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COORDINATED BREATHING IN BOTTLENOSE DOLPHINS (TURSIOPS TRUNCATUS) AS COOPERATION: INTEGRATING PROXIMATE AND ULTIMATE EXPLANATIONS

by

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Coordinated Breathing in Bottlenose Dolphins (*Tursiops truncatus*) as Cooperation: Integrating Proximate and Ultimate Explanations

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In this study, coordinated breathing was studied in 13 common bottlenose dolphins because of its links with spontaneous coordinated behaviors (e.g., swimming, foraging, and playing). A strong link was shown between dyadic coordination levels and age/sex categories when both association patterns and spatial formation are considered. This is consistent with a significant influence of social relationships on cooperating and contrasts with an economic perspective based on immediate material outcomes alone. This cooperation bias is explained by linking proximate processes that evoke performance with ultimate evolutionary processes driven by long-term adaptive outcomes. Proximate processes can include 2 kinds of immediate outcomes: material reinforcements and affective states associated with acts of cooperating that can provide positive reinforcement regardless of immediate material benefits (e.g., when there is a time lag between cooperative acts and material outcomes). Affective states can then be adaptive by strengthening social relationships that lead to eventual gains in fitness.

Keywords: cooperation bias, coordinated cooperation, proximate and ultimate explanations, time lag, *Tursiops truncatus*

Cooperation is usually defined and explained by biologists from a pure economic perspective that emphasizes the outcomes that benefit all participants by increasing their individual or inclusive fitness (Clements & Stephens, 1995; Dugatkin, 1997; Kéfi, Bonnet, & Danchin, 2007; Stephens & Anderson, 1997; Trivers, 1985). In behavioral terms, individuals are expected to act rationally by choosing to cooperate in a way that maximizes expected utility, a quantity that reflects the eventual adaptive value of the outcomes obtained (Edwards, 1954). From this perspective, the behaviors used to gain outcomes when cooperating are not analyzed as relevant to the reasons why individuals cooperate, regardless of whether individuals actually work together for shared outcomes or use other means that do not require joint action (Dugatkin, 1997; Stephens & Anderson, 1997). Instead, what matters most is that behavioral decisions by individuals should maximize access to beneficial outcomes when there is an interdependent contingency that also links outcomes to the actions of others. From a pure economic perspective, therefore, cooperation can even be claimed in the complete absence of social interaction (Hake & Vukelich, 1972; Stephens & Anderson, 1997). Minimizing or eliminating social interaction has also been the dominant strategy in laboratory models of cooperation with anonymous subjects that are physically isolated (Colman, 2003; Hake & Vukelich, 1972; Skinner, 1953).

The present research arises from an explanatory perspective regarding cooperation that focuses not only on material outcomes but also on the *behavioral dimensions of cooperating*, that is, on the irreducible social dimensions associated with cooperating in the natural world that are absent when behaving noncooperatively, and the potential influence of such dimensions on both the motivation and reinforcement for cooperating, and on the choice of whether to cooperate (Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004). For both animals and humans, a widespread type of cooperation is based on familiar individuals that learn to use each other's behaviors and locations when coordinating joint actions for shared outcomes, for example, in group hunting (Boesch & Boesch, 1989; Kruuk, 1972; Schaller, 1972) or aggression (Grinnell, 2002; Heinsohn & Packer, 1995; Kruuk,

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1972; Watts & Mitani, 2001). Noncooperation is then represented by situations in which outcomes are obtainable by individuals behaving on their own. Lions (*Panthera leo*), for example, often have the option of hunting with pride members or individually (Packer, Scheel, & Pusey, 1990).

One reason to focus on the behavioral dimensions of cooperation is accumulating evidence for a tendency to cooperate more than expected from the receipt of immediate material outcomes alone. This "apparent irrationality" at the time of cooperating is well documented even in game theory experiments with human subjects that are isolated and anonymous (for reviews, see Colman, 2003; Dawes & Thaler, 1988; Palameta & Brown, 1999). To explain the human bias in such games, it is assumed that participants have some awareness of the interdependent social contingencies despite the impoverished social conditions. Animals, in contrast, do not choose to cooperate under these conditions (Baker & Rachlin, 2002; Clements & Stephens, 1995; Flood, Lendenmann, & Rapoport, 1983; Green, Price, & Hamburger, 1995). To show the bias to cooperate in animal models, it appears as if the cooperative behavior has to explicitly incorporate the kinds of social dimensions that are typical of free-ranging conditions. In this article, we consider two expressions of the bias (for a detailed description, see Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004). First, the bias is revealed when the likelihood of social cooperation is higher than the levels predicted from access to material outcomes at the time of cooperating (Packer et al., 1990; Scheel & Packer, 1991; Schuster, 2001, 2002; Schuster & Perelberg, 2004); and second, the bias is expressed when there is a considerable time lag—hours, weeks, months, or even years—between the performance of cooperative acts and eventual access to the kinds of material outcomes that determine fitness (Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004).

The present study was conducted on free-swimming dolphin dyads within a large seminatural enclosure that was designed as a tourist attraction in Eilat, Israel, and focused on coordinated breathing. This behavior does not in itself represent any special or distinctive category of behavior, but it has close links with other coordinated acts, such as cooperative foraging/hunting (Acevedo-Gutierrez, 1999; Connor, Wells, Mann, & Read, 2000; Reynolds, Wells, & Eide, 2000), resting (Gnone, Benoldi, Bonsignori, & Fognani, 2001; Sekiguchi & Koshima, 2003), inter- and intraspecific aggression (Herzing, 1996; Pryor & Shallenberger, 1991), consorting with females by male alliances (Connor & Mann, 2006; Connor et al., 2000), and playing (Bel'kovich, 1991). Coordinated breathing/surfacing can also reveal both long-lasting, stable relationships, such as between mothers and calves (Connor et al., 2000; Mann & Smuts, 1999; Miles & Herzing, 2003; Würsig, 1978) and male alliances among subadults and adults (Connor & Mann, 2006; Connor, Smolker, & Bejder, 2006), as well as short-term, context-dependent associations (Ballance, 1990). Coordinated breathing thereby offers an indirect way to measure dolphin cooperation and to analyze some of the factors that influence its occurrence by means of an event that is objective, discrete, unambiguous and easily observed from above the water (Hastie, Wilson, Tufft, & Thompson, 2003).

