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Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies

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Male bottlenose dolphins (*Tursiops* sp.) in Shark Bay have one of the most complex male societies outside humans. Two broad mating strategies have been identified in males. In the first strategy, there are two types of alliances: stable 'first-order' pairs and trios that herd individual females in reproductive condition, and 'second-order' teams of two first-order alliances (five or six individuals) that join forces against rivals in contests for females. In the alternative strategy, a 'super-alliance' of *ca.* 14 individuals, males form pairs or trios to herd females, but in contrast to the stable alliances, these pairs and trios are highly labile. Here, we show that males in stable first-order alliances and the derived second-order alliances are often strongly related, so that they may gain inclusive fitness benefits from alliance membership. By contrast, members of the super-alliance are no more closely related than expected by chance. Further, the strength of the association of alliance partners within the super-alliance, as measured by an index of joint participation in consorting a female, was not correlated with their genetic relatedness. Thus, within one population and one sex, it appears that there may be simultaneous operation of more than one mode of group formation.

Keywords: alliance formation; bottlenose dolphins; kinship; relatedness; skew theory; *Tursiops* sp.

1. INTRODUCTION

We have studied the association between genetic relatedness and grouping behaviour in a population of coastal bottlenose dolphins (*Tursiops* sp.) from Shark Bay, Western Australia, which show complex hierarchies of male alliances. One of the fundamental questions in evolutionary biology is 'Why should animals form groups—and even more interestingly, cooperate or exchange altruistic acts—when benefits might be unequal among group members?' Over the past decades, four main models have been developed that seek to explain the evolution and maintenance of cooperative or altruistic behaviours on an individual level: by-product mutualism, reciprocity, pseudo-reciprocity and kin selection (Hamilton 1964*a,b*; Trivers 1971; West-Eberhard 1975; Brown 1983; Connor 1986). The first three models do not assume that cooperating individuals are related, but genetic relatedness among cooperating individuals is one of the key assumptions of the kin selection model. Ever since the seminal work by Hamilton (1964*a,b*) on kin selection, genetic relatedness has been considered as one of the critical variables in the understanding of any social phenomenon.

Hamilton argued that cooperation among related individuals may be favoured by kin selection, because individuals can increase their inclusive fitness by assisting relatives' reproduction, even if the direct benefits of cooperation in terms of increased reproductive success accrue to only one or a few of the cooperating individuals. Such benefits have been demonstrated in eusocial (Reeve *et al.* 1990) and cooperatively breeding mammalian species (Packer *et al.* 1991), and also in lekking birds (Petrie *et al.* 1999). Individuals that jointly participate in aggression against conspecifics constitute a 'coalition' or 'alliance' (Harcourt 1992). Alliances between social groups are commonly observed in mammals, but within-group alliances are rare outside of primates.

Cooperation among males has received considerable attention in the past, because of the indivisibility of the resources for which males primarily compete, namely, females and conceptions (Van Hooft & Van Schaik 1992, 1994). Compared with females, males form coalitions less often. Coastal bottlenose dolphins (*Tursiops* sp.) live in fission–fusion societies, where group structure is variable rather than fixed (Wells *et al.* 1987; Smolker *et al.* 1992). During a long-term study, Connor *et al.* (1992*a,b*, 1999, 2001) demonstrated that in Shark Bay, sexually mature male dolphins show at least two coexisting mating strategies within a single population, involving two different

