Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins

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Maternal care varies across taxa from brief, minimal care to long-term, intensive care. Mammalian mothers provide extensive and energetically expensive care by definition through pregnancy and lactation, which can extend for years, resulting in behavioural trade-offs between resource acquisition and direct care. In marine environments, mammalian mothers face unique challenges, such as the inability to cache or den their offspring while diving for prey. Dolphin newborns are precocious, accomplishing shallow dives in the first few weeks of life, however, fully mature diving and breath-holding capabilities take years to develop. Consequently, mothers are faced with a trade-off between diving and foraging or remaining close to and protecting their calves at the surface. Here we examined this trade-off, specifically by investigating whether mothers change their dive durations, especially during foraging, as a function of calf age. We used a longitudinal (1988–2014) data set on wild bottlenose dolphins, *Tursiops aduncus*, in Shark Bay, Western Australia, which included 27 388 dive bouts from mothers ($N = 26$) and calves ($N = 41$). Our results show that maternal diving behaviour changes in response to calf age and sex. While both male and female calves increased their dive durations with age as expected, mothers were more likely to adjust their diving behaviour to accommodate female but not male calves, especially when daughters were in close proximity. This is consistent with findings that vertical social learning is more critical for daughters than for sons, and may reflect the sex-specific foraging and social tactics of the males and females more generally.

In some iteroparous taxa, females provide extensive care to offspring lasting from months to years (e.g. marsupials, ungulates: Fisher, Blomberg, & Owens, 2002; delphinids: Whitehead & Mann, 2000; primates: Campbell, Fuentes, MacKinnon, Panger, & Bearder, 2011). While direct care increases offspring survival, such care can compromise resource acquisition (e.g. Thometz et al., 2016) resulting in trade-offs between maternal care and foraging (Royle, Smiseth, & Kölliker, 2012). Females engage in multiple strategies of care designed to guard, hide, assist and protect offspring. Females that den or cache their offspring, such as birds (Royle et al., 2012), carnivores (spotted hyaenas, *Crocuta crocuta*: Boydston,

Kapheim, & Holekamp, 2006; African wild dogs, *Lycaon pictus*: van der Meer, Mpofu, Rasmussen, & Fritz, 2013; Pallas's cats, *Otocolobus manul*: Ross, Kamnitzer, Munkhtsog, & Harris, 2010) and pinnipeds (Australian sea lion, *Neophoca cinerea*: Fowler, Costa, & Arnould, 2007; Steller sea lions, *Eumetopias jubatu*: Milette & Trites, 2003; harp seals, *Pagophilus groenlandicus*: Van Opzeeland, Corkeron, Risch, Stenson, & Van Parijs, 2009), leave their young unguarded in relatively safe locations. In other species, females adjust their foraging patterns to remain in close proximity to their offspring. For example, Sardinian mouflon, *Ovis orientalis musimon*, shift to lower-quality foraging areas to reduce the costs of separation and predation (Ciuti, Pipia, Grignolio, Ghiandai, & Apollonio, 2009). In the marine environment, female southern sea otters, *Enhydra lutris nereis*, with young pups exhibit suboptimal diving behaviour in comparison to adult females without pups, likely due to trade-offs between optimal foraging and pup care, as they spend more time at the surface attending to their pups (Thometz et al., 2016). Primates (Altmann & Samuels, 1992; Caperos, Morcillo, Peláez, Fidalgo, & Sánchez, 2012), bats (Ross, 2001) and marsupials (Fisher et al., 2002) typically carry offspring. Lastly, some

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females use a following strategy, such as ungulates (Fisher et al., 2002) and cetaceans (e.g. humpback whales, *Megaptera novaeangliae*: Szabo & Duffus, 2008; Tyson, Friedlaender, Ware, Stimpert, & Nowacek, 2012), in which offspring travel in close proximity to their mother. Each of these strategies imposes energetic costs because they impact maternal time budgets and foraging efficiency.

Female cetaceans combine following and carrying strategies in response to limited calf abilities in a marine environment. Immediately after birth, cetacean calves must be precocious enough to swim and reach the surface to breathe and to avoid predators as there are few places to safely hide. However, young calves have limited swimming and diving abilities. Thus, delphinid females 'carry' offspring in the form of echelon or infant position (Noren, 2008; Noren, Biedenbach, Redfern, & Edwards, 2008) in which the calf is parallel to or underneath its mother (Mann & Smuts, 1999; Mann & Watson-Capps, 2005), allowing calves to gain the hydrodynamic benefits of drafting off their mothers, but exerting an energetic cost in terms of increased drag on the mother (Noren & Edwards, 2011; Noren, 2008; Weihs, 2004). Cetaceans also use the following strategy since offspring can travel independently (e.g. humpback whales: Szabo & Duffus, 2008; Tyson et al., 2012). In several species, adult cetaceans have been observed carrying calves on their backs (Smultea et al., 2017). The most common example of this is during predatory attacks by killer whales, *Orcinus orca*, where humpback whale females physically carry their vulnerable calves on their heads or backs (Pitman et al., 2015).

For species such as cetaceans that use the following and carrying strategies, maternal foraging still adds an additional challenge as mothers must typically separate from calves for brief periods in order to find and catch prey. Calves also begin to separate from their mothers well before weaning to develop foraging skills and meet their nutritional needs (bottlenose dolphins, *Tursiops aduncus*: Mann & Smuts, 1999; killer whales: Guinet & Bouvier, 1995; long-finned pilot whales, *Globicephala melas*: Gannon, Ready, Craddock, & Mead, 1997). Mysticete mothers such as humpback and grey whales, *Eschrichtius robustus*, also incur high travel costs during migration from breeding to the feeding grounds (Braithwaite, Meeuwig, & Hipsey, 2015; Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016; Rodríguez de la Gala-Hernández, Heckel, & Sumich, 2008).

Like most cetaceans, bottlenose dolphin (*Tursiops truncatus* and *T. aduncus*) mothers face a number of costs by adopting the carrying or following strategy. Young calves have limited swimming, diving and breath-holding abilities. Bradycardia, an important reflex that slows the heart rate when the animal dives to conserve oxygen is not fully developed in bottlenose dolphins until approximately 3.5 years of age (Noren, Cuccurullo, & Williams, 2004), close to the average weaning age (Mann, Connor, Barre, & Heithaus, 2000). Breath-holding capability also develops with age as it is positively correlated with body size, with blood oxygen storage reaching adult capacity at age 3 (Noren & Williams, 2000; Noren, Lacave, Wells, & Williams, 2002). Calf swimming efficiency, measured as distance per stroke, also increases with age, tapering off around age 2 (Noren, Biedenbach, & Edwards, 2006), enabling the calf to begin to travel, socialize, dive and hunt more independently (Mann & Sargeant, 2003; Sargeant & Mann, 2009; Stanton, Gibson, & Mann, 2011). As a result, young dolphin calves are unable to dive as long, deep or often as their mothers. Thus females may face costs because their offspring are not as physically capable as adults and may hinder their mothers' mobility, especially during maternal foraging bouts.

Some studies show that delphinid mothers spend more time at the surface to accommodate their young calves (e.g. bottlenose dolphins: Mann & Smuts, 1999; beluga whales, *Delphinapterus leucas*: Heide-Jørgensen, Hammeken, Dietz, Orr, & Richard, 2001).

Increased surface time imposes two major costs: decrease in swimming efficiency due to drag at the surface (Fish, 2000) and decrease in time spent foraging, especially if preferred prey species are found at depth. For example, lactating spotted dolphins, *Stenella attenuata*, shift from deep-water squid to less nutritional, surface-swimming flying fish presumably so they do not have to dive for long periods and leave their calves at the surface (Bernard & Hohn, 1989). Sperm whales balance foraging dives with calf care by staggering their deep foraging dives, presumably so at least one group member remains near the calf at the surface (Gero, Engelhaupt, & Whitehead, 2008; Whitehead, 1996).

