

Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.)

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ABSTRACT In Shark Bay, Western Australia, male bottlenose dolphins (*Tursiops* sp.) cooperate in pairs and triplets to sequester and control the movements of females. We refer to this behavior as “herding” and to the male pairs and triplets as alliances. During a 25-month study (1987–1989) on the social relationships of males, we documented herding in 10 alliances. Males preferentially herded nonpregnant females likely to be in estrus. Alliance members associated with one another consistently when not herding females. Each alliance associated preferentially with one or two other alliances. Occasionally, two alliances combined and took females from another alliance or defended females against such efforts. This study documents multiple-level male alliances within a social group outside of humans.

The social groups of many birds and mammals function as alliances against nonmembers (e.g., refs. 1–4). Alliances within social groups are reported commonly in primates but rarely elsewhere (5). Prior to this study there were only two reports of coalition or alliance formation in cetaceans [bottlenose dolphins (*Tursiops truncatus*) and spotted dolphins (*Stenella attenuata*)] and in neither case was the function of the behavior clear (6, 7).

In Shark Bay, Western Australia, wild bottlenose dolphins (*Tursiops* sp.) have become exceptionally tame, allowing detailed studies of dolphin social behavior, including alliance formation (8). Since 1984 we have observed a social network of >300 individually identified bottlenose dolphins in a 130-km² area around the Monkey Mia campground on the Peron Peninsula in Shark Bay (25°47'S, 113°43'E). For 25 months during 1987–1989 we studied the social relationships of 21 males. We observed three of these males in shallow water at Monkey Mia where they were fed daily by tourists (8). Most results reported here are from scan samples of group composition, follows of focal individuals (range, 1–9.5 hr; total, 535 hr), and ad libitum observations (9).

Scar patterns and shapes of dorsal fins are used for individual identification; photographs of identifying features of each individual are on file. Sixteen of 21 focal males were sexed by observing an erection, two by a ≥ 2.5 -cm gap between the genital and anal slits and by the absence of mammarys, and three by the gap alone.

Male–Male Associations

Bottlenose dolphins live in “fission–fusion” societies (10, 11) in which party size and membership are variable and in which all members of the social network are never together in one party (7, 12). Foraging and feeding assemblages of dolphins in Shark Bay are typically ephemeral and poorly defined. We restrict our analysis of associations to resting, traveling, and socializing parties. We include as party members any individuals within 10 m of at least one other dolphin in the group.

The modal distance between individuals in such groups is typically ≤ 2 m. We use pairwise “half-weight” association coefficients (13), defined as $100 \times 2N_{ij}/(N_a + N_b)$, where N_{ij} is the number of parties in which A and B are found together and N_a and N_b are the total number of party sightings for A and B, respectively. This equation yields association coefficient values ranging from 0 for two individuals that are never sighted together in parties to 100 for individuals that are always sighted together.

Association coefficients for some male “pairs” are in the same range as those found between females and their nursing calves (80–100). Members of male pairs rank as each other’s closest associate. Groups of three males (“triplets”) are also common; members of a triplet rank as each other’s first or second closest associate. Five years of survey data on party composition (1985–1989) show that male pairs and triplets typically remain stable for years (unpublished data). We do not know how males in pairs and triplets are genetically related. Similar high levels of association between males have been reported from Sarasota Bay, Florida (7). In Shark Bay, each pair or triplet also preferentially associates with one or two other pairs or triplets (Fig. 1).

First-Order Alliances: Aggressive Herding of Females

During 1987–1988, the three provisioned males herded single dolphins or mother/calf pairs for periods ranging from a few minutes to 13 days. We sexed 30 of 48 dolphins herded by the provisioned males; all 30 were females, and we assume that the other 18 were as well.

