whistles typically comprise approximately 85% of the hundreds to thousands of whistles produced in the catch-and-release context (33).

Individual females were selected from the Sarasota Dolphin Whistle Database based on whether they had been recorded both with and without dependent calves. The list of females was then narrowed down to include only those who were both independent from their own mothers and at least 5 y of age in both recording sessions; this is the youngest age at which a female in the Sarasota population was known to have become pregnant (38), and thus was used as a proxy for adulthood. Most dolphins are of known age due to visual observations during the year of birth or dental examinations (38, 62). One dolphin was excluded because we were not able to measure the maximum frequencies of her signature whistles, as they exceeded the upper limit of the recording system used in the 1980s (33). These criteria resulted in a dataset of 19 females for which there were sufficient data both with and without a dependent calf (*SI Appendix,*

Table S1), for a total of 38 recording sessions. All 19 females produced the same signature whistle contour (identified by visual classification; refs. 33 and 61) in both of their analyzed recording sessions (Fig. 1 B and C).

All whistles produced in the chosen recording sessions were selected and labeled in Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, Cornell, NY, USA) using the selection marquee tool. Spectrogram settings included a Hamming window with a size of 512 samples, and 50 percent overlap. As noted above, in each recording, the predominant whistle type was labeled as the signature. For each individual, 20 whistles were randomly chosen from all signature whistles produced in a single recording session using an online random number generator. These 20 randomly selected whistles were then subjected to further analyses. The fundamental frequency contour was extracted using a semi-supervised method, using a manual ridge tracker to detect and select local peaks in the spectrogram with a 5 ms temporal resolution (63), using MATLAB R2020b (MathWorks, Natick, MA, USA). For whistles with multiple disconnected loops (e.g., Fig. 1 B and C), gaps were measured manually between loop repetitions to determine the duration of interloop intervals. For each whistle contour, the following frequency measures were extracted: minimum, 50th percentile (median), maximum, and 90% contour bandwidth (the difference between 95th percentile and 5th percentile contour frequency). Duration of each whistle loop was extracted and averaged across each whistle, and the total number of loops was scored. For whistles with disconnected loops, interloop intervals were also averaged across each whistle.

Statistical analysis was conducted in MATLAB R2020b (MathWorks, Natick, MA, USA). A linear mixed-effects model was used to test how acoustic parameters depended on calf presence, which was modeled as a fixed effect, and individual identity modeled as a random effect on both slope and intercept. For all variables, data from each individual were Z-transformed by subtracting the mean and dividing by the SD for that individual. Initially, effects on maximum contour frequency were tested using the *fitlme* function with the formula $F_{max} \sim 1 + TYPE + (1|FBID) + (TYPE|FBID)$, where F_{max} was maximum contour frequency, TYPE was a categorical variable indicating whether the whistle was from a calf session or control (without calf) session, and FBID was a categorical variable with the individual freezebrand ID of the study subject fitted as a random effect on both intercept and slope. Subsequently, effects on other acoustic variables were tested with the same model formulation but with different response variables. Mixed-effects models were fitted with a maximum likelihood method, and fixed-effects hypothesis tests were conducted using an F-test implemented with the *anova* function in MATLAB, with modified degrees of freedom calculated using the Satterthwaite method.

Data, Materials, and Software Availability. Whistle contour extraction measurements used in this study have been deposited in the Woods Hole Open Access Server (WHOAS; (64); dataset URL is <https://hdl.handle.net/1912/66193> and DOI is [10.26025/1912/66193](https://doi.org/10.26025/1912/66193).

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