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levels with two distinct *strategies*. The two alliance *levels* are defined functionally. First, males form stable first-order (1°) alliances of two or three individuals to aggressively maintain consortships of females in reproductive condition. Second, two 1° alliances may cooperate, forming so-called second-order (2°) alliances, to take females being herded by another 1° alliance or to defend females from theft attempts (Connor *et al.* 1992a). The two *strategies* of alliances are concerned with the durability of 1° alliances and the size of the 2° alliances. There are 1° alliances that can be extremely stable, lasting for up to 17 years or more (R. C. Connor, unpublished data). By contrast, in the second *strategy*, males regularly change their 1° alliance partners within a large 2° alliance, sometimes called a 'super-alliance', while exhibiting significant partner preferences and avoidances (Connor *et al.* 1999, 2001). Cooperation between male dolphins has also been reported from Atlantic bottlenose dolphins (*Tursiops truncatus*) Sarasota Bay, Florida (Wells *et al.* 1987), and bottlenose dolphins (*Tursiops aduncus*) in Port Stephens, Australia (Möller *et al.* 2001), where pairs or triplets separate females from their groups, but 2° alliances have not been documented at either site despite extensive study. However, taxonomic relationships among populations of *Tursiops* remain unclear (LeDuc *et al.* 1999).

Over the past two decades, various models have been developed to explain evolutionarily stable strategies (*sensu* Maynard Smith 1982) when animal social groups cooperate in reproductive behaviour (Vehrencamp 1983a,b; Cant 1997; Clutton-Brock 1998; Reeve *et al.* 1998; Kokko & Johnstone 1999; Crespi & Ragsdale 2000; Johnstone 2000). Depending on the model, there is either negative, positive or zero correlation between relatedness and group size or skew (i.e. the asymmetry of reproductive shares). In transactional models, group members help each other to reproduce by offering reproductive incentives of different kinds in return for specific benefits (Reeve & Keller 2001). The two main transactional models are the restraint model and the concession model. In the restraint model, the subordinate completely controls its own breeding, while group membership is controlled by the dominant. Genetic relatedness is expected to be positively correlated with group size (Reeve & Keller 2001), as shown in male lions (*Panthera leo*), where the tendency of males to form coalitions with non-relatives drops sharply with increasing coalition size (Packer *et al.* 1991). In the concession model, group membership and breeding are both controlled by the dominant individual (Reeve & Keller 2001), which tolerates a certain amount of breeding of the subordinate. Under such a scenario, dominants would maximize their fitness by preferring relatives as subordinates. Importantly for our study, the concession model predicts a negative association between relatedness and group size (Reeve & Keller 2001). An expansion of the concession model is the bidding model, in which different groups bid for the help of subordinates (Reeve 1998). Under such a model, frequent group switching by subordinates, low relatedness and low reproductive skew are expected. In cases where dominance is not achieved by concession but by coercion, the manipulation model is appropriate (Crespi & Ragsdale 2000). Under this model, there is expected to be complete reproductive skew in favour of the dominant, and significant relatedness between

dominant and subordinate, to provide a fitness incentive for the subordinate to join the group.

The two different strategies of alliance formation within a single dolphin population allow clear tests of some model predictions concerning relatedness, group membership and group size, avoiding the confounding factors of comparisons across populations or species. In this paper, we aim to test the relationship between genetic relatedness and alliance membership. Estimation of genetic relatedness between cooperating individuals is becoming more frequent (Packer *et al.* 1991; Möller *et al.* 2001; Vigilant *et al.* 2001). However, relatedness estimators usually have high variances (Lynch & Ritland 1999), and their performance can be affected by the population composition and the loci chosen (Lynch & Ritland 1999; Van de Castele *et al.* 2001). It is particularly important that a relatedness estimator should have high precision (low standard deviation) and high accuracy (represent the actual relatedness of individuals). Ideally, one should choose a relatedness estimator that reflects true relatedness considering a given population composition. The number of loci studied and their level of polymorphism may affect relatedness estimates. Locus-specific weights seem to greatly improve the performance of estimators, if loci differ strongly in allele frequency distribution (Van de Castele *et al.* 2001). Choosing the best performing relatedness estimator for a given dataset can be achieved by carrying out Monte Carlo simulations to assess which estimator reflects the true relatedness best (Van de Castele *et al.* 2001).

