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**BOTTLENOSE DOLPHINS (TURSIOPS
TRUNCATUS) PREFER TO COOPERATE WHEN
PETTED: INTEGRATING PROXIMATE AND
ULTIMATE EXPLANATIONS II**

by

AMIR PERELBERG and RICHARD SCHUSTER

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Bottlenose Dolphins (*Tursiops truncatus*) Prefer to Cooperate When Petted: Integrating Proximate and Ultimate Explanations II

Amir Perelberg
University of Haifa, and International Laboratory
for Dolphin Behaviour Research, Israel

Richard Schuster
University of Haifa, Israel

Cooperation poses theoretical problems because the behaviors of individuals can benefit others. Evolutionary and game-theory explanations that focus on maximizing one's own material outcomes are usually supported by experimental models with isolated and anonymous subjects. Cooperation in the natural world, however, is often a social act whereby familiar individuals coordinate behaviors for shared outcomes. Social cooperation is also associated with a *cooperation bias* expressed as a preference for cooperation even when noncooperation is immediately more beneficial. The authors report on evidence for such a bias in a captive group of bottlenose dolphins that voluntarily preferred to receive petting from human guides by using a pairwise coordinated approach, even though this was more difficult, and total petting amount was thereby reduced. To explain why this bias occurs, the authors propose an integrated behavioral-evolutionary approach whereby performance is determined by two kinds of immediate outcomes: material gains and intrinsic affective states associated with cooperating. The latter can provide reinforcement when immediate material gains are reduced, delayed, or absent. Over a lifetime, this proximate mechanism can lead to cooperative relationships whose long-term ultimate consequences can be adaptive.

Keywords: cooperation bias, coordinated cooperation, intrinsic reinforcement, proximate causes, *Tursiops truncatus*

Why cooperate? Cooperation poses theoretical problems because of the implication that individuals behave for the benefit of others. Definitions and explanations of cooperation have histori-

cally emphasized a predominantly economic and selfish perspective focusing on the outcomes that individuals can gain when these outcomes are also contingent on the behaviors of others, that is, by interdependent contingencies of reinforcement (Dugatkin, 1997; Perelberg & Schuster, 2008; Perelberg, Schuster & Motro, 2008; Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004, 2008; Skinner, 1953). When explaining cooperative behavior, the emphasis has usually been on the kinds of material outcomes such as food, copulations, and for humans—money, that are attractors, motivating and reinforcing behaviors at the time of performance (Skinner, 1953; Thorndike, 1911). The same kinds of outcomes also have the potential to influence natural selection because of fitness implications (Dugatkin, 1997; Mesterton-Gibbons & Dugatkin, 1992; Stephens & Anderson, 1997). Individuals are then expected to cooperate when this is more profitable relative to the predicted gains from not cooperating.

Studying Cooperation: The Economic/Evolutionary Perspective

The economic perspective is also characterized by downplaying behavioral differences between the expressions of cooperation and noncooperation (Dugatkin, 1997; Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004, 2008; Skinner, 1953; Stephens & Anderson, 1997). In the most popular laboratory models, interdependent contingencies determine the reinforcements available to two or more subjects deprived of meaningful social interaction by physical isolation and anonymity. In simple models in which cooperation is the only available option, subjects are reinforced for

synchronizing the performance of simple individual acts such as bar pressing or key pecking (Schmitt & Marwell, 1968; Skinner, 1953; for a review, see Hake & Vukelich, 1972). To enable coordination to develop between isolated subjects, timing cues must be available. These can be provided either by transparent partitions that allow each individual to time its responses by directly observing the actions of the other, or by opaque partitions that eliminate all social interaction and allow for coordination only if the behavior of one individual is accompanied by a nonsocial cue—for example, light or tone—that is presented to the other. In more complex game-theory models of social dilemmas, isolated and anonymous individuals choose between the options of cooperating and noncooperating that are defined a priori by differences in outcomes that depend upon how all subjects have chosen (Colman, 2003; Rapoport & Chammah, 1965). In this way, both the act of cooperating and the receipt of outcomes are reduced to events experienced individually (Schuster & Perelberg, 2004; Stephens & Anderson, 1997).

In addition to minimizing social interactions, isolation models neutralize behavioral differences between the expressions of cooperation and noncooperation by representing both as identical and individual acts. In social dilemmas, cooperation and noncooperation usually differ only in the locations to which responses are directed; for example, to two different keys (Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004). Given the absence of behavioral differences between individual and cooperative acts, what remains is to link levels of cooperation to the immediate material reinforcements that follow individual behaviors according to both behavioral/psychological processes such as the Law of Effect (Skinner, 1953; Thorndike, 1911) and ultimate biological theories that focus on natural selection (Dugatkin, 1997; Stephens & Anderson, 1997). Indeed, the same game-theoretical models, such as the popular prisoner's dilemma, have been used as models of both evolution (e.g., Clements & Stephens, 1995; Dugatkin, 1997; Maynard-Smith, 1982) and social behavior (e.g., Rapoport & Chammah, 1965; Stephens & Anderson, 1997; for a review, see Colman, 2003).