Despite extensive research on cetacean diving, no study has investigated how mothers and calves simultaneously change their diving behaviour over the entire period of dependency and the implications for trade-offs between calf care and maternal foraging requirements. To investigate this trade-off, we examined the diving behaviour of females and their calves from birth to weaning in bottlenose dolphins in Shark Bay, Australia, where females have an extended lactation period of 3–8 years per calf (Mann et al., 2000). We hypothesized that females shorten dives most when calves are young and mortality risk is highest (Mann et al., 2000), but as calves matured, both calf and maternal dive durations would increase accordingly. In addition, we predicted that mother–calf proximity would be an important factor; mothers were predicted to shorten dives most when calves were close and thereby able to nurse and benefit from their mother's protection. When mothers and calves were separated, mothers were not expected to shorten their dives as this would not benefit the mother or the calf. These hypotheses assume that mothers are balancing calf care when near offspring with maximizing foraging opportunities when far from offspring.

METHODS

Study Site and Population

The Shark Bay Dolphin Research Project has been collecting demographic, behavioural, genetic, ecological and life history data on Indo-Pacific bottlenose dolphins (*T. aduncus*) in Shark Bay, Western Australia since 1984. The population is residential and bisexually philopatric (Tsai & Mann, 2013), such that individuals can be monitored from birth to death. The study site is a 300 km² area in the eastern gulf of Shark Bay off Monkey Mia (25°47′S, 113°43′E). To date over 1600 individual dolphins have been monitored using photo-identification of unique dorsal fin markings and shape, and other distinctive features (Bichell, Krzyszczyk, Patterson, & Mann, 2017; Mann, 2000). Sexes for dolphins in this study were determined by views of the genital area or by association with a calf (Smolker, Richards, Connor, & Pepper, 1992). We use the term calves here to refer to dependent offspring that are still nursing, or not yet weaned (Mann et al., 2000). Weaning age was determined by taking the midpoint between the last sighting of a calf in infant position or spending at least 80% of time with the mother, and when mother–calf association decreased to less than 50% (Mann et al., 2000). All calves in this study were of known age and sex. Birth dates were estimated from the last sighting of a mother before the birth of her calf to first sighting of a mother with the calf, as well as physical features of the calf such as fetal folds, behaviour and body size (Mann et al., 2000). All birth dates were accurate to within a single birth season, and more than half of birth dates could be pinpointed to within a month. Ages used in models were to the estimated day of birth (in years). Calves ranged in age from less than 1 month to 3.8 years old. We excluded calves older than 4 years of age but still nursing because of limited sample size.

Data Collection and Subjects

For this study, we used data from individual focal follows collected from 1989 to 2014. Focal follows are detailed quantitative behavioural observations in which we observed individual animals and recorded activity, group composition and associated environmental data (location, habitat, depth, temperature, etc.) (Karniski et al., 2015). Prior to 1997, maternal and calf predominant activity was noted for each dive bout. After 1997, activity state was recorded using 1 min point sampling, but continuous dive data were still collected. Despite the different sampling methods, activity budgets are virtually identical (Mann, 1999). During mother–calf focal follows, mother–calf distance and dive bouts were recorded using continuous sampling. A dive bout indicates the length of a dive (in seconds) recorded as the time the dolphin dives under the surface to the time that the dolphin resurfaces. For each dive, we assigned the depth (range 2.00–12.50 m, mean $\pm$ SD $= 7.28 \pm 1.82$ m) as the closest depth recording in time from the boat's depth-sounder within 5 min of the dive onset (mean $\pm$ SD $= 75.02 \pm 48.36$ s). Because we were interested in discrete diving rather than near-surface underwater behaviour, we excluded dives by dolphins that were in water less than 2 m deep, the average body length of Shark Bay dolphins, or surfacing by dolphins within 20 s of their previous breath ($N = 16$). This 20 s cutoff point was determined based on breathing rates from calves and adults in relatively shallow water (<6 m depth) that were exhibiting surface behaviour rather than deliberate dives (Appendix, Table A1). At each surface interval or point sample, we also assigned mother–calf distance and activity state as the distance and activity observed prior to the onset of the dive. Mother–calf distance was estimated by distance codes that refer to ranges ($\leq$30 cm, 30 cm–2 m, 2–5 m, 5–10 m, 10–20 m, 20–50 m, 50–100 m, >100 m, >200 m). Dives in infant or echelon position were included in the $\leq$30 cm distance category. Activity states of foraging, resting, socializing and travelling were assigned as in Karniski et al. (2015).

Because we were interested in mother–calf behaviour, specifically the influence of calf proximity and age on maternal diving behaviour, we analysed dive bouts with regard to three mother–calf distance categories: contact, near, and far. We defined 'contact' as when mother and calf were in echelon position, infant position or $\leq$30 cm, 'near' as when mother and calf were >30 cm and $\leq$10 m, and 'far' as when mother and calf were >10 m apart. We chose these categories because we define mother–calf separations as being >10 m (Mann & Smuts, 1999; Smolker, Mann, & Smuts, 1993), which is consistent with dolphin spatial patterns in Shark Bay and our definition of association (in the same group) based on a 10 m chain rule (Smolker et al., 1992). The 10 m chain rule tends to describe the general spatial grouping of dolphins in Shark Bay: individuals that are within 10 m of one another are often engaged in the same behaviour and stay close for at least a short duration, whereas individuals farther than 10 m do not appear to be engaged in similar behaviours nor do they remain within any predictable distance of one another. Thus, calves that are >10 m from their mothers are typically not in the same group as their mothers unless they are connected by other individuals. Although mothers and calves can likely hear each other even when they are hundreds of metres apart, visual contact is likely only in the contact and near categories (Smolker et al., 1993). There were more dives when mothers and calves were in contact (15 803) and near (8097) compared to when they were far (3488). When mothers and calves separated, researchers continued to record observations on both individuals until one of the pair was out of visual range. At this point, researchers continued to follow either the mother or the calf depending on a number of factors, such as whether the mother or the infant was the predetermined focal animal, the visibility of the individual, or other data collection priorities. However, calves spend most of their time near their mothers and are only more than 10 m away on average 17% of the time (Gibson & Mann, 2008a).

We further specifically isolated foraging dives in order to investigate how mothers balance the trade-offs between calf care and foraging effort. Maternal foraging dives were characterized by frequent changes in direction, accelerations, irregular movement and intermittent prey catches (Karniski et al., 2015). For this subset of dives, we examined both the mothers' dive durations and calves' dive durations during maternal foraging bouts.

Statistical Analysis

We explored the effects of multiple predictors on calf and mother dive durations, which were treated as response variables in generalized linear mixed models (GLMM). For all models, dive durations were measured in seconds and age was a continuous variable measured in decimal years. In total, we ran 13 models under multiple conditions with two different response variables, mother dive duration and calf dive duration (detailed below). To construct these models, we used *R* v.3.4.1 (R Core Team, 2017) and the package MCMCglmm (Hadfield, 2010), which employs a Bayesian approach to GLMMs using Markov-chain Monte Carlo simulations. We used a Gaussian error distribution since the response variable was near normal and the Gaussian model fit our data most closely. We used the default weak priors (nu = 0, V = 1, alpha.mu = 0, alpha.V = 0), 1 000 000 iterations, a burn-in of 3000 and a thinning interval of 10. Convergence and mixing were assessed after each model run using trace and posterior distribution plots. For all analyses, significance was set at $\alpha = 0.05$.

Our first model examined how calf dive durations changed with age, regardless of the calf's distance from its mother. Fixed factors included calf sex, calf age, their interaction, and depth, and random factors included mother and calf identity. Based on results from this model (further detailed in Results below) we included calf age in the maternal model as a proxy for calf diving abilities. We included calf age rather than actual calf dive duration for two reasons. First, if dives are paired, for example when mother and calf are in infant or echelon position, their dive durations will be the same and thus no longer independent from one another. Second, since we were interested in how mothers adjust their diving behaviour in response to overall calf development, including swimming ability and independence, not just diving ability, calf age is perhaps more informative. As calf age and dive duration were highly correlated, we only used calf age, rather than calf dive duration, when modelling maternal dive bouts.

Next, we ran 12 models to examine the mother–calf diving relationship under multiple conditions. For each, the response variable was either calf dive duration or maternal dive duration, fixed factors were calf sex, calf age, their interaction, depth, and random factors were mother identity and calf identity. We ran three models (contact, near, far) with calf dive duration as the response and three models (contact, near, far) with the mother dive duration as the response. We also ran the same six models (calf dive duration: contact, near, far; mother dive duration: contact, near, far), for maternal foraging bouts only. Since social factors may influence mother and or calf diving behaviour, we included group size as a fixed factor in all of our models; however, effects of group size on maternal dive duration were nonsignificant ($P > 0.1$) and there was no evidence of mothers adjusting dive duration based on group size, so we removed this variable from our analyses. Furthermore, foraging is a relatively solitary activity. Out of our data set, 60% of dives and 87% of foraging dives occurred when mothers and calves were alone. For all models, if there was a significant calf age $*$ sex interaction, we ran separate models for each sex. We examined

variance inflation factors, which indicated that collinearity between calf age and depth was not a major concern (VIFs < 2). That is, calves did not necessarily spend more time in deeper water with age.

