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Original Article

Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins

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Effective foraging is necessary for nearly all animals, but most animals are not born with adult-like foraging performance. Instead, foraging skills are developed during an individual's lifetime. Life-history theory predicts that adult-level foraging performance should be reached prior to the start of reproduction, but for most species, we know little about age-specific foraging in the wild. Here, we examine lifetime changes in foraging performance for a group of female wild bottlenose dolphins that use marine sponge tools to forage. After controlling for ecological effects and developmental changes in activity budgets, we show that females continue to improve in 3 aspects of foraging until a peak at around midlife, well after dolphins reach physical and sexual maturity. The factors that lead to this improved performance are unknown, but likely include learning and increasing physical ability. Dolphins' peak in foraging performance also coincided with a peak in reproduction, with middle-aged females maximizing foraging efficiency and having the highest probability of lactating. Thus, inadequate mastery of foraging behaviors, such as tool use in bottlenose dolphins, does not limit the onset of reproduction, but improvement in foraging skill may help maximize age-specific reproduction and lifetime fitness.

Key words: bottlenose dolphin, foraging performance, life history, reproduction, tool use.

INTRODUCTION

Successful foraging is necessary for nearly all animals in order to provide energy to support survival, growth, and reproduction. However, many species, particularly those that receive parental care, do not exhibit adult-like foraging performance at the start of life (e.g., Hunt et al. 2012). Instead, individuals develop foraging skills over the course of their life span as the result of changes in physiology, social and/or individual learning, or both (Schippers et al. 2006; Dukas 2008; Hoppitt et al. 2012). Not surprisingly, foraging competency in many species is developed before adulthood (Janson and van Schaik 2002; Schuppli et al. 2012) likely because of its direct ties to fitness and the strong selection pressure on early-life traits (Stearns 2000). Part of the improvement in foraging performance during development is probably the result of growth and maturation because in many animals productivity scales with body size (Lavigne 1982). Thus, by allocating energy to growth, animals can increase productivity and ultimately fecundity. However, birds and mammals usually cannot support extensive growth

and reproduction simultaneously, and thus, time spent growing is time not spent reproducing. In considering the trade-offs between growth and reproduction, life-history theory predicts that female mammals should first allocate energy to growth, but at some optimal age, switch and divert energy to reproduction (Charnov 2001). The timing of this switch (age at first parturition) is based on balancing the benefits of increasing reproductive rate with the costs of decreasing reproductive life span so as to maximize lifetime fitness.

Although substantial research in life history has focused on explaining when animals shift energy allocation from growth to reproduction, less has been dedicated to understanding how the timing of this shift relates to developmental changes in energy acquisition (i.e., foraging). This may, in part, be due to the assumption that animals should reach adult-level foraging performance before they begin to reproduce, as otherwise they should continue to allocate energy to growth in order to increase foraging productivity and other fitness-enhancing skills. Although a recent analysis of data from birds and mammals suggests this may be the case, species with complex foraging niches, slow physical development, and cooperative foraging, particularly intergenerational food transfer, appear to reach adult-level foraging performance rather late and in some cases, even after first parturition (Schuppli et al.

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2012). However, here one must distinguish between adult-level performance and peak performance given that age-related changes in foraging performance have been documented even within adults for several avian and mammalian species (Forsslund and Pärt 1995; Kaplan et al. 2000; MacNulty et al. 2009; Lecomte et al. 2010). For example, after controlling for differences in life expectancy, humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), oystercatchers (*Haematopus ostralegus*), and honey bees (*Apis mellifera*) all reach peak foraging efficiency at a similar life-history stage, well after reaching adulthood (Helton 2008). Moreover, many taxa exhibit age-related variation in female reproduction at, and even after, first parturition, with female reproduction following an inverted U-shaped pattern, starting out relatively low, increasing to a peak around midlife, and declining into old age (Clutton-Brock 1988), which in some cases coincides with age-related changes in foraging performance (Forsslund and Pärt 1995; Kaplan et al. 2000; Lecomte et al. 2010). Thus, although there is likely a coupling of foraging performance and reproduction in many animal life histories, outside of birds (Forsslund and Pärt 1995), we currently lack detailed longitudinal data on age-related changes in foraging performance as it relates to age-specific reproduction.

In this vein, we examine age-related changes in foraging performance and reproduction in wild bottlenose dolphins (*Tursiops cf. aduncus*), a study species well suited to address the coupling of foraging and reproduction in life histories for several reasons. First, bottlenose dolphins (*Tursiops* spp.) are well known for their complex foraging behaviors (Patterson and Mann 2015), some being cooperative (Bel'kovich et al. 1998; Torres and Read 2009), which may suggest a late onset of adult-level foraging performance (Schuppli et al. 2012). Second, like many cetaceans, they have slow physical development and extended life histories with a late age at first parturition (10 years) compared with other mammals (Mann et al. 2000; Chivers 2009). In addition, similar to terrestrial mammals, available data on bottlenose dolphins indicate an inverted U-shaped pattern of age-related changes in reproduction (Marsh and Kasuya 1986; Whitehead and Mann 2000; Chivers 2009; Fruet et al. 2015). However, how this late age of first parturition and inverted U-shaped pattern of reproduction relates to foraging performance, if at all, is not known.