The main aim of this study was to compare the extent to which the performance of this behavior can be predicted from pure economic self-interest based on immediate individual gains from behaving in close proximity or whether the likelihood of this behavior was better predicted from social dimensions associated with cooperating that have long-term fitness implications. Among the potential immediate economic benefits that have been proposed are the following: hydrodynamic facilitation of calf swimming (Mann & Smuts, 1999; Weihs, 2004), communication enhancement in acoustically polluted environments (Hastie et al., 2003), and antipredator defense (Hastie et al., 2003). Less tangible benefits linked to the social dimensions of cooperating have also been proposed, including emotional states linked to tension reduction and bond maintenance (Connor & Mann, 2006; Connor et al., 2006).

Method

Study Site and Subjects

The study group consisted of 13 (5 males, 8 females) common bottlenose dolphins living in a 14,000-m^2 semifree, natural marine enclosure at the Dolphin-Reef facility, located south of the city of Eilat, Israel, at the northern part of the Gulf of Aqaba, the Red Sea (34°56′13′"E 29°31′37"N; see Figure 1). Water depth inside the enclosure gradually slopes from the shore to 15 m along the circumference net. A gate was open to the sea all year round, 24 hr/day, enabling the dolphins to have unlimited access to the open sea. We categorized the group into three age classes: adults (sexually mature male and females; 1 male, 4 females), adolescents (dolphins between 3 and 8 years of age, before sexual maturity; 2 males, 2 females), and calves (dolphins under 2 years of age, still dependent on their mothers; 2 males, 2 females). All resident dolphins were observed and included in the analysis. Individual identification of the dolphins was based on distinct shapes and marks of dorsal fins, as well as body size, girth, and color.

For the purposes of this study, we regarded this facility as a seminatural simulation of free-ranging conditions in the wild that provided the dolphins with unlimited opportunities for social interaction and association among representatives of all age and sex categories. No forced restriction or separation of any dolphin (except for medical reasons) took place at the site, which allowed the dolphins to freely segregate without any external intervention. Feeding was provided four times a day (1000, 1200, 1400, and 1600 hr) from designated platforms along the tourists' pier (see Figure 1C) and was never contingent upon any training performance. Training sessions took place between feeding times as a means of environmental enrichment for the dolphins and included performance of individually performed simple tricks that did not require any cooperation between dolphin subjects. Participation by the dolphins was completely voluntary, and food reward was never related to training. Two guided and supervised programs for tourists took place between feeding times: swimming with dolphins and diving with dolphins. Participation by the dolphins was also completely voluntary and spontaneous; that is, dolphins were free to approach any person, and tourists were not permitted to chase after or touch the dolphins. Dolphins were also free to access large regions inside the enclosure that were prohibited to human access and functioned as shelter areas. Housing conditions of the dolphins complied with the (currently suspended) Animal and Plant Health Inspection Service (2001) swim-with-the-dolphin program regulations. Following a formal application, this study was approved by the University of Haifa Ethical Committee for Experiments on Animals, following Israeli legal regulations.

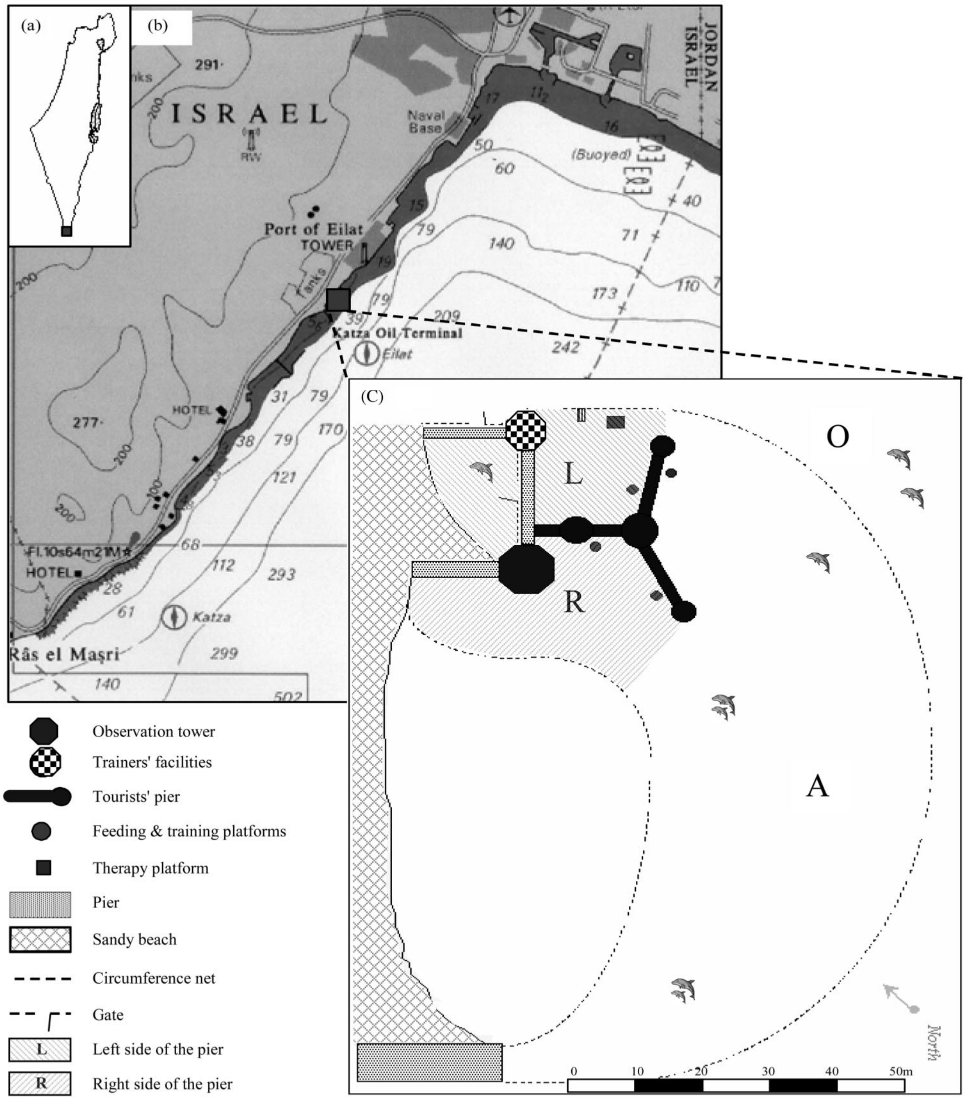

Figure 1. Dolphin-Reef site map. Section (C) demonstrates the four areas defined before feeding time to decipher association patterns: L = left side of the tourists' pier; R = right side of the tourists' pier; A = away from the tourists' pier; O = outside the enclosure in the open sea.