Ethical Note

This work was approved by the Georgetown University Animal Care and Use Committee (permits 07-041, 10-023, 13-069), the West Australian Department of Biodiversity, Conservation and Attractions (DBCA) (permits SF009311, SF008076, SF009876) and the University of Western Australia (animal ethics permit 600-37). The study was entirely observational and care was taken when approaching and following animals (e.g. to not approach the dolphins erratically or too closely (50 m) and to drive alongside rather than behind the dolphins).

RESULTS

Our data set included 27 388 dive bouts, 13 586 from mothers ($N = 26$, 754 focal hours) and 13 802 from calves ($N = 41$, 782 focal hours). Of the 13 802 dives from calves, 7231 dives were from female calves ($N = 20$) and 6571 dives were from male calves ($N = 21$). The number of dives per calf ranged from 7 to 1761 (mean ± SD = 336.6 ± 346.2). The number of dives per mother ranged from 7 to 2206 (522.5 ± 484.9). The subset of maternal foraging dives included 5274 calf dives and 5255 maternal foraging dives for 37 calves and 26 mothers.

Calf Diving Development

First, we analysed all calf diving data to identify the relationship between calf age and dive duration. We found a significant interaction between calf age and calf sex on calf dive duration (coefficient $\beta = -1.76$, 95% confidence interval, CI (-3.10, -0.43), $P < 0.001$). Both female calves ($\beta = 4.28$, CI (3.25, 5.29), $P < 0.001$) and male calves ($\beta = 12.67$, CI (1.78, 3.55), $P < 0.001$) increased dive duration with age, but the significant interaction indicated that they did so at different rates, with females increasing dive duration faster with age. These results indicate that calf age is an adequate proxy for dive duration, allowing us to use calf age in mother dive duration models as previously mentioned. Additionally, depth was positively correlated with calf dive duration for both sexes (females: $\beta = 6.36$, CI (5.88, 6.85), $P < 0.001$; males: $\beta = 5.74$, CI (5.16, 6.35), $P < 0.001$), regardless of mother–calf distance (Tables 1, 2).

Mother–Calf Proximity and Calf Dives

When calves were in contact with their mothers, we found an interaction between calf age and calf sex on calf dive duration. Both female and male calves significantly increased their dive duration with age (Fig. 1a, b, Table 1). However, the estimate for female calves was higher, indicating a steeper slope for the increase in dive duration. When calves were near their mothers (<10 m), the interaction between calf age and calf sex on calf dive duration was not significant. Both female and male calves significantly increased their dive duration with age (Fig. 1c, Table 1). When calves were far from their mothers (>10 m), the calf sex∗age interaction on dive durations was not significant (Table 1). Both female and male calves significantly increased their dive duration with age (Fig. 1d, Table 1).

Mother–Calf Proximity and Calf Dives during Maternal Foraging

When calves were in contact with their foraging mothers, we found an interaction between calf age and calf sex on calf dive duration (Table 2). In contrast to the full data set, during maternal foraging, female calves significantly increased dive duration with age (Fig. 2a, Table 2), but male calves did not (Fig. 2b, Table 2). When calves were near their foraging mothers (<10 m), the interaction between calf sex∗age on calf dive duration was not significant (Table 2). However, we also examined the sexes separately, given the interaction in previous models, and found that female calves near foraging mothers significantly increased dive duration with age (Fig. 2c) while male calves did not (Fig. 2d, Table 2). Similar to all dive bouts, the interaction between calf sex∗age on calf dive duration when calves were far from their foraging mothers (>10 m) was not significant (Table 2). Both female and male calves significantly increased their dive duration with age (Fig. 2e, Table 2).

Mother–Calf Proximity and Maternal Dives

When mothers were in contact with their calves, the interaction between calf sex and age on mother dive duration was significant (Table 1). We found an increase in the mother's dive duration with female calf age (Fig. 3a, Table 1), but not with male calf age (Fig. 3b, Table 1). The analysis for mothers when calves were near (<10 m) did not show a significant interaction between calf age and calf sex on mother dive duration (Table 1). We found a marginally nonsignificant increase in the mother's dive duration with calf age (Fig. 3c, Table 1). When mothers were far from their calves (>10 m), the interaction for calf sex∗age on mother's dive duration was not significant, so we analysed the sexes together (Table 1). Mothers did not significantly change their dive duration with calf age (Fig. 3d, Table 1).

Mother–Calf Proximity and Maternal Foraging Dives

While mothers were foraging in contact with their calves, the calf age∗sex interaction on mother dive duration was marginally nonsignificant, so we analysed the sexes separately (Table 2). Mothers significantly increased their dive duration with calf age when foraging in contact with female calves (Fig. 4a), but not when foraging in contact with male calves (Fig. 4b, Table 2). While mothers were foraging near their calves (<10 m), the calf age∗sex interaction on mother dive duration was not significant (Fig. 4c, Table 2). Mothers did not significantly adjust their dive duration in response to calf age (Table 2). While mothers were foraging far from their calves (>10 m), the calf age∗sex interaction on mother dive duration was not significant (Table 2), so we analysed the sexes together. Mothers did not significantly change their dive duration with calf age (Table 2, Fig. 4d).

DISCUSSION

To our knowledge, this is the first study to examine longitudinal changes in mother–calf diving behaviour in a wild cetacean from birth to weaning. Consistent with research on captive dolphins (Noren et al., 2004, 2006), we found that dolphin calves of both sexes increased dive duration with age. This is similar to diving development in other marine mammals (e.g. New Zealand fur seals, *Arctocephalus forsteri*: Baylis et al., 2005; harbour seals, *Phoca vitulina*: Bowen, Boness, & Iverson, 1999; southern sea otters: Payne & Jameson, 1984; humpback whales: Cartwright & Sullivan, 2009), and may suggest that longer dive durations coincide with the acquisition of foraging skills. As early as 3 months of age, bottlenose dolphin calves in Shark Bay engage in shallow-water

Table 1
Mother and calf diving parameter estimates from the Markov-chain Monte Carlo GLMMs for dive duration.

	Fixed effect	Estimate	95% CI		N_e	P
			Lower	Upper		
Maternal dives						
Contact						
Female calves	Calf age	4.171	2.921	5.409	99700	**<0.001**
	Depth	6.950	6.332	7.572	99700	**<0.001**
Male calves	Calf age	0.4276	−0.8541	1.7028	99700	0.513
	Depth	7.0152	6.1521	7.8696	99700	**<0.001**
Near						
	Calf age	1.6678	−0.1487	3.4130	99436	**0.0658**
	Calf sex	1.1825	−6.1784	8.6402	99700	0.7570
	Depth	6.8335	6.1992	7.5083	99700	**<0.001**
	Calf age*sex	−0.8024	−3.2213	1.6195	99700	0.5160
Far						
	Calf age	0.4382	−2.5480	3.3433	99700	0.765
	Calf sex	5.9532	−5.6582	17.4311	86654	0.301
	Depth	5.0273	3.5935	6.4319	37826	**<0.001**
	Calf age*sex	0.3919	−4.3180	5.0494	13454	0.842
Calf dives						
Contact						
Female	Calf age	5.257	4.017	6.501	99700	**<0.001**
	Depth	6.981	6.367	7.582	100727	**<0.001**
Male	Calf age	2.205	1.021	3.375	99700	**<0.001**
	Depth	5.725	4.892	6.524	86057	**<0.001**
Near						
	Calf age	3.605	1.810	5.425	99700	**<0.001**
	Calf sex	−2.326	−9.650	4.865	99700	0.5247
	Depth	5.870	5.222	6.511	99700	**<0.001**
	Calf age*sex	−0.591	−2.955	1.871	99700	0.6299
Far						
	Calf age	3.9584	0.4059	7.5864	99700	**0.0318**
	Calf sex	0.9811	−12.9031	15.1565	98177	0.8978
	Depth	3.3920	2.2336	4.5824	99700	**<0.001**
	Calf age*sex	−0.6042	−5.2470	4.1157	99700	0.8019

CI: confidence interval; N_e: effective sample size. Statistically significant P values are shown in bold.

foraging tactics that do not require long dives (e.g. 'snacking' sensu Mann & Sargeant, 2003; Mann & Smuts, 1999). While such tactics are important for young calves, older calves decrease time spent engaged in such foraging behaviour and begin to adopt deeper-water tactics (Mann & Sargeant, 2003; Mann & Smuts, 1999). With improving diving capability, calves increase both their rate of foraging and proportion of time spent foraging with age (Foroughirad & Mann, 2013; Mann & Sargeant, 2003). Tactics requiring deeper dives begin to occur regularly at 7–8 months. One deep-diving foraging tactic, sponge tool use, does not occur until at least 2 years of age (Mann & Sargeant, 2003). In our study, calves increased their dive duration until weaning; however, average dives were still shorter than average dive duration for adult females without calves (131.1 ± 8.90 s) and adult males (132.9 ± 11.50 s), whereas average dive duration for calves age 3–4 years was 84.30 ± 5.23 s.