Studying Cooperation: The Behavioral/Psychological Perspective

In the natural world, however, cooperation and noncooperation differ not only in outcomes but also in the behaviors generated by reinforcement contingencies when these are interdependent or individual. Cooperation is typically performed by individuals already familiar to one another from a shared social context. The performance of cooperation is then likely to incorporate irreducible social dimensions that are absent when the same individuals engage in noncooperation. For example, a widespread form of cooperation in both humans and other animals involves individuals that work together for shared outcomes by using each other's actions and locations to coordinate behaviors (Perelberg & Schuster, 2008; Schuster & Berger, 2006; Schuster & Perelberg, 2004). Highly coordinated actions are common in animals in contexts that include hunting, aggression, defense, reproduction, and foraging (e.g., Boesch, 1994; Boesch & Boesch, 1989; Connor, Smolker, & Richards, 1992; Krützen, Barré, Connor, Mann, & Sherwin, 2004; Packer, Scheel, & Pusey, 1990; Stander, 1992; for a review, see Dugatkin, 1997). The performance of coordinated behaviors can

then incorporate complementary roles and communication, as well as unrestricted social interactions that can occur before and after an act of cooperation (Boesch & Boesch, 1989; Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004; Stander, 1992). Moreover, additional social behaviors are likely when cooperation leads to a single shared outcome whose allocation depends upon competition and dominance (e.g., Boesch & Boesch, 1989; Noë, 1990).

In contrast to behaving cooperatively, the noncooperative alternative is then represented by the alternative strategy of behaving alone for individual outcomes, when this is feasible. The hunting behavior of both lions (*Panthera leo*) and common chimpanzees (*Pan troglodytes*) illustrates these options, as the same individuals are known to employ either tactic (Boesch, 1994; Packer et al., 1990). In humans as well, group action for shared outcomes is also widespread (Hutchins, 1995). Highly coordinated behaviors are also common in orchestrated ceremonies associated with religion, politics, and the military (McNeill, 1995), and also in a spontaneous and unconscious tendency toward "behavior matching" between individuals (Chartrand & Bargh, 1999).

If cooperation differs in its behavioral expression from noncooperation, this invites examination of the possibility that the motivation and reinforcement for cooperating arise not only from access to immediate material outcomes but also from positive affective states associated with engaging in cooperation that can function as additional reinforcements (Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster, 2002; Schuster & Perelberg, 2004, 2008). The latter could then provide the potential for positive reinforcement even when immediate material outcomes are minimal or entirely absent. A decision about whether or not to cooperate would then be based not only on a choice between material outcomes, as in typical game-theoretical models (e.g., Clements & Stephens, 1995; Dugatkin, 1997; Mesterton-Gibbons & Dugatkin, 1992; Stephens & Anderson, 1997), but also on a choice between qualitatively different behaviors when one of them, cooperation, is associated with additional reinforcement from positive affect (Schuster & Perelberg, 2004). Based on observations of chimpanzees that hunt in groups, Boesch and Boesch (1989) suggested that there is intrinsic motivation and reinforcement associated with the group hunting of chimpanzees.

The Cooperation Bias

Both field and laboratory studies of social cooperation provide evidence consistent with intrinsic motivation and reinforcement when material outcomes alone cannot predict levels of performance. Instead, in both animals and humans, there is evidence for a *cooperation bias* expressed as an overall tendency to cooperate more than expected from immediate material outcomes alone (Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster & Berger, 2006; Schuster & Perelberg, 2004, 2008). In the field, the bias is expressed in several ways that include the following:

(a) Individuals chose cooperation over noncooperation (individual action) even when the latter was more profitable (Boesch, 1994; Packer et al., 1990).

(b) Shared outcomes were not always allocated equally, with the possibility that subordinate individuals gained nothing at all (Boesch, 1994; Boesch & Boesch, 1989; Krützen et al., 2004; Noë, 1990).

(c) Cooperative coordination was learned despite extended periods without evidence of material success (in chimpanzees estimated at 10 years; see Boesch, 2002). Repeated failures become likely because of the inherent complexity of a behavior such as cooperative hunting that places demands on individuals to coordinate not only with each other, but also to adjust strategies according to the behavior of unpredictable targets (Boesch, 2002; Scheel & Packer, 1991). An additional complication is the development of a stable division of labor that can emerge in groups of experienced cooperators (Boesch & Boesch, 1989; Stander, 1992).

(d) The performance of cooperation can be unrelated to immediate biological needs, such as the example of cooperative hunting in chimpanzees that was more likely to occur when other foods were plentiful (Mitani & Watts, 2001). The behavior instead was best predicted from social relationships among participants, including evidence for outcome sharing with both participants and nonparticipants based on social and political ties (Boesch, 1994; Boesch & Boesch, 1989).

(e) There can be a considerable *time lag* between the performance of cooperative acts and eventual access to the kinds of material outcomes with the potential to determine fitness (Connor et al., 1992; Packer et al., 1990). This time lag poses a problem for explaining how the same material outcomes can influence both the likelihood of cooperating and fitness because the value of delayed reinforcements is likely to be sharply discounted with the passage of time, especially in animals (Kagel, Green, & Caraco, 1986; Stephens, Nishimura, & Toyer, 1995). Mechanisms of intrinsic reinforcement have the potential to compensate for delayed benefits.