A herding event begins when two or three males capture a female. We observed 19 captures by the provisioned males, of which 17 included obvious chases and 2 merely involved the males rushing up to and around the female. In one capture the chasing, displays, and aggression continued for 85 min and covered 7 km. The male displays often included striking synchronous underwater turns and aerial leaps. Male aggression toward a consort included chasing, hitting with the tail, head-jerks (sharp lateral or vertical movements of the head), charging, biting, or slamming bodily into the female. Males enforced herding partly by making a “popping” vocalization which induced the herded female to approach (R.C.C. and R.A.S., unpublished data). When a female failed to approach a popping male, he sometimes threatened or attacked her. During travel, males typically remained just behind and to either side of a herded female, behavior which we call formation swimming. Herded dolphins bolted from the provisioned males on 179 occasions, escaping in 45 (25%) of the attempts. The males chased in 25 (56%) of the escapes. The manner in which males chased bolting females illustrates the cooperative nature of herding: rather than chasing directly behind the female, the males often angled off to either side, effectively cutting the distance if she changed direction. Herding ended when the female escaped.

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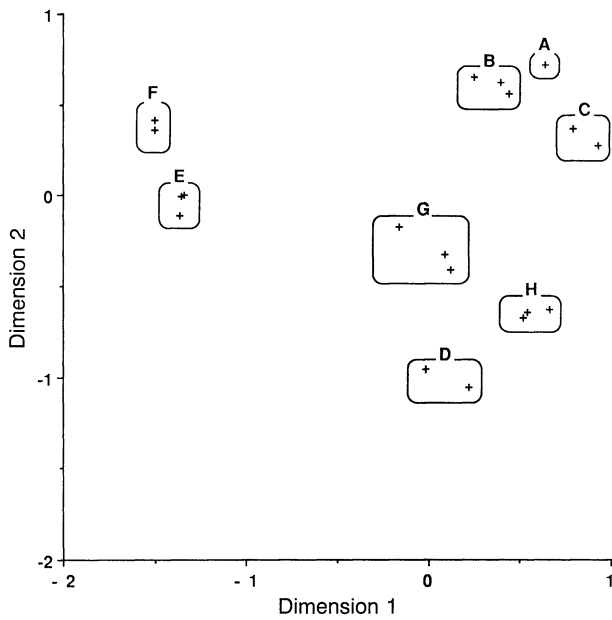


FIG. 1. Associations within and between dolphin alliances are represented by scaling, in two dimensions, the association matrix for the 21 focal males in all male groups (refs. 14 and 15; Kruskal's stress formula 1; stress = 0.048). The letters (A–H) correspond to those given for alliances in the text and Fig. 2. Each point represents one individual except for the point in A and one in C in which the points for two dolphins overlap exactly.

Only two of the three provisioned males herded a female together at a time; we refer to the males with the female as “partners” and the remaining male as the “odd-male-out.” Partners often moved with remarkable synchrony. There were frequent changes in which male was odd-male-out. We recorded which two males were partners during the males’ daily visits to the provisioning area. The odd-male-out would sometimes form a partnership with either member of a pair of nonprovisioned males (alliance D) that frequently associated with the provisioned males (Fig. 1).

Because we cannot observe the dolphins 24 hr per day we can only estimate the total number and duration of many herding events. On 13 occasions we observed a herding association between a female and the provisioned males terminate only to reform later the same day or on the following day. From this we assume that some herding associations were terminated and reestablished between observation periods. Thus, if we define the length of a herding event as the number of consecutive days that males spend with a female, we may underestimate the number of herding events and overestimate their durations.

Most partner changes among the provisioned males occurred when the males were not herding a female (we observed only one partner change during a herding event). In 8 of the 13 cases in which an association with a female terminated and was reestablished by the next day, partners changed between events. Partner changes can therefore be used to detect some of the cases where associations were terminated and reestablished while we were not observing. However, incorporating partner changes into our estimation of the number of herding events may also bias our estimate upward to the small extent that partner changes occur while a herded female is with the males. Incorporating data on partner changes increases the estimate of herding events involving the provisioned males from 240 events derived from the “consecutive female day” method to 255, an increase of only 6%.