In summary, we used a combination of behavioural and genetic data to test whether the evolution and maintenance of alliance formation in male bottlenose dolphins in Shark Bay may be influenced by kinship. In particular, we tested whether:

- (i) members of 1° alliances are more closely related to each other than expected by chance;
- (ii) males who are members of the same 2° alliance but not the same 1° alliance are more closely related to each other than expected by chance;
- (iii) members of the super-alliance are more closely related to each other than expected by chance;
- (iv) members of the super-alliance form labile pairs or trios with closely related males.

2. MATERIAL AND METHODS

(a) *Study area and sample collection*

Shark Bay is a large and relatively shallow embayment complex ca. 850 km north of Perth in Western Australia (ca. $25^\circ 30'$ S, $113^\circ 30'$ E), where bottlenose dolphins have been systematically studied since the mid-1980s (Smolker *et al.* 1992; Connor *et al.* 1992a,b). Between 1994 and 1999, we opportunistically collected tissue samples from free-ranging bottlenose dolphins in the eastern gulf of Shark Bay. Biopsy samples were obtained employing a biopsy system designed for small cetaceans (Krützen *et al.* 2002), and stored in a saturated NaCl/20% (v/v) dimethyl sulphoxide solution (Amos & Hoelzel 1991) until further processing in the laboratory. Alliance membership was known from ongoing surveys and focal animal sampling (Smolker *et al.* 1992; Connor *et al.* 1992a, 1999; R. C. Connor,

Table 1. Mean relatedness \pm variance for simulated populations consisting of 1000 pairs of UR, HS, FS or PO pairs^a. (In parentheses are two-tailed p -values of t -tests for difference from expected relatedness value (0.0 for UR, 0.25 for HS, 0.5 for FS and PO). The smallest sampling variances that did not show significant bias are given in bold.)

	relationship			
	UR	HS	FS	PO
\hat{r}_{Swavl}	-0.0058 ± 0.0215 (0.210)	$0.2444 \pm \mathbf{0.0206}$ (0.216)	$0.5038 \pm \mathbf{0.0204}$ (0.396)	$0.4992 \pm \mathbf{0.0078}$ (0.771)
\hat{r}_{R}	$-0.0027 \pm \mathbf{0.0074}$ (0.315)	0.2483 ± 0.0345 (0.775)	0.5096 ± 0.0451 (0.155)	0.5028 ± 0.0320 (0.617)
$\hat{r}_{\text{QrsI,rsi}}$	-0.0088 ± 0.0200 (0.050)	0.2433 ± 0.0208 (0.140)	0.4975 ± 0.0213 (0.591)	0.4961 ± 0.0082 (0.175)
$\hat{r}_{\text{QrsI,avi}}$	-0.0089 ± 0.0205 (0.050)	0.2456 ± 0.0213 (0.340)	0.5013 ± 0.0214 (0.779)	0.5010 ± 0.0083 (0.725)
$\hat{r}_{\text{Qwavl,rsi}}$	-0.0037 ± 0.0161 (0.359)	0.2299 ± 0.0179 (0.000 ^a)	0.4846 ± 0.0191 (0.000 ^a)	0.4633 ± 0.0081 (0.000 ^a)
$\hat{r}_{\text{Qwavl,avi}}$	-0.0073 ± 0.0202 (0.107)	0.2465 ± 0.0216 (0.454)	0.5039 ± 0.0208 (0.392)	0.4979 ± 0.0095 (0.499)

^a The significance level after sequential Bonferroni correction (Rice 1989) for the four tests was 0.013.

unpublished data). For a detailed description of alliance definition see Connor *et al.* (1992a, 1999).