The existence of a cooperation bias has also been demonstrated in the laboratory when animal models incorporated the kinds of social dimensions that characterize the cooperative behaviors of wild populations (Brosnan & de Waal, 2002; de Waal & Berger, 2000; Schuster, 2002; Schuster & Berger, 2006; Schuster & Perelberg, 2004). Using capuchin monkeys (*Cebus apella*), individuals were more likely to share outcomes if they had been achieved by coordinating behaviors of pulling on a tray to gain access to a single food reward (de Waal & Berger, 2000). In a model using laboratory rats (*Rattus norvegicus*), pairs were reinforced in one chamber for cooperating together by coordinating back-and-forth shuttling or for noncooperation in a second chamber by shuttling individually (Schuster & Berger, 2006; Schuster & Perelberg, 2004). The differences between cooperation and noncooperation became analogous to the differences in the natural world between working together or alone. When individuals could choose between entries into the two chambers, there was an overall 3:1 preference for entering the chamber associated with cooperating even though there was no difference between the chambers in the numbers or rates of material reinforcements that were obtainable. In humans, the bias can even emerge in game-theory models such as the prisoners' dilemma despite the isolation and anonymity (Colman, 2003; Fehr, Fischbacher, & Gächter, 2002; Fehr & Gächter, 2002; Fehr & Rockenbach, 2004; Palameta & Brown, 1999). The levels of cooperation generated by such models are consistent with some degree of awareness that outcomes are also influenced by other players.

The existence of a bias to cooperate does not imply that cooperative behavior thereby becomes altruistic. One important difference between altruism and cooperation lies in the degree to which the cost/benefit balance is free to vary between participants. Altruistic behavior is usually said to occur when there is an actor that invests time and effort in a behavior that only benefits the recipient (Trivers, 1985). When cooperating, in contrast, there are at least two actors that mutually (but not necessarily equally) invest in the behavior and then determine how the outcomes will be allocated. Gains from cooperation can therefore vary widely from equal sharing to total access by only some individuals, depending on factors such as competition, dominance and free riders. When cooperating, there is the potential for each cooperator to gain at least some of the time, for example, in chimpanzee cooperative hunting when prey is large (Boesch & Boesch, 1989). The existence of a bias to cooperate means only that an individual can on average gain more immediate benefit by *not* cooperating, and this begs the question why cooperation should then be preferred. This issue will be addressed in the Discussion (see also Perelberg & Schuster, 2008; Schuster & Perelberg, 2004).

Human–Dolphin Interactions

In the present article, we use the behavior of a captive group of free-swimming common bottlenose dolphins (*Tursiops truncatus*) to examine the issue of cooperation bias by measuring the tendency of dolphins to spontaneously approach familiar human guides for petting without any additional reinforcement. Wild dolphins are highly social animals, living in groups with a defined social structure based on familiarity, kinship, and dominance (Connor, Wells, Mann, & Read, 2000). Social petting/rubbing between dolphins is regarded as an analogy to social grooming in primates, with both physical (e.g., removal of excess skin or body cleaning from skin parasites) and social functions (e.g., strengthening social bonds, see Dudzinski, 1998; Sakai, Hishi, Takeda, & Kohshima, 2006). Thus, for example, Indo-Pacific bottlenose dolphins (*T. aduncus*) were found to have preferred partners for flipper rubbing, with same-sex and same-age category pairs rubbing together more frequently than intersexual pairs. Males were also providers of rubbing more often than females in intersexual rubs, and rubbing was usually initiated by the recipient and terminated by the provider, suggesting that rubbing may inflict some cost to the provider (Sakai et al., 2006). Similar results were also reported in social rubbing/petting of Atlantic spotted dolphins (*Stenella frontalis*, see Dudzinski, 1998).

Dolphins seek relationships not only with conspecifics, but also with humans, for reasons that are not always clear. Human–dolphin relationships are interwoven into myth and folklore for thousands of years in various locations around the world, from Maori, New Zealand, to ancient Greeks and Romans (Busnel, 1973; Lockyer, 1990; Orams, 1997). Some cases have been explained by mutual benefits when humans and dolphins cooperate in fishing and share the outcomes (Busnel, 1973; Neil, 2002; Orams, 1997; Pryor, Lindbergh, Lindbergh, & Milano, 1990). Dolphins also approach humans for provisioned feeding, at least during an initial phase of habituation (Dill, Dill, & Charles, 2003; Dudzinski, Frohoff, & Crane, 1995; Orams, 1997), but there are also examples of dolphins refusing to accept fish handouts from humans (Lockyer, 1990).

Overall, human–dolphin relationships seem to go beyond the influence of food reinforcement and point instead to the intrinsic attraction of social and physical contact. Lone dolphins have sought human company, at least temporarily, as compensation for

lack of stable social relationships with members of their own species (Frohoff & Packard, 1995; Goffman, 2005; Lockyer, 1990; Müller, Battersby, Buurman, Bossley, & Doak, 1998; Müller & Bossley, 2002; Orams, 1997; Webb, 1978). When interacting with humans, such dolphins use affiliative social behaviors such as touching, rubbing, and petting that are part of their natural social repertoire toward conspecifics (Dudzinski et al., 1995; Frohoff & Packard, 1995; Goffman, 2005; Lockyer, 1990; Lockyer & Morris, 1986; Müller et al., 1998; Webb, 1978). Dolphins in groups have also shown a spontaneous tendency to approach humans in the water when conditions allow for the option of either approach or avoidance. This occurs in the wild (Lockyer, 1990), but also when conditions of captivity are "seminatural"; that is, when dolphins can roam freely within enclosures that are large and deep marine bays surrounded by netting that enable free in- and out-flow of marine water and organisms. Such enclosures can also include sanctuary regions that restrict human access and close supervision of interactions with humans by staff members who are familiar to the dolphins (Brensing & Linke, 2004). In contrast, when captive dolphins are confined to concrete pools or small marine enclosures where proximity to humans cannot be avoided, it may evoke signs of stress that include avoidance, arousal, and aggression toward either conspecifics or humans (Brensing & Linke, 2004; Frohoff & Packard, 1995).

