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Original Article

Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins

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Male alliances are an intriguing phenomenon in the context of reproduction since, in most taxa, males compete over an indivisible resource, female fertilization. Adult male bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, form long-term, multilevel alliances to sequester estrus females. These alliances are therefore critical to male reproductive success. Yet, the long-term processes leading to the formation of such complex social bonds are still poorly understood. To identify the criteria by which male dolphins form social bonds with other males, we adopted a long-term approach by investigating the ontogeny of alliance formation. We followed the individual careers of 59 males for 14 years while they transitioned from adolescence (8–14 years of age) to adulthood (15–21 years old). Analyzing their genetic relationships and social associations in both age groups, we found that the vast majority of social bonds present in adolescence persisted through time. Male associations in early life predict alliance partners as adults. Kinship patterns explained associations during adolescence but not during adulthood. Instead, adult males associated with males of similar age. Our findings suggest that social bonds among peers, rather than kinship, play a central role in the development of adult male polyadic cooperation in dolphins.

Lay Summary: Multilevel cooperation in adult male bottlenose dolphins is based on friendships that are formed among similarly aged males during their adolescence. Although cooperative behaviors in many animals are found among relatives, this is not the case in dolphins. Our findings reveal the existence of enduring friendships in a complex marine mammal society, similar to those that have been described in many primate species including humans.

Key words: bottlenose dolphin, cooperation, kin selection, male alliance, multilevel society, social bonds.

INTRODUCTION

Social animals frequently interact with their group members. Although such interactions can occur among different sets of

individuals (e.g., Henzi et al. 2009; Braun and Bugnyar 2012; Schweinfurth et al. 2017), some individuals interact repeatedly in beneficial contexts and over a longer period of time (Schino and Aureli 2017). In many studies on wild animal populations, such long-term stable interactions among the same individuals have previously been referred to as “social bonds” (Massen 2017), defined as persistent,

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affiliative, and cooperative relationships that may generate benefits through support which may be approximately balanced between the partners (Silk 2002; Ostner and Schülke 2014). It has previously been shown that “social bonds” involve some degree of differentiation and selectivity in that individuals maintaining these bonds showed high rates of association (Silk 2002; Whitehead 2008; Ostner and Schülke 2014; Thompson 2019). Here, we follow this convention by referring to two individuals as having a social bond whenever they show significantly higher association rates than the group average over an extended period of time (Whitehead 2008; Ostner and Schülke 2014).

Benefits of social bonds include increased reproductive output (e.g., feral horses *Equus ferus*, Cameron et al. 2009; chimpanzees *Pan troglodytes*, Langergraber et al. 2013; Assamese macaques *Macaca assamensis*, Schülke et al. 2010; house mice *Mus musculus*, Weidt et al. 2008), life span (e.g., savannah baboons *Papio cynocephalus*, Silk et al. 2010), infant survival (e.g., savannah baboons, Silk et al. 2003, 2009), and decreased mortality (e.g., humans, Holt-Lunstad et al. 2010). Social bonds are thus crucial determinants of an individual’s fitness. Fitting with predictions of kin selection theory (Hamilton 1964), relatives are often preferred social partners, with closer kin being preferred over distant kin (see Smith 2014 for a review).

Philopatry facilitates the formation of persistent social bonds and permits close association with kin postweaning. Most mammals are characterized by female philopatry and male dispersal (Greenwood 1980), allowing females to form close and enduring social bonds. This sex-bias can be explained by the different reproductive constraints faced by both sexes. Although reproductive success of females is limited by access to resources and safety, male reproductive success is constrained by access to fertile females (Trivers 1972).

Due to the indivisibility of fertilizations, a paradox exists where males cooperate to reproduce (Díaz-Muñoz et al. 2014). Males often engage in temporary coalitions, in which 2 or more males cooperate to compete against others in contests over resources or rank (Smith 2014), thereby increasing individual access to females. Recurring coalitions among the same males, also known as male alliances (Harcourt 1992), are an unusual phenomenon (Díaz-Muñoz et al. 2014). Alliances occur in, though are not limited to, humans (Chagnon 1988), nonhuman primates (e.g., chimpanzees, Mitani et al. 2002a; savannah baboons, Noë 1992), lions (*Panthera leo*, Packer et al. 1991), cheetahs (*Acinonyx jubatus*, Caro 1994), lekking birds (e.g., manakins *Chiroxiphia linearis*, McDonald and Potts 1994), fish (reviewed in Taborsky 1994), and bottlenose dolphins (*Tursiops aduncus*, Connor et al. 1992).