(b) Genetic data analysis

Total genomic DNA was extracted from skin biopsies using standard methods (Davis *et al.* 1986). All samples were genotyped using the polymerase chain reaction (PCR) with a panel of 12 highly polymorphic dinucleotide microsatellite loci, MK3, MK5, MK6, MK8, MK9 (Krützen *et al.* 2001); EV1, EV14, EV37 (Valsecchi & Amos 1996); KWM12 (Hoelzel *et al.* 1998); 199/200 (Amos *et al.* 1993); and D14, D22 (Shinohara *et al.* 1997). We sized the PCR products using an ABI 377 DNA automated sequencer (Applied Biosystems). To measure the size of the fragments obtained, we used the software GENOTYPER, v. 1.1.1 (Applied Biosystems). The animals were genetically sexed following the protocol of Gilson *et al.* (1998). To test the suitability of the 12 loci for relatedness analyses, we estimated levels of expected heterozygosity (H_E), checked for physical linkage of microsatellite loci, and also checked for the presence of null alleles by comparing mother–offspring pairs, as well as by using an iterative algorithm based on the difference between observed and expected frequency of homozygotes (Summers & Amos 1997), using CERVUS v. 2.0 (Marshall *et al.* 1998).

Relatedness analysis requires detailed knowledge about genetic population structure, so that an appropriate base population can be chosen for calculation of allele proportions. Previous studies on the dolphin population in East Shark Bay—the core study area—have shown that for microsatellites and mitochondrial DNA, there is only weak isolation by distance, with gene flow (Nm) estimated to be 9–130 among different parts of the core study area (M. Krützen, unpublished data). This very high gene flow between areas prevents population subdivision; hence there was no need to partition the dataset to accommodate population structure.

To assess which relatedness estimator performs best for our dataset, Monte Carlo simulations were performed for six different estimators (Van de Castele *et al.* 2001). Mean pairwise relatedness (\hat{r}) estimators were the similarity index \hat{r}_{Swavl} (Li *et al.* 1993), a regression-based method-of-moments estimator \hat{r}_{R} (Lynch & Ritland 1999) and four different regression-based symmetric estimators: $\hat{r}_{\text{QrsI,rsi}}$, $\hat{r}_{\text{QrsI,avi}}$, $\hat{r}_{\text{Qwavl,rsi}}$, $\hat{r}_{\text{Qwavl,avi}}$ (Queller & Goodnight 1989); for definitions see Van de Castele *et al.* (2001). Four datasets of 1000 pairwise genotypes were created using the observed allele proportions in the Shark Bay dolphin population for four possible types of relationship: parent–offspring (PO), full siblings (FS), half siblings (HS) and unrelated

(UR). We then calculated pairwise relatedness values and tested for significant departure from expected levels, using a two-tailed t -test. The proportion of the total variance in microsatellite estimates explained by true relatedness was calculated (Van de Castele *et al.* 2001). For all subsequent work, we used the best performing \hat{r} (see § 3).

(c) Statistical analysis of pairwise relatedness values

To test the first three hypotheses, we used a resampling simulation (Sokal & Rohlf 1995) to produce randomized pairwise relatedness values among all males 1000 times; we then counted the number of occasions on which the randomized \hat{r} for each alliance type was larger than the observed. We tested the fourth hypothesis by counting the number of times that the correlation coefficient between randomized coefficient of association (COA) (Connor *et al.* 1999) and pairwise relatedness matrices exceeded the actual correlation coefficient of randomized COA and \hat{r} (Manly 1997), using PopTools v. 2.3 (<http://www.cse.csiro.au/poptools/>).

3. RESULTS

(a) Sample collection and behavioural data

During our field seasons, we collected 305 biopsy samples. We were able to identify 224 individuals either directly in the field, or by comparing a photograph of the dorsal fin to an established photographic catalogue. We sampled 161 males (128 sighted at least five times) and 139 females (96 sighted at least five times). For five animals, we were not able to assign sex using either behavioural or genetic methods. Based on previous surveys and focal follows, we assigned 28 different sexually mature males to different alliance types: 16 males were members of seven 1° alliances, with two individuals being members of different 1° alliances in different years (Smolker *et al.* 1992; R. C. Connor, unpublished data). Eight of these males formed two different 2° alliances (one 1° alliance was found in both sampled 2° alliances). We also sampled 13 of the 14 males in one intensively studied super-alliance.

