Why become speckled? Ontogeny and function of speckling in Shark Bay bottlenose dolphins (*Tursiops* sp.)[1]

Ewa Krzyszczyk

Janet Mann

Georgetown University,
37th and O Street, NW,
406 Reiss Building, Washington, District of Columbia 20057, U.S.A.
E-mail: ewakrzyszczyk@gmail.com

Abstract

To date, color patterns have been used to assess cetacean age and taxonomic status, but few studies have determined precise correlates of coloration with known age or investigated its function. Here, we examine the ontogeny of speckling in 88 bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia, of known age, tracked from birth to age 34. Ventral speckles first appear in the genital area at a mean age of 10.2 ± 0.35 yr (range $= 7.6$–12.7 yr). Throughout their life span, speckles increase in number and density, particularly along the ventral and lateral sides. The timing of speckle onset does not significantly differ by sex but is related to sexual maturity in females. The age of speckle onset in the genital area correlates with the age of first known parturition. In terms of speckle function, we discuss two hypotheses commonly proffered to explain color variation, concealment, and communication. Concealment from predators or prey is unlikely to explain speckle development in Shark Bay *Tursiops* because the onset occurs long after peak predation risk and initial hunting success (at 3 mo of age). We suggest that speckle patterns offer reliable cues on reproductive status and/or condition and could, thus, serve a communicative or some other function.

Key words: speckles, spots, ontogeny, bottlenose dolphin, *Tursiops*, function.

Adaptive hypotheses explaining animal coloration date at least as far back as Darwin (1871), and many have received empirical support (reviewed in Caro 2005). Specifically, color typically serves three broad adaptive functions: concealment, communication, and regulation of physiological processes (Cott 1940, Ortolani 1999, Stoner *et al*. 2003, Caro 2005, Bradley and Mundy 2008, Mills and Patterson 2009). Vibrant coloration is often linked to sexually selected traits or ornament(s) (Caro 2005), with males exhibiting brighter coloration than females in birds (*e.g.*, Butcher and Rohwer 1989), fish (*e.g.*, Houde 1997), reptiles (*e.g.*, Cooper and Greenberg

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[1]This paper is dedicated to the memory of Dr. Amy R. Samuels, one of our inspired colleagues in Shark Bay for many years.

1992), amphibians (*e.g.*, Doucet and Mennill 2010), and occasionally, mammals (Dixson 1998, Caro 2005). Cetacean coloration has received only modest attention, in part because color variation is limited to variations on pink, gray, black, white, and yellow and because cetaceans are typically sexually monochromatic and appear to lack color vision (Madsen and Herman 1980, Peichl *et al*. 2001, but see Griebel and Schmid 2002). However, ontogenetic changes in coloration are widespread in cetaceans and interspecific differences aid in taxonomic identification (Perrin 2009). Specifically, the ventral speckling in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) is one of the salient features that helps distinguish them from common bottlenose dolphins (*T. truncatus*, Ross 1977; LeDuc *et al*. 1999; Hale *et al*. 2000; Möller and Beheregaray 2001). Despite the similarities in social structure and behavior between *T. aduncus* and *T. truncatus* (*e.g*., Connor *et al*. 2000), this physical difference between them has received little attention. The current study investigates the ontogeny and possible functions of ventral speckling in bottlenose dolphins in Shark Bay, Australia, where basic individual demographic data are available. Although their taxonomic status is uncertain (see Krützen *et al*. 2004), their speckling pattern is similar to *T. aduncus* and similarly informative.