For the provisioned males, we recorded a confirmed herding event if we observed any of the following: (i) a capture,

(ii) a bolt, (iii) a male “popping,” or (iv) aggression (charge, head-jerk, bite, or hit) directed at a nonprovisioned (and unhabituated) dolphin in the feeding area. We observed one or more of these four behaviors in 208 (82%) of the total sample of 255 suspected herding events. Although we did not confirm herding in the remaining 47 cases, the behavior of the males was otherwise typical of herding (traveling in formation, displays, etc.), and nearly all the females involved were unhabituated and would be unlikely to enter the feeding area without coercion. We believe we failed to confirm herding in these cases because of inadequate observation time. In a restricted sample of 149 events in which we had at least 20 min of continuous observation of the provisioned males with a female, we confirmed herding in 142 cases (95%).

During 1987–1989 we documented 58 cases of herding by nine alliances of nonprovisioned males from observations of a capture, a bolt, pops, or a theft (in which two alliances took a female from another alliance). The longest association between an alliance and a female spanned 28 days ($n = 8$ sightings). A Mantel test (16, 17) revealed a strong association between male–male association in all-male groups and joint participation in herding for 13 nonprovisioned focal males ($n = 13$; $t = 6.65$, $P < 0.001$; Fig. 2). The persistence of male pairs and triplets in nonherding contexts implies that such relationships have a cooperative basis.

Second-Order Alliances: Thefts of Females

On six occasions two first-order alliances joined forces to take females aggressively from other alliances. In five of the six thefts, both alliances participated in chasing and fighting the defending alliance; in the other case we could not determine if one of the alliances participated. Only one of the two attacking alliances herded the female after a theft. In three thefts, the alliance that did not obtain the stolen female already had a female that they herded before, during, and after the theft.

In two thefts the defending alliance was assisted by another alliance, resulting in a “two alliances against two” (five

	12	12	24	26	20	21	23	21	31	28	35	31	25
	A1	A2	B1	B2	B3	C1	C2	C3	D1	D2	E1	E2	E3
A1	-	100	44	37	44	24	39	24					
A2	15	-	44	37	44	24	39	24					
B1			-	92	82	13	21	13					
B2			15	-	83	8	16	8					
B3			15	16	-	14	23	14					
C1						-	91	100					
C2	1	1	1			10	-	91					
C3						10	10	-					
D1									-	88			
D2									5	-			
E1											-	93	81
E2											1	-	80
E3											1	1	-

FIG. 2. Association coefficients from all-male groups (upper right) and the number of times males herded together (lower left) for the 13 nonprovisioned focal males who were observed herding. Blank cells have zero values. A Mantel test ($t = 6.65$, $P < 0.001$) reveals a strong association between male–male association and herding partners. The numbers above each of dolphin’s letter code are the number of sightings in all-male groups for each individual.

individuals against five individuals) encounter. The outcome of the four "two alliances against one" thefts was decided in <2 min each. One of the "two against two" thefts was discovered in progress and lasted 10–20 min; in the other, chasing and fighting lasted for 70 min and covered 8–9 km.

In four thefts, male pair A combined with triplet B to take females from the provisioned males (alliance H, which was assisted by alliance D on two occasions). Once, A accompanied C when they took a female from B, but we did not see whether A participated in aggression against B. The next day A and B took a female from H, which B herded. One week later, A and B again took a female from H, which A herded. This sequence shows that alliances between alliances shift, perhaps in response to changes in the social context in which such alliances occur.

Alliances may recruit other alliances to participate in thefts. During 9 months of observation (1986–1987) before the two thefts described above involving alliances A and B, A and B had been sighted in the feeding area only once each and on both occasions the provisioned males (H) were absent. Prior to both thefts, however, B visited the feeding area, approaching as close as four meters to H with no apparent response by H. Alliance B then left the provisioning area but returned for the thefts accompanied by alliance A 150 and 105 min later, respectively. In one of the two thefts we found A and B together 1.5 km north of the feeding area after B's visit and 85 min prior to the theft.