While calves increased their dive duration with age, sex differences were notable. Female calves increased their dive durations at a faster rate than males. There are several possible explanations for these sex differences. First, sexual dimorphism helps explain sex differences in diving development in some species (Noren & Williams, 2000), but Shark Bay bottlenose dolphins are monomorphic (Connor, Wells, Mann, & Read, 2000; Smolker et al., 1992). Second, sex differences in mother–calf separation rate could impact diving behaviour. However, no such sex differences have been found in previous work (Gibson & Mann, 2008a; Mann & Watson-Capps, 2005), and we controlled for distance in our analyses, rendering sex differences in mother–calf separation rate an unlikely explanation. Third, and most plausible, the sex differences observed in this study could be due to sex-specific socioecological strategies that are well documented in Shark Bay dolphins, with

females spending more time foraging and exhibiting greater foraging specialization than males at all stages of development (Gibson & Mann, 2008a; Krzyszczyk, Patterson, Stanton, & Mann, 2017; Mann & Patterson, 2013; Mann & Sargeant, 2003; Mann et al., 2008; Sargeant, Mann, Berggren, & Krützen, 2005; Smolker et al., 1992). Finally, females may mature more quickly than males, allowing them to dive longer at a younger age. Bimaturism, differential timing of maturity between sexes due to different durations of growth, occurs in some species, especially those with a polygynous mating system. For example, female pinnipeds generally reach sexual maturity faster than males (Riedman, 1990) and female great apes reach adult body weight faster than males (Watts & Pusey, 2002). Read et al. (1993) found that female *T. truncatus* grew at a faster rate than males during the first 6 years of life, even though this species is sexually dimorphic, with males reaching larger adult size. Bimaturism is consistent with the socioecological strategy hypothesis, for which we have most support.

As mothers did not adjust their dive durations when at a distance from their calves, we suggest that mothers change their diving behaviour as a function of their immediate caregiving responsibilities, at least for daughters. Remarkably, mothers only adjusted their dive durations when in contact with female, but not male, calves. This suggests that mothers are biasing their diving and foraging behaviour to benefit female calves more than male calves, possibly because foraging skill development is more critical for daughters than for sons, consistent with the socioecological hypothesis. Males and females in Shark Bay exhibit different reproductive strategies, which are apparent during development. Calves of both sexes are physically precocious and begin to separate for brief periods at a young age (Mann & Watson-Capps, 2005). During these separations, calves, especially males, begin to form their own

Table 2
Mother and calf diving parameter estimates from the Markov-chain Monte Carlo GLMMs for dive duration during maternal foraging bouts

	Fixed effect	Estimate	95% CI		N_e	P
			Lower	Upper		
Maternal dives						
Contact						
Female calves	Calf age	5.753	3.541	8.062	98804	**<0.001**
	Depth	7.200	6.028	8.372	34626	**<0.001**
Male calves	Calf age	1.506	−1.330	4.352	99265	0.299
	Depth	10.295	8.342	12.266	56498	**<0.001**
Near						
	Calf age	1.5625	−0.8801	4.0530	28625	0.20869
	Calf sex	−0.4808	−8.4329	7.6871	17570	0.87637
	Depth	8.0046	6.9346	9.0710	20977	**<0.001**
	Calf age*sex	−1.3898	−5.2190	2.3221	6218	0.47661
Far						
	Calf age	0.3187	−2.6268	3.2065	95901	0.823
	Calf sex	8.6396	−3.1984	20.8082	98704	0.154
	Depth	5.6732	4.1697	7.1606	45699	**<0.001**
	Calf age*sex	0.5516	−4.1747	5.2529	68926	0.809
Calf dives						
Contact						
Female	Calf age	7.111	4.826	9.427	99700	**<0.001**
	Depth	7.429	6.263	8.611	97600	**<0.001**
Male	Calf age	2.2392	−0.3209	4.8722	99700	0.0909
	Depth	7.7355	5.9875	9.4747	100707	**<0.001**
Near						
	Calf age	3.9392	0.9538	6.9426	99700	**0.011**
	Calf sex	0.4852	−10.1960	10.7509	99700	0.927
	Depth	6.1181	5.0291	7.2024	99700	**<0.001**
	Calf age*sex	−2.2504	−6.2548	1.8070	101611	0.271
Near						
Female	Calf age	3.9340	0.8292	7.1369	99700	**0.0159**
	Depth	5.8887	4.4586	7.3083	99700	**<0.001**
Male	Calf age	1.861	−0.930	4.591	26149	0.1857
	Depth	6.558	4.923	8.227	82889	**<0.001**
Far						
	Calf age	4.6875	0.5332	8.7178	2030	**0.0285**
	Calf sex	−0.9591	−16.8916	14.6101	6057	0.9057
	Depth	3.4684	2.0435	4.8644	99700	**<0.001**
	Calf age*sex	0.3669	−5.6709	6.4131	3839	0.9121