The research reported here was conducted with a captive dolphin group housed in the kind of seminatural conditions described earlier; a "swim-with-the dolphins" tourist site in which dolphins remained free to approach or avoid human contact (for details, see Methods section below). As petting by familiar humans seemed to be an attractor for free-swimming dolphins, we treated it as representative of an available material resource offering the options of approach or avoidance, and if approach, of gaining access either alone, in pairs, or in larger groups. Approach in pairs or groups can then be classified as an act of cooperation from a behavioral perspective that considers how individuals use each other to co-ordinate for shared outcomes, with additional evidence for pre-ferred partners (Boesch & Boesch, 1989; Brosnan & de Waal, 2002; Perelberg & Schuster, 2008; Roberts, 1997; Schuster, 2002; Schuster & Perelberg, 2004). In the case of petting, this requires that dolphin pairs coordinate their pace and distance both with each other and with the petter, and then share the physical contact that is available. The noncooperative alternative is to approach individually and gain all of the available contact.

The central research question was the extent to which dolphins used individual or coordinated dyadic approach and how this behavioral choice affects the contact time and frequency of petting that individuals gain. As outlined in the Method section, petting was only available from guides who had either one or two hands available for physical contact with dolphins. In either case, approach by pairs meant that the amount of contact petting was approximately halved (sharing the resource); with one-handed petters, the frequency of petting was also halved (sequential instead of simultaneous petting). Evidence for the use of a dyadic coordinated approach at the expense of petting amount or frequency would be consistent with the bias. We will also discuss the validity of two alternative hypotheses: competition and anxiety. Competition suggests that dolphins are not cooperating in order to gain access to a petter, but to compete over this limited resource,

and anxiety reduction suggests that dolphins approach in pairs in order to reduce stress.

In the Discussion section, an explanation for the cooperation bias will be offered that integrates behavioral/psychological and evolutionary processes within a time-extended developmental framework. The cornerstone of this explanatory framework is a distinction between short- and long-term outcomes. Short-term outcomes are the kinds of immediate events that function as attractors, influencing proximate behavioral processes such as emotion, motivation, and reinforcement that determine the likeli-hood that an individual would cooperate. Long-term outcomes, in contrast, are the kinds of material benefits linked to the past performance of cooperation with the potential to elevate fitness and thereby influence the evolution of cooperation in a species via the process of natural selection (Perelberg, 2005; Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster & Perelberg, 2004; Thierry, 2007).

Method

Study Site and Subjects

The study group consisted of 14 (5 males, 9 females) common bottlenose dolphins (*T. truncatus*) living in a 14,000-m^2 natural marine enclosure at the "Dolphin-Reef" swim-with-the-dolphins tourist site, including large shelter areas for the dolphins where human access was prohibited. The site is located south of the city of Eilat, Israel, at the northern part of the Gulf of Aqaba, the Red Sea (for a map and a diagram of the study site, see Perelberg & Schuster, 2008). Water depth inside the enclosure gradually slopes from the shore to 15 m along the circumference net.

The dolphin group was composed of all age and sex classes: adults (sexually mature male and females; 1 male, 4 females), adolescents (dolphins between 7 and 10 years of age, that had yet to sire offspring; 2 males, 1 female), juveniles (weaned dolphins between 2 and 6 years of age; 1 male, 3 females), and calves (dolphins under 1 year of age that were still nursing from their mothers; 1 male, 1 female). All resident dolphins were observed and included in the analysis. There was no forced restriction or separation of any dolphin (except for medical reasons), allowing the dolphins to freely aggregate in ways that represented the expression of social relationships under free-ranging conditions (for further data on relationships, see Perelberg & Schuster, 2008). Feeding was provided by the trainers five times a day (at 0900, 1000, 1200, 1400, and 1600 hr) from designated platforms along the tourists' pier. Feeding was not contingent on performing any behaviors for show, and dolphins never displayed any training-related behaviors before feeding (for more details on prefeeding behaviors, see Perelberg & Schuster, 2008). Training sessions were performed between feeding times as a means of "environ-mental enrichment" for the dolphins, and included individually performed simple tricks such as leaping out of the water that were not contingent on any form of cooperation between dolphins. Participation was completely voluntary, and food reward was never related to training. Only vocal cheers and applause were used as reinforcers for dolphin performance.