Measurement of Association Patterns

Association patterns, coordination levels, and spatial formation of dolphin dyads were collected by Amir Perelberg from April 2002 to January 2003 from an observation tower adjacent to the enclosure, 8 m above sea level (see Figure 1C). The determination of association patterns was facilitated by the tendency of the dolphins to spontaneously congregate around the tourists' pier about 20 min before feeding time, where they could observe the trainers coming out to the feeding stations with the fish buckets. There was no spatial relation between feeding station location and dolphin location during this waiting period (Amir Perelberg, unpublished raw data). We defined four distinct areas inside and outside the enclosure that enabled us to quickly and unambiguously define the location of each dolphin. These four areas were separated by readily identifiable physical obstacles such as the tourists' pier and the circumference net: right side of the pier (R); left side of the pier (L); inside the enclosure but away from the pier (A); and outside the enclosure in the open sea (O; see Figure 1C). Associations while freely swimming in the water were reliably reflected by differences in the clustering of dolphins among the four defined areas while waiting for food (Perelberg, 2005). This enabled the use of scan sampling, a method that requires the identification of the locations of all participants and is considered more rigorous for estimating association patterns than focal-animal sampling (Altmann, 1974). The locations of all dolphins were recorded on a check sheet once per minute during the prefeeding observation sessions. A 1-min interval was selected because it is sufficient for both identifying the locations of all the dolphins and for the dolphins to move from any defined area to any other area between consecutive observations. An association matrix of all possible dyads was calculated for each prefeeding observation session.

Association patterns were estimated by the Half Weight Index (HWI; see Cairns & Schwager, 1987; Maze-Foley & Würsig, 2002). This index was selected because it produces a very low mean square error when sample size is large (Cairns & Schwager, 1987) and it is also widely used in cetacean research. Although this index is often used in field studies as a means to identify the associations between individuals in separate occasions when observed with the same or separate schools, we believe that our observations are conceptually similar, although in a finer scale. Therefore, regarding comparability of our study with field studies, use of the same index might provide insights regarding the factors that influence the segregation of groups under free-ranging conditions. The index provides a number between 0 (*no association*) and 1 (*tight association*) indicating a relative estimation to the strength of the association: $\mathrm{HWI} = x/[x + y_{\mathrm{AB}} + 0.5(y_{\mathrm{A}} + y_{\mathrm{B}})]$, where x is the number of observations of A and B together at the same location, y_{AB} is the number of observations where A and B were observed in separate locations at the same time, y_{A} is the number of observations of only A, and y_{B} is the number of observations of only B. To identify the quality of any association (i.e., attraction, avoidance, or random), we used Monte–Carlo procedure iterations on the dolphins' locations by generating a frequency distribution for each dyad on the basis of 1,000 iterations from permutations of the original data. In such a case, any value exceeding 0.025 probability on the high or low tails of the distribution (in a two-tailed test) was considered significant (see Bejder, Fletcher, & Bräger, 1998). We defined attraction as a level of association significantly above random and avoidance as a level of association significantly below random. Because association levels of age/sex categories were not normally distributed, we used Kruskal–Wallis nonparametric tests followed by post hoc comparisons using Mann–Whitney U tests with Bonferroni correction for threshold α values. As there were 10 age/sex groups, adjusted value was set to $\alpha'' = \alpha/45 = 0.05/45 = 0.0011$.

Measurement of Breathing Coordination

Surface breathing was used to quantify the level of coordination between two or more dolphins swimming in close proximity (i.e., within one body length in the same direction and pace). When more than two dolphins were swimming together, we analyzed all possible pairings (three pairings in a triad, six pairings in a quartet, etc.). The event-sampling method (Altmann, 1974) was used to record breathing coordination, whereby all observed dyadic breathing events were recorded on a check sheet. Each observation session lasted ca. 1 hr, at various times of the day and only between feeding times. Breathing was determined either by observing the open blowhole at the surface or by hearing the sound of the breath (Mann & Smuts, 1999). We defined four easily observed and discrete levels of dyadic coordination in descending order, on the basis of variation in the timing of breathing between two animals: (a) simultaneous (<1 s); (b) the second dolphin breathes while the first is still out (1–3 s); (c) the second dolphin breathes only after the first dolphin is already submerged (4–10 s); and (d) an interval greater than 10 s between the breathing of two dolphins. The last two categories were differentiated because preliminary observations revealed that the interval between breathing events of a single dolphin was $M = 15$ s $\pm$ $SD = 5$ s (Amir Perelberg, unpublished raw data). Therefore, this definition allowed the identification of two consecutive breathing events when one dolphin breathes more frequently than its associate (i.e., when one dolphin breathes twice while its associate breathes only once or less). For each observation session, we calculated mean breathing coordination level for each observed dyad. To test for significant breathing coordination levels, two normal distributions ($M = 15$ s, $SD = 5$ s) of 50,000 breathing events, randomly arranged, were coupled and scored as the above. We selected the measure of 50,000 comparisons because the variance of the standard error of the mean stabilized at less than 0.001 at this stage. The resulting random breathing coordination level distribution was compared to each dyad breathing distribution and to age/sex categories using Mann–Whitney U tests. To compare among age/sex categories, we used Kruskal–Wallis tests followed by post hoc comparisons using Mann–Whitney U tests with Bonferroni correction for threshold α values. As there were 10 age/sex categories, adjusted value was set to $\alpha'' = \alpha/45 = 0.05/45 = 0.0011$.

Measurement of Dyadic Spatial Formation

To assess the relations between the spatial formation of dyads and their coordination levels, we recorded the configuration of each pair during the observations of breathing coordination, as described earlier. We defined five distinct levels of spatial configurations: (F) subject dolphin is in front of its partner, up to one body length apart; (A) subject is ahead of its partner, with an overlap of up to half-body length; (P) subject and partner dolphins are swimming in parallel, up to half-body-length difference; (L) subject is lagging after its partner, with an overlap of up to half-body length; and (B) subject is behind its partner, up to one body length apart (see Figure 2). To measure the correlation between spatial formation and coordination levels, we considered categories F,B and A,L as equivalent regarding the distance between the members of a dyad. Distances were ranked as follows: $p = 0$; A/L = 1; F/B = 2. To overcome unequal sample sizes, we used the proportions of the frequency distributions of the above spatial formation categories among age/sex groups. To test for deviations from even distribution across spatial formations, we used χ^2 tests (two-tailed). In correlation analysis, we used one-tailed significance tests because we assumed directionality: positive correlation between association levels and coordination levels, and negative correlation between distance and coordination levels.