One complex foraging behavior that shows a late onset and can easily be observed in the wild involves tool use (Sargeant and Mann 2009). In Shark Bay, Western Australia, a subset of bottlenose dolphins (primarily females) use marine basket sponge tools to forage (Smolker et al. 1997; Mann et al. 2008). These females (hereafter spongers) are highly specialized foragers, spending approximately 96% of their foraging time using sponge tools and rarely engaging in other foraging tactics (Mann et al. 2008). By tearing up sponges from the seafloor and placing them over their beaks (Figure 1), they gain protection from sharp rock and shell debris that litters the seafloor while they search for prey (Mann et al. 2008; Patterson and Mann 2011). Given that sponge tools are required for safely accessing these prey (Patterson and Mann 2011), and that spongers appear to differ in diet compared with nonspongers (Patterson and Mann 2011; Krützen et al. 2014), this form of tool use has been suggested to reduce intraspecific competition and provide spongers access to a unique niche.

The onset of sponge foraging (hereafter sponging) is delayed by at least a year compared with other foraging tactics (Sargeant and Mann 2009), suggesting that it may require greater physical maturation and/or be more difficult to learn. For predatory animals such as dolphins, finding, capturing, and handling prey are



Figure 1

A female bottlenose dolphin (*Tursiops cf. aduncus*) with a marine sponge tool (*Ircinia* sp.) in Shark Bay, Western Australia.

often the most difficult foraging skills to develop, but for spongers, previous work suggests that this may not be the case. The majority of prey spongers encounter are small, abundant, and easy to catch (Patterson and Mann 2011). They also swallow their prey quickly, usually before resurfacing, indicating that minimal prey handling is required (Mann et al. 2008; Patterson and Mann 2011). Thus, unlike other dolphin foraging tactics (e.g., beach hunting, Sargeant et al. 2005), sponging likely requires less skill development with respect to capturing and handling prey. Nonetheless, in order to gain access to these prey, dolphins must use a sponge tool, which fortunately they bring to the surface allowing us to quantify a variety of aspects of their foraging performance.

Although it is clear that calves of spongers learn the basics of this behavior from their mothers (Sargeant and Mann 2009), it is not known whether spongers continue to improve in their tool use beyond initially adopting the behavior. To explore age-related changes in foraging performance, that is, the ratio of foraging gains to costs (Stephens and Krebs 1986; Ydenberg 1998). Because spongers specialize in small, abundant, and easy-to-catch prey that require little handling time, (Mann et al. 2008; Patterson and Mann 2011), their energy gain is likely proportional to the amount of time they spend sponging. This assumption is further supported by the fact that spongers spend a much larger proportion of their activity budgets foraging compared with nonspongers (~53% vs. 30%) who often hunt more difficult to catch larger or schooling prey (Mann et al. 2008; Patterson and Mann 2011) and do not appear to differ in size or condition. Nonetheless, spongers must also dedicate part of their time to acquiring tools, which has energetic costs and no immediate gain. Therefore, to maximize efficiency, spongers should minimize time spent acquiring tools and maximize time spent using them. One way of achieving this is to forage with each sponge tool for as long as possible. Though spongers must drop their tools in order to consume prey (Figure 1), we have observed spongers regularly retrieving and reusing their tools, and sometimes even traveling with their sponges to use them in new foraging areas (Mann et al. 2008; Patterson and Mann 2011). Such behavior is clearly beneficial, as it negates the need to acquire a new tool after each prey capture, and ultimately increases foraging efficiency.

In this study, we examine age-related changes in time spent acquiring tools per unit time spent foraging (acquiring-to-foraging ratio), time spent foraging per tool, and time spent traveling per tool.

In doing so, we control for differences in the availability of sponge tools and developmental changes in foraging effort and traveling. We then examine how age-related changes in foraging performance relate to changes in female reproduction. To do so, we focus on the likelihood of having a dependent calf (lactating), because in most mammals (Gittleman and Thompson 1988; Clutton-Brock et al. 1989), lactation is the most costly aspect of dolphin reproduction (Cheal and Gales 1991; Oftedal 1997).

METHODS

Study site and data collection

The Shark Bay Dolphin Research Project has an extensive 30-year database of demographic, genetic, association, life history, ecological, and behavioral data on ~1800 individually identified dolphins residential to a 500 km² area offshore of Monkey Mia (Figure 2). Behavioral data for this study were collected during boat-based focal follows of individual females or mother–calf pairs from 1989 to 2012 in which systematic point (every minute) and continuous samples of behavior were collected (Mann 1999; Karniski et al. 2014). All dolphin identities were determined using standard photo ID methods (Würsig B and Würsig M 1977). Age was determined by birth date estimates based on first calf sighting, first reproductive event (Mann et al. 2000), degree of ventral speckling (Krzyszczuk and Mann 2012), and/or size. All dolphins used in this study could be assigned an age to an average estimated accuracy of 1.18 years (standard deviation [SD] = 1.27). Sex was determined by the presence of mammary slits or a dependent calf (Mann et al. 2000).