CI: confidence interval; N_e: effective sample size. Statistically significant P values are shown in bold.
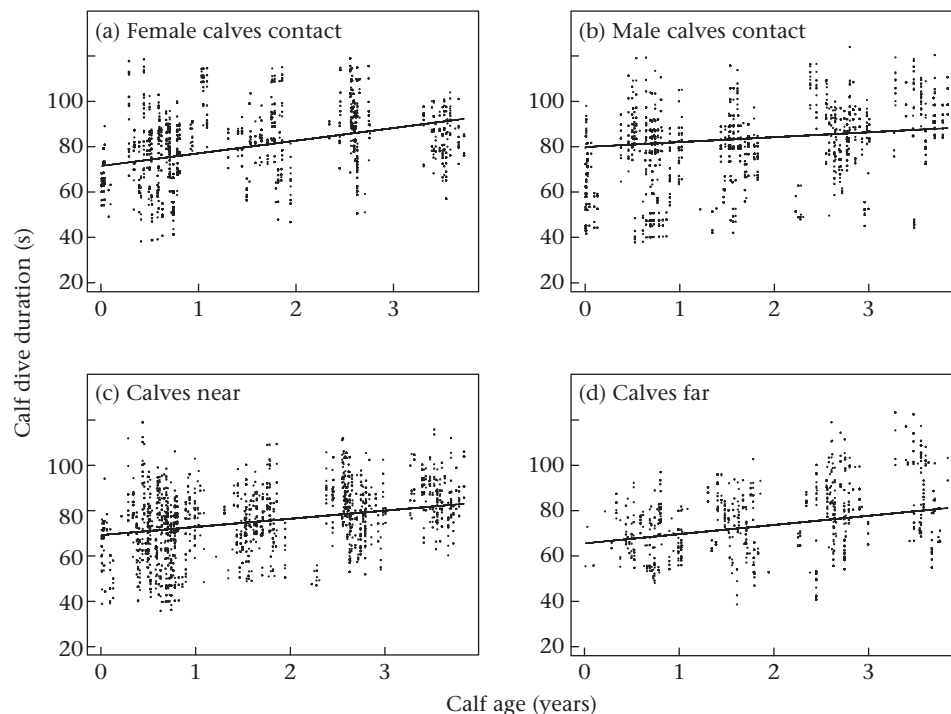
Figure 1. Partial effects of age on calf dive duration for (a) female calves in contact with mothers, (b) male calves in contact with mothers, (c) calves near mothers and (d) calves far from mothers. Points are predictions from the full model and lines are the partial effects of age after marginalizing all other factors.
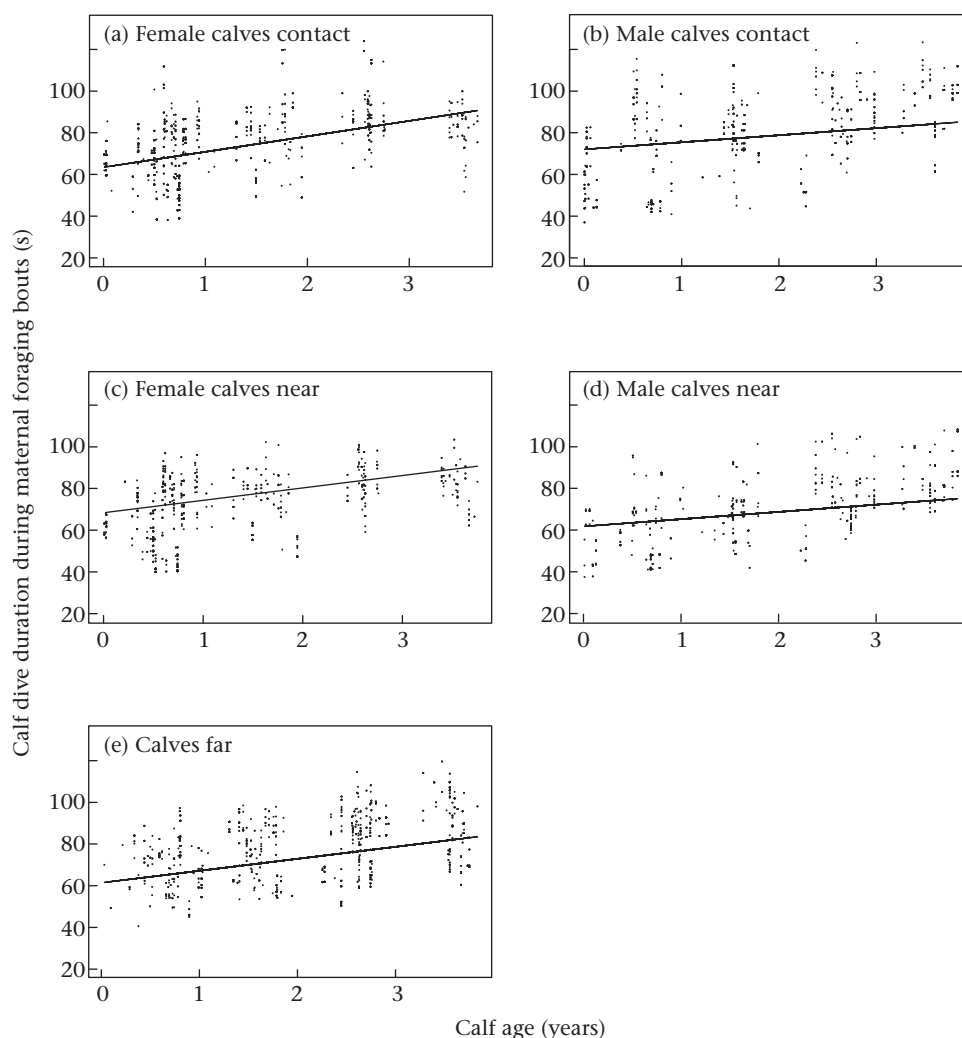
Figure 2. Partial effects of age on calf dive duration during maternal foraging bouts for (a) female calves in contact with mothers, (b) male calves in contact with mothers, (c) female calves near mothers, (d) male calves near mothers and (e) calves far from mothers. Points are predictions from the full model and lines are the partial effects of age after marginalizing all other factors.

social bonds (Stanton et al., 2011). In comparison to females, male calves have stronger ties to other males during separations (Stanton et al., 2011), socialize more preweaning (Krzyszczyk et al., 2017) and spend more time in groups on longer separations. Female calves emulate their mothers (usually by foraging) more during separations; males prioritize finding associates, particularly when their mother is relatively solitary (Gibson & Mann, 2008b). These social bonds are particularly significant for male calves (1) because it predicts survival into the juvenile period (Stanton & Mann, 2012) and (2) because male alliance formation is critical to reproductive success (Krützen et al., 2004). In contrast to males, Shark Bay females tend to adopt and specialize in their mothers' foraging tactics (Mann & Sargeant, 2003; Sargeant & Mann, 2009; Sargeant et al., 2005) and associate more with their mothers than sons do post-weaning even though both sexes remain in their natal area (Tsai & Mann, 2013).

Given these different sex-specific socioecological strategies, we suggest that dolphin mothers adjust their dive behaviour when in contact with female calves to preferentially allow females to observe maternal foraging tactics while physically entraining with her movement, breathing and diving. Average dive duration for all maternal dives ranged from 72.85 ± 3.64 s to 82.09 ± 5.18 s. In contrast, average dive duration for females without calves was

131.05 ± 8.98 s. This suggests that mothers are adjusting to some degree for all calves, however, mothers with female calves adjust to a greater degree. Observational learning has been identified in both captive and wild dolphins (for review, see Yeater & Kuczaj, 2010) and there is evidence from our study population of vertical social learning (mother to offspring) for multiple specialized foraging tactics (Sargeant & Mann, 2009). Thus, in order for vertical transmission of foraging tactics to occur, calves must be close enough to their mothers to observe their mothers' foraging behaviour. While in contact, entrainment may be occurring, which can facilitate observational learning (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014). Calves in contact position can visually and acoustically observe their mothers during foraging bouts, receiving acoustic feedback from the mother's echolocation during foraging. Furthermore, many species, including dolphins, are capable of vocal mimicry (Reiss & McCowan, 1993; Schachner, Brady, Pepperberg, & Hauser, 2009). In another population, wild Atlantic spotted dolphin, *Stenella frontalis*, mothers appeared to alter their foraging behaviour in the presence of calves, and calves assumed an observation position, in which they faced their mothers during foraging (Bender, Herzing, & Bjorklund, 2009). In our study, calves increased dive duration when far from their mothers, which may be evidence that they are practising and developing their foraging
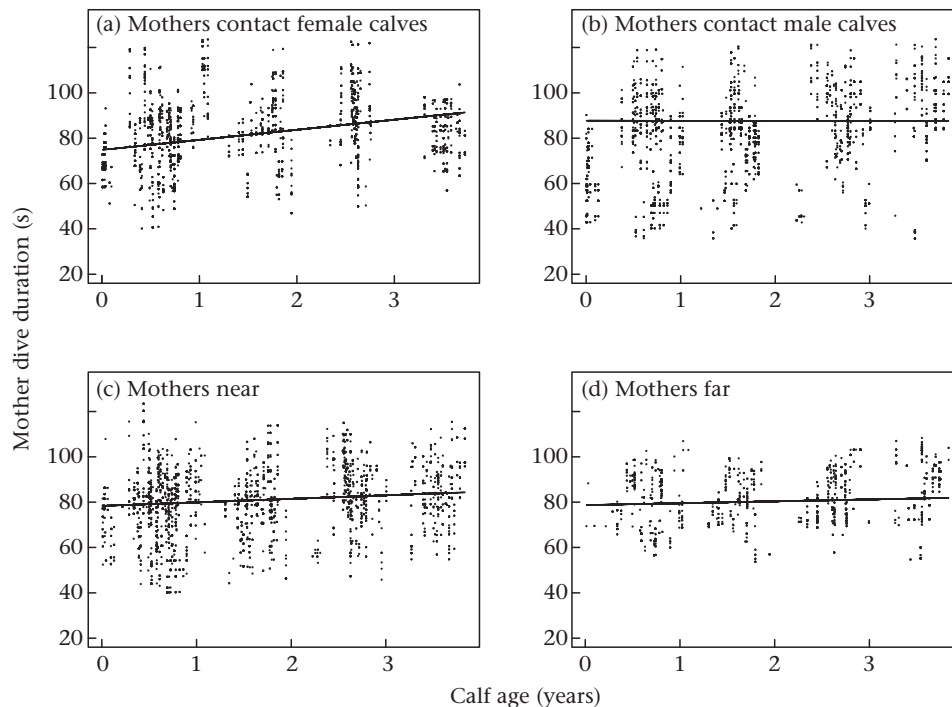
Figure 3. Partial effects of calf age on mother dive duration for (a) mothers in contact with female calves, (b) mothers in contact with male calves, (c) mothers near calves and (d) mothers far from calves. Points are predictions from the full model and lines are the partial effects of age after marginalizing all other factors.
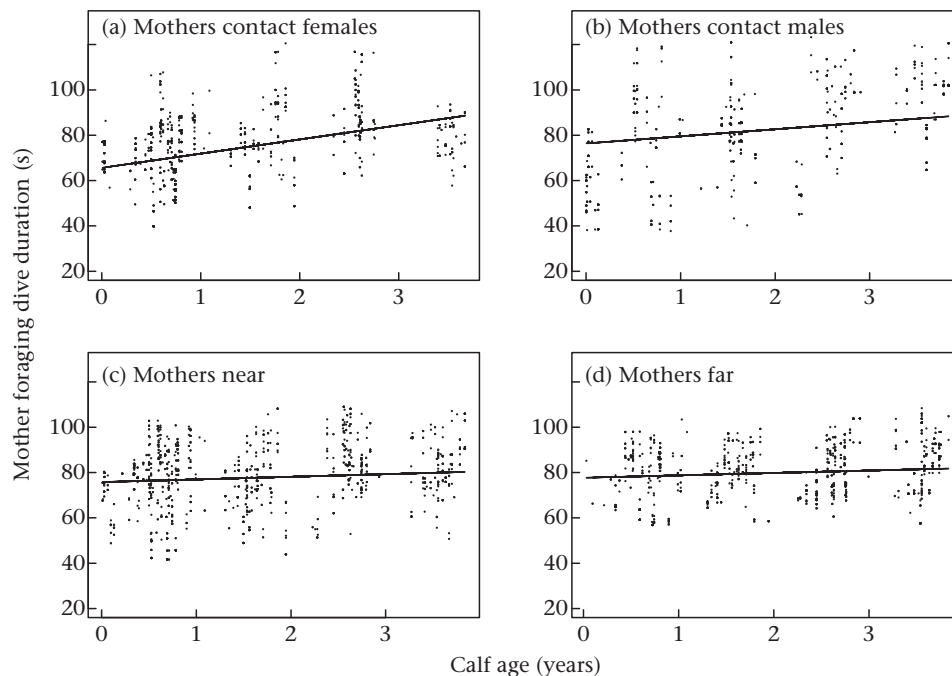