Human–Dolphin Interactions: Approach and Petting

Guided and closely supervised programs for tourists occurred between feeding times, including both swim-with-dolphins and

dive-with-dolphins. These differed with regard to the number of hands that accompanying guides had available for petting dolphins that approached. Petting was limited to one hand when guides were holding on to a client with the other hand. This occurred during introductory dives (IDs) and dolphin-assisted-therapy swims (TSs). In contrast, guides had two hands available for petting dolphins during guided dives (GDs) with certified tourist divers, and guided swims (GSs), when the role of the guide was only to lead the tourists but not hold on to them. During these swims and dives, human–dolphin interactions remained voluntary and spontaneous; that is, dolphins voluntarily approached staff for petting or play. Clients were not permitted to either chase after dolphins or touch them. We defined a petting bout as the time a petted dolphin remained next to the petter, until the departure of the dolphin out of the video camera recording frame. Coordination level was defined as the number of separations/minute within a petting bout between a dolphin and its petter's hand. Thus, better coordination was defined as less separations/min between the petter and the dolphin.

The main point to note in the present context is that pairwise approach meant that individual dolphins were sacrificing reinforcement because the resource (i.e., contact with petter's hands) had to be shared whether the number of hands available for petting was one or two. When a dolphin approached a "single-handed petter" in a pair rather than alone, the dolphin was forced to share a single resource because simultaneous petting of both dolphins was not possible. Instead, guides had to pet the dolphin pairs sequentially, thereby halving both contact amount and frequency of contact relative to the reinforcement for individual approach. When a dolphin approached a "two-handed petter" in a pair rather than alone, only the amount of contact was halved relative to approach by a single dolphin because a noncooperating single dolphin could receive two-handed petting whereas both members of a pair could be petted simultaneously but with reduced physical contact (one hand instead of two). In either case, whether with a one- or two-handed petter, pairwise approach meant that reinforcement was substantially reduced in contact amount, frequency or both.

Data Collection and Analysis

Data were collected by scuba diving, using a Sony (Tokyo, Japan) DCR-TRV950E video camera with an attached wide-angle lens Raynox (Tokyo, Japan) DVR-5000 0.5X, housed in an underwater Ikelite (Indianapolis, Indiana) #6037.95 video case. All observed human–dolphin interactions were videotaped using event-sampling method (Altmann, 1974). In addition, all observations that did not involve interactions with humans were recorded ad libitum (Altmann, 1974). The sound track of the video was used during the underwater recording for simultaneous verbal commentary.

Research was conducted over 8 months from May to December 2004. We observed 688 IDs in 118 sessions ($M = 27$, 95% confidence interval [CI] $= \pm 0.36$ min), 118 GDs in 81 sessions ($M = 30$, 95% CI $= \pm 1.52$ min), 260 GSs in 174 sessions ($M = 28$, 95% CI $= \pm 0.45$ min), and 22 TSs in 19 sessions ($M = 26$, 95% CI $= \pm 3.60$ min). Total recorded petting time of single dolphins was 19:03:22 hr, and total recorded petting time of dolphin pairs was 27:39:26 hr. Events where more than two dolphins were petted together by the same petter were excluded from analysis.

Because all data were collected by Amir Perelberg, no measure of interobserver consistency was taken. To ensure reliability and accuracy, data collection commenced only after reaching >95% proficiency on dolphin identification, behavioral categorization, and information on spatial and temporal parameters of behavior, as judged by the manager of the research laboratory (F. Veit). Nonparametric statistical tests were used in data analysis because there was no compliance with homoscedasticity or normal distribution requirements (Sokal & Rohlf, 1995). For all analyses, 95% CIs were calculated for significance level of $\alpha = .05$. 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). Association indices and cluster analysis were performed using the SOCPROG2.2 software, and average linkage was used for clustering (Whitehead, 2004). Statistical analysis was conducted using the SPSS 14.0 for Windows software package (SPSS Inc., Chicago). Dolphin housing conditions comply with the (currently suspended) Animal & Plant Health Inspection Service (APHIS, 2001) swim-with-the-dolphin programs regulations. Following a formal application, this study was approved by the University of Haifa Ethical Committee for Experiments on Animals, following Israeli legal regulations.

Results

Can Dolphins Differ Between Single-Handed and Two-Handed Petters

Because we based our analysis on differences in reinforcement associated with single-handed and two-handed petters, we first assessed whether the dolphins could tell the difference between petter types. If dolphins could not differentiate between petter types, then there would have been no difference in the time that the dolphins were petted by each. Because sessions varied in duration, recorded petting times were standardized to percentages of total session duration. The results showed that, for dolphins approaching alone, the percentage of petting time received from single-handed petters ($M = 5.44\%$, 95% CI $= \pm 2.09\%$) and two-handed petters ($M = 4.50\%$, 95% CI $= \pm 1.82\%$) did not significantly differ (two-sided Wilcoxon signed-ranks test; $z = 0.384$, $N = 14$, $p = .701$, $p_{rep} = .361$, $d = -0.251$, Figure 1B). This result suggests that the frequency of petting (either one hand or two) may not be an important factor for the dolphins. In contrast, for dolphins that approached in pairs, there was a significant difference between petting time with the different petter types: dolphin pairs spent significantly less petting time with single-handed petters ($M = 2.57\%$, 95% CI $= \pm 1.02\%$) than with two-handed petters ($M = 6.03\%$, 95% CI $= \pm 1.61\%$; two-sided Wilcoxon signed-ranks test; $z = -2.62$, $N = 14$, $p = .008$, $p_{rep} = .972$, $d = 1.347$, Figure 1A). This result is consistent with the ability of the dolphins to distinguish between the two types of petters, because even if petting frequency was not an important factor for the dolphins, the contact amount (sequential vs. simultaneous petting) was easily distinguishable.