Because all data were collected by Amir Perelberg, no measure of interobserver consistency was taken. To ensure the reliability and accuracy of the data collection, a training period of ca. 3 months was conducted by the manager of the research laboratory (F. Veit) before the beginning of the study. Data collection commenced only after reaching >95% proficiency on dolphin identification, behavioral categorization, and information on spatial and temporal parameters of behavior. For all analyses, 95% confidence intervals (CIs) were calculated for significance level of $\alpha = 0.05$. Realization variance was defined as $\sigma_{\delta}^{2} = 0.08$ and the probability of replicating an effect (p_{rep} statistic), was calculated following Killeen (2005). All statistical analysis was conducted using the SPSS 14.0 for Windows software package (SPSS Inc., Chicago).

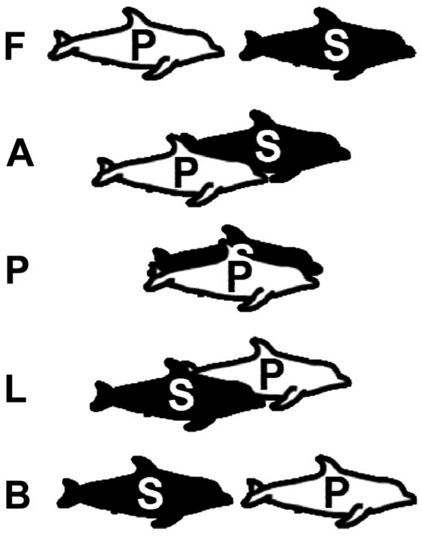

Figure 2. Spatial formations of dolphin dyads (S = subject, P = partner). F = subject dolphin is in front of its partner, up to one body length apart; A = subject is ahead of its partner, with an overlap of up to half-body-length; P = subject and partner dolphins are swimming in parallel, up to half-body-length difference; L = subject is lagging after its partner, with an overlap of up to half-body-length; and B = subject is behind its partner, up to one body length apart.

Results

Association Patterns

Association patterns were obtained from 2,840 min of scan sampling, collected during 140 observation sessions ($M = 20$, CI = ±0.66 scans/session). Association levels differed significantly among age/sex categories, Kruskal–Wallis test, $\chi^2(9) = 1608.85$, $p < .001$, $p_{\text{rep}} > .986$, two-tailed; and post hoc Mann–Whitney U tests (see Figure 3). Consistent with attraction, the highest levels of association were found between adolescent males and, as expected, between mothers and calves. Consistent with avoidance, the lowest levels of association were found between the adult male and both adolescent males, between the younger adolescent female and two adult females, and between one adolescent male and the oldest adult female. Positive medium-to-low levels were found between the adult male and both adult and adolescent females. Association levels between pairs of adult females varied from avoidance between the two youngest females to random up to medium-level positive relations among other pairs. Except for mother–calf associations, there was no apparent relationship between kinship and association levels (see Table 1).

Coordinated Breathing

We recorded 3,969 events of dyadic breathing during 3,856 min of observation time, collected in 73 observation sessions ($M = 55$, CI = ±0.92 events/session). Coordination levels differed significantly among age/sex categories, Kruskal–Wallis test, $\chi^2(9) = 77.98$, $p < .001$, $p_{\text{rep}} > .986$, two-tailed; and post hoc Mann–Whitney U tests (see Figure 4). When compared with the calculated random level coordination ($M = 2.72$, CI = ±0.01), the same-sex adolescent pairs and mother–calf pairs had shown better coordination than expected from random level ("good" coordinators). Lower than random coordination levels ("poor" coordinators) were found in adult male–female pairs. Other categories did not significantly differ from random coordination level (see Figure 4). When breathing coordination levels of individual pairs were

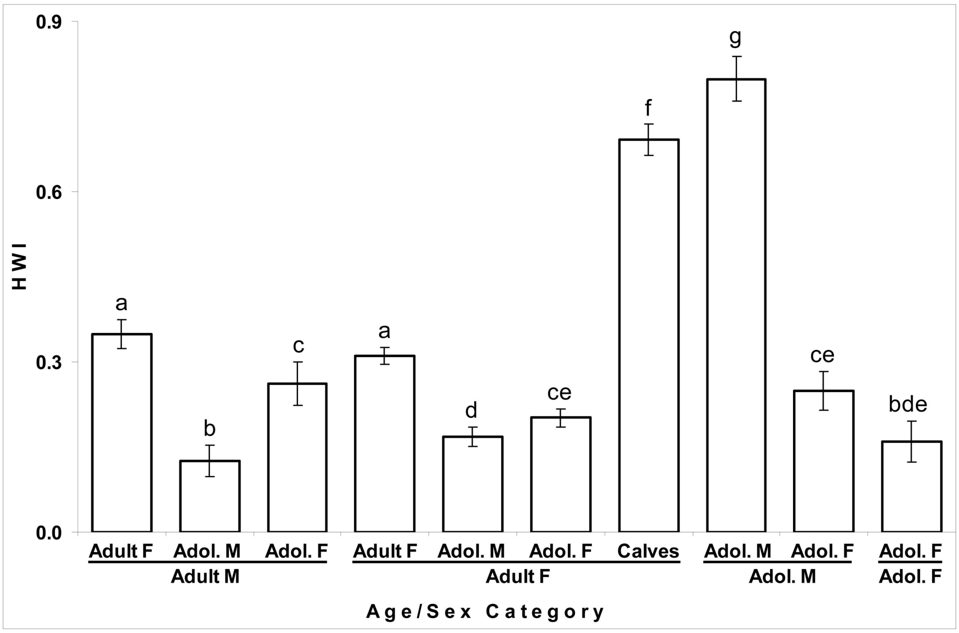

Figure 3. Mean association patterns measured by the Half Weight Index (HWI) between age/sex categories (M = male, F = female, Adol. = adolescent). Adult F/Calves category refers only to mother-calf pairs. Letters above bars denote Mann–Whitney U test post hoc groupings. Error bars represent 95% confidence interval.