Dolphin behavior was classified based on the following ethogram. Dolphins were considered to be searching for sponges if they were performing relatively short dives (1–2 min) in a haphazard direction in sponge habitat while not wearing a sponge (Sargeant

et al. 2007; Patterson and Mann 2011). Dolphins were considered to be detaching sponges if, following searching behavior, they were repeatedly performing relatively long dives (2–3 min) in the same location until surfacing with a new sponge. Because it was not always possible to determine when an animal shifted from searching for a sponge to detaching a sponge, we collapsed these 2 behaviors and collectively call this acquiring a sponge. Dolphins were considered to be foraging with a tool if they were wearing a sponge on their beak and performing relatively long dives (2–3 min) separated by multiple breaths (Mann et al. 2008). Dolphins were considered to be traveling with a sponge if they were carrying a sponge, performing relatively short dives (1–2 min), and exhibiting regular and consistent spatial progress. Dolphins sequentially use multiple sponge tools during a sustained foraging period, and most sponges were uniquely identifiable by color and shape, allowing observers to record the duration that each sponge was used. However, photographs were used to help confirm sponge switches (e.g., Figure 1). We did not always observe the full duration a sponge tool was used and so adjusted our analyses to handle these censored data (see Statistical analyses for details). Additional detail on the ethogram and data collection methods can be found in Karniski et al. (2014) and Mann et al. (2008).

To sample sponge density, divers performed 39 belt transects randomly located in 2 areas containing ~78% of all sponging sightings (Figure 2). Divers weighted one end of a 50-m tape measure at each transect's midpoint, and then swam away at a speed of ~0.3 m/s at a bearing either with or against the direction of water current, while filming a 2-m-wide strip of the substrate using a Sony HDR-XR500V HD video camera in an AquaticaHD housing. Swimming in line with the tidal currents minimized within transect heterogeneity because habitat types within channels tend to occur in strips oriented along the direction of water flow. After completing the swim in one direction, divers returned to the transect midpoint and then repeated the filming in the exact opposite direction so that the entire transect covered a distance of 100 m. All video transects were viewed and logged by E.M.P., and only basket sponges estimated to be of appropriate diameter (10 cm < diameter < 50 cm) were included in sponge density estimates. Because video transect data were only available from one field season (2011), we were unable to account for longitudinal changes in sponge abundance. However, given that our study site is remote, well protected, and we have observed dolphins sponging in the same locations year after year (~66% overlap between *a*-LoCoH home ranges constructed from 100 sponging locations observed over 4 time periods between 2002 and 2012), we assume fairly stable sponge densities throughout the study period.

Female home ranges were constructed using an adaptive local convex hull method (*a*-LoCoH, Calenge 2006; Getz et al. 2007) with GPS data from surveys (5–60-min behavioral observations, see Mann 1999; Karniski et al. 2014 for survey details). The average maximum distance between any 2 location points for each animal was used as the *a* parameter following the heuristic rule proposed by Getz et al. (2007). Spatial data were pooled across ages because Shark Bay dolphins have stable home ranges throughout their lives (Tsai and Mann 2013), but only the last location point per day was used to reduce spatial autocorrelation and biases associated with our boat-launching site. Home-range boundaries were constructed using 90% isopleths and intersected with video transect data using QGIS 2.6 (QGIS Development Team 2014). Sponge density estimates were then calculated within each female's home range separately (e.g., Figure 2). All methods for data collection

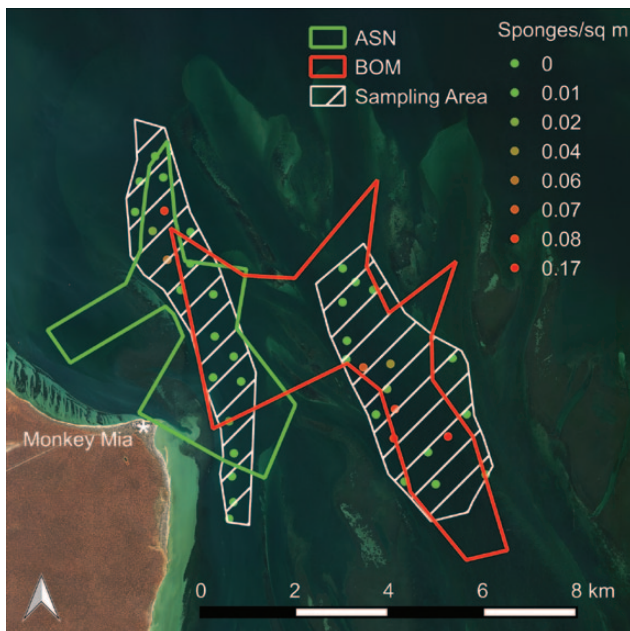


Figure 2

Map of study area. The white hatched polygons denote the 2 sponge transect sampling areas, the colored polygons are example home ranges for 2 spongers with low (green) and high (red) sponge densities, the asterisk shows the location of our boat-launching site, and the points denote estimates of basket sponge densities.

were approved by the Georgetown University Animal Care and Use Committee (permits 07–041 and 10–023) and the Western Australian Department of Parks and Wildlife (permits SF007418, SF007975, SF006897, and SF007457).