(b) Genetic data and performance of relatedness estimators

The mean number of alleles per locus was 13.8 (\pm s.d. 5.3, range 8–23 alleles) and mean H_E was 0.77 (range

Table 2. Alliance memberships and pairwise relatedness values (\hat{r}_{Swavl}).

(Each three-letter code represents a single individual. The lower half of the matrix shows all pairwise combinations for the super-alliance. The upper half of the matrix shows the possible pairwise combinations of members of seven first-order alliances. Each alliance is enclosed by solid lines, and two second-order alliances are shaded in grey; BUM, BAM and BJA were members of both sampled 2° alliances.)

	HII	BOT	POI	LUC	WAV	SPU	SHK	CRC	SYL	BJA	BUM	BAM	BIF	BOH	
	0.256	0.091													REA
		0.093													HII
GRI	-0.238		0.153												BOT
VAX	0.015	0.077		-0.192											POI
KRI	0.020	-0.040	-0.187												LUC
MYR	-0.269	0.443	-0.025	-0.110		-0.408									WAV
WOW	0.224	0.105	0.322	-0.096	0.098										SPU
HOB	-0.044	0.110	-0.168	-0.127	-0.082	-0.121		0.009	-0.004	0.116	0.229	-0.186			SHK
WBE	0.149	0.074	-0.083	0.077	-0.083	0.227	0.125		0.302	0.104	0.415	0.154			CRC
HOR	-0.078	0.211	-0.135	-0.230	0.182	0.121	0.106	0.261		-0.095	0.029	0.065			SYL
AJA	-0.235	0.228	-0.044	-0.161	-0.011	-0.160	0.069	0.246	0.322		0.489	-0.044	0.108	0.148	BJA
PIK	-0.105	0.350	-0.069	0.042	0.023	-0.050	0.086	0.600	0.213	0.270		0.283	0.464	0.491	BUM
ANV	-0.050	-0.233	-0.391	-0.391	-0.211	-0.125	-0.406	0.114	0.106	0.022	-0.055		0.158	0.126	BAM
VEE	0.141	0.021	0.152	-0.109	-0.078	0.003	-0.089	-0.045	0.058	0.007	-0.169	-0.166		0.255	BIF
	LAT	GRI	VAX	KRI	MYR	WOW	HOB	WBE	HOR	AJA	PIK	ANV			

Table 3. Mean relatedness (\hat{r}_{Swavl}) and 95% confidence intervals (c.i.) for all possible pairwise combinations (PC) for all sampled members (n) within seven 1°, two 2° alliances and one super-alliance.

(Second-order alliance comparisons are only between members of different first-order alliances. p indicates the proportion of randomizations on which \hat{r} values were larger than the observed.)

alliance type	\hat{r}_{Swavl}	c.i.	PC	n	p
1°	0.104	±0.057	13	15	0.008
2°	0.155	±0.095	15	8	<0.001
super-alliance	0.003	±0.042	78	13	0.328
all males	-0.006	±0.005	5663	162	

0.64–0.89). All loci used for relatedness analysis were in Hardy–Weinberg equilibrium, no linkage disequilibrium could be observed, none of the loci were sex-linked, and the proportions of null alleles, if present, were below 0.03 (data not shown).

For the three categories concerning related animals (HS, FS, PO), $\hat{r}_{\text{Qwavl,rsi}}$ showed the lowest variance. However, $\hat{r}_{\text{Qwavl,rsi}}$ is biased: simulated values are significantly lower than expected (table 1). The estimator with the lowest variance for categories concerning related animals with no significant bias is \hat{r}_{Swavl} (table 1). For different types of population composition, $\hat{r}_{\text{Qrsi,rsi}}$ and \hat{r}_{Swavl} explain most of the true variance (data not shown), but computation of \hat{r}_{Swavl} is much less time consuming than that of $\hat{r}_{\text{Qrsi,rsi}}$. Therefore, we chose \hat{r}_{Swavl} for calculating pairwise relatedness between all individuals, on the basis of its high level of precision, accuracy and ease of computation.