Figure 4. Partial effects of calf age on mother dive duration during maternal foraging bouts for (a) mothers in contact with female calves, (b) mothers in contact with male calves, (c) mothers near calves and (d) mothers far from calves. Points are predictions from the full model and lines are the partial effects of age after marginalizing all other factors.

tactics while on separations. Gibson and Mann (2008a) found that during separations greater than 50 m, female calves spent a greater proportion of time foraging than male calves. Thus, we suggest that females are observing their mothers foraging and then practising those techniques during separations more than males. Such observation- and practice-based learning may not be surprising given that in order to reach peak performance in some foraging

tactics, such as sponging, individuals must learn the behaviour at a young age, specialize in it, and then continue to improve well into adulthood (Patterson, Krzyszczyk, & Mann, 2016).

When we analysed maternal foraging dive bouts separately, we found that mothers again only adjusted their dive durations when in contact with female calves. This is consistent with our explanation that foraging behaviour likely explains the observed sex differences.

To illustrate this point further, we return to an example with sponge foraging, a highly female-biased, habitat-specific foraging tactic in which individuals tend to specialize (Mann & Sargeant, 2003; Mann et al., 2008). To become a sponger, one's mother must be a sponger, and even then, typically more females become spongers, as 91% of daughters and only 50% of sons adopted sponging from their mothers (Mann & Patterson, 2013; Mann et al., 2008). Females adopt sponging earlier (Mann et al., 2008) and sponge more often as adults than males (Mann & Patterson, 2013). Thus, dependency, when calves have ample opportunities to observe their mothers, is a critical period of time for females to develop this tactic. Although sponging is only used by a small fraction of the females in Shark Bay (Mann & Sargeant, 2003), and in this study, 29% of calves and 39% of mothers were spongers, Shark Bay dolphins have been observed using over 13 different foraging tactics, a number of which appear to be vertically transmitted (Mann & Sargeant, 2003; Sargeant & Mann, 2009; Sargeant et al., 2005, 2007). Thus, the same principles for sponging likely apply to other sex-biased foraging tactics.

There are several costs and benefits to mothers and calves associated with adjusting diving behaviour. Maternal foraging bouts may require mothers to increase distance from calves as they must accelerate rapidly in order to catch prey. These separations may leave calves vulnerable to predators, such as tiger sharks, Galeocerdo cuvier, which are seasonally abundant in Shark Bay (Heithaus & Dill, 2002; Heithaus, 2001) and pose a threat, with approximately one-third of nursing calves having shark bite scars (Mann & Barnett, 1999). Therefore, mothers and calves likely benefit by adjusting in terms of decreased predation risk. However, such behavioural adjustments may increase drag at the surface, decrease foraging opportunities and lead to a loss of successful foraging events. Nevertheless, maternal foraging rate and percentage of time foraging does not significantly change as a function of calf age (Mann & Sargeant, 2003), which indicates that mothers forage just as frequently with young, inexperienced calves as they do with older calves, regardless of the demands of their calves. Adult females appear to become more efficient foragers with age, but likely suffer foraging costs with a young calf regardless. For example, female spongers increase their efficiency in this tactic as they increase in age, but peak in their mid-20s, when they are most likely to be experiencing the high costs of motherhood (Patterson et al., 2016).

Since our data suggest that mothers only adjust their diving behaviour in response to daughters, it raises an important question: do mothers invest more in daughters? In species with extensive maternal care, and no paternal care, mothers have greater influence on the reproductive value of female offspring than of male offspring (Leimar, 1996). A mother might influence her daughter's reproductive success more than her son's by vertical transmission of foraging skills. Males are less likely to adopt maternal foraging tactics and show less specialization (e.g. Mann & Patterson, 2013). In this way mothers can behaviourally influence the quality of grand offspring through daughters but not through sons. This logic follows Zefferman (2016), who proposed support for uniparental teaching hypothesis in which Shark Bay mothers preferentially teach daughters to sponge over sons due to benefits gained from future generations.

Our results confirm that dolphin calves increase their dive durations with age, similar to other species. Because young dolphins are incapable of repeated long, deep dives, mothers appear to adjust their behaviour in order balance their own needs to forage while maintaining close proximity to calves, but do so more for female calves than for male calves. Most work examining sex-biased investment has examined polygynous follower species, namely ungulates (e.g. feral horses, Equus caballus: Cameron, Linklater, Stafford, & Veltman, 1999; red deer, Cervus elaphus: Clutton-Brock, Albon, &

Guinness, 1984; bighorn sheep, Ovis canadensis: Bérubé, Festa-Bianchet, & Jorgenson, 1996). In contrast, dolphins are a promiscuous species that use a combination of following and carrying strategies. Studies on promiscuous primate species provide inconsistent evidence regarding sex-biased maternal investment (reviewed in Brown, 2001). We found that mothers favour their female offspring in terms of adjusting maternal behaviour, here, diving. Evidence to support sex-biased maternal care has also been observed in a few species outside ungulates (e.g. pinnipeds: Trillmich, 1996; primates: Brown, 2001); however, examining such biases in natural settings, especially in long-lived marine mammals, is rare. Here we provide new insights into calf diving development and the associated behavioural trade-offs made by mothers. Our results contribute to a better understanding of the intricacies of the mother–calf relationship and how females mitigate the demands of motherhood by selectively altering behaviour. Future studies investigating the fitness costs of such behavioural adjustments would allow for an important analysis of how mothers balance resource acquisition with calf care and learning.

Acknowledgments

References

Altmann, J., & Samuels, A. (1992). Costs of maternal care: Infant-carrying in baboons. Behavioral Ecology and Sociobiology, 29(6), 391–398. https://doi.org/10.1007/BF00170168.

Baylis, A. M. M., Page, B., Peters, K., McIntosh, R., Mckenzie, J., & Goldsworthy, S. (2005). The ontogeny of diving behaviour in New Zealand fur seal pups (Arctocephalus forsteri). Canadian Journal of Zoology, 83(9), 1149–1161. https://doi.org/10.1139/z05-097.

