



The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins



Ewa Krzyszczyk^{a,*}, Eric M. Patterson^{a,b}, Margaret A. Stanton^c, Janet Mann^{a,d}

^a Department of Biology, Georgetown University, Washington, D.C., U.S.A.

^b Office of Protected Resources, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Silver Spring, MD, U.S.A.

^c Center for the Advanced Study of Hominid Paleobiology, The George Washington University, Washington, D.C., U.S.A.

^d Department of Psychology, Georgetown University, Washington, D.C., U.S.A.

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Sex differences in adult behaviour are well documented, but less is known about the ontogeny of these differences. In mammals, the transition to independence, from infancy to the juvenile period, is when these sex differences are likely to become prominent. Here, we examined sex differences in behavioural development among calf and juvenile bottlenose dolphins, *Tursiops aduncus*, from 2 years preweaning to 2 years postweaning and whether these differences were consistent, or not, with three nonmutually exclusive hypotheses regarding the function of the juvenile period: the social skills, protection/safety and energy allocation hypothesis. All hypotheses received some support, but strikingly so for females. First, sex differences in the nature and quality of juvenile social bonds appear to foreshadow adult association patterns. Juveniles had a greater proportion of same-sex associates than calves. Second, although neither sex increased their number of associates from infancy to juvenility, a pattern that might mitigate predation risk, avoidance between juveniles and adult males suggests that both sexes reduce the likelihood of conspecific aggression. This pattern was more marked for juvenile females. Third, females, but not males, increased foraging rates from late infancy to the early juvenile period, even surpassing typical adult female foraging rates. This is likely related to the future energetic demands of maternal investment and skill development required for specialized foraging tactics, which are female biased in this population. This study provides a first step towards understanding the transition into independence for cetaceans, insight into how sex differences develop and a glimpse into the function of the juvenile period. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sex differences in foraging, ranging and sociality have been widely documented in adults in a variety of taxa (reviewed in Meredith, 2013; Wearmouth & Sims, 2008). For example, in some species females travel shorter distances, forage in smaller core areas and are less gregarious than males (e.g. double-crested cormorants, *Phalacrocorax auritus*: Anderson, Roby, & Collis, 2004; chimpanzees, *Pan troglodytes*: Murray, Mane, & Pusey, 2007; Gilby & Wrangham, 2008; Wrangham & Smuts, 1980; bottlenose dolphins, *Tursiops aduncus*: Mann, Stanton, Patterson, Bienenstock, & Singh, 2012; Randić, Connor, Sherwin, & Krützen, 2012). These differences are often associated with sex-biased dispersal where the philopatric sex is typically more gregarious and forms stronger same-sex associations (Dobson, 2013; Smith, 2014). In species with bisexual philopatry, bonds are strongly driven by kinship (e.g. killer

whales, *Orcinus orca*: Parsons, Balcomb, Ford, & Durban, 2009) or reproductive strategy (e.g. bottlenose dolphins, *Tursiops* spp.: Connor et al., 2000). Beyond social behaviour, in some species, females exhibit distinct foraging strategies from males, including use of rare techniques and niche specialization (chimpanzees: Murray et al., 2007; bottlenose dolphins: Mann & Sargeant, 2003; Mann et al., 2008; sea otter, *Enhydra lutris*: Fujii, Ralls, & Tinker, 2015). These sex differences are strongly linked to sex-specific reproductive strategies (e.g. socioecological theory, reviewed in Gowaty, 2004). Because female reproduction is usually limited by food, females tend to focus their efforts on foraging. Conversely, male reproduction is often limited by access to mates, and consequently males tend to focus on enhancing their access to mating opportunities (e.g. through rank acquisition or alliance formation) (Connor & Krützen, 2015; Rodriguez-Llanes, Verbeke, & Finlayson, 2009). Despite a well-established socioecological theory predicting sex differences in the behaviour of adult animals, there are few studies that directly examine the ontogeny of such sex differences in

* Correspondence: E. Krzyszczyk, Department of Biology, Georgetown University, Reiss Science building Rm 406, 37th & O St, NW, Washington, D.C. 20057, U.S.A.