(c) Analysis of pairwise relatedness values for different alliance types

Patterns of relatedness differed between the different alliance types (table 2). The mean relatedness for all 1° alliances was 0.104 (range -0.408 to 0.489), which was significantly above random expectations (table 3). This

elevated level of relatedness was also seen in five out of seven of the 1° alliances (table 2). In 2° alliances, the mean relatedness among all members, calculated only between members of different 1° alliances, was 0.155 (range -0.186 to 0.491; table 3); this value was significantly above random expectations (table 3). The mean relatedness values for the two 2° alliances were 0.248 and 0.124 (ranges -0.044 to 0.491 and -0.186 to 0.489, respectively). In the super-alliance, the mean relatedness among all members was 0.003 (range -0.406 to 0.600; table 2), which was not significantly above random expectations (table 3). The fact that males within the super-alliance are, on average, not more closely related than expected by chance does not rule out the possibility that super-alliance members might prefer to associate with males to which they are more closely related. Each male forms highly labile pairs or trios with a limited number (5–11) of other super-alliance members, exhibiting significant preferences and avoidances (Connor *et al.* 1999, 2001). Surprisingly, this is not reflected by pairwise relatedness values among males with strong preferences for each other, as there was no significant correlation between pairwise COAs and corresponding \hat{r}_{Swavl} ($p = 0.956$).

4. DISCUSSION

Male dolphins in Shark Bay within a single social network show two different modes of alliance formation with different evolutionary histories. In this paper, we demonstrated that different patterns of relatedness are found in two distinct strategies of male alliance formation. Males that cooperate in stable 1° alliances are, on average, significantly more closely related to each other than expected by chance, and they are also significantly related to their 2° alliance partners. By contrast, the average relatedness among all super-alliance members was not significantly different from the average relatedness of all males, and the strength of the association of alliance partners within the super-alliance was not correlated with their genetic relatedness. To date, there seems to be no model that

could adequately explain all aspects of nested alliance formation in male bottlenose dolphins. One possible explanation for these apparently different modes of alliance formation would be that they are based on different ecological constraints. However, the extensive home range overlap of different alliance types renders this possibility unlikely (Connor *et al.* 1999).

Another possible explanation of the patterns of relatedness and alliance formation is that there is more than one evolutionarily stable strategy in this population. As there is significantly elevated relatedness in stable 1° alliances and their 2° alliance partners, it is conceivable that the first strategy of formation of 1° and 2° alliances for the purposes of sexual coercion and intrasexual competition may be favoured at least in part by inclusive fitness benefits. By contrast, the second strategy of labile 1° alliance structure within the super-alliance may be based on short-term expedience, and the size of the super-alliance may allow individuals to hold their own in competition with stable alliances of related males (Connor *et al.* 1999). Thus, the disadvantage for super-alliance members of allying with unrelated individuals might be offset by their ability to succeed in most conflict situations.

5. CONCLUSION

It appears that no single existing model of the evolution of social behaviour can adequately explain all aspects of multi-level alliance formation in Shark Bay male dolphins. The negative association between relatedness and group size (super-alliance versus other 2° alliances) is consistent with predictions of either the concession or manipulation models, and this inference may be supported by high reproductive skew within the stable 1° alliances (M. Krützen, unpublished data). However, within the super-alliance, the frequent partner switching irrespective of relatedness is inconsistent with these models, but supports the bidding model. Thus, within one sex, it appears that there may be simultaneous operation of more than one mode of group formation and its evolution.

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