Kin selection theory can resolve the apparent paradox of persisting social bonds between allied males when individuals are related (Caro 1990; Pope 1990; Qi et al. 2017). Polytocous species, those that give birth to multiple offspring at once, may produce “ready-made” male alliances from single litters (Caro 1990) or synchronized litters of related individuals (Packer et al. 1991). In contrast, many monotocous species, which produce single offspring, share the demographic challenge of maternal same-sex half-siblings being scarce and, if present, separated in age by at least several years. In chimpanzees, for instance, Langergraber et al. (2007) found that, although males do favor maternal siblings as allies, the majority of cooperative male dyads were formed among nonrelatives.

In some species, for example, long-tailed manakins and boat-tailed grackles (McDonald and Potts 1994; *Quiscalus major*, Poston 1997), nonkin male cooperation can be attributed to social queuing, where subordinates remain in a group to acquire dominant status (Kokko and Johnstone 1999). However, neither kin selection nor social queuing can explain the persisting social bonds formed among

unrelated males observed in, for example, humans (Boehm 2009), baboons (Guinea baboons *Papio papio*, Patzelt et al. 2014), chimpanzees (Watts 1998), Galapagos hawks (*Buteo galapagoensis*, Faaborg et al. 1995), and dolphins (Wiszniewski et al. 2012b; Connor and Krützen 2015). To understand how persisting social bonds among unrelated males emerge, we need to investigate how, when, and with whom such bonds are formed.

Male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, exhibit one of the most remarkable male alliance systems known (Connor and Krützen 2015). The system is unusual because male dolphins exhibit long-term, multilevel alliances with context-dependent interactions within an open social network (Connor et al. 2000a, 2017). This sets them apart from the multilevel alliances observed in baboon species (Grueter et al. 2012). Although male dolphins in other populations form alliances (Owen et al. 2002; Parsons et al. 2003; Wiszniewski et al. 2012a), Shark Bay appears to be the only population where up to 3 levels of nested alliances occur (Randić et al. 2012; Connor and Krützen 2015).

Alliance membership provides male dolphins with mating opportunities they would otherwise not obtain, as nonallied males have been shown to sire very few, if any, offspring (Krützen et al. 2004a). On the level of first-order alliances, 2 to 3 males cooperate to coerce individual estrus females. Members of first-order alliances belong to larger groups of second-order alliances, consisting of 4–14 males, which compete against other such alliances over access to females (Connor et al. 1992, 2011). Males select their first-order allies from within their second-order alliance (Connor et al. 2011). Thus, second-order alliances are now recognized as the core social unit of male dolphins in Shark Bay (Connor and Krützen 2015). Once formed in early adulthood, second-order alliances can persist over decades (Connor and Krützen 2015). Adult male dolphins are characterized by high levels of association year-round (Smolker et al. 1992), increased rates of affiliative behaviors such as petting (Connor et al. 2000a, 2006) and high levels of cooperation during consortships (Connor and Krützen 2015). Male alliances in dolphins therefore differ from the purely reproductive alliances or coalitions observed in other species (Silk 2002; Díaz-Muñoz et al. 2014; Thompson 2019). Male alliance partners in dolphins can therefore be said to exhibit social bonds based on the definition used in this study.

Preliminary work on relatedness among males in Shark Bay was ambiguous in that relatedness patterns differed markedly between alliances of different sizes and levels of stability (Krützen et al. 2003). However, Krützen et al. (2003) and studies on other dolphin populations (Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012a; Diaz-Aguirre et al. 2018) assessed the potential effect of kinship based on average group relatedness within established alliances relative to a population mean. In order to reveal the development of male alliance formation, however, individual males and their social bonds with others during alliance development need to be considered. Furthermore, the individual-based approach we employed here has an additional advantage in that it accounts for the availability of an individual’s potential associates, unlike earlier studies assuming equal availability of potential associates.

Previous work demonstrated that male calves and juveniles (2 years pre-weaning and 2 years post-weaning, respectively) invest more time into developing social skills compared with females of the same age (Stanton et al. 2011; Krzyszczyk et al. 2017). The persistence of specific dyadic associations, though, has never been tested. Adolescence is a critical period during which males become sexually and socially mature (Connor and Krützen 2015). In contrast to adult

males, adolescent males have not yet established alliance membership and do not engage in consortships. Thus, patterns of associations are expected to differ qualitatively and quantitatively between adolescent and adult males. To close this important gap in our understanding of alliance formation, we explored the development and maintenance of social bonds during the transition from adolescence to adulthood.

Here, we describe the ontogeny of social bonds and thus, alliance formation among male bottlenose dolphins relative to patterns of genetic relatedness, affiliation history, and age-similarity. We focus on social bonds of individual males during the transition from adolescence to adulthood. This approach permitted us to gain insights into the underlying dynamics of friendships among male bottlenose dolphins.

MATERIALS AND METHODS

Data collection and study subjects

Data were collected at our long-term field site in the eastern gulf of Shark Bay, Western Australia. Standardized observations, hereafter “surveys,” have been conducted on this Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population since 1984 (Connor and Krützen 2015). In this study, we extracted survey data on group composition recorded between the years 1988 and 2015. Group composition was determined during the first 5 min of each survey according to the 10-m “chain rule” using photographs of dorsal fins to identify individuals (Smolker et al. 1992).

