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Allomaternal Care and Allonursing Behaviors by a Primiparous Bottlenose Dolphin

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Allocare—alloparenting or allomaternal care—has been documented for both sexes in terrestrial, aquatic, and avian species (for a review, see Riedman, 1982), and may be linked to the evolution of an increased brain size in some social mammals (Isler & van Schaik, 2012). The benefits afforded through an allocare strategy enable mothers to travel and forage unencumbered, minimize energy expenditure, and increase energy intake, thereby allowing these species to invest more heavily or efficiently in offspring than mothers who exclusively care for their offspring (Burkart et al., 2009; Isler & van Schaik, 2012). Allocare occurs when supportive care is provided for conspecific young by individuals other than the genetic parents (i.e., siblings, aunts, uncles, or unrelated individuals identified as "helpers"). These helper individuals behave in a way that benefits a young animal (Wilson, 1975; Riedman, 1982; Whitehead, 1996; Gero et al., 2009; Schubert et al., 2009; Stanton & Mann, 2012), but their action(s) may also have advantages to the alloparent (Whitehead, 1996; Lewis & Pusey, 1997; Mann & Smuts, 1998; Roulin, 2002; Gero et al., 2009; Isler & van Schaik, 2012).

Numerous non-mutually exclusive functions have been proposed for allocare and include added protection for the offspring, opportunities to rest or forage for the mother, a chance to secure favor from an adult female for future mating opportunities, experiences for naïve females to practice or learn to care for young animals (e.g., Mann & Smuts, 1998; Simard & Gowans, 2004; Hill & Campbell, 2014; Augusto et al., 2016), among others. Allonursing has also been confirmed for several species of social mammal (see Roulin, 2002, for a review of the alternative hypotheses for why lactating females nurse non-offspring young). Spontaneous lactation by females (multiparous and primiparous) has also been reported for some mammals (e.g., bottlenose dolphins [*Tursiops truncatus*]: Kastelein et al., 1990; Ridgway et al., 1995; belugas [*Delphinapterus leucas*]: Leung et al., 2010).

In this paper, we describe the behavior and potential reproductive development of a primiparous common bottlenose dolphin ("Poli") as related to allomaternal care, including allonursing positioning, that suggests she was practicing maternal actions as well as receiving potential mentoring by an unrelated, multiparous adult female.

In 2022, Poli was an adult female common bottlenose dolphin resident to The Roatan Institute for Marine Sciences (RIMS) at Bailey's Key, Roatan, Honduras. In June 2011, Poli was the second calf (and first female) born to "Mika," an adult female also born at The RIMS. Mika died when Poli was ~4.5 y old; loss of her mother at this young age might have impacted the onset of Poli's reproductive maturity. Three other female dolphins born at The RIMS in summer 2011 and 2012 each had their first pregnancies in 2019 (The RIMS, unpub. data, 2011-2019); Poli did not exhibit follicular development until December 2021 (confirmation via voluntary ultrasound). In late 2020/early 2021, Poli was observed in Dolphin Communication Project (DCP) video data appearing to show interest in the newest calf ("Sandy"); this calf was from one of the other three females who were the same age as Poli. Poli often swam in infant position to Sandy when Sandy was in infant position to "Tilly." ("Infant position," often referred to as "P3," is defined as when the calf swims below the mother near the genital slit and mammary openings.) Poli also initiated pectoral fin contacts and body rubs with Sandy whether or not Tilly was present. These exchanges between Poli and Sandy were documented when Sandy was more than 6 mo old (DCP, unpub. data, 2020-2021). Still, Poli appeared to be readily distracted from Sandy by other dolphins, swimmers, fish, and objects. Poli was also observed sharing allomaternal

actions toward Sandy with two other young adult female dolphins when Tilly was not within visual range.

In October/November 2021, three calves were born to The RIMS group: two calves (to "Gracie" and "Elli") were born in late October, and the third calf (to "Calli") was born in mid-November. All three neonates were present during DCP's underwater video data collection in late 2021 and early 2022, with observations discussed herein from the video data collected from 28 November to 3 December 2021 and from 2 to 21 January 2022. Underwater observations were collected in 30- to 45-min videotaped sessions between 0630 and 0800 h daily (see Dudzinski et al., 2010, for details of the video collection process at The RIMS, and Dudzinski et al., 1995, for details of the underwater recording system). Specifically, three 30-min sessions yielded several observations of Poli interacting with Gracie's calf (born in October 2021) while Gracie was nearby—either within visual range or out of view of the camera and Poli and the calf (Table 1). In the December video data, Poli is more visible than Gracie and her calf (Table 1), suggesting Poli was spending less time with this mother–calf pair or that she might have been readily distracted by other dolphins, the researcher, or other objects in or near the lagoon. In January 2022, Poli was in view for almost the same amount of time as Gracie and her calf, suggesting Poli might have been spending more time with Gracie and her calf (Table 1).