Cost of Approaching in Pairs

As noted earlier, a pairwise approach to a petter was associated with the cost of a reduction in the contact amount and/or frequency
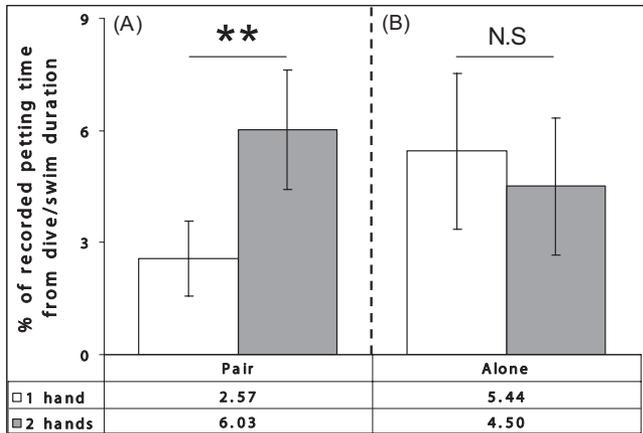
Figure 1. Percentage of recorded petting time from total dive/swim duration. A, dolphin pair; B, single dolphin (Pair = dolphin pair; Alone = single dolphin; 1 hand = petter with one available hand for petting; 2 hands = petter with two available hands for petting). $N = 14$. Error bars denote 95% confidence interval. ** Denotes significance level of $p < 0.01$.

of petting because the resource was shared. An additional cost was the difficulty in coordinating a pairwise approach. Coordination levels between individual dolphins and the human petters were significantly lower when dolphins approached in pairs ($M = 3.05$, 95% CI $= \pm 0.37$ separations/min) rather than alone ($M = 2.54$, 95% CI $= \pm 0.27$ separations/min; two-sided Wilcoxon signed-ranks test; $z = 2.27$, $N = 13$, $p = .023$, $p_{rep} = .870$, $d = 0.817$).[1] Combining the reduction in reinforcement with the difficulty of coordinating, there were higher costs associated with coordinated swimming by pairs to receive petting relative to individuals that approached alone.

Cooperation Bias in Approach to Petters

Evidence for the cooperation bias was obtained by comparing the proportions of petting bouts by dolphins that approached guides individually or in pairs. The data showed no difference between single dolphins ($M = 0.48$, 95% CI $= \pm 0.12$) and dolphin pairs ($M = 0.52$, 95% CI $= \pm 0.12$) when approaching single-handed petters (two-sided Wilcoxon signed-ranks test; $z = -0.22$, $N = 14$, $p = .824$, $p_{rep} = .600$, $d = 0.178$, Figure 2A), even though both contact amount and frequency of reinforcement were halved for cooperators. When two-handed petters allowed for simultaneous petting of both dolphins, there was a preference of ca. 4:1 to approach in pairs even though the amount of physical contact was thereby limited to one hand, and coordination level was reduced ($M = 0.79$, 95% CI $= \pm 0.08$ for pairs, and $M = 0.21$, 95% CI $= \pm 0.08$ for single dolphins; two-sided Wilcoxon signed-ranks test; $z = 3.29$, $N = 14$, $p = .001$, $p_{rep} = 1.000$, $d = 3.875$, Figure 2B).

Coordination Levels and Social Factors

Additional evidence for the existence of the cooperation bias comes from social factors that may affect preference for cooperating with particular partners. A significant positive correlation was found between the time that dolphins were petted by a human

guide and the coordination level of approaching pairs; that is, more petting was received by pairs that better coordinated with their petters ($r_s = .508$, $N = 106$, $p < .001$, $p_{rep} > .992$).[2] This is consistent with dolphins having learned to coordinate both with each other and with the petter, and to prefer better partners as petting-mates. However, if coordination between a dolphin and a guide was predominantly affected by learning, this also predicts that there would be a positive correlation between age and coordination level (i.e., better coordination in older subjects). For individual dolphins, there was no significant correlation between age and coordination levels with petters ($r_s = -.207$, $N = 13$, $p = .498$, $p_{rep} > .713$). In contrast, for dolphin dyads, mean coordination levels of each dolphin in a pair with the petter were negatively correlated with age categories ($r_s = -.386$, $N = 112$, $p < .001$, $p_{rep} > .970$, Figure 3). Moreover, when each age category was separately tested, the trend was also significant within categories of adults with others ($r_s = -.415$, $N = 76$, $p < .001$, $p_{rep} > .975$, Figure 3, black); and juveniles with others ($r_s = -.420$, $N = 64$, $p < .001$, $p_{rep} > .974$, Figure 3, pale gray). Coordination levels of adolescents with others ($r_s = .036$, $N = 32$, $p = .845$, $p_{rep} = .920$, Figure 3, dark gray) and calves with others (Mann–Whitney *U test*: $U = 12$, $N = 4, 12$, $p = .145$, $p_{rep} = .774$, $d = 0.770$, Figure 3, white) did not differ among categories, perhaps due to the small sample size. These results are consistent with social factors having a stronger effect on coordination levels relative to learning per se.