We extracted association data on 59 focal males, each of which we followed over 14 years. Data were extracted for 2 periods in the lifespan of each focal male, creating 2 age groups: from 8 to 14 years (“adolescence”) and from 15 to 21 years old (“adulthood”). By age 8, male bottlenose dolphins have typically been weaned for approximately 4 years and have transitioned to being independent juveniles (Mann et al. 2000a). Male bottlenose dolphins reach sexual maturity between 12 and 15 years of age (Kemper et al. 2014) and start forming stable alliances at approximately 15 years of age (Connor et al. 2000a). Only alliance membership enables males to successfully consort females (Connor et al. 1992). Males under 13 years of age have never been observed consorting an adult female, although this does not exclude the possibility that some males might start at a younger age (Connor and Krützen 2015). To avoid biases introduced by unbalanced age ranges, we limited the upper age in the adult category to 21 years of age, although dolphins may live past 40 in this population (unpublished data).

Whenever possible, birth dates were assigned based on the first sighting of a dolphin as a calf. Calf age was estimated using behavioral and physical criteria, including surfacing patterns, presence of fetal folds, as well as the last sighting of the mother before birth (Smuts and Mann 1999). In cases where there were no early-life demographic data available, we used ventral speckle density to infer approximate birth date, which is highly correlated with age in our study population (Krzyszczyk and Mann 2012).

Association rates

Socio-positive behaviors such as grooming in primates (Dunbar 2010) are often used to infer social bond strength on the qualitative level. However, social bonds can also be identified quantitatively by increased rates of affiliation over a prolonged period of time compared with other relationships in the group (Silk 2002; Whitehead 2008; Ostner and Schülke 2014; Thompson 2019).

Since socio-positive behaviors cannot be observed systematically underwater, we used association rates to identify social bonds among male dolphins. Association rates are well-established indicators for social bond strength in cetaceans (Mann et al. 2000b) and have been demonstrated to correlate with social bond strength (Silk 2002; Mitani 2009). To quantify associations between focal males and their male associates, we calculated Half-Weight Association Indices (HWIs, Cairns and Schwager 1987) for each focal male twice: once during its adolescence and for a second time while adult. A focal male’s associates consisted of all males with whom a focal was observed. Both focal males and all their associates had to have been observed at least 30 times in each age group. We used SOCPROG V2.6 (Whitehead 2009) to generate HWIs with the sampling period set to 1 day. Group composition data were collected during surveys, and re-sights, that is, the same group encountered within 2 h, were excluded.

To identify social bonds among focal males and their associates in each age group, we conducted a change point analysis. Change points are those where statistical properties of the data to either side differ, as is expected for different levels of social structures in multilevel societies (e.g., Wittemyer et al. 2005; Patzelt et al. 2014). To locate change points, we used the “changepoint” (Killick and Eckley 2014) R package employing the Pruned Exact Linear Time (PELT) method. The data set for the change point analysis comprised all dyads associating during the focal male’s adulthood, denoted by a HWI larger than 0 ($N = 1,755$). Adulthood HWIs were higher (mean \pm sd = 0.12 ± 0.18 , $N = 1,755$) than those in adolescence (mean \pm sd = 0.10 ± 0.13 , $N = 1,544$). Including adulthood HWIs only resulted in a more conservative cutoff for the adolescence period while reliably identifying a focal male’s alliance partner once adulthood was reached.

Based on the changepoint analysis, we defined a cutoff HWI value above which we regarded 2 males as sharing a social bond due to association rates well-above random expectations (Silk 2002; Whitehead 2008; Ostner and Schülke 2014). For focal adolescent males and any other male above the cutoff value, we chose the term “close associates.” Correspondingly, for focal adult males and any other male above the cutoff, we used “alliance partners.” Exploring the dyadic nature of male bonds in 2 separate age periods allowed us to determine some of the proximate mechanisms that predict alliance formation in adult male dolphins for the first time.

Pairwise relatedness and mitochondrial matriline membership

To explore the potential role of kinship in male association patterns, we used both maternal mitochondrial DNA (mtDNA) haplotypes and pairwise autosomal relatedness estimates. DNA was extracted from tissue samples which were collected using a remote biopsy system for small cetaceans (Krützen et al. 2002). To assign individuals to their maternal haplotype, we sequenced a 468 base-pair fragment of the hypervariable region I of mtDNA, as described in Bacher et al. (2010). We estimated pairwise relatedness based on 22 hypervariable autosomal microsatellite markers, which we generated and scored using previously established protocols (Kopps et al. 2014). We provide summary statistics on genetic diversity indices in Supplementary Material, see Tables S2–S4 and Figures S1 and S2.