In December, when her calf was about 1 mo old, Gracie's placement (within 3 to 5 adult dolphin body lengths) and vigilance (inferred from attention and gaze oriented toward her calf and Poli) indicated that she was attentive to, if not overseeing, Poli's interactions with her calf (Table 2). During one session in December, these three dolphins were observed in a triad swim formation (150.81 s; Table 2) more than in either possible dyad with the calf (Poli–calf: 57.78 s; Gracie–calf: 39.11 s; Table 2). This trend shifted between December 2021 and January 2022, with the triad swim formation per session ranging from 61.47 to 83.07 s (Table 2). Similarly, the amount of time Poli spent with Gracie's calf in both infant and echelon positions increased between December and January (Table 2). It is possible that once the mother–calf bond was stable, then Gracie might have been more relaxed in her calf vigilance when Poli was with her calf. Additionally, Gracie's vigilance with Poli might also have been a form of mentoring given that Poli was primiparous and did not have an available kin maternal model (Riedman, 1982; Komdeur, 2006; Schubert et al., 2009; Briga et al., 2012).

Table 1. Total time Gracie, her calf, and Poli are observed during three sessions recorded on video

	Total time observed on screen (s)		
Session ID	Gracie's calf	Gracie	Poli
December A42146	285.69	281.45	337.61
January A42209	213.41	200.80	228.66
January A42210	162.47	164.80	169.64
Total (s)	661.57	647.04	735.92
Total (min)	11.00	10.80	12.30

Note: Please see Supplemental Video.

Our hypothesis that Gracie could be mentoring Poli is supported anecdotally by Gracie's retrieval of her calf when Poli was distracted by the camera, other dolphins, or other objects when the calf was 1 mo old (i.e., in December). On several occasions (3 in November/December 2021; 2 in January 2022), when Poli had Gracie's calf in echelon or infant position, Poli's attention to the calf waned—for example, she investigated the researcher/camera by shifting her attention toward the camera lens and echolocating on the camera. In each instance, Gracie swam forward, "scooped" her calf into echelon position with her body, and slowly moved out of visual range (~12 m away). Poli responded by circle swimming the camera/researcher once and then made a fast swim in the direction that Gracie and her calf went (see Supplemental Video; the Supplemental Video for this paper is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Additionally, in our December observations, Gracie swam in close proximity to her calf with the calf often in echelon position to Gracie (Table 2); however, in January, there was more distance between Gracie and her calf, and other positions (e.g., parallel or staggered parallel positioning to Poli and the calf or to the calf; Table 2) were used.

In addition to infant or echelon swim positions, Gracie's calf was observed attempting to nurse from Poli's mammary slits (Figure 1; Supplemental Video). While Gracie's calf was observed (and recorded) nursing from her mother, six apparent nursing events were also documented by Gracie's calf toward Poli's genital area/mammary slits (Table 2). The only time Poli used the "mom" position for infant swims was when Gracie's calf was in the nursing position and made contact to Poli's mammary slits (Table 2). Poli's mammary glands were not developed nor was milk evident from her, though Gracie's calf placed her rostrum at Poli's mammary slits (Figure 1). Gracie's calf was observed twice nursing from Gracie for an average

Table 2. Observations of Poli and Gracie's calf; Gracie and her calf; and Poli, Gracie, and the calf together during three 30-min sessions in December 2021 and January 2022. P3 is the acronym for infant position. Time spent in the mom and calf positions by Poli when she was in P3 or echelon with the calf were documented. The triad included all three females in a "stacked P3" swim formation.

			Time Poli swims in each position w/calf (s)				Time of Gracie's position during triad (s)		Calf "nursing" Poli	
Date (session)	Total time swimming in dyad or triad (s)		P3 mom	P3 calf	Echelon mom	Echelon calf	Echelon w/calf	Parallel w/Poli	Events	Mean duration (s)
1 Dec 2021 (A42146)	Poli–calf	57.78	0.00	43.60	14.18	0.00	--	--	0	0.00
	Gracie–calf	39.11	0.00	0.00	39.11	0.00	--	--		
	Triad*	150.81	0.00	109.10	33.21	0.00	69.05	74.05		
10 Jan 2022 (A42209)	Poli–calf	135.69	17.81	105.03	12.85	0.00	--	--	2	1.50
	Gracie–calf	0.00	0.00	0.00	0.00	0.00	--	--		
	Triad*	61.47	0.00	40.07	11.08	0.00	12.87	33.95		
11 Jan 2022 (A42210)	Poli–calf	57.95	63.23	25.71	19.31	0.00	--	--	4	2.85
	Gracie–calf	5.28	0.00	0.00	5.28	0.00	--	--		
	Triad*	83.07	29.29	0.00	50.30	0.00	22.63	56.60		

*When in the triad formation, Gracie is either Echelon mom to calf or following Poli/calf in parallel staggered (swimming in the same horizontal plane but slightly before or behind) or parallel (swimming perfectly in line) to Poli.