Coloration often varies with age, reproductive status, and stress (Marcoux 2008, Wang *et al*. 2008, West and Packer 2002). In many species, young have characteristic natal coats that differ from adult pelage (*e.g*., Pampus deer, *Ozotocerus bezoarticus*, Jackson 1987; tapirs, *Tapirus terrestris*, Padilla and Dowler 1994; gibbons, *Hylobates* sp., Treves 1997; mountain lion, *Puma concolor*, Pierce and Bliech 2001; red-fronted lemurs, *Eulemur fulvus rufus*, Barthold *et al*. 2009). Cetacean natal coloration also differs widely; some species have the same coloration throughout development (*e.g*., franciscana, *Pontoporia blainvillei*, Brownell 1981), but most calves have muted or paler coloration than adults (*e.g*., Commerson's dolphin, *Cephalorhynchus commersonii,* Robineau 1984; right whale dolphins, *Lissodelphis*, Jefferson *et al*. 1994; Fraser's dolphins, *Lagenodelphis hosei*, Jefferson *et al*. 1997). By contrast, belugas, *Delphinapterus leucas*, are dark gray at birth but lighten to white as adults (Brodie 1981). Indo-Pacific humpbacked dolphins (*Sousa chinensis*) near Hong Kong are solid gray as calves, but are heavily speckled as juveniles, and become mostly white in adulthood (Jefferson and Leatherwood 1997). Suggested functions for natal coloration include enhanced infant care, reduced infanticide risk, sexual mimicry (*e.g*., primates, Treves 1997; Barthold *et al*. 2009), heat conservation, and camouflage against predators (*e.g*., pinnipeds, Bonner 1990). Such explanations may be relevant for cetaceans but have received little attention to date. Coloration can also differ by geographic area (*e.g*., *Orcinus orca*, Evans *et al*. 1982; humpback whales, *Megaptera novaeangliae*, Rosenbaum *et al*. 1995; humpback dolphin, *S. chinensis*, Wang *et al*. 2008). Thus, studying the ontogeny of coloration in cetaceans can inform about function and facilitate species identification and sex or age determination at sea, which is essential for understanding life history and social structure.

Here, we describe and investigate the ontogeny and possible function(s) of speckling in Shark Bay bottlenose dolphins (*Tursiops* sp.). We examine sex differences and the development of ventral speckles in individuals of known age and reproductive history. Speckling ontogeny has been studied in spotted dolphins (*Stenella frontalis*, Perrin *et al*. 1994; Herzing 1997; *S. attenuata*, Perrin and Hohn 1994; Mignucci-Giannoni *et al*. 2003; *S. a. graffmani*, Perrin 1970) and bottlenose dolphins (*T. aduncus*, Ross and Cockcroft 1990; *Tursiops* sp., Smolker *et al*. 1992). However, these studies were based either on few or no animals of known age or limited age range and none discussed the possible function(s) of speckles. That

said, of the three main functional hypotheses described above, concealment, communication, and regulation of physiological processes, one can be readily discarded. Regulation of physiological processes (regulation of body temperature by reflecting or absorbing light, or reducing glare from the sun) is not likely to be the function of speckling because it occurs ventrally (Ross and Cockcroft 1990, Smolker *et al*. 1992). The function of speckles is also unlikely to be related to aposematism; since, *Tursiops* are not known to be unpalatable or poisonous. Concealment is also unlikely given that young dolphins do not have speckles and are likely to be most vulnerable to predators. Since dolphins begin hunting soon after birth and typically exhibit adult hunting tactics before weaning (Mann and Sargeant 2003, Sargeant and Mann 2009), camouflage from prey also seems to be an unlikely function. Three communication functions are possible; speckles could signal or provide cues on age, reproductive maturity, or species identity. These nonexclusive functions will be discussed.

<center>METHODS</center>

Speckling data were collected opportunistically from wild Indian Ocean bottlenose dolphins (*Tursiops* sp.) between 1985 and 2010 as part of the ongoing long-term research project (established in 1984) in Shark Bay, Western Australia (25°47′S, 113°43′E). Shark Bay *Tursiops* have uncertain taxonomic status with control region haplotypes characteristic of both *T. aduncus* and *T. truncatus* (Krützen *et al*. 2004). Therefore, we refer to them as *Tursiops* sp., although their speckling patterns are similar to those in *T. aduncus* (Ross and Cockcroft 1990). Individual dolphins are identified by natural dorsal fin shape and markings with the aid of a photographic catalogue (Würsig and Jefferson 1990). Over 1,500 dolphins have been identified since 1982, and approximately 550 dolphins are seen frequently and monitored each year in the main study area (roughly 300 km^2). Birth dates and weaning ages were determined as in Mann *et al*. (2000). For this analysis, all birth dates were accurate to within 1 yr, but most estimates were accurate to within months, weeks, or even days. Sexes of individuals were determined by (1) the presence of a dependent calf (Smolker *et al*. 1992), (2) views of the genital area, (Smolker *et al*. 1992), and/or (3) DNA analyses (Krützen *et al*. 2003). Dolphins of unknown age, sex, or ambiguous identity were not used in analyses.