Relatedness estimators perform differently based on the inherent relatedness composition of a population (Csillery et al. 2006). We identified the best performing relatedness estimator (i.e., high precision, low standard deviation) for our population by choosing the

estimator with the highest correlation between simulated relatedness estimates and true relatedness values, that is, the values expected for a certain relationship, using the software Coancestry V1.0.1.5 (Wang 2011). We included all individuals with no more than 3 missing loci and simulated 1,000 relatedness values based on the allele frequency distribution in our population. Simulations were completed for each of the following relationships: parent–offspring (PO), half-siblings (HS), and unrelated individuals (UR). We then compared the correlations between the simulated values and the expected true relatedness values (PO = 0.5, HS = 0.25, UR = 0) for all estimators. The triadic likelihood estimator TrioML (Wang 2007) showed the highest correlation and was therefore our relatedness estimator of choice.

Male–male associations during adolescence and adulthood

We quantified the effect of shared mtDNA haplotype, pairwise relatedness, age, and association rates during adolescence on adulthood association rates by building 2 linear mixed models. For both models, the response variables were the HWIs between focal males and their close associates during adolescence, and their alliance partners in adulthood, respectively. Advancing upon previous research in this area (Möller et al. 2001; Krützen et al. 2003; Parsons et al. 2003; Wiszniewski et al. 2012a; Diaz-Aguirre et al. 2018), this approach allowed us to analyze the ontogeny of alliance formation on an individual level during this critical period.

For the adolescence model (Model 1), the explanatory variables we tested were age difference in years, pairwise relatedness, and the presence or absence of a shared mtDNA haplotype. In the adulthood model (Model 2), we investigated association patterns of the focal males during their adulthood and included the same variables as Model 1, as well as a dyad's HWI during the focal male's adolescence. This additional variable permitted us to test whether a dyad's association during the focal male's adolescence predicts their association once the focal male reached adulthood. To control for repeated measures of individuals, we included the ID code of the focal male and his close associates (Model 1) or alliance partners (Model 2) as random effects. All analyses were carried out in R (R Core Team 2017), V3.4.0 and linear mixed models were built using the R package “lme4” (Bates et al. 2015).

To identify which combination of the above variables best described the observed association patterns during adolescence and adulthood, we first calculated a global model including all variables (Supplementary Table S1: Models 1 and 2). Subsequently, we used the “dredge” function in MuMIn (Barton and Barton 2018) to obtain second-order Akaike's Information Criterion values corrected for small sample size (AICc) for models containing only a subset of variables. Differences in AICc (Δ AICc) allowed us to determine the best models among candidate solutions (Zuur et al. 2007). We then averaged across the top model set separately for the adolescence (Model 1) and the adulthood model (Model 2), where Δ AICc < 2 (Burnham and Anderson 2003; Grueber et al. 2011). All models with Δ AICc < 2 are shown in Table 1.

Within-dyad relationship development

We wanted to determine whether age, relatedness, or shared mtDNA haplotype influenced the formation, maintenance, or termination of social bonds between adolescence and adulthood. For this, we combined data from the previous analyses to classify each dyad in one of the following 3 categories of within-dyad

relationship development (“RD”): close associates during adolescence and alliance partners in adulthood (“ASA”); close associates during adolescence but not alliance partners in adulthood (“ASO”); alliance partners in adulthood without having been close associates during adolescence (“AO”).

We built a total of 9 binomial generalized linear mixed models (Supplementary Table S1: Models 4a–c), in which we entered either pairwise relatedness, shared mtDNA haplotype or age difference as explanatory variables, and investigated their effect on the 3 relationship development scenarios. The variables were tested separately because models including combinations of the explanatory variables did not converge. To account for multiple tests, we adjusted the significance level to 0.0056 (Bonferroni correction, Dunnett 1955). In models (a), we were interested in whether males who became alliance partners without having been close associates (AO) differed in either age, relatedness, or shared haplotype from males that became alliance partners and were close associates during adolescence (ASA). In models (b), we investigated if any of the 3 variables were correlated with whether close associates during adolescence became alliance partners once adulthood was reached (ASA) or not (ASO). Lastly, in models (c), we tested whether male dyads with social bonds only during either adolescence or adulthood, that is, either being close associates (ASO) or alliance partners (AO) only, differed with respect to age difference, relatedness, or haplotype similarity.

Statistical significance of fixed effects was assessed using Satterthwaite's method as implemented in the package “lmerTest” (Kuznetsova et al. 2017). All models presented above were validated by likelihood ratio tests where we compared each model to a null model containing only the intercept and random effects. All models performed significantly better than their respective null models. To test for multicollinearity among our explanatory variables, we calculated the Variance Inflation Factors (VIFs), running the script containing the “corvif” function provided by Zuur (2009). None of our variables were correlated (Supplementary Table S5). Lastly, we checked the model assumptions visually by Q-Q plots, as well as histograms of the residuals (provided in Supplementary Material). Interactions were not significant in all models and were, thus, not incorporated.