Alliances and Reproduction

Pregnancy becomes obvious to observers 2–3 months prior to parturition, when the female's abdomen becomes very swollen. Of 28 females herded by the provisioned males in 1987, we were able to monitor 16 individuals for visible signs of pregnancy throughout the late austral winter and early summer of 1988 (July–November). Eight of these females gave birth during the 1988–1989 austral summer, and the other 8 did not give birth and clearly did not attain an advanced stage of pregnancy (it is possible that these females conceived in 1987 but lost the fetus at an earlier stage). To determine whether or not males herd nonpregnant (and potentially receptive) females differentially, we compared the number of times each female was herded during April–November 1987 with the number of times she was herded during the same period in 1988 (Table 1). Females who gave birth in late 1988 or early 1989 were herded much less during 1988, when they were pregnant, than during 1987, when they were not pregnant (Wilcoxon signed-ranks test, $P = 0.018$). Females who did not give birth in the summer of 1988–1989 showed a trend toward being herded more often in 1988 than in 1987, but the difference was not significant (Wilcoxon signed-ranks test, $P = 0.093$). The single herding event for "Cro" in 1988 was excluded from this analysis because it occurred after she gave birth in October. The change in herding between 1987 and 1988 for pregnant versus nonpregnant females demonstrates that males more frequently herd nonpregnant females (Mann–Whitney U test, $U = 3$, $P = 0.002$). Based on birth dates, most of the pregnant females would have been pregnant for at least 2 months by April 1988, and so our results apply only to mid–late pregnancy.

Researchers have been unable to detect reliable estrus cues in bottlenose dolphins (18). Herding, however, is a useful behavioral indicator (19). We have observed sexual behavior, including mounting, during herding as well as in other social contexts (e.g., infant males mounting adult males). In 8 of 26 herding events in which we saw a male mount a herded female, two males mounted the female synchronously from either side. Although it is often difficult to see whether a mounting male has an erection, on some occasions both males had erections. In right whales (*Eubalaena glacialis*)

Table 1. Herding by the provisioned males in 1987 and 1988: Females that calved in spring–summer 1988–1989 versus those that did not

Female	No. of times herded	
	1987	1988
Calved		
Puc	6	0
Cro	15	1
Pdx	9	0
Mun	2	0
Hol	7	0
Yog	3	0
Psu	1	1
Mer	5	0
(Subtotal)	48	2
Did not calf		
Jfr	4	9
Squ	2	0
Ton	1	2
Sur	5	10
Yan	2	0
Jag	10	16
Wav	3	7
God	6	8
(Subtotal)	33	52

Females that were pregnant in 1988 were less attractive than they were in 1987 compared with females that did not calve (Mann–Whitney U test of between-year differences for pregnant versus nonpregnant females, $U = 3$, $P = 0.002$).

two males have been observed to achieve intromission simultaneously (20). We have not been able to observe intromissions, so we do not know how copulations are distributed within an alliance of males.

Two Levels of Alliance Formation: A Comparative Perspective

Social interactions among first-order alliances of male dolphins resemble interactions among individual males of some primate species. Thus, both *individual* male chimpanzees (*Pan troglodytes*) and *alliances* of male dolphins (*i*) associate consistently with one another in nonagonistic as well as agonistic contexts, (*ii*) form alliances with the same parties with which they have agonistic interactions on other occasions, and (*iii*) form aggressively maintained but temporary consortships with receptive females (21–24). Second-order alliances in male bottlenose dolphins are used to acquire access to (apparently) estrous females as are (first-order) alliances in savanna baboons (25). Both chimpanzee and baboon males may recruit alliance partners (21, 26).

In both common chimpanzees and bottlenose dolphins, herding may be a strategy to monopolize females. Female chimpanzees typically mate with multiple males (27). Testis size, sperm concentration, and association patterns also predict multi-male mating for female *Tursiops* (7, 28). In support of this prediction, we observed females being herded by as many as 13 males during the season they conceived.

Two-level male alliances with triadic interactions among alliances and with both hostile and affiliative interactions between particular alliances appear not to have been identified except in dolphins and humans (29). Connor *et al.* (29) suggest that complex social relationships, including multiple-level alliance formation, may have played a role in the evolution of the large delphinid brain. The brains of many delphinids, including *Tursiops*, are 2–3 times larger than those of some other toothed whales (odontocetes) of similar

body size (29–31). The “social complexity” hypothesis for large-brain evolution (32–35) predicts that social relationships, including alliance formation, will be more complex among these large-brained forms than in small-brained genera.

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