Table 1
Half Weight Index Association Levels of Dolphin Dyads by Age/Sex Categories

		Adult F				Adol. F		Adol. M		Calf			
Age/sex category	Subject/partner	Sh	Da	Do	Pa	Na	Ja	Sn	Le	Ne	Lu	Su	Mi
Adult M	Ci	0.23^{a}	0.47^{a}	0.35^{a}	0.38^{a}	0.37^{a}	0.17^{a}	0.13^{b}	0.12^{b}				
Adult F	Sh		0.06	0.22	0.32^{a}	0.08^{a}	0.19^{a}	0.04	0.03^{b}	0.65^{a}			
	Da			0.51^{a}	0.46^{a}	0.41^{a}	0.15^{b}	0.28^{a}	0.29^{a}		0.80^{a}		
	Do				0.36^{b}	0.26^{a}	0.16	0.19^{a}	0.17			0.66^{a}	
	Pa					0.23^{a}	0.16^{b}	0.18^{a}	0.18				0.64^{a}
Adol. F	Na						0.16^{a}	0.38^{a}	0.37				
	Ja							0.15^{a}	0.17^{a}				
Adol. M	Sn								0.82^{a}				

Note. Each age category is ordered by age. Associations of calves were reported only with their mothers. Underlined values represent mother–offspring relations. Significance levels of interactions were obtained by Monte Carlo permutations over the original data (two tailed, $p < .05$). M = male; F = female; Adol. = adolescent.
[a]Positive association. [b]Negative association. Values without superscripts associations did not significantly differ from random levels.

compared with the calculated random coordination level, all mother–calf pairs, as well as the pairs of adolescent males and females, had shown coordination levels significantly better than random. Coordination levels lower than random were found between the adult male and the youngest adult female (see Table 2).

Spatial Formation

From the same observations of coordinated breathing events described earlier, the spatial formations of the dolphin dyads were analyzed. In all age/sex categories, formations did not distribute evenly among positions: the adult male, $\chi^2(4) = 180.67, p < .001, p_{\text{rep}} > .986$; the adult females, $\chi^2(4) = 4155.55, p < .001, p_{\text{rep}} > .986$; the adolescent males, $\chi^2(4) = 103.69, p < .001, p_{\text{rep}} > .986$; and the adolescent females, $\chi^2(4) = 104.87, p < .001, p_{\text{rep}} > .986$. As interactions are reciprocal (e.g., adult male/adult female interaction equals adult female/adult male interaction with reversed roles), the results here are described only once for every age/sex interaction category.

The adult male tended to be in A/B positions with adult females, $\chi^2(4) = 19.60, p < .001, p_{\text{rep}} > .986$; in the A position with adolescent males, $\chi^2(4) = 162.30, p < .001, p_{\text{rep}} > .986$; and in A/L positions with adolescent females, $\chi^2(4) = 34.40, p < .001, p_{\text{rep}} > .986$ (see Figure 5). Adult females were in F/A positions

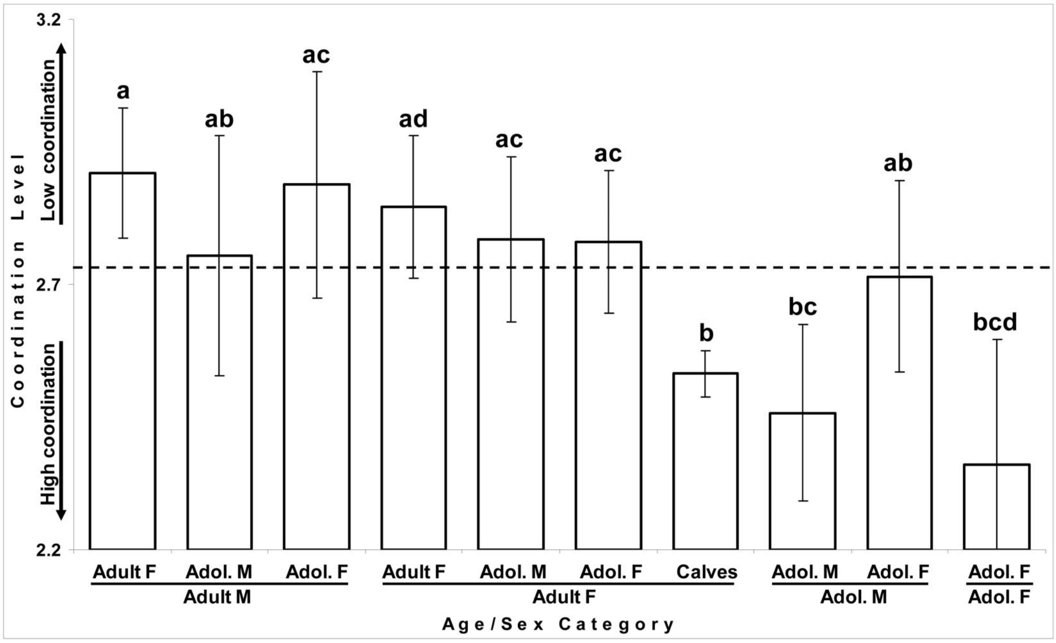

Figure 4. Mean breathing coordination levels between age/sex categories (M = male, F = female, Adol. = Adolescent). Adult F/Calves category refers only to mother-calf pairs. Letters above bars denote Mann–Whitney U test post hoc groupings. Error bars represent 95% confidence interval. Dashed line indicates calculated random breathing coordination level (2.72).

Table 2
Breathing Coordination Levels of Dolphin Dyads by Age/Sex Categories

Age/sex category	Subject/ partner	Adult F				Adol. F		Adol. M		Calf			
		Sh	Da	Do	Pa	Na	Ja	Sn	Le	Ne	Lu	Su	Mi
Adult M	Ci	2.80	2.79	2.95	3.38[b]	2.90	2.88	2.99	2.59				
Adult F	Sh		2.95	2.74	2.98	2.67	3.13		2.50	2.14[a]			
	Da			2.87	2.65	2.70	2.85	2.64	2.53		2.51[a]		
	Do				2.98	3.00	2.58	3.00	3.00			2.59[a]	
	Pa					2.83	2.86	2.88	2.93				2.60[a]
Adol. F	Na						2.36[a]	2.50	2.62				
	Ja							2.79	2.73				
Adol. M	Sn								2.46[a]				

Note. Each age category is ordered by age. Coordination levels of calves were reported only with their mothers. Underlined values represent mother–offspring relations. Significance was assessed by comparing each coordination level to a randomly arranged distribution of two normal distributions of singly breathing dolphins. (Random coordination level: $M = 2.72$, confidence interval = ±0.01, Mann–Whitney U tests, two-tailed, $p < .05$.) M = male; F = female; Adol. = adolescent.