RESULTS

Identification of “close associates” and “alliance partners”

We identified 3 change points (Figure 1) reflecting the multilevel social structure of male associations in our population. The first change point, observed at HWI of ≥ 0.38 , separates first-order alliance partners from second-order alliance partners ($N = 201$, mean = 0.55). The second change point, at HWI ≥ 0.19 , divides second-order alliance partners from males that occasionally associate ($N = 160$, mean = 0.28). The third change point, at HWI ≥ 0.09 , separates males that occasionally associate ($N = 182$, mean = 0.12) from those that randomly associate ($N = 1,212$, mean = 0.03). We treated all dyads with a HWI ≥ 0.19 (i.e., the second change point detected) as close associates during adolescence. The same value was used to identify alliance partners once the focal males transitioned into adulthood. This value is supported by earlier studies on the same population, showing that a HWI ≥ 0.2 validly clustered males into their respective second-order alliances (Smolker et al. 1992; Connor et al. 2001; King et al. 2018).

Table 1
Models with $\Delta\text{AICc} < 2$ compared with the top models

	Model	AICc	ΔAICc	Weight
1a	$\text{HWI}_{\text{adolescence}} \sim r + \Delta\text{age} + (1 \text{ID}_F) + (1 \text{ID}_A)$	-304.72	0	0.42
1b	$\text{HWI}_{\text{adolescence}} \sim r + (1 \text{ID}_F) + (1 \text{ID}_A)$	-304.54	0.18	0.39
1c	$\text{HWI}_{\text{adolescence}} \sim r + \Delta\text{age} + \text{haplotype} + (1 \text{ID}_F) + (1 \text{ID}_A)$	-303.11	1.6	0.19
2a	$\text{HWI}_{\text{adulthood}} \sim \text{HWI}_{\text{adolescence}} + \Delta\text{age} + (1 \text{ID}_F) + (1 \text{ID}_A)$	-448.1	0	0.63
2b	$\text{HWI}_{\text{adulthood}} \sim \text{HWI}_{\text{adolescence}} + \text{haplotype} + \Delta\text{age} + (1 \text{ID}_F) + (1 \text{ID}_A)$	-446.99	1.1	0.37

Results of model selection including model details of all models with $\Delta\text{AICc} < 2$. Models 1a–c were averaged to identify the effect of relatedness (r), shared haplotype, and age difference (Δage) on associations during adolescence. Individual ID codes are included as random effects ($\text{ID}_F = \text{ID focal}$, $\text{ID}_A = \text{ID Close Associate}$). Models 2a–b were averaged to explore how associations during adolescence, age difference, and shared haplotype influence adulthood association patterns. For the adulthood models, ID_A denotes alliance partners but all other abbreviations are consistent with the ones described for Models 1a–c. Relatedness was not included in the best adult models. Weight describes the proportion of a given model to the averaged model.

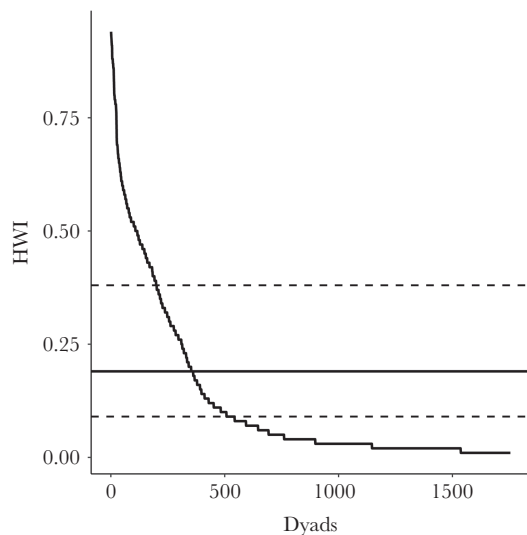


Figure 1
 Change point analysis showing HWI values defining various levels of association. Distribution of adulthood HWI among 1,755 dyads of focal males and all their male associates, with lines representing change points. The continuous line denotes the HWI value of 0.19 separating males with social bonds above the line from males that associate occasionally below. The dashed line ($\text{HWI} = 0.38$) differentiates second-order from first-order alliance partners. The dotted line ($\text{HWI} = 0.09$) separates random associations from occasional associates.

Furthermore, the identified value of $\text{HWI} \geq 0.19$ is well above average rates of association (mean $\text{HWI} = 0.12 \pm 0.17$, excluding zeros, $N = 1,755$). Since HWIs were calculated per age period, they reflect increased levels of association over a prolonged period of time. Thus, this value indicates differentiated relationships among male dolphins that fit our definition of social bonds.

Male–male associations during adolescence and adulthood

During adolescence, pairwise relatedness significantly correlated with HWI ($z = 2.974$, $P = 0.003$; Table 2), indicating that adolescent focal males associated more frequently with related males. Age difference between a focal adolescent male and its close associates, as well as shared mtDNA haplotype, was not a significant predictor of association patterns during adolescence.