Statistical analyses

We first used LOESS smoothing curves to visualize the acquiring-to-foraging ratio (#min acquiring/#min foraging), foraging per tool (#min foraging per tool), traveling per tool (#min traveling per tool), and the proportion of the sponger population lactating (Figure 3) as a function of age. A span value of 0.75 and a second-order polynomial with a redescending M-estimator with Tukey's biweight function were used, and to visualize the SD, we plotted the square root of the variance function (Cleveland 1979; Fox and Weisberg 2011). For data that were censored (foraging per tool and traveling per tool), we plotted all uncensored data in addition to censored data that fell above the mean of the uncensored data in order to avoid biases toward short durations. After this initial inspection, we employed Markov chain Monte Carlo generalized linear mixed models (MCMC glmm) in a Bayesian framework (Hadfield 2010) to explore age-related changes in foraging performance and reproduction.

The acquiring-to-foraging ratio was modeled with a binomial error structure, the logit link function, and additive overdispersion. Age was included as a fixed effect and individual identity as a random effect. To control for differences in the availability of sponges for each female, we also included sponge density as a fixed effect.

Based on the LOESS smoothing curve (Figure 3a), which indicated a decline in the acquiring-to-foraging ratio up until ~25 years of age and possibly no relationship between age and the acquiring-to-foraging ratio thereafter, we fit a piecewise model. We estimated a breakpoint by iteratively adjusting a breakpoint to minimize the deviance of an overall piecewise model (Hastie and Tibshirani 1993; Muggeo 2003; Toms and Lesperance 2003). We then computed bootstrap confidence intervals (CIs) for this final breakpoint estimate, which is recommended when sample sizes are not particularly large (Toms and Lesperance 2003). Subsequently, 2 models were created, one before and one after the breakpoint. Although sponging constitutes a large portion of a sponger's overall activity budget (Mann et al. 2008), sponge-acquiring behavior generally makes up a small percentage of an individual's activity budget, so we restricted our sample for this analysis to females with at least 3 h of follow data per age analyzed (age rounded to nearest year, number of hours each dolphin was observed per age: mean = 7.52, SD = 3.43; number of years each dolphin was observed: mean = 3.53, SD = 1.87; number of dolphins: $N = 19$).

Foraging per tool and traveling per tool were modeled using a censored Poisson error structure, the log link function, and additive overdispersion. Age and sponge density were included as fixed effects and individual identity as a random effect. In addition, to control for developmental changes in foraging effort (which were inherently controlled for in the acquiring-to-foraging ratio) and time spent traveling, we included percent time spent sponging and traveling at a given age as fixed effects in the foraging and traveling

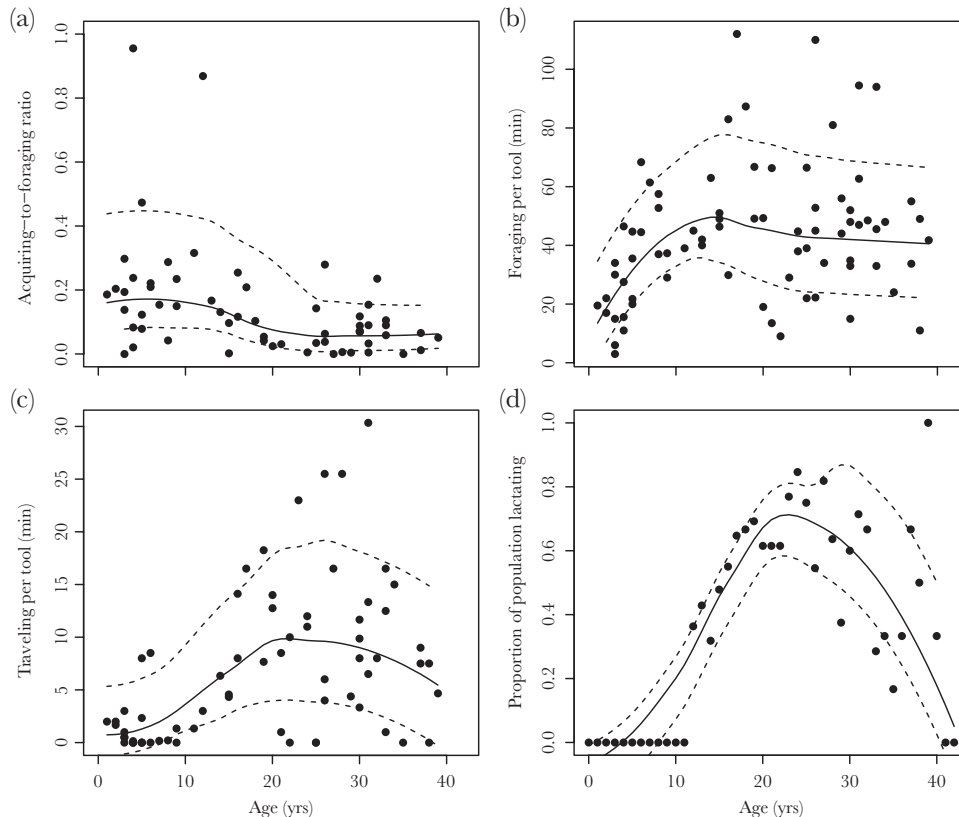


Figure 3

Age-specific foraging performance and lactation. (a) Age-specific acquiring-to-foraging ratio, (b) age-specific foraging per tool, (c) age-specific traveling per tool, (d) proportion of population lactating. For foraging data (a–c), points represent raw data from individual dolphins at a given age. For lactation data (d), points represent the proportion of the sponger population lactating at a given age. In all panels, solid lines represent LOESS smoothing curves, and the dashed lines denote square roots of the variance functions.

models respectively. Similar to the acquiring-to-foraging ratio, we fit piecewise models because the LOESS smoothing curves (Figure 3b,c) appeared to show an increase in foraging and traveling per tool up until ~16 and ~25 years, respectively, and no apparent increase afterwards. We estimated the breakpoints and CIs as above and created 2 models for each behavior, one before and one after the breakpoint. Because these models focus on individual sponge tools ($N = 327$), we included data from all dolphins that were followed while sponging (number of dolphins: $N = 22$; number of sponge tools per dolphin, per age: mean = 3.72, SD = 2.84; number of years each dolphin was observed: mean = 4.00, SD = 2.20).