[a] Better than random-level coordination; [b] Worse than random-level coordination. Coordination levels without superscripts did not significantly differ from random.

with adolescent males, $\chi^2(4) = 73.41$, $p < .001$, $p_{\text{rep}} > .986$; in the A position with adolescent females, $\chi^2(4) = 50.60$, $p < .001$, $p_{\text{rep}} > .986$; and almost exclusively in the A position with their calves, $\chi^2(4) = 264.20$, $p < .001$, $p_{\text{rep}} > .986$. Pairs of adult females did not show any tendency for a specific formation, $\chi^2(4) = 2.40$, $p = .663$, $p_{\text{rep}} = .383$ (see Figure 5). Adolescent males tended to be in P position when together, $\chi^2(4) = 9.80$, $p = .044$, $p_{\text{rep}} = .886$; and in L/P positions with adolescent females, $\chi^2(4) = 16.40$, $p = .003$, $p_{\text{rep}} = .974$. Adolescent females tended to be in A/L positions when together, $\chi^2(4) = 68.70$, $p < .001$, $p_{\text{rep}} > .986$ (see Figure 5).

Relationship Between Association and Coordination Levels

Overall, there was a significant but weak positive correlation between HWI and coordination levels (Pearson $r = .293$, $n = 39$, $p = .035$, $p_{\text{rep}} = .879$, $d = 0.605$, one-tailed), with great variation

Figure 5. Frequency distributions of spatial formations of all age/sex pair combinations (M = male, F = female, Adol. = adolescent, S = subject, P = partner). Frequency distributions of all but adult F/F pairs were significantly different from even distribution, $\chi^2(4)$ tests, $p < .05$, two tailed).

among pairs; that is, association levels were not good predictors of coordination levels. Instead, the relationship between levels of association and coordination varied widely. Both scores of coordination and association levels were predictably high in mother–calf pairs and in the pair of adolescent males (see Figure 6A); in contrast, all mixed adult–adolescent pairs had both low associations and coordination levels (see Figure 6D). Low association but high coordination level characterized the pair of adolescent females (seeFigure 6B), whereas low coordination with intermediate association levels characterized the adult male with the adult females (see Figure 6C).

Relationship Between Spatial Formation and Coordination Levels

A clear negative correlation was found between the spatial distances and coordination levels (Pearson $r = -.528$, $n = 39$, $p < .001$, $p_{\text{rep}} > .991$, $d = 1.227$, one-tailed; see Figure 7). The closer the dolphins were, the higher coordination level achieved. However, as with association patterns and coordination levels, there was a large variance among age/sex categories. Both close proximity and high coordination levels characterized mother–calf pairs, as well as same-sex adolescent pairs (see Figure 7A). In contrast, similar proximity between the adult male and the adolescent males was typified by low coordination levels (see Figure 7C). Both low coordination levels and distant formation were characteristic of adult females paired with all age/sex categories except with their calves (see Figure 7D).

Discussion

The main finding reported here is that, in free-swimming bottlenose dolphin dyads, an important factor that affects coordination levels was the age/sex group of each member of a dyad. When this factor is ignored, there was only a weak correlation between the apparent coordination levels of their movements and both association levels and proximity. There was also high variability across pairs in the degree of linkage between coordination, association, and proximity. As expected, mother–calf dyads were strongly associated, displayed high coordination levels, and maintained close proximity (mothers in A position, calves in L position). Likewise, the pair of adolescent males revealed a strong positive link between coordination and association levels and was usually observed swimming in parallel (P position). In contrast, weak associations and low coordination levels were characteristic of the relationships between the single adult male and his potential opponents, the pair of adolescent males, in spite of keeping relatively close proximity (adult male in A position, adolescent males in L position). However, association did not always predict coordination. The relationships between the adult male and the adult females were relatively strong but with highly variable coordination levels and distant spatial formation. In contrast, the pair of adolescent females had shown only weak association but was highly coordinated and maintained close proximity. Unlike the adolescent male pair that was swimming in parallel (P position), the adolescent female pair was usually swimming in a formation similar to a mother–calf pair (A and L positions).

We suggest here, and in more detail elsewhere (Perelberg & Schuster, 2008; Schuster, 2002; Schuster & Perelberg, 2004), that the coordinated breathing of dolphins represents an act of cooperation that is influenced not only by immediate material outcomes for individuals (Clements & Stephens, 1995; Dugatkin, 1997; Trivers, 1985), but also by the social dimensions of cooperation when it is performed by individuals that coordinate behaviors for jointly obtained outcomes (Brosnan & de Waal, 2002; Roberts,

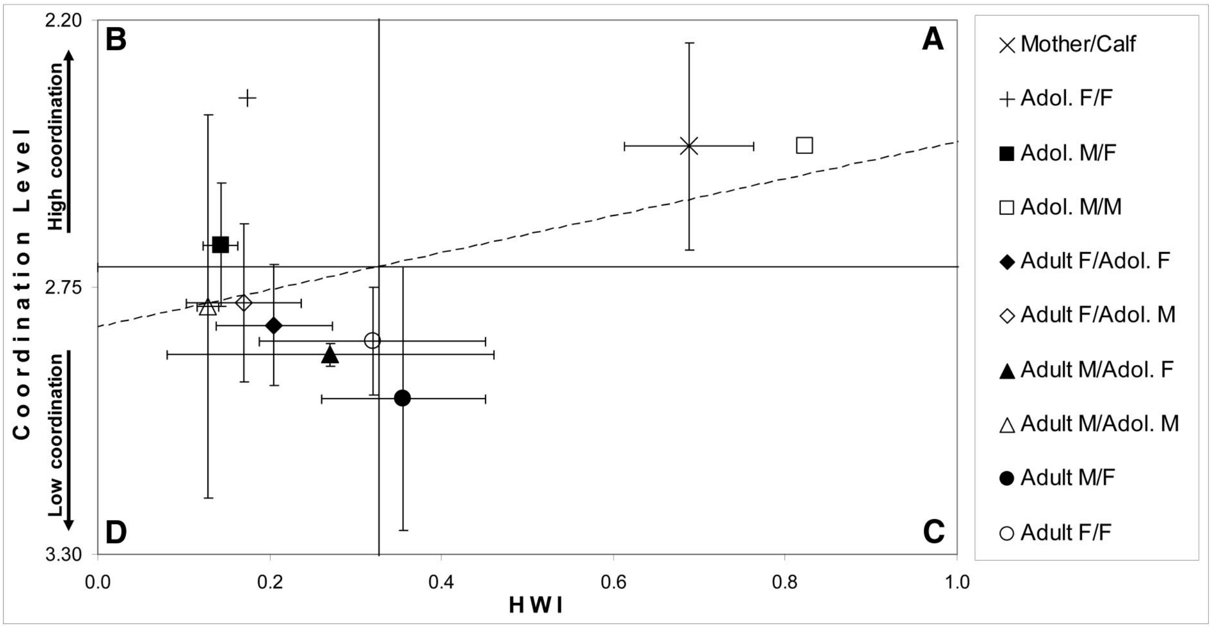

Figure 6. Correlation between association levels and coordination levels (M = Male, F = Female, Adol. = Adolescent). Figure splits into four quadrants by mean values of the Half Weight Index (HWI) and coordination levels. Linear correlation denoted by dashed line. Error bars represent 95% confidence interval.