Speckling information was obtained during surveys and focal follows for most dolphins (Mann 1999), or at the beach while the semiprovisioned dolphins visited (see Mann and Kemps 2003). Speckle information was collected from photographs or views of the lateral and ventral area. Speckles were classified by density and body part: 1 = no speckles, 2 = few speckles, 3 = moderate speckles, and 4 = heavy speckles (Fig. 1). Speckles were rated by body part: genital area, belly, chest, axillae, and throat/jaw (Fig. 2). The type of view was further classified as ventral (when the dolphin was belly-up) or lateral (side view, Fig. 3). Speckling information was collected when water clarity was good and Beaufort was 1 or less.

Our analyses focused on 88 identified dolphins of known age and sex, 58 females and 30 males, between the ages of 3 mo and 34 yr. Only speckle data from reliable observers were used. These observers had more than one field season and were trained by experienced observers. Any ambiguous data, such as comments not corresponding with speckle scores, were excluded from analyses. If a transition from one classification to another was missing, we excluded that case from some analyses.
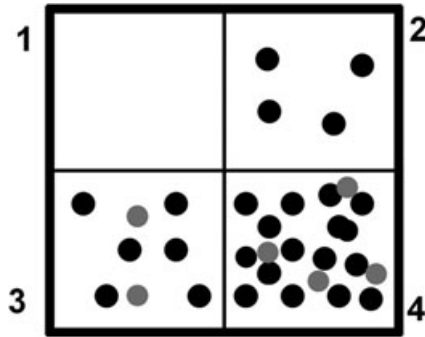
Figure 1. Speckle classifications: 1 = none, 2 = few, 3 = moderate, 4 = heavy.

For example, if a dolphin had moderate speckles at age 20, and heavy speckles when next observed at age 25, we have missed the transition year and would exclude that case.

To examine differences in speckling as a function of age, sex, body view, and body part, we restricted our sample to one speckling data point per body part and view at a given age for each individual unless speckle classification changed within the year, in which case both points were used. Males and females were combined for some analyses when there was no detectable sex difference determined by a Mann-Whitney *U* test. To analyze differences in speckle onset between body views, we used a mixed linear regression model to account for intercorrelated observations (*i.e.*, within and between subject) or Wilcoxon Matched Pairs Signed Rank test for within-subject comparisons.

For growth curve analysis (Singer and Willett 2003), all data points were used to analyze speckling state as a function of time and to examine the shape of the curve (linear or quadratic). The growth curve was analyzed using Proc Mixed in SAS statistical software v9.2 (SAS Institute, Inc., Cary, NC, USA). To examine the relationships between speckling and maturation, we correlated weaning age (both sexes) and age at first-birth (females only) with age of speckling onset using Spearman's rank test. Differences were considered significant at $P < 0.05$ for all analyses.
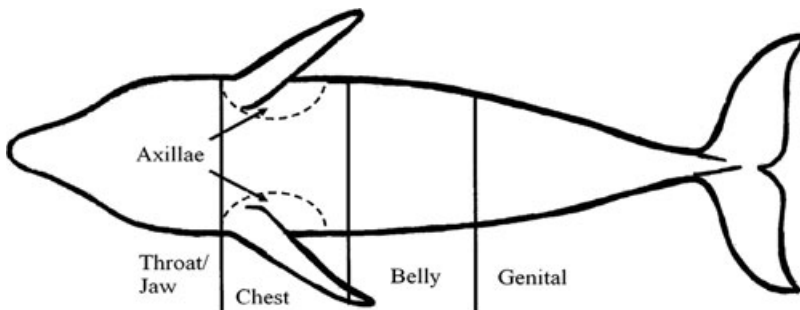

Figure 2. Speckles were rated by body part: genital area, belly, chest, axillae, throat/jaw.
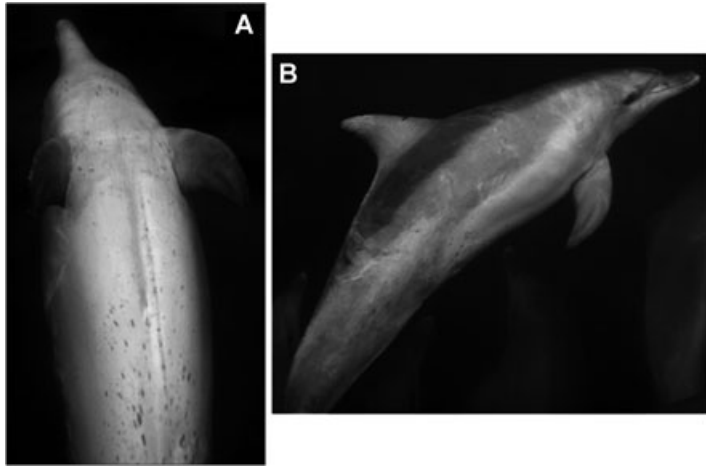
Figure 3. Classification of view: (A) ventral (when the dolphin was belly-up), (B) lateral (dolphin turned on side). Photos by Kirk Gastrich.