Table 3. Nursing positions by calf to Poli and Gracie with descriptions of each event documented on video in January 2022

Session ID	Mom position	Duration (s)	Comments
A42209	Poli	1.25	Calf angles toward genital area but cannot confirm contact; not really nursing. Poli responds by slowing down, directing her genitals to calf, and then doing it again a bit later before the next bout.
	Poli	1.75	Far and blurry but does look like nursing position.
	Gracie	1.99	Might be nursing position but very far and blurry.
A42210	Poli	1.00	Calf angles toward genital area but cannot confirm contact; kind of "checking the area."
	Poli	2.50	Could be nursing position, but very far and blurry. Poli is on left side pushing genital area to calf.
	Poli	6.15	Calf clearly at mammary slits. Poli is stationary, on her right side, and head is vertically down. Gracie is near KD and looks at Poli/calf when it starts and gets closer, starting a triad swim/parallel staggered on left of Poli.
	Poli	1.72	Quite sure nursing position happens again in background. Poli is turning on her right side. Gracie is still parallel staggered on left of Poli.

of ~2 s (Table 3). The nursing position bouts by Gracie's calf to Poli ranged from 1.00 to 6.16 s ($\bar{x}$ = 2.38 s), which seemed to be similar in length to the observed time spent by the calf nursing from her mother (Table 3). Poli's posture to the calf during nursing attempts included mostly horizontal, mostly on her right side, and occasionally on her left side. The calf initiated the attempted nursing bouts and placed her rostrum against Poli's genital area/mammary slits. Poli reacted by remaining stationary or shifting her position slightly (Table 3; Figure 1; also see Supplemental Video).

In 2022, Poli was a primiparous, adult (~11 y) female bottlenose dolphin who had only showed interest in calves that might be considered allomaternal care in the last 1 to 2 y. As a subadult female, Poli shared physical contact (e.g., pectoral fin and body contact) and engaged in play

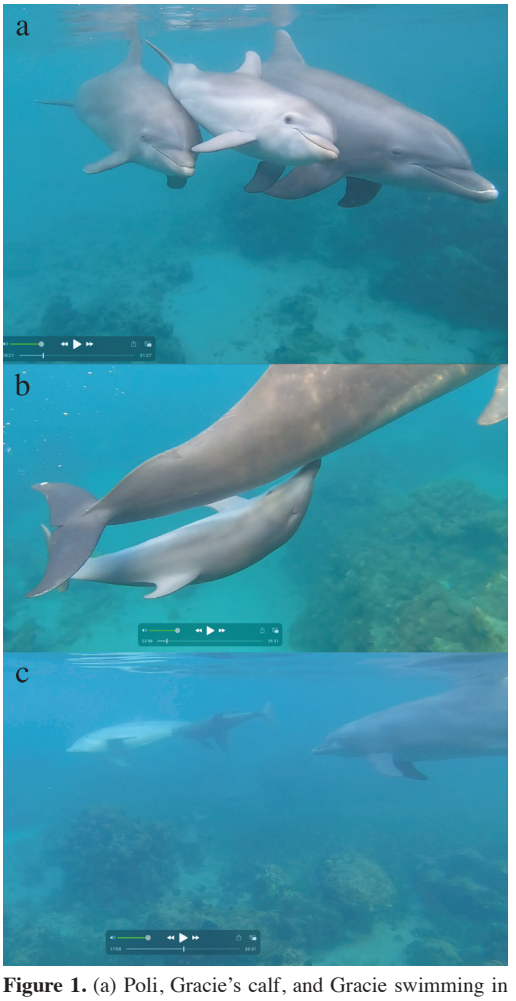

Figure 1. (a) Poli, Gracie's calf, and Gracie swimming in a staggered parallel formation; (b) Gracie's calf with her rostrum against Poli's genital area; and (c) Poli on her right side, stationary, while Gracie's calf presses her rostrum to Poli's mammary area with Gracie watching from about 3 m distance. All images taken from DCP video recorded in January 2022. See Supplemental Video for sequences.

behaviors (e.g., chases, circle swims, object play) with older (6 mo to 1 to 2 y old) calves. Her recent, more focused attention to other adult females with neonate calves, and to the calves specifically, suggests that Poli might have been maturing both socially and developmentally as would be required for her future potential maternal role (Levengood & Dudzinski, 2015; Harvey et al., 2017). This increase in allomaternal behavior exhibited by Poli coincided with her follicle development and observed mating activity with an adult male (all coauthors, pers. obs., 2022). Poli also seemed to practice a holding position for Gracie's calf to attempt nursing, even though Poli was not lactating and did not produce milk during our observations. Gracie is an experienced mother with several successful offspring. It is possible that Gracie displayed this nursing posture to Poli out of our camera's view, and Poli was simply imitating Gracie's behavior. It is also possible that Poli's position at the bottom of the triad with Gracie and her calf afforded her the opportunity to observe how Gracie and her calf interacted. That is, Gracie and her calf could be a model for Poli as she learns skills required to parent and that allomaternal care might offer (e.g., Whitehead, 1996; Mann & Smuts, 1998). With this logic, the increased allomaternal behavior by Poli could represent her practice of behaviors she will likely need in the future with her own offspring. Future observations of Poli with her own calves may offer insight into the benefits of her actions as an alloparent.

Epilogue

In October 2022, Dudzinski visited the RIMS and AKR to continue long-term data collection of the dolphins. Poli was confirmed to be pregnant, due in early 2023.

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