To examine how changes in foraging performance relate to reproduction, we modeled whether or not a female sponger was lactating using a binomial error structure and the logit link function. A female was considered to be lactating at a specific age if she had a dependent calf for greater than half that year of her life (Mann et al. 2000). The response variable was binary (lactating or not) so overdispersion cannot occur (Collett 2003), and the residual variance was fixed at 1 to allow proper mixing. As indicated by the quadratic relationship in Figure 3d, both age and age² (as orthogonal polynomials to reduce multicollinearity, Narula 1979) were included as fixed effects and mother identity was included as a random effect. Only females greater than age 10 were used in this model, as this is the youngest recorded pregnancy in our population. For this analysis, all spongers with sufficient reproductive data for a given year of their life were included (number of dolphins: $N = 31$, number of years each female's reproductive status was known: mean = 12.00, SD = 8.83).

For all models, we employed the method described by van de Pol and Wright (2009) to distinguish between within-subject age effects (longitudinal), which represent developmental changes in behavior within an individual, and between-subject age effects (cross-sectional), which represent differences in behavior between dolphins of different ages. Briefly, this constitutes using subject centered and subject mean age terms in the models and testing whether the within- and between-subject effects are effectively the same. All models were fit using the MCMC glmm package in R (Hadfield 2010, R Development Core Team 2015), with weak priors, 1 000 000 iterations, a burn-in of 10 000, and a 1000 thinning interval. Mixing and convergence were assessed using trace and posterior plots, and Raftery and Lewis's (1992) diagnostic, Heidelberger

and Welch's (1983) diagnostic, and Geweke's (1992) diagnostic from the coda package in R (Plummer et al. 2006).

RESULTS

Acquiring tools

From the initial LOESS smoothing curve (Figure 3a), it appeared that there was a decrease in the acquire-to-foraging ratio up until spongers were in their early 20s (around midlife) and no change thereafter. Indeed, minimizing the deviance of a 2-piece MCMC glmm resulted in a breakpoint at 23.72 years (lower [L] 95% CI = 6.28, upper [U] 95% CI = 33.80). Before the breakpoint, the acquiring-to-foraging ratio significantly decreased with age, whereas after, there was no significant relationship between age and the acquiring-to-foraging ratio (Table 1). In fact, of the total time, older females (>23.73 years) spent on sponging-related activities (acquiring sponges and foraging with them), only ~6% (mean = 6.41%, SD = 5.66) was typically dedicated to acquiring sponges, less than half as much time as younger females (mean = 14.60%, SD = 11.30 for females <23.73 years). Examining the within- versus between-subject age effects revealed that the observed age effects before the breakpoint may have been driven by between-subject variation (Table 1). However, the term for the difference of the between- and within-subject effects in the model revealed that the 2 effects were not statistically different (between-within age: estimate = -0.1151, L 95% CI = -0.2402, U 95% CI = 0.0545, $P = 0.1212$), indicating that the overall standard glmm results can be used. As expected, neither the within- nor the between-subject age effects were significant in the model after the breakpoint (Table 1), nor were the 2 significantly different from each other (between-within age: estimate = -0.0460, L 95% CI = -0.3578, U 95% CI = 0.2608, $P = 0.7820$). Sponge density had a marginally significant negative effect on the acquiring-to-foraging ratio in all models before the breakpoint, but not after (Table 1).

Foraging with a tool

Based on the initial plot of the raw data and a LOESS smoothing curve (Figure 3b), foraging per tool appeared to increase until roughly 16 years of age, and then remain stable. The piecewise MCMC glmm of foraging per tool confirmed a positive relationship

Table 1
Parameter estimates from the MCMC glmms for the acquiring-to-foraging ratio

Fixed effect	Estimate	L 95% CI	U 95% CI	ESS	<i>P</i>
Acquiring-to-foraging before the breakpoint					
Age	-0.0966	-0.1770	-0.0233	990	0.0162
Sponge density	-0.0133	-0.0299	0.0028	839	0.0788
Acquiring-to-foraging after the breakpoint					
Age	0.0045	-0.1315	0.1598	990	0.9720
Sponge density	-0.0027	-0.0267	0.0236	1426	0.8000
Acquiring-to-foraging within-between age effects before the breakpoint					
Within-subject age	0.0019	-0.1441	0.1493	990	0.9535
Between-subject age	-0.1117	-0.1885	-0.0372	897	0.0020
Sponge density	-0.0148	-0.0295	0.0017	935	0.0566
Acquiring-to-foraging within-between age effects after the breakpoint					
Within-subject age	0.0137	-0.1834	0.1798	1058	0.8850
Between-subject age	-0.0319	-0.3101	0.2449	1801	0.7780
Sponge density	-0.0067	-0.0412	0.0244	990	0.6670