RESULTS

When and Where Do Speckles First Appear? Do Speckles Increase with Age?

Shark Bay bottlenose dolphins are born with only the basic counter-shading coloration (dark dorsal, white ventral) and no speckles. Table 1 summarizes the speckling onset for each body part for each view (ventral and lateral). Speckles first appeared ventrally in the genital area at a mean age of 10.2 ± 0.35 yr (females at 10.27 ± 0.44 yr [$n = 13$] and males at 10.22 ± 0.42 yr [$n = 5$]), with a minimum of 7.6 yr and a maximum of 12.7 yr ($n = 19$).

Soon after the onset of speckles in the genital area (ventral view), speckles appeared on the belly (ventral view). Table 2 summarizes the development of speckling from onset in the genital area to heavy speckles at the throat. All growth curve analyses indicated that speckles increased quadratically with age in all body parts (Fig. 4).

Is There a Difference in Speckling Onset with Body View?

Linear mixed model tests indicated that onset of speckling differed between lateral and ventral view in the genital and belly area only (AIC = 143.5, $t = 2.52$,

Table 1. Age of mean speckle onset for Shark Bay bottlenose dolphins.

Body view	Body part	n	Mean $\pm$ SE (yr)	Minimum	Maximum
Ventral	Genital area	19	10.2 ± 0.35	7.6	12.7
Ventral	Belly	16	11.2 ± 0.52	8.5	14.5
Lateral	Genital area	17	11.5 ± 0.57	7.6	13.9
Lateral	Belly	9	13.4 ± 0.46	10.9	15.5
	Axillae	6	12.3 ± 0.79	9.7	13.9
	Chest	9	14.9 ± 0.75	11.7	18.4
	Throat	4	15.7 ± 1.21	12.8	17.3

Table 2. The onset age of speckles by body part (lateral and ventral views combined).

Age (yr)	Few speckles	Moderate speckles	Heavy speckles
10	Genital area		
11	Belly		
12	Axillae		
↓			
14	Chest	Genital area	
15	Throat		
16		Belly	
↓			
20			Genital area
↓			
23			Belly
24–26		Chest/Throat Axillae[a]	Axillae[a]
↓			
29			Chest/Throat[a]

[a]= few data.

$P = 0.045$, $n = 33$; AIC $= 140.8$, $t = 6.18$, $P = 0.004$, $n = 28$, respectively), with speckles first appearing in the ventral area. No significant difference was found for lateral and ventral views of the chest, probably due to small sample size (ventral $n = 6$, lateral $n = 4$). Sample sizes were too small for the axillary (ventral $n = 6$, lateral $n = 1$) and throat (ventral $n = 3$, lateral $n = 3$) areas to analyze.

Is Onset of Speckles Linked to Weaning or Sexual Maturity?

Spearman's correlation analyses showed that speckle onset did not significantly correlate with weaning age for either sex (female $n = 18$, $P = 0.224$; male $n = 8$, $P = 0.456$). However speckle onset in the genital area highly correlated with the age of first parturition ($r = 0.867$, $P < 0.002$, $n = 9$), averaging 2.5 ± 0.5 yr (range 1–4.3 yr) from when speckles occur at the genital area to when the female gave birth to her first calf.

DISCUSSION

Our data show that speckling variation is primarily determined by age and maturation. Speckles first appear at 10 yr of age around the genital area, though speckle onset occurs as early as 7 yr or as late as 12 yr of age. Throughout their lifespan, speckles increase in number and density, particularly along the ventral and lateral sides. Age of speckle onset in the genital area was found to correlate significantly with the age of first known parturition, confirming the relationship of speckling to sexual maturation. Using speckling data, it would be possible to estimate the percentage of sexually mature females in the population regardless of whether or not they have a dependent calf.