Once focal males reached adulthood, the averaged model indicated age similarity ($z = 2.314$, $P = 0.021$; Table 2) and adolescence HWI ($z = 11.844$, $P < 0.001$; Table 2) as significant predictors explaining patterns of association. These results suggested that adult males affiliated more often with males of similar age, as well as males with whom they already closely associated during adolescence (Figure 2). In contrast to the best adolescence models, pairwise relatedness was not included in the best adulthood models and, thus, did not hold explanatory power for male associations. As in the adolescence model, shared mtDNA haplotype was not significant.

Within-dyad relationship development

We identified 209 dyads (53%) that were close associates during adolescence and became alliance partners in adulthood (ASA). In contrast, relatively few dyads ($N = 32$, 8%) were close associates during adolescence without becoming alliance partners in adulthood (ASO). Notably, this was not due to some individuals missing from the adulthood dataset because of permanent emigration or death; instead, this result may reflect selective termination of social bonds. We found 152 dyads (39%) that became alliance partners during adulthood without having closely associated during adolescence (AO). This result implies a significant overall net gain of social bonds during the transition from adolescence to adulthood (mean close associates \pm se adolescent males = 4.1 ± 3.2 ; mean alliance partners adulthood \pm se = 6.1 ± 3.8 ; Poisson Generalized Linear Mixed Model, $z = 4.414$, $se = 0.083$, $P < 0.001$; Figure 3; Supplementary Table S1: Model 3). To ensure that this result was not biased by the conservative cutoff of $\text{HWI} \geq 0.19$ for adolescence, we re-ran the change point analysis including adolescence HWIs > 0 only. The change point separating close associates during adolescence was found at $\text{HWI} \geq 0.15$. On average, individual males still had significantly more social bonds in their adulthood (mean close associates \pm se adolescence males = 4.9 ± 3.4 ; mean alliance partners \pm se adulthood = 6.1 ± 3.8 ; Poisson Generalized Linear Mixed Model, $z = 2.728$, $se = 0.078$, $P = 0.006$).

The within-dyad relationship models (Models 4) showed no effect of either shared haplotype or pairwise relatedness on within-dyad relationship development between adolescence and adulthood (Table 3, *Hap.*, r). Hence, neither the persistence nor the formation of social bonds between adolescence and adulthood seemed to be influenced by relatedness. However, age difference was significant in 2 out of the 3 models (Table 3, Δage). Dyads that were close associates in adolescence but did not become alliance partners in adulthood (ASO) had a significantly larger age difference

Table 2
Results of averaged models on male association rates during adolescence and adulthood

	β		SE		z-value		P-value	
	Adolescent	Adult	Adolescent	Adult	Adolescent	Adult	Adolescent	Adult
Intercept	0.352	0.426	0.014	0.015	26.016	29.053	< 0.001	< 0.001
Relatedness	0.047	NA	0.016	NA	2.947	NA	0.003	NA
Haplotype	0.002	0.005	0.009	0.011	0.269	.474	0.788	0.636
HWI _{Adolescent}	NA	0.187	NA	0.016	NA	11.844	NA	< 0.001
Age difference	-0.019	-0.039	0.020	0.017	0.927	2.314	0.354	0.0207

Results of averaged Models 1a–c and averaged Models 2a–b (Table 1), investigating the effect of age similarity, HWI during the focal male's adolescence (Models 2), pairwise relatedness, and shared haplotypes on association patterns during adolescence and adulthood in males. P-values in bold indicate significant results after Bonferroni correction.

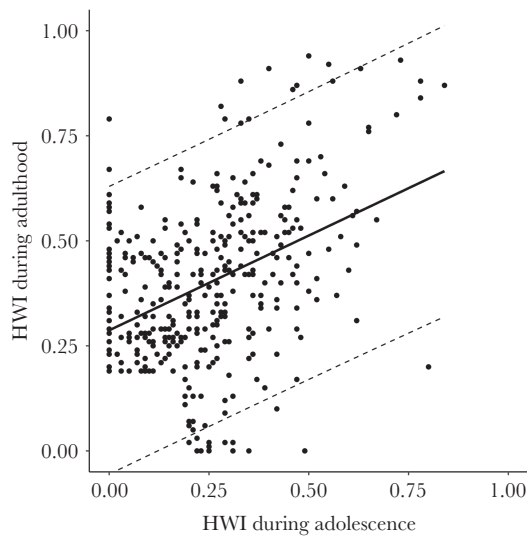


Figure 2

Positive correlation between adolescent and adult association rates within dyads. The association rate between an adolescent male and a second individual predicts the same dyad's association rate once a male matured into an adult, suggesting adolescent close associates foreshadow alliance partners ($N = 361$ dyads, Model 2). The dashed lines enclose the 95% confidence interval.