ESS, effective sample size. Bold lines indicate significance at $P < 0.05$.

with age before an estimated break point at 19.50 years (L 95% CI = 7.43, U 95% CI = 33.82), and no significant relationship with age afterwards (Table 2). Here, both within- and between-subject effects drove the relationship between age and foraging per tool before the breakpoint (Table 2), and they were not significantly different from each other (between-within age: estimate = -0.0462 , L 95% CI = -0.1897 , U 95% CI = 0.0825 , $P = 0.5172$) indicating that the standard model results are applicable. After the breakpoint, neither the within nor the between age effects were significant (Table 2), nor were they significantly different than each other (between-within age: estimate = 0.0130 , L 95% CI = -0.0836 , U 95% CI = 0.0997 , $P = 0.7576$). Both standard models (before and after the breakpoint) indicated that dolphins increased foraging per tool with an increase in sponging activity budget, but this positive relationship was only marginally significant in the within and between models (Table 2). In the standard models, sponge density had a significant positive effect on foraging per tool before the breakpoint and a marginally significant positive effect after the breakpoint. In the within and between models, this positive effect was marginally significant both before and after the breakpoint.

Traveling with a tool

The initial LOESS smoothing curve of traveling per tool (Figure 3c) suggested an increase in traveling per tool until ~25 years of age, and either a decline or no change in traveling per tool thereafter. Minimizing the deviance of a piecewise model estimated a break point at 23.34 years (L 95% CI = 8.79, U 95% CI = 33.82), before which there was a significant positive relationship between age and traveling per tool and after which there was no significant relationship between age and traveling per tool (Table 3). Examining the within and between effects suggested that the positive relationship between traveling per tool and age before the breakpoint was driven primarily by between-subject effects (Table 3). However, the within- and between-subject effects before the breakpoint were not significantly different from each other (between-within age: estimate = 0.2888 , L 95% CI = -0.0611 , U 95% CI = 0.6734 , $P = 0.1131$), and so the standard model can be interpreted. As expected, neither the within- nor the between-subject effects were significant after the breakpoint (Table 3), nor were they significantly

different from each other (between-within age: estimate = 0.0140 , L 95% CI = -0.2748 , U 95% CI = 0.2840 , $P = 0.9475$), so as above, the standard model can be interpreted. In all traveling models, percent time traveling had a significant positive effect on traveling per tool, whereas sponge density did not have a significant effect (Table 3).

Reproduction

Given that the cost of lactation is high compared with other reproductive states, improved foraging performance is particularly important for spongers with dependent offspring. As suggested by the LOESS smoothing curve (Figure 3d), we found a negative quadratic relationship between age and the probability of a female lactating with a predicted peak at 25 years of age, near the age of highest foraging performance (Table 4). This quadratic relationship appeared to be driven by both between- and within-subject effects, although the linear age term was not significant for the within-subject effects (Table 4). Indeed, the linear age terms for the within- and between-subject effects were significantly different from each other (between-within age: estimate = 14.7004 , L 95% CI = 3.0984 , U 95% CI = 25.9272 , $P = 0.0141$), but importantly, the quadratic age² terms did not differ (between-within age²: estimate = -5.9178 , L 95% CI = -19.9326 , U 95% CI = 10.1052 , $P = 0.4485$).

DISCUSSION

Our data indicate that dolphins continue to improve performance in a tool-use foraging behavior well into adulthood. Models of 3 aspects of foraging efficiency that controlled for differences in foraging effort, time spent traveling, and sponge availability revealed that females improved in multiple aspects of foraging up until roughly midlife, well beyond sexual and physical maturity. Although large CIs indicate considerable variation in the breakpoint estimates, the raw data and LOESS smoothing curves in Figure 3 closely agree with the model breakpoint estimates and strongly suggest continued lifetime improvement in all 3 aspects of foraging efficiency. Because the within- and between-subject effects were similar for all 3 aspects of foraging efficiency, female spongers improve in their foraging

Table 2
Parameter estimates from the MCMC glmms for foraging per tool

Fixed effect	Estimate	L 95% CI	U 95% CI	ESS	<i>P</i>
Foraging per tool before the breakpoint					
Age	0.1222	0.0545	0.1855	990	0.0009
Sponge density	0.0106	0.0000	0.0210	990	0.0465
% sponging	1.1110	0.1406	2.1140	990	0.0343
Foraging per tool after the breakpoint					
Age	0.0081	-0.0357	0.0521	749	0.6788
Sponge density	0.0100	-0.0020	0.0207	990	0.0828
% sponging	1.2908	-0.0331	2.6066	990	0.0485
Foraging per tool within-between age effects before the breakpoint					
Within-subject age	0.1575	0.0351	0.2930	990	0.0202
Between-subject age	0.1105	0.0425	0.1877	990	0.0020
Sponge density	0.0095	-0.0025	0.0208	990	0.0889
% sponging	1.0012	-0.1227	2.1507	990	0.0909
Foraging per tool within-between age effects after the breakpoint					
Within-subject age	-0.0020	-0.0808	0.0631	1044	0.9758
Between-subject age	0.0106	-0.0397	0.0701	990	0.7071
Sponge density	0.0103	-0.0002	0.0247	990	0.0929
% sponging	1.3221	0.0856	2.9688	990	0.0647

ESS, effective sample size. Bold lines indicate significance at $P < 0.05$.