Speckling ontogeny in Shark Bay bottlenose dolphins differs from that of other delphinids. In the Atlantic spotted dolphin (*S. frontalis*), dark ventral spots begin to appear near weaning, not sexual maturity, and light dorsal spots begin to appear with
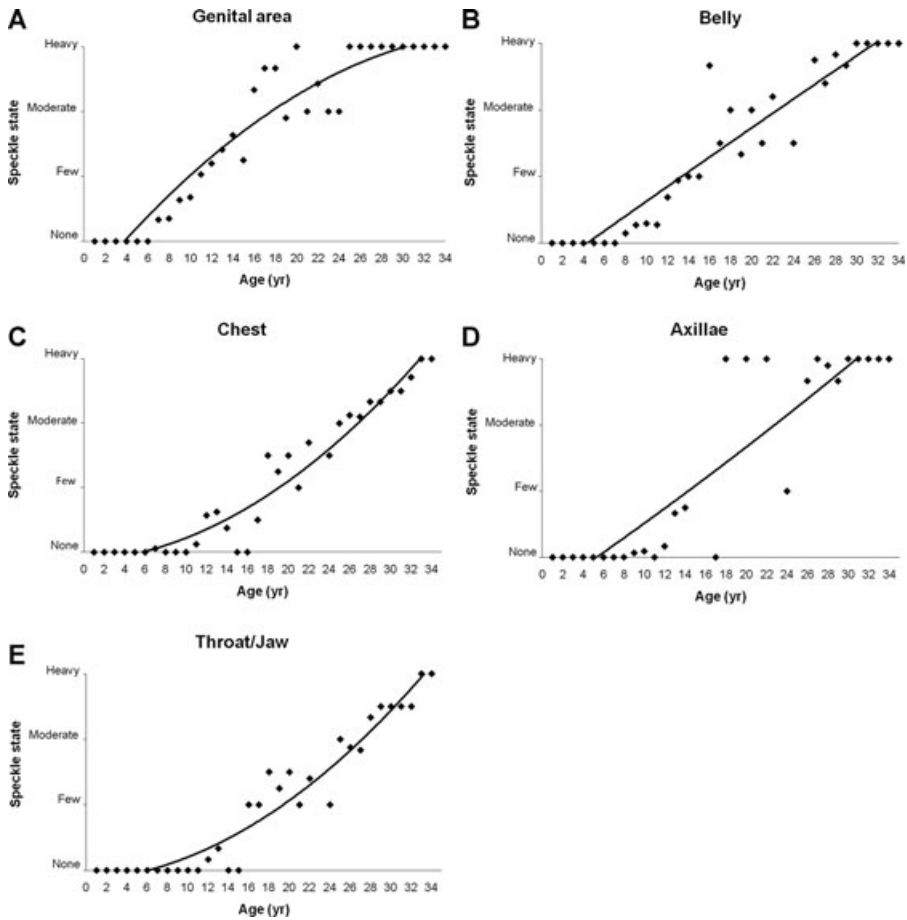
Figure 4. The development of *Tursiops* sp. speckles with age at each body part. Means and quadratic trend lines were added for visual presentation. Growth curve analysis was used, as it is able to account for unbalanced, incomplete, and/or missing data, as seen in the axillae region. Genital area: y = speckle state = $-0.0025x^2 + 0.1979x + 0.2881$, x^2 = age^2 = $F_{1,317}$ = 17.96, P = 0.0001, x = age = $F_{1,317}$ = 192.54, $P < 0.0001$. Belly: $y = -9E - 05x^2 + 0.1128x + 0.5115$, $x^2 = F_{1,361}$ = 5.15, P = 0.0239, $x = F_{1,361}$ = 58.53, $P < 0.0001$. Chest: $y = 0.0026x^2 + 0.0108x + 0.8533$, $x^2 = F_{1,377}$ = 220.60, $P < 0.0001$, $x = F_{1,377}$ = 1.09, P = 0.2971. Axillae: $y = 0.0004x^2 + 0.104x + 0.4378$, $x^2 = F_{1,216}$ = 27.25, $P < 0.0001$, $x = F_{1,216}$ = 3.61, P = 0.0589. Throat/jaw: $y = 0.0025x^2 + 0.0108x + 0.8406$, $x^2 = F_{1,342}$ = 327.56, $P < 0.0001$, $x = F_{1,342}$ = 14.82, P = 0.0001.

age. However, similar to the case in Shark Bay, dark ventral spots increase in number and size (Perrin *et al*. 1994, Herzing 1997). The same ontogeny is observed in the pantropical spotted dolphin (*S. attenuata*), with the spots first appearing in puberty on the side of the lower jaw, in the flipper band, on the throat, or in the abdominal region (Perrin 1970, Perrin and Hohn 1994, Mignucci-Giannoni *et al*. 2003).