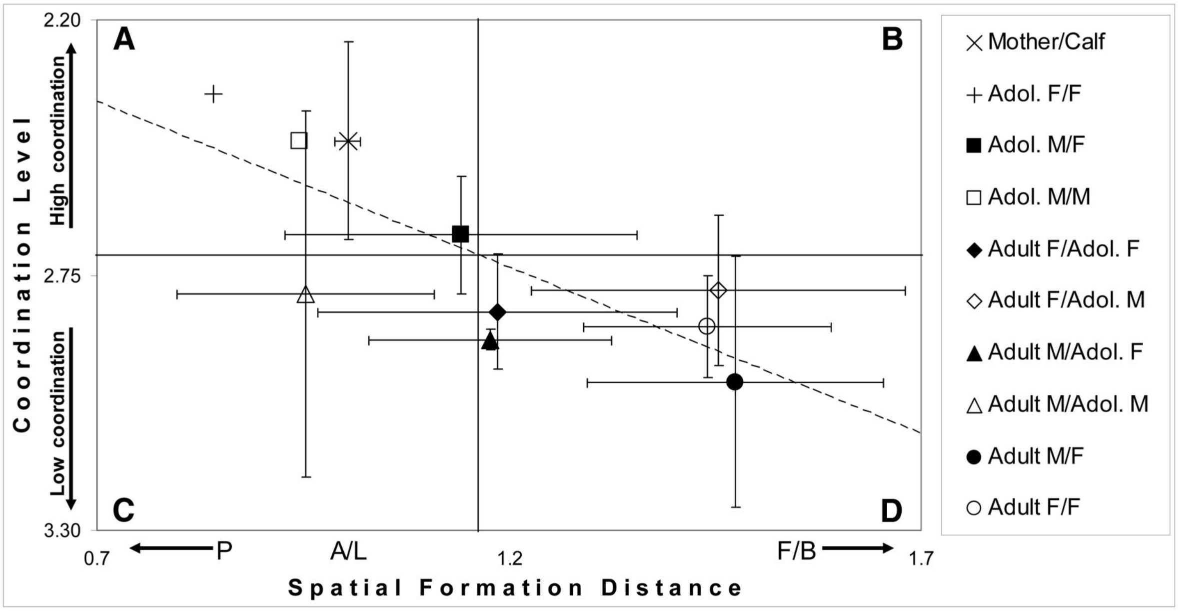

Figure 7. Correlation between spatial formation distance and coordination levels (M = Male, F = Female, Adol. = Adolescent).Figure splits into four quadrants by mean values of spatial distance and coordination levels. Linear correlation denoted by dashed line. Error bars represent 95% confidence interval.

1997; Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004). Another example of cooperation not entirely predicted by outcomes is the cooperative hunting of chimpanzees (*Pan troglodytes*), in which behavioral dimensions include coordination, signaling, complementary roles, and adjunct social interactions among cooperators (Boesch & Boesch, 1989). In explaining why cooperation in chimpanzees, as in bottlenose dolphins, cannot be fully predicted by immediate material outcomes, it seems as if the behavioral differences between cooperation and noncooperation also exert strong influence on the likelihood of cooperating. Hence, the decision of whether to cooperate becomes a choice not only between immediate outcomes but also between alternative ways of gaining access to material outcomes: by joint action with shared success, or by individual action and individual success (Schuster & Perelberg, 2004).

If individual access to material outcomes was the dominant factor influencing coordinated swimming and breathing, there should have been a stronger relationship with association patterns and spatial formation. Across a variety of species that display coordinated cooperation, including dolphins and a variety of mammalian and avian species, five explanations (not mutually exclusive) have been suggested as sources of profitable outcomes at the individual level: (a) decreased drag effects while swimming in order to increase swim efficiency, especially in dolphin calves (Mann & Smuts, 1999; Weihs, 2004); (b) decreased predation risk (Buckstaff, 2004; Hastie et al., 2003; Whitehead, 1996); (c) increased bonding relations in male–female pairs (as, e.g., in birds, see Todt, 1975; Todt, Hultsch, & Duvall, 1981) or between dolphin males in alliances (Connor et al., 2006); (d) decreased stress between competitors (Connor & Mann, 2006; Dugatkin, 1997; Schuster, 1976; Todt, 1981); and (e) enhanced vocal, visual, and tactile communication, especially in areas exposed to high ambient noise pollution (Buckstaff, 2004; Hastie et al., 2003). The first four of the these explanations predict higher coordination levels related to specific association patterns and spatial formations: Calves in mother–calf pairs would benefit from decreased drag effects and predation risk; male–female pairs and male–male pairs would benefit from increased bonding relations; and same-sex pairs (males or females) would benefit from decreased stress between competitors. The fifth explanation, enhanced communication, predicts that there should have been no significant difference across association patterns and spatial formations on coordination levels.

The potential benefits of decreased predation risk could not be directly evaluated in this study, because there was no predation risk inside the enclosure and calves never left the enclosure for the open sea. Predation risk, however, is inconsistent with elevated mother–calf coordination that continued well into the calves' second year. Predation risk was also unable to account for the results of a study of wild bottlenose dolphin calves in which coordination levels of mother–calf breathing declined rapidly after the first month of age, when calves gradually altered "echelon swimming position" to "infant position" (Mann & Smuts, 1999), even though predation risk in the wild was presumably much higher than in our captive group.

Remaining Explanations

The four remaining explanations that remain relevant to our study group are briefly addressed here.

(a) Decreased drag effects. This explanation predicts that younger dolphins, more affected by drag, will tend to keep the L position when swimming with older dolphins and have higher coordination levels. As expected, mother–calf pairs had the highest coordination levels, with calves keeping the most effective L

position. Similar spatial position effect was also found between same-sex adult and adolescent pairs, but this did not translate into association or coordination levels. Adult–adolescent pairs of the opposite sexes did not even match in spatial formation.