E-mail address: ewakrzyszczyk@gmail.com (E. Krzyszczyk).

behaviour in the wild postindependence from the mother (but see Barale, Rubenstein, & Beehner, 2015; Cords, Sheehan, & Ekernas, 2010; Pereira & Fairbanks, 2002). Nevertheless, such studies are essential not only for understanding developmental processes that shape adult sex differences but also why some species have more prolonged juvenile periods than others. In this study, we define juvenile period, also referred to as juvenility, as the time between weaning and sexual maturity.

Both intrinsic and extrinsic factors have been shown to be important in the emergence of sex-typical behaviours (Beck, Iverson, Don Bowen, & Blanchard, 2007; Clotfelter, Bell, & Levering, 2004; Dulac & Kimchi, 2007; Lonsdorf, Eberly, & Pusey, 2004; Maekawa, Tsukahara, Kawashima, Nohara, & Ohki-Hamazaki, 2014; McIntyre & Edwards, 2009; Wallen & Hassett, 2009). Early in life, circulating androgens are responsible for many male-specific behaviours (Wallen & Hassett, 2009). Sex differences can also emerge with changes in predation risk or food availability, for example female adult grey seals, *Halichoerus grypus*, select fewer and higher-quality prey species than males in the spring, during the postbreeding period when energy acquisition is important for females to support pregnancy (Beck et al., 2007; Croft et al., 2006).

Learning and/or social factors during early development are associated with differences in male and female attention towards the same event or stimulus. For example, young female chimpanzees spend more time watching their mothers fish for termites (with tools) and acquire termite-fishing skills earlier than males, who spend more time playing during termite-fishing sessions (Lonsdorf, 2005; Lonsdorf et al., 2004).

Despite extensive knowledge on mammalian life histories, infant and adult behavioural development, juveniles remain the least studied life-history stage. Few longitudinal data sets are available in long-lived mammals outside of primates (Cohas, Berger, Lematre, Allainé, & Gaillard, 2015; Holekamp, Smith, Strelhoff, Van Horn, & Watts, 2012; Lonsdorf & Ross, 2012; Pereira & Fairbanks, 2002). This is due in part to juvenile mammals being difficult to observe, especially in natural settings, because they move fast and unpredictably, are small in size, lack distinctive markings and one sex often emigrates, making individual identification difficult (Pereira & Fairbanks, 2002). Moreover, for species with an extended period of juvenility, years of study might be necessary. The juvenile period is critical given that it is flanked by two transitions fraught with risks to fitness: (1) the transition to nutritional independence (i.e. weaning) (nursing offspring to juvenile: Maestriperi & Mateo, 2009) and (2) the transition to adulthood (juvenile to adult: Rubenstein, 2002; Tecot, Gerber, King, Verdolin, & Wright, 2013).

In most species with slow life histories (e.g. primates: Altmann, Altmann, Hausfater, & McCuskey, 1977; Pusey & Packer, 1987; Wrangham, 1980; elephants: Fernando & Lande, 2000; Moss & Poole, 1983; cetaceans: Whitehead & Mann, 2000), juveniles remain in relatively stable groups with their mothers and are thus somewhat protected from ecological and social threats. However, in some species such as bottlenose dolphins (*Tursiops* spp.) that are characterized by high fission–fusion dynamics, juveniles do not remain with the mother postweaning (Mann, Connor, Barre, & Heithaus, 2000; McHugh, Allen, Barleycorn, & Wells, 2011a; Tsai & Mann, 2013). In bottlenose dolphins, male mortality is high postweaning (Stanton & Mann, 2012), and juveniles face a number of challenges such as the loss of maternal nutrition and protection from predators and conspecifics. Considering the immediate mortality risk and the potential importance of acquiring social (e.g. development of bonds, fighting skill, avoiding aggressive individuals) and ecological (e.g. foraging, predator avoidance) skills necessary for adult fitness, the ‘choices’ that individuals make to mitigate or meet these challenges during the transition to nutritional independence are vital.