Overall, our results generally support the conclusions reached by other studies of *Stenella* and *Tursiops* spp. that speckles correlate with sexual maturity (Perrin 1970,

Kasuya *et al*. 1974, Hohn *et al*. 1985, Myrick *et al*. 1986, Ross and Cockcroft 1990, Smolker *et al*. 1992, Herzing 1997). Studies of *S. attenuata* (Perrin 1970, Kasuya *et al*. 1974, Hohn *et al*. 1985, Myrick *et al*. 1986) found a higher percentage of sexually mature dolphins (presence of corpora in females and spermatogenesis or full-size testes in males) in the mottled (extensive and merging gray and white spots on the dorsal surface and continued increase in ventral black spots) and fused (dark and white spots become extensive and coalesced on the ventral and dorsal surfaces) coloration phases. Herzing (1997) found that female Atlantic spotted dolphins (*S. frontalis*) did not give birth until after they had reached the mottled color phase, similar to our findings that females become speckled before their first parturition. However, in contrast to Smolker *et al*. (1992), we found that speckling often occurs before the attainment of adult size, which is thought to occur after age 10.

Yablokov (1963, in Mitchell 1970) proposed that coloration in cetaceans could aid in prey acquisition; Mitchell (1970) also noted that nursing calves in *Stenella* sp. (referred to as *S. frontalis* by Perrin *et al*. 1987), are unspotted and only begin to develop spots at about the age when they begin to forage on their own, inferring that spotting aids in hunting rather than against predators. However *Turiops* in Shark Bay are often weaned by age 3 or 4 (Mann *et al*. 2000), successfully hunt by 3–4 mo of age, and typically exhibit adult hunting tactics before weaning (Mann and Sargeant 2003, Mann *et al*. 2008, Sargeant and Mann 2009), years before any speckling has occurred. As such, this hypothesis may help explain spotting in *Stenella* but not *Turiops* spp.

Coloration in cetaceans could be directed at conspecifics and provide information on reproductive status and physiological condition, or for species, kin, and individual recognition (Bradley and Mundy 2009). Pigment patterns act as individual-recognition cues in some insects (*e.g.*, Tibbetts 2002) and birds (*e.g.*, Dale *et al*. 2001). Although speckles might aid in individual or kin recognition in dolphins, it would not be the most reliable cue given the lack of ventral speckles early in life and the age-determined changes.

Species recognition is another possibility, given that Indo-Pacific bottlenose dolphins overlap with other delphinids at several locations in Australia (Hale *et al*. 2000, Best 2007, Parra and Ross 2009). Speckling occurs in bottlenose dolphins along the coastlines of New South Wales, Queensland, and Western Australia, but is absent in South Australia, Victoria, Tasmania, and the Bass Strait (Ross and Cockcroft 1990). Genetic analyses in a recent paper by Möller *et al*. (2008) suggested a new species of bottlenose dolphin in Southern Australia. Given that speckling occurs before sexual maturity, speckles could offer cues on with what species to avoid breeding. On rare occasions, we have observed Shark Bay *Turiops* interacting with *Sousa* at our study site.

The most promising functional explanation is that speckles offer cues to reproductive maturity, social status (age), or condition. Speckles could be a byproduct of hormonal changes (see Ketterson and Nolan 1992, Jawor and Breitwisch 2003), but still serve communicative functions. Their onset suggests that they are a secondary sexual characteristic. Although most secondary sexual traits are sexually dimorphic, their presence or absence can be similar between the sexes (*e.g.*, armpit and genital hair in humans, perineal and facial coloration in macaques, Waitt *et al*. 2003, 2006). Although the occurrence and onset of speckles appear not to be sexually dimorphic, further investigation could reveal sex differences in speckle patterns. In sexually monomorphic species, speckles may provide obvious cues for sexual maturity. For

example, females might avoid mating with unspeckled males (immature) or very heavily speckled males (potential fathers), particularly as recent data suggest that breeding with close kin is a real risk, especially for young females (Frère *et al*. 2010). Within sex, speckles might signal social status (Samuels and Gifford 1997) or deter older males from behaving aggressively toward younger ones (Graham and Nadler 1990, Wahlström 1994, Setchell and Dixson 2001).

Our results suggest that speckling patterns in Shark Bay and Indo-Pacific dolphins could be used for estimating age, sexual maturation, and social status. They might also aid in species identification. We are currently using the speckle data to develop a robust age structure of the Shark Bay population and to better estimate age-specific mortality and life span.

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