The influence of social factors on cooperation is also shown by nonrandom associations between dolphins that approached guides in pairs. Cluster analysis of dolphin associations both when petted and when swimming freely showed a clear segregation of the population into subgroups according to age-category and maternal status: juvenile subgroup (Su-Mi-Ja), adolescent subgroup (Na-Sn-Le), mothers accompanied by calves or juvenile (Do-Ba, Sh-Ni, Da-Lu), and a barren female with the adult male (Ci-Pa) (see Figure 4). Mean Half-Weight Index (HWI) association levels when petted ($M = 0.097$, 95% CI $= \pm 0.024$) were significantly higher than associations when not petted ($M = 0.065$, 95% CI $= \pm 0.024$; two-sided Wilcoxon signed-ranks test; $z = 4.88$, $N = 14$, $p < .001$, $p_{rep} = .845$, $d = 0.713$).

Discussion

Overall, the data are consistent with petting from familiar human guides as an attractor that functioned as a reinforcement for dolphins. The data are also consistent with a marked bias to approach guides in pairs rather than alone, even though there was an economic cost from pairwise approach. The influence of economic factors was evident in the observation that dolphin pairs spent significantly less petting time with single-handed petters than with two-handed petters, because there was an economic cost associated with pairs choosing one-handed petters. But overall, total reinforcement alone did not predict choice. The cooperation bias was revealed by the strong preference to approach two-handed

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[1] One of the calves never approached alone for petting. Thus, the sample size in this test was limited to $N = 13$.

[2] Of the 91 possible pairs $[N * (N - 1)]/2$, where $N = 14$, 53 were observed in a dyadic approach to a petter. Coordination levels with the petter were analyzed separately for each member of a pair, averaged over all same-pair approaches.
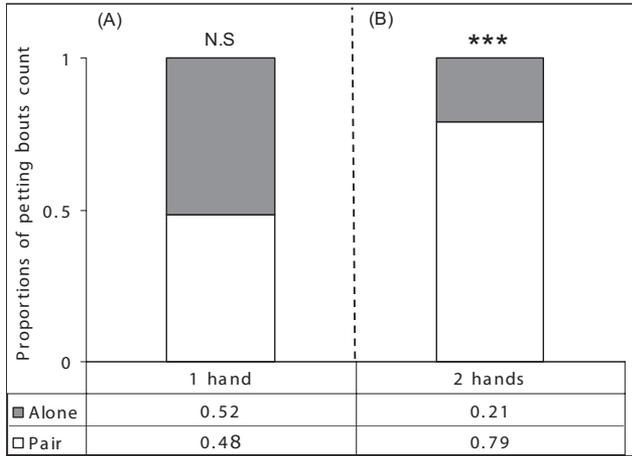
Figure 2. Proportions of petting bouts count. A, single-handed petters; B, two-handed petters (Pair = dolphin pair; Alone = single dolphin; 1 hand = petter with one available hand for petting; 2 hands = petter with two available hands for petting). $N = 14$. *** Denotes significance level of $p = 0.001$.

petters in pairs even though this entailed a sacrifice of total petting amount (one hand per dolphin instead of two hands, and lower coordination levels). The indifference between approaching single-handed petters alone or in pairs is also consistent with the bias because pairwise approach meant sharing the total contact time due to successive petting.

The previous conclusion also implies that the dolphins were capable of discriminating between the amounts of petting received from single- and two-handed petters when they approached alone or in pairs. The fact that dolphin pairs spent significantly less petting time with single-handed petters is consistent with the ability to distinguish between the two types of petters. Although not directly tested, it is likely that the dolphins were readily able to detect the large differences between the contact amount and frequency of petting reinforcement obtainable from single-handed and two-handed petters. Yet the dolphins were indifferent between approaching single-handed petters alone or in pairs even though

this meant sacrificing both contact amount and frequency of petting by about 50%, and preferred 4:1 to approach two-handed petters in pairs even though each dolphin received only one hand.

The cooperation bias is also consistent with the evidence that pairwise approach to human guides for petting was performed nonrandomly, with partners that were also strongly associated when not being petted. Moreover, the negative correlation between pair coordination levels and age, and its sensitivity to age category, imply that social factors, not only learning processes per se, affect pairing for petting. Although our study group was small, with few subjects in each age category, segregation into subgroups by age category and maternal status is consistent with the social structure of this species in the wild (Connor et al., 1992) and also with the social structure of this group in a previous study (Perelberg, 2005; Perelberg & Schuster, 2008). Thus, the structure of cooperating pairs is consistent with the observed social structure of dolphin groups. Together with the influence of partner identity and the increased association levels during paired petting, the results provide evidence that petting was an attractor and support the role of social processes in explaining the likelihood of cooperation (Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster, 2002; Schuster & Perelberg, 2004, 2008).