Bender, C. E., Herzing, D. L., & Bjorklund, D. F. (2009). Evidence of teaching in Atlantic spotted dolphins (Stenella frontalis) by mother dolphins foraging in the presence of their calves. Animal Cognition, 12(1), 43–53. https://doi.org/10.1007/s10071-008-0169-9.

Bernard, H. J., & Hohn, A. A. (1989). Differences in feeding habits between pregnant and lactating spotted dolphins (Stenella attenuata). Journal of Mammalogy, 70(1), 211–215.

Bérubé, C. H., Festa-Bianchet, M., & Jorgenson, J. T. (1996). Reproductive costs of sons and daughters in Rocky Mountain bighorn. Behavioral Ecology, 7, 60–68. https://doi.org/10.1093/beheco/7.1.60.

Bichell, L. M. V., Krzyszczyk, E., Patterson, E. M., & Mann, J. (2017). The reliability of pigment pattern-based identification of wild bottlenose dolphins. Marine Mammal Science, 34(1), 113–124. https://doi.org/10.1111/mms.12440.

Bowen, W. D., Boness, D. J., & Iverson, S. J. (1999). Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. Canadian Journal of Zoology, 77(6), 978–988. https://doi.org/10.1139/z99-065.

Boydston, E. E., Kapheim, K. M., & Holekamp, K. E. (2006). Patterns of den occupation by the spotted hyaena (Crocuta crocuta). African Journal of Ecology, 44(1), 77–86. https://doi.org/10.1111/j.1365-2028.2006.00618.x.

Braithwaite, J. E., Meeuwig, J. J., & Hipsey, M. R. (2015). Optimal migration energetics of humpback whales and the implications of disturbance. Conservation Physiology, 3, 1–15. https://doi.org/10.1093/conphys/cov001.

Brown, G. R. (2001). Sex-biased investment in nonhuman primates: Can Trivers & Willards theory be tested? Animal Behaviour, 61, 683–694. https://doi.org/10.1006/anbe.2000.1659.

Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Veltman, C. J. (1999). Birth sex ratios relate to mare condition at conception in Kaimanawa horses. Behavioral Ecology, 10(5), 472–475. https://doi.org/10.1093/beheco/10.5.472.

Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M., & Bearder, S. K. (2011). Primates in perspective. New York, NY: Oxford University Press.

Caperos, J. M., Morcillo, A., Peláez, F., Fidalgo, A., & Sánchez, S. (2012). The effect of infant body mass on carrier travel speed in cotton-top tamarins (Saguinus oedipus). International Journal of Primatology, 33(2), 447–459. https://doi.org/10.1007/s10764-012-9594-3.

Cartwright, R., & Sullivan, M. (2009). Behavioral ontogeny in humpback whale (Megaptera novaeangliae) calves during their residence in Hawaiian waters.

Marine Mammal Science, 25(3), 659–680. https://doi.org/10.1111/j.1748-7692.2009.00286.x.

Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere, 7*(10), 1–18. https://doi.org/10.1002/ecs2.1468.

Ciuti, S., Pipia, A., Grignolio, S., Ghiandai, F., & Apollonio, M. (2009). Space use, habitat selection and activity patterns of female Sardinian mouflon (*Ovis orientalis musimon*) during the lambing season. *European Journal of Wildlife Research, 55*(6), 589–595. https://doi.org/10.1007/s10344-009-0279-y.

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1984). Maternal dominance, breeding success and birth sex ratios in red deer. *Nature, 308*, 358–360.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission–fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago, IL: University of Chicago Press.

Fish, F. E. (2000). Biomechanics and energetics in aquatic and semiaquatic mammals: Platypus to whale. *Physiological and Biochemical Zoology, 73*(6), 683–698. https://doi.org/10.1086/318108.

Fisher, D. O., Blomberg, S. P., & Owens, I. P. F. (2002). Convergent maternal care strategies in ungulates and macropods. *Evolution, 56*(1), 167–176.

Foroughirad, V., & Mann, J. (2013). Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biological Conservation, 160*, 242–249. https://doi.org/10.1016/j.biocon.2013.01.001.

Fowler, S. L., Costa, D. P., & Arnould, J. P. Y. (2007). Ontogeny of movements and foraging ranges in the Australian sea lion. *Marine Mammal Science, 23*(3), 598–614. https://doi.org/10.1111/j.1748-7692.2007.00134.x.

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. *Scientific Reports, 4*. https://doi.org/10.1038/srep05283. srep05283.

Gannon, D. P., Ready, A. J., Craddock, J. E., & Mead, J. G. (1997). Stomach contents of long-finned pilot whales (*Globicephala melas*) stranded on the US mid-Atlantic coast. *Marine Mammal Science, 13*(3), 405–418. https://doi.org/10.1111/j.1748-7692.1997.tb00648.x.

Gero, S., Engelhaupt, D., & Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology, 63*(1), 143–151. https://doi.org/10.1007/s00265-008-0645-x.

Gibson, Q. A., & Mann, J. (2008a). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour, 76*, 375–387. https://doi.org/10.1016/j.anbehav.2008.01.021.

Gibson, Q. A., & Mann, J. (2008b). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour, 76*, 389–405. https://doi.org/10.1016/j.anbehav.2008.01.022.

Guinet, C., & Bouvier, J. (1995). Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Canadian Journal of Zoology, 73*(1), 27–33.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software, 33*(2), 1–22. http://www.jstatsoft.org/v33/i02/.

Heide-Jørgensen, M. P., Hammeken, N., Dietz, R., Orr, J., & Richard, P. R. (2001). Surfacing times and dive rates for narwhals (*Monodon monoceros*) and belugas (*Delphinapterus leucas*). *Arctic, 54*(3), 284–298.

Heithaus, M. R. (2001). The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes, 61*(1), 25–36. https://doi.org/10.1023/A:1011021210685.

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology, 83*(2), 480–491. https://doi.org/10.2307/2680029.

Karniski, C., Patterson, E. M., Krzyszczyk, E., Foroughirad, V., Stanton, M. A., & Mann, J. (2015). A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans. *Marine Mammal Science, 31*(3), 839–852. https://doi.org/10.1111/mms.12198.

Krützen, M., Barré, L. M., Connor, R. C., Mann, J., & Sherwin, W. B. (2004). 'O father: Where art thou?': Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology, 13*(7), 1975–1990. https://doi.org/10.1111/j.1365-294X.2004.02192.x.

Krzyszczyk, E., Patterson, E. M., Stanton, M. A., & Mann, J. (2017). The transition to independence: Sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behaviour, 129*, 43–59. https://doi.org/10.1016/j.anbehav.2017.04.011.

Leimar, O. (1996). Life-history analysis of the Trivers and Willard sex-ratio problem. *Behavioral Ecology, 7*(3), 316–325. https://doi.org/10.1093/beheco/7.3.316.

Mann, J. (1999). Behavioral sampling methods of cetaceans: A review and critique. *Marine Mammal Science, 15*(1), 102–122.

Mann, J. (2000). Unraveling the dynamics of social life: Long-term studies and observational methods. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago, IL: University of Chicago Press.

Mann, J., & Barnett, H. (1999). Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: Defense and reactions by the mother. *Marine Mammal Science, 15*(2), 568–575. https://doi.org/10.1017/CBO9781107415324.004.

Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology, 11*(2), 210–219.

Mann, J., & Patterson, E. M. (2013). Tool use by aquatic animals. *Proceedings of the Royal Society B: Biological Sciences, 368*(20120424). https://doi.org/10.1098/rstb.2012.0424.

Mann, J., & Sargeant, B. (2003). Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In D. Fragaszy, & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 236–266). Cambridge, U.K.: Cambridge University Press.

Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C., et al. (2008). Why do dolphins carry sponges? *PLoS One, 3*(12), e3868. https://doi.org/10.1371/journal.pone.0003868.

Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour, 136*(5), 529–566.

Mann, J., & Watson-Capps, J. J. (2005). Surviving at sea: Ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Turisops* sp. *Animal Behaviour, 69*, 899–909. https://doi.org/10.1016/j.anbehav.2004.04.024.

Milette, L. L., & Trites, A. W. (2003). Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. *Canadian Journal of Zoology, 81*, 340–348. https://doi.org/10.1139/Z03-008.