(mean \pm sd = 8.6 ± 7.1 years) than dyads that were close associates during adolescence and became alliance partners later on (ASA, mean age difference 3.5 ± 3.4 years; Binomial Generalized Linear Mixed Model, $P < 0.001$). These results indicated that similarly aged males were more likely to form persistent social bonds and, thus, become alliance partners. We also found significantly larger age differences between males who were close associates during adolescence without becoming alliance partners (ASO, Binomial Generalized Linear Mixed Model, $P < 0.001$) compared with dyads that were alliance partners but had not been close associates (AO, mean age difference 3.8 ± 3.1 years). It appeared that adult males formed social bonds with other males of more similar age than they did during adolescence.

DISCUSSION

Affiliation history and age similarity predicted social bonds and thus alliance partnerships among adult male bottlenose dolphins. Individual social bonds formed during adolescence, particularly

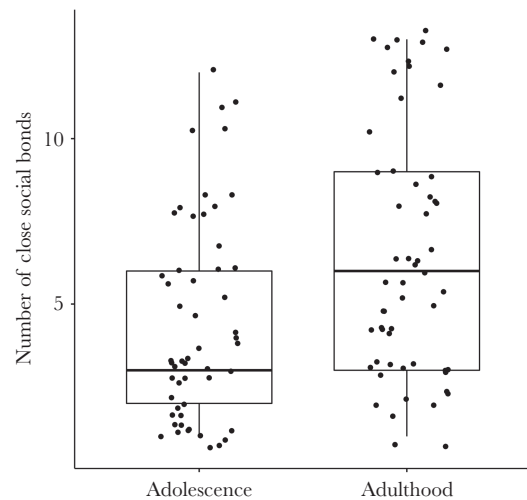


Figure 3

Increase in number of social bonds during the transition from adolescence to adulthood. Boxplot showing the average number of social bonds during the focal male's adolescence (i.e., number of close associates) and adulthood (i.e., number of alliance partners) including 95% confidence intervals. The average number of social bonds (HWI ≥ 0.19) is higher in a male's adult age bracket compared with its adolescence. This result suggests that males form additional social bonds during the transition into adulthood (Poisson Generalized Linear Mixed Model, including age period, i.e., adolescence or adulthood, as explanatory, number of close associates/alliance partners as dependent, and IDs as random variable, $P < 0.001$, $N = 118$, Model 3).

those among similar-aged males, persisted into adulthood. Kinship explained social bonds of adolescents, most likely due to bisexual philopatry (Krützen et al. 2004b; Tsai and Mann 2013). However, kinship did not predict the persistence of social bonds into adulthood or the existence of social bonds among adult males. Social bonds were maintained during the transition from adolescence to adulthood, yet, relatedness no longer predicted patterns of associations among adult dolphins. This effect is likely due to males increasing their number of social bonds between adolescence and adulthood.

Our finding that association rates during adolescence were positively correlated with relatedness may be best explained by associations with their mothers' related associates. In Shark Bay, adult females maintain high association rates with female relatives (Frère et al. 2010). This is in line with recent work that social networks in a large range of species, including bottlenose dolphins (Ilany and

Table 3
Results from within-dyad relationship analyses

	β			SE			z-value			P-value		
	r	Δ age	Hap.	r	Δ age	Hap.	r	Δ age	Hap.	r	Δ age	Hap.
ASA-AO	1.54	-0.10	0.36	1.06	0.05	0.20	1.45	-2.04	1.86	0.15	0.04	0.06
ASA-ASO	-0.11	-5.45	-0.67	5.89	1.11	1.50	-0.02	-4.90	-0.45	0.99	<0.001	0.66
ASO-AO	-20.08	1.38	3.37	11.80	0.24	2.13	-1.70	5.70	1.59	0.089	<0.001	0.11

Results of Models 4a–c, top to bottom.

ASA = close associates during adolescence and alliance partners in adulthood, ASO = close associates during adolescence without becoming alliance partners in adulthood, and AO = alliance partners in adulthood but not close associates during adolescence. r = pairwise relatedness, Δ age = age difference in years, Hap. = shared or nonshared haplotype.

P-values in bold indicate significant results after Bonferroni correction.

Akçay 2016), were shaped by social inheritance of maternal bonds (Goldenberg et al. 2016; Kerhoas et al. 2016).