Consequently, in this study, we examine behavioural sex differences from 2 years preweaning (i.e. calf) to 2 years postweaning (i.e. juvenile) in a long-lived cetacean, the bottlenose dolphin. Only a handful of studies have examined the juvenile period in cetaceans (*Tursiops* spp.: McHugh et al., 2011a; McHugh, Allen, Barleycorn, & Wells, 2011b; Tsai & Mann, 2013; Atlantic spotted dolphin, *Stenella frontalis*: Kaplan & Connor, 2007), and none have focused on the transition from calf to juvenile. Here, we use a 30-year data set from Shark Bay, Australia to examine sex differences in behaviour across the transition to nutritional independence, as well as how they might inform our understanding of function of the juvenile period. Thus, we explore how these data are consistent or inconsistent with three nonmutually exclusive hypotheses regarding the function of the juvenile period: (1) the social skills and bonds hypothesis (Joffe, 1997); (2) the protection/safety hypothesis (Gibson & Mann, 2008b; van Noordwijk, Hemelrijk, Herremans, & Sterck, 1993); (3) and the energy allocation hypothesis (Blueweiss et al., 1978; Calder, 1984; Charnov, 1993) (Table 1). As these hypotheses are not exclusive from each other (e.g. gregariousness supports social bonds and reduces predation risk), results might be consistent with more than one hypothesis.

Social Skills and Bonds Hypothesis

The social skills and bonds hypothesis suggests that immature animals benefit by focusing on social skill development prior to adulthood when the costs of error, such as poor mate choice or losing a ‘play’ fight, are low (Fairbanks, 1993; Janson & van Schaik, 1993; Joffe, 1997; Pagel & Harvey, 1993; Pereira & Altmann, 1985). Adult bottlenose dolphins have preferred and avoidance relationships (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Lusseau et al., 2003; Wiszniewski, Allen, & Möller, 2009) in part based on kinship (Frère et al., 2010; Krützen et al., 2003; Mann et al., 2012; Parsons et al., 2003) and multilevel male alliances (Connor & Krützen, 2015). Both sexes in Shark Bay remain in their natal area for life, providing opportunities for occasional association with their mother and natal network (Tsai & Mann, 2013). The social environment that individuals experience is highly fluid, dynamic and complicated due to the fission–fusion social system with a large number of individuals available for interaction and the elaborate network structure (Mann et al., 2012). Early social interactions may aid in the development of agonistic or affiliative skills for concurrent or future use in navigating this complicated social landscape (Pereira & Fairbanks, 2002). Play in many species helps to establish social relationships among individuals likely to interact with each other in the future (Beckoff, 2001; Holmes, 1994; Palagi, 2006) and in the development of innovation by preparing individuals for unexpected and novel environmental and social circumstances (Spinka, Newberry, & Bekoff, 2001). Through play fighting and sociosexual interactions, individuals learn ground rules that are acceptable to others (how hard they can bite, how roughly they can interact) and how to resolve conflicts (Spinka et al., 2001). Immediate benefits to juveniles could include testing social roles and improving communication skills that contribute to current survival in the juvenile stage (Palagi, 2006).

Partner preference has been shown to be influenced by the expectation of partner availability in the future (Fairbanks, 1993), which appears to contribute to reproductive success as adults (e.g. via close bonds and stable, enduring relationships, reviewed in Seyfarth & Cheney, 2012). Several studies have focused on spatial and affiliative relations of social behaviour, finding sex differences in immature animals that match adult patterns (primates: Pereira, 1988; Strier, 1993; van Noordwijk et al., 1993; ungulates: Mathisen, Landa, Andersen, & Fox, 2003; canids: Holekamp & Smale, 1998; elephants: Merte, Goodwin, & Schulte, 2010). Given the importance

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