Table 3
Parameter estimates from the MCMC glms for traveling per tool

Fixed effect	Estimate	L 95% CI	U 95% CI	ESS	P
Traveling per tool before the breakpoint					
Age	0.2581	0.0961	0.4269	738	0.0009
Sponge density	0.0060	-0.0335	0.0397	990	0.7030
% traveling	10.6482	2.6488	19.3518	990	0.0040
Traveling per tool after the breakpoint					
Age	0.0021	-0.1180	0.1173	898	0.9680
Sponge density	0.0164	-0.0082	0.0443	1116	0.2040
% traveling	6.1430	1.7565	9.8414	990	0.0009
Traveling per tool within-between age effects before the breakpoint					
Within-subject age	0.0072	-0.2608	0.2910	800	0.9354
Between-subject age	0.3313	0.1399	0.5380	897	0.0020
Sponge density	0.0183	-0.0173	0.0545	990	0.2970
% traveling	7.8462	0.6953	16.3116	990	0.0303
Traveling per tool within-between age effects after the breakpoint					
Within-subject age	-0.0016	-0.1286	0.1310	990	0.9939
Between-subject age	0.0200	-0.2262	0.2891	990	0.8727
Sponge density	0.0181	-0.0136	0.0546	990	0.2647
% traveling	6.2558	1.9362	10.3975	803	0.0061

ESS, effective sample size. Bold lines indicate significance at $P < 0.05$.

Table 4
Parameter estimates from the MCMC glms for lactating

Fixed effect	Estimate	L 95% CI	U 95% CI	ESS	P
Lactating					
Age	9.9888	3.6786	15.2314	990	0.0001
Age²	-18.6335	-24.1368	-13.3746	990	0.0001
Lactating within-between age effects					
Within-subject age	4.7832	-2.1476	11.2482	990	0.1394
Within-subject age²	-17.7088	-24.2163	-11.9165	990	0.0001
Between-subject age	19.6286	10.0407	29.5108	990	0.0020
Between-subject age²	-23.9521	-37.6178	-10.4357	1184	0.0020

ESS, effective sample size. Bold lines indicate significance at $P < 0.05$.

performance with age until midlife, which leads to a population-level pattern of middle-age peak foraging competency.

First, females increased their foraging efficiency with age by continuing to decrease the amount of time spent acquiring tools per unit time spent foraging with them (acquiring-to-foraging ratio; Figure 3a). One possible explanation for this improved performance is that as females gain more experience sponging, they learn the spatial distribution of sponges within their home ranges. Basket sponges are only found in the channels of Shark Bay (Sargeant et al. 2007; Tyne et al. 2012), but even within channels, sponges grow in patches (Figure 2). Throughout females' lives their home ranges are stable (Tsai and Mann 2013) and within their ranges, the distribution of sponges, which are sessile and take years to grow, should be reliably found in the same locations. Thus, spongers experience conditions that would favor the learning sponge locations (Stephens 1991). Yet, few aspects of dolphins' lives likely require this type of long-term spatial memory. Most dolphin prey are highly mobile and have ephemeral distributions. Furthermore, even though their home ranges are stable (Tsai and Mann 2013), they lack hard boundaries and are not defended (Randić et al. 2012). Thus, although dolphins are likely capable of georeferencing, acquiring sponges likely demands atypical object location memory that may take years to develop. Alternatively, females could be decreasing their acquiring-to-foraging without learning sponge distributions. Up until midlife, females increased their foraging per tool (Figure 3b), which should

reduce the number of tools needed, and ultimately their acquiring-to-foraging ratio. Indeed, this is why using a single tool for longer is more efficient. Regardless of how females are able to reduce time spent acquiring sponges, there are likely also ecological factors at play. For example, sponge density had a marginally significant negative effect on the acquiring-to-foraging ratio (Table 1), suggesting that if there are more sponges around to choose from, it may take less time to find an appropriate tool.

Second, females increased their foraging efficiency with age by increasing their foraging per tool (Figure 3b). Such a result is consistent with foraging theory in that animals are expected to employ long foraging bouts when resources are easy to obtain and/or when the cost of switching behaviors is high (Dukas and Clark 1995). Spongers target easy-to-catch prey and incur a high cost of switching behavior due to the loss of a tool, so one would expect spongers to forage as long as possible with each sponge tool. By midlife, females appear do this, possibly because by this age they know how to select the most robust sponges. We identified dolphins using at least 5 different sponge species (*Echinodictyum* sp., *Ircinia* sp., *Pseudoceratina* sp., and 2 undetermined sponge species, Fromont J, personal communication), which vary in toughness and presumably durability (Hooper and van Soest 2002). Perhaps it takes years of experience to learn which tools last the longest. However, tool selectivity is probably also a function of sponge density. We found a positive relationship between foraging per tool and sponge density (Table 2).