Simple rules based on proximity and familiarity, without requiring sophisticated mechanisms to distinguish kin from nonkin, may operate where partner choice is kin biased. This is found in many primate species characterized by female philopatry (e.g., cercopithecine primates, Chapais 2002). Persistent social bonds during the transition from adolescence to adulthood suggest that male dolphins might apply the same rules. Yet, the outcome is very different when individuals are expected to have access to a limited number of close relatives and where kin discrimination may be limited (Lewis et al. 2013). Moreover, in order to maximize individual fitness, the identification of competent and compatible alliance partners may be more important than kin-biased partner choice. Traits that might be valued in alliance partners include resource holding potential (Parker 1974), cooperativeness (Heinsohn and Packer 1995), including the propensity to return received favors (Taborsky et al. 2016), competence (Chapais 2006), and other characteristics, such as behavioral homophily (e.g., in chimpanzees, Massen and Koski 2014) or dominance rank (e.g., hyenas *Crocuta crocuta*, Smith et al. 2007). The amount of time that individuals have been associated and their relationship quality may also be important factors influencing partner choice, as recently shown in female mangabeys (*Cercocebus atys*) and chimpanzees (Mielke et al. 2018), as well as ravens (*Corvus corax*, Asakawa-Haas et al. 2016). Furthermore, a modeling approach as well as experimental evidence from humans suggests that individuals are more likely to cooperate with previously helpful partners (Wang et al. 2012; Campenni and Schino 2014). Multiple positive experiences with the same partners can thus lead to persisting social bonds, although this may not always be the case (Schweinfurth and Taborsky 2018).

Adult male bottlenose dolphins in Shark Bay primarily cooperate to sequester estrus females within consortships, or in conflicts over access to females with other alliances; the latter entailing risk of injury (Connor et al. 2011; Connor and Krützen 2015; Hamilton et al. 2019). Hence, a male's reproductive success is not only determined by his own competence but also by that of his alliance partners, and how well these individuals can synchronize and coordinate their joint behaviors (Connor et al. 2006). Evidence that males selectively choose partners for activities whose payoff is affected by partner competency, independently of kinship, has also been described in chimpanzees. Males will participate in alliances, take part in risky boundary patrols, or share meat with the males that they either associate with most often and trust to take the same

risk (Watts and Mitani 2001), or with males of similar age and rank, rather than kin (Mitani et al. 2000, 2002b).

Bisexual philopatry and a slow life history, including a long developmental period, provide male dolphins in Shark Bay with opportunities to assess each other's competencies and compatibilities, as well as to form social bonds with desirable future alliance partners. Indeed, similar to chimpanzees (Kawanaka 1989; Pusey 1990), rats (*Rattus norvegicus*, Auger and Olesen 2009), and elephants (*Loxodonta africana*, Evans and Harris 2008), juvenile male dolphins in Shark Bay invest more time into social activities compared with females (Krzyszczuk et al. 2017). Social activities often involve play-herding, a behavior where adolescents practice consortship behavior (Connor et al. 2000a), which potentially serves to increase efficacy of future consortships through joint practice or to identify valuable alliance partners.

The persistence of social bonds during the transition from adolescence to adulthood implies that the actual formation of alliances is a protracted process, likely starting years before males become reproductively active. Even though social bonds among unrelated, similar-aged males could also arise by demographic constraints without invoking partner choice (Connor et al. 2000b), our finding of persistent social bonds and the fact that they are subject to directional changes suggest otherwise. During the transition from adolescence to adulthood, focal males increased the overall number of social bonds with new social bonds typically arising among male dolphins of similar age. The few social bonds that were discontinued were observed among males with larger age disparities. Hence, male dolphins showed a preference for a larger number of similar-aged alliance partners.

In bats, individuals can benefit from expanding their social networks by forming social bonds with nonkin (*Desmodus rotundus*, Carter et al. 2017). Individuals with larger networks consisting of kin and nonkin alike coped better with partner loss compared with individuals who had smaller networks consisting predominantly of kin. Considering the importance of alliance partners for male dolphins, expanding the social network with valuable nonkin individuals might lead to an increase in reproductive success and, thus, fitness. Under such a scenario, males might benefit from a larger number of alliance partners composed of kin and nonkin alike. Because of the different constraints on reproductive success between the sexes, males might prefer a large number of competent but unrelated partners. This is not necessarily the case for females. Therefore, social bond formation might underlie different criteria in the two sexes and might explain why males form social bonds

with nonkin, whereas the social partners of females usually consist of kin (Möller et al. 2006; Frère et al. 2010).

Male bottlenose dolphins might apply similar rules based on proximity, homophily, and familiarity for alliance formation as other species. Due to their social system, however, these do not necessarily lead to kin-biased cooperation. Thus, rather than kin selection, we propose that other evolutionary mechanisms, such as forms of intra-species mutualism (Connor 1986), reciprocity (reviewed in Trivers 1971; Taborsky et al. 2016), or a combination thereof, should be invoked when explaining the evolution of social bonds in male bottlenose dolphins (reviewed in Connor 2010). Our results reveal that long-term familiarity and age similarity, but not necessarily relatedness, influence the formation of multilevel alliances in male Indo-Pacific bottlenose dolphins. With this study, we add to the growing body of research highlighting the occurrence of enduring social bonds, or friendships, in animals, independent of relatedness.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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