(b) Bonding. Bonding between male–female pairs was unable to account for the variation linked to age category: adult male–female pairs exhibited varying levels of associations and breathing coordination, and distant spatial formation; in contrast, adolescent male–female pairs maintained intermediate proximity and positive association levels, but coordination levels that were not different from random. These observations fit well with the fluid social organization of this species, in contrast to the behavioral coordination patterns that characterize monogamous species—for example, primates (Müller & Anzenberger, 2002) and birds (Wachtmeister, 2001). Bonding between all-male pairs, however, was strongly supported by our findings, in which the pair of adolescent males scored high in all three measures: association, proximity, and coordination levels. Whereas their parallel swimming formation excludes the possibility of hydrodynamic advantage (Weihs, 2004), the possibility of using coordinated swimming and breathing as a method for strengthening the bond and as a mutual signal for the quality of the alliance (Connor et al., 2006) remains valid.

(c) Reducing stress. Stress reduction between competitors was also not a good predictor of coordination levels. The pairs with the highest levels of conflict, mixed adult–adolescent pairs, and especially the adult–adolescent male pairs, maintained close proximity but were poor coordinators with lower than random association levels.

(d) Maintaining communication. This explanation predicts similar levels of coordination among all group members and was clearly contradicted by significant differences in coordination within and between categories.

In summary, with the exception of possible benefits to the calf from decreased drag effects and predation risk, all other data showed a tendency for coordinated swimming and breathing in the absence of any observed immediate individual profitable outcomes. As observed in the adolescent male pair, coordinated breathing was instead associated mainly with social factors that are related to age and sex groups, such as strengthening of a bond.

Explaining the Bias to Cooperate: Linking Proximate and Ultimate Causes

We suggest that the bias to cooperate can be explained by integrating the proximate behavioral processes that govern behavior—for example, learning, reinforcement, and emotion—with long-term outcomes that influence natural selection. Applying a proximate–ultimate explanatory approach to dolphin cooperation, however, remains tentative because of the difficulty in studying this species under free-ranging conditions. Immediate economic gains are usually not clear, and their ultimate function, although hypothesized (Buckstaff, 2004; Gnone et al., 2001; Hastie et al., 2003; Mann & Smuts, 1999; Sekiguchi & Koshima, 2003; Whitehead, 1996), remains to be tested. One example in dolphins that is consistent with a link between short- and long-term outcomes comes from Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) males in Shark Bay, Western Australia (Connor & Mann, 2006; Connor et al., 2000, 2006). Males were observed to form a sophisticated nested structure of coalitions and alliances as adolescents, with no apparent material gain when these relationships were first formed. However, the same males later cooperated as adults in herding and guarding females for mating. Thus, the behavior of remaining together at adolescence led to increased reproductive success about a decade later as adults. Because coordinated breathing, swimming, and surfing are also linked to certain relationships, the preliminary hypothesis is that such behaviors are characterized by a short-term bias to cooperate that will eventually pay off in ways that elevate fitness by cooperating in fishing, defense, aggression, and/or reproduction. This remains to be tested in wild populations.

The proximate processes that enhance cooperation are suggested to include immediate reinforcement from two kinds of outcomes: (a) tangible economic gains (i.e., material reinforcers with immediate benefits such as money, food, and mating opportunities) that can be directly observed and measured and (b) positive affective states evoked by the social dimensions associated with behaving cooperatively (Schuster, 2001, 2002; Schuster & Perelberg, 2004). Thus, in highly social species such as dolphins, lions, and chimpanzees, the likelihood of cooperation would be explained partially by immediate material outcomes, if any, but also by additional outcomes linked to the behavioral expression of cooperation that are absent when engaging in noncooperation. The latter may provide the motivation to induce cooperation even when material gains are insufficient or even absent at that time (Schuster, 2002; Schuster & Perelberg, 2004). Rachlin (2002) has offered a similar explanation of human altruism, and others have proposed links between cooperation and affect (Butler, 2003; Rapoport, 2003; Sigmund, 2003).

At the present time, the dimensions of cooperation associated with positive affect are largely unknown, but one likely candidate is a high level of behavioral coordination (Schuster & Perelberg, 2004). The long-term alliances of Indo-Pacific bottlenose dolphin males are characterized by highly synchronized activity (Connor & Mann, 2006; Connor et al., 2006), and alliances of common bottlenose dolphin males are associated with greater similarity in signature whistle when compared with whistles of nonpartners (Watwood, Tyack, & Wells, 2004). In an experiment with laboratory rats (*Rattus norvegicus*), a preference for social cooperation over individual noncooperation for the same outcomes was strongly correlated with the level of intrapair coordination while cooperating (Schuster & Perelberg, 2004). Also, in humans, emotions evoked by coordinated action may explain the rapport associated with behavior matching (Lakin & Chartrand, 2003) and the excitement and unity evoked by orchestrated group ceremonies that incorporate coordinated marching, praying, singing, and dancing (Fiske, 2000; McNeill, 1995).

In the long term, a cooperation bias can be adaptive if it eventually raises the mean probability for an increase in fitness at any time during an individual's lifetime or that of its kin—even if this is realized months, years, or decades later. Cooperation may thus be analogous to play that seems designed to evoke behaviors at an early stage in life even though the evolutionary implications are only realized far in the future (Bekoff & Allen, 1998; Pellis & Pellis, 1998). In this way, hedonic processes provide a behavioral mechanism that bridges the substantial time gaps between immediate performance and ultimate outcomes (Schuster & Perelberg, 2004). Thus, behaviors such as group hunting by lions and chimpanzees need not lead to immediate payoffs in terms of increased caloric intake. However, the same behaviors would remain adaptive if they increase the likelihood that adults will later cooperate in aggression and defense, behaviors with direct implications for fitness (Schuster & Perelberg, 2004). Female lions, for example, jointly defend cubs against other prides, infanticidal males, and hyenas (Packer et al., 1990). Male lions, after associating together as nomads, fight together to gain and hold territories for mating (Grinnell, 2002; Heinsohn & Packer, 1995). Male chimpanzees engage both in hunting and in intergroup "warfare" that increases territory and numbers of mates (Watts & Mitani, 2001).

In general, we suggest that the analysis of cooperation poses problems because it is sometimes expressed in widely spaced components, and in different contexts, as linked components of an adaptive developmental sequence mediated by social bonds forged at an early age. Cooperation, therefore, does not always seem to be adaptive on the basis of immediate material gains, and the search for immediate material payoffs can be futile. Hence, the integration of proximate and ultimate processes offers a better fit when there is a substantial time lag between the outcomes that determine behavior and those that determine fitness. In this way, the cooperation of dolphins, like that of other sophisticated social species, can perhaps be better understood.

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