This was somewhat surprising as we anticipated a negative relationship, reasoning that if a female had a greater sponge density in her home range, she would be less likely to retrieve a sponge after each prey capture as ample replacements are available. Although this relationship could be a spurious result of differences in our sampling periods for sponge density (2011) and foraging per tool (1989–2012), we would expect this limitation to lead to not detecting any relationship at all (increasing Type I error, i.e., false negative), rather than biasing toward a positive or negative relationship specifically. Instead, it may be that an increase in sponge density allows females to select longer lasting tools, and thus, tool selectivity is the result of a dolphin's lifetime experience, but ecologically constrained by the available tools. Alternatively, or in addition, as spongers gain more experience, they may alter their foraging behavior to allow each tool to be used longer. Spongers may become better at reducing damage to their tools and/or become better at retrieving tools for reuse. Shark Bay channels experience strong tidal currents that likely wash away any unattached sponges (Burling et al. 2003; Patterson 2012), but after years of experience, a sponger might become skilled at predicting where her tool will be based on its last location and the direction of water flow.

Finally, females increased their foraging efficiency with age by increasing their traveling per tool (Figure 3c). Similar to what has been suggested for New Caledonian crows (*Corvus moneduloides*), chimpanzees, and capuchin monkeys (*Cebus libidinosus*) (Seed and Byrne 2010), it is possible that this tool transportation indicates some level of planning and forethought. Before foraging, females may travel to superior sponge patches to obtain tools and then transport these tools to preferred foraging areas. Likewise, after sponging in one area, females may transport their tools to other areas to forage, especially if they know that no suitable sponges exist near their next location. Regardless, using the same sponge over multiple foraging bouts and in multiple locations is certainly advantageous and ultimately increases foraging efficiency.

The late peak in foraging performance documented here provides insight into several previously unexplained aspects of this unique form of tool use. First, because the peak in foraging performance is not achieved until a female is in her mid-20s, spongers probably need to adopt sponging early in life and then specialize in it, in order for sponging to be a profitable lifetime foraging tactic. This would explain why sponging is almost exclusively vertically socially transmitted and female biased (Mann et al. 2008; Sargeant and Mann 2009). If dolphins were to begin sponging later in life, peak performance may not be reached until well after their maximum life span. Thus, substantial early exposure seems critical and given dolphins' extended period of maternal dependency, a maternal demonstrator is likely necessary. After being exposed to sponging, daughters of spongers quickly become tool-use specialists, but most sons do not, presumably because doing so would restrict their ranging and ultimately their ability to form and maintain alliances necessary for gaining access to mates (Randić et al. 2012; Mann and Patterson 2013). Thus, the female sex bias and vertical cultural transmission of sponging may simply be the result of the amount of time and specialization required to make sponging a profitable foraging tactic.

What is perhaps most striking from our data is that multiple aspects of foraging efficiency coincide with a peak in reproduction (Figure 3). Female spongers in their mid-20s spend minimal time acquiring tools, forage longer with each tool, and travel more with their tools to different foraging areas, all of which may help them cope with the energetic demands of maternal care. Thus, similar to humans and several

avian species (Forslund and Pärt 1995; Kaplan et al. 2000; Lecomte et al. 2010), spongers' reproduction and foraging performance appear tightly linked over the course of their life history. Whether or not the same pattern exists for nonsponging dolphins is unclear largely because we lack sufficient means to document their foraging efficiency. That said, reproduction might be more closely linked to foraging efficiency for spongers than nonspongers given the complex nature of this foraging tactic. What is clear is that despite their atypical foraging behavior, spongers have similar calving success compared with nontool users (Mann et al. 2008). Thus, even though in many ways sponging seems more costly than other foraging tactics, through specialization and continued improvement in foraging efficiency, spongers achieve similar fitness to the rest of the population.

Together, these results have important implications for the evolution of life histories. They contrast with the notion that only food-sharing species can afford to delay peak foraging performance until after physical development is complete (Schuppli et al. 2012). Dolphins are known to forage cooperatively in some locations (Bel'kovich et al. 1998; Torres and Read 2009), but they do not share food (Mann et al. 2007). Yet, spongers clearly peak in foraging performance well after physical maturation. Although reproduction in many species likely relates to foraging performance, it is not necessary that animals reach peak foraging performance prior to, or at, first parturition. This is not to say that below-peak foraging performance has no impact on calving success, only that spongers do not delay reproduction as a consequence. In fact, there are likely other physiological and behavioral traits that still favor early reproduction. Therefore, the dichotomy of an absolute trade-off between allocating energy to growth to increase productivity or to reproduction may be too simplistic. It may be that selection favors individuals that begin to reproduce as soon as their foraging skills are good enough and then continue to improve their foraging performance with age in order to further increase reproduction. Other tool-using iteroparous animals that have slow life histories and show interindividual variation in tool use such as chimpanzees (Kendal et al. 2015; Sirianni et al. 2015), capuchin monkeys (*Cebus apella*; Ottoni et al. 2005), and sea otters (*Enhydra lutris*; Fujii et al. 2014), show age-related improvement in foraging performance at young ages and may also continue to improve in foraging performance well after the onset of reproduction. Nonetheless, we might also expect age-related changes in foraging performance after first parturition for nontool users when successful foraging requires considerable skill or knowledge, which may be true for many predatory animals (Forslund and Pärt 1995; Kaplan et al. 2000; MacNulty et al. 2009; Lecomte et al. 2010). Thus, despite the importance of the link between foraging and reproduction in the evolution of life histories, we should not be surprised that animals increase their foraging expertise after reaching adulthood and that such expertise likely has fitness consequences.

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