Noren, S. R. (2008). Infant carrying behaviour in dolphins: Costly parental care in an aquatic environment. *Functional Ecology, 22*(2), 284–288. https://doi.org/10.1111/j.1365-2435.2007.01354.x.

Noren, S. R., Biedenbach, G., & Edwards, E. F. (2006). Ontogeny of swim performance and mechanics in bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology, 209*, 4724–4731. https://doi.org/10.1242/jeb.02566.

Noren, S. R., Biedenbach, G., Redfern, J. V., & Edwards, E. F. (2008). Hitching a ride: The formation locomotion strategy of dolphin calves. *Functional Ecology, 22*(2), 278–283. https://doi.org/10.1111/j.1365-2435.2007.0.

Noren, S. R., Cuccurullo, V., & Williams, T. M. (2004). The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 174*(2), 139–147.

Noren, S. R., & Edwards, E. F. (2011). Infant position in mother–calf dolphin pairs: Formation locomotion with hydrodynamic benefits. *Marine Ecology Progress Series, 424*, 229–236. https://doi.org/10.3354/meps08986.

Noren, S. R., Lacave, G., Wells, R. S., & Williams, T. M. (2002). The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): Implications for diving capacity. *Journal of Zoology, 258*(1), 105–113. https://doi.org/10.1017/S0952836902001243.

Noren, S. R., & Williams, T. M. (2000). Body size and skeletal muscle myoglobin of cetaceans: Adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology A, Molecular & Integrative Physiology, 126*(2), 181–191. https://doi.org/10.1007/s00360-003-0398-9.

Patterson, E. M., Krzyszczyk, E., & Mann, J. (2016). Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. *Behavioral Ecology, 27*(2), 401–410. https://doi.org/10.1093/beheco/arv164.

Payne, S. F., & Jameson, R. J. (1984). Early behavioral development of the sea otter, Enhyrda lutris. *Journal of Mammalogy, 65*(3), 527–531.

Pitman, R. L., Totterdell, J. A., Fearnbach, H., Ballance, L. T., Durban, J. W., & Kemps, H. (2015). Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science, 31*(2), 629–657. https://doi.org/10.1111/mms.12182.

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology, 107*, 301–312.

Riedman, M. (1990). Reproduction and life history. In M. Riedman (Ed.), *The pinnipeds: Seals, sea lions, and walruses* (Vol. 12, pp. 222–263). Berkeley, CA: University of California Press.

Rodríguez de la Gala-Hernández, S., Heckel, G., & Sumich, J. L. (2008). Comparative swimming effort of migrating gray whales (*Eschrichtius robustus*) and calf cost of transport along Costa Azul, Baja California, Mexico. *Canadian Journal of Zoology, 86*(4), 307–313. https://doi.org/10.1139/Z07-141.

Ross, C. (2001). Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology, 22*(5), 749–771. https://doi.org/10.1023/A:1012065332758.

Ross, S., Kamnitzer, R., Munkhtsog, B., & Harris, S. (2010). Den-site selection is critical for Pallas's cats (*Otocolobus manul*). *Canadian Journal of Zoology, 88*(9), 905–913. https://doi.org/10.1139/Z10-056.

Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). *The evolution of parental care*. Oxford, U.K.: Oxford University Press.

Sargeant, B. L., & Mann, J. (2009). Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour, 78*, 715–721. https://doi.org/10.1016/j.anbehav.2009.05.037.

Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology, 83*, 1400–1410. https://doi.org/10.1139/Z05-136.

Sargeant, B. L., Wirsing, A. J., Heithaus, M. R., & Mann, J. (2007). Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behavioral Ecology and Sociobiology, 61*(5), 679–688. https://doi.org/10.1007/s00265-006-0296-8.

Schachner, A., Brady, T. F., Pepperberg, I. M., & Hauser, M. D. (2009). Report spontaneous motor entrainment to music in multiple vocal mimicking species. *Current Biology, 19*, 831–836. https://doi.org/10.1016/j.cub.2009.03.061.

Smolker, R. A., Mann, J., & Smuts, B. B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology, 33*(6), 393–402. https://doi.org/10.1007/BF00170254.

Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour, 123*, 38–69.

Smultea, M. A., Fertl, D., Bacon, C. E., Moore, M. R., James, V. R., & Würsig, B. (2017). Cetacean mother–calf behavior observed from a small aircraft off southern California. *Animal Behavior and Cognition, 4*(41), 1–23. https://doi.org/10.12966/abc.01.02.2017.

Stanton, M. A., Gibson, Q. A., & Mann, J. (2011). When mum's away: A study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops* sp.). *Animal Behaviour, 82*, 405–412. https://doi.org/10.1016/j.anbehav.2011.05.026.

Stanton, M. A., & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One, 7*(10), e47508. https://doi.org/10.1371/journal.pone.0047508.

Szabo, A., & Duffus, D. (2008). Mother–offspring association in the humpback whale, *Megaptera novaeangliae*: Following behaviour in an aquatic mammal. *Animal Behaviour, 75*, 1085–1092. https://doi.org/10.1016/j.anbehav.2007.08.019.

Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. G., & Tinker, M. T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology, 27*(5), 1552–1566. https://doi.org/10.1093/beheco/arw089.

Trillmich, F. (1996). Parental investment in pinnipeds. *Advances in the Study of Behavior, 25*, 533–577. https://doi.org/10.1016/S0065-3454(08)60342-3.

Tsai, Y.-J. J., & Mann, J. (2013). Dispersal, philopatry, and the role of fission–fusion dynamics in bottlenose dolphins. *Marine Mammal Science, 29*(2), 261–279. https://doi.org/10.1111/j.1748-7692.2011.00559.x.

Tyson, R. B., Friedlaender, A. S., Ware, C., Stimpert, A. K., & Nowacek, D. P. (2012). Synchronous mother and calf foraging behaviour in humpback whales *Megaptera novaeangliae*: Insights from multi-sensor suction cup tags. *Marine Ecology Progress Series, 457*, 209–220. https://doi.org/10.3354/meps09708.

van der Meer, E., Mpofu, J., Rasmussen, G. S. A., & Fritz, H. (2013). Characteristics of African wild dog natal dens selected under different interspecific predation pressures. *Mammalian Biology, Zeitschrift für Säugetierkunde, 78*(5), 336–343. https://doi.org/10.1016/j.mambio.2013.04.006.

Van Opzeeland, I. C., Corkeron, P. J., Risch, D., Stenson, G., & Van Parijs, S. M. (2009). Geographic variation in vocalizations of pups and mother–pup behavior of harp seals pagophilus groenlandicus. *Aquatic Biology, 6*, 109–120. https://doi.org/10.3354/ab00170.

Watts, D. P., & Pusey, A. E. (2002). Behavior of juvenile and adolescent great apes. In M. E. Pereira, & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 148–167). Oxford, U.K.: Oxford University Press.

Weihs, D. (2004). The hydrodynamics of dolphin drafting. *Journal of Biology, 3*(2), 8.1–8.16. https://doi.org/10.1186/jbiol2.

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology, 38*(4), 237–244. https://doi.org/10.1007/s002650050238.

Whitehead, H., & Mann, J. (2000). Female reproductive strategies in cetaceans. In J. Mann, R. C. Connor, P. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 219–246). Chicago, IL: University of Chicago Press.

Yeater, D. B., & Kuczaj, S. A., II (2010). Observational learning in wild and captive dolphins. *International Journal of Comparative Psychology, 23*(3), 379–385.

Zefferman, M. R. (2016). Mothers teach daughters because daughters teach granddaughters: The evolution of sex-biased transmission. *Behavioral Ecology, 27*(4), 1172–1181. https://doi.org/10.1093/beheco/arw022.

Appendix

Table A1
Breathing rates of bottlenose dolphin mothers ($N = 4$) and calves ($N = 4$) collected in relatively shallow water (<6 m) in Monkey Mia

Subject ID	No. of minutes observed	Mean breathing rate
Calves		
BUD	85	2.58
EDE	120	3.03
INI	130	3.12
YAD	105	2.69
Mothers		
SUR	150	2.40
PIC	120	3.10
PUC	115	2.71
NIC	140	3.34

Average breathing rates were 2.86 breaths/min for calves (2–4 years old) and 2.90 breaths/min for mothers (13–31 years old). Average breathing rates presented here indicate approximately 20 s between breaths.