There are two alternatives to the bias hypothesis for explaining why dolphins might approach guides in pairs rather than individually: competition and anxiety. Both predict higher association levels of dolphin pairs when petted than when not petted. The competition explanation also suggests that dolphins were not congregating to gain access to a petter but to compete over the resource. But this hypothesis seems unlikely because competition is relevant to situations with a limited resource. The petters, however, were an abundant resource that was approached by the dolphins for only a fraction of the time that the guides were present. Second, if competition was a dominant influence, the dolphins should have spent more time congregating around single-handed petters that provided less contact. But the results showed the opposite: there was no difference in preference between single- and paired-dolphins when petters had only one hand, and strong preference of dolphin pairs toward two-handed petters.

The second hypothesis, that dolphins approached in pairs in order to reduce anxiety is inconsistent with the observation that
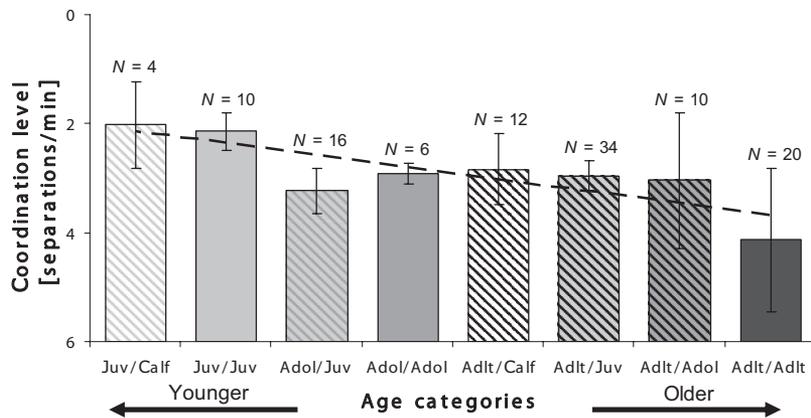

Figure 3. Coordination levels of dolphin dyads by age category (Adlt = Adult; Adol = Adolescent; Juv = Juvenile). Dashed line denotes linear regression. Error bars denote 95% confidence interval.
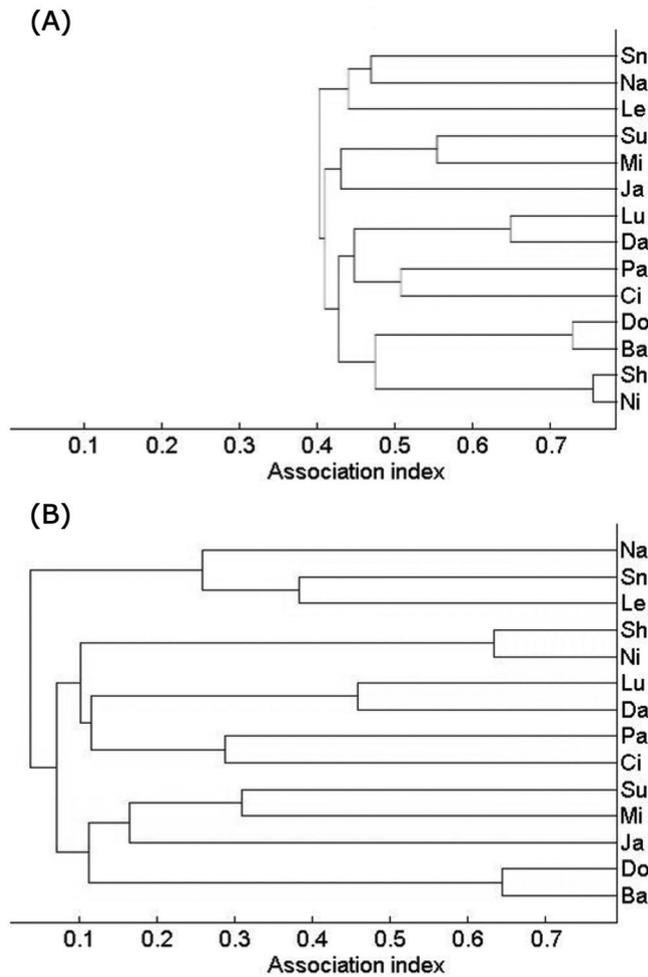
(A)

(B)

Figure 4. Cluster analysis dendogram (average linkage) of dolphin associations. A, when petted; B, when freely swimming in the water (i.e., when not petted). Half-Weight Index (HWI) was used for estimating association levels (adult male: Ci; adult females: Da, Pa, Do, Sh; adolescent males: Sn, Le; adolescent female: Na; juvenile male: Su, juvenile females: Mi, Ja, Lu; male calf: Ba; female calf: Ni).

dolphins did not approach novice guides. Only after several months of habituation, the now-familiar guides were approached for petting (Amir Perelberg, unpublished raw data). Furthermore, the anxiety-reduction hypothesis predicts that there would be no preference between single-handed and two-handed petters, and even a preference to approach single-handed petters in pairs, if one assumes that inexperienced clients (in TSs and IDs) cause more anxiety than more experienced ones (in GSs and GDs). As noted earlier, our results show the opposite effect: dolphins strongly preferred to approach only familiar petters when they had two available hands. It seems that a combination of cooperation, sharing, and tolerance rather than competition or anxiety reduction characterizes how dolphins use this resource.

Overall, the pattern of results is consistent with a behavioral approach to the understanding of cooperation that is anchored in the differences between the behavioral expressions of cooperation and noncooperation in the natural world (Boesch & Boesch, 1989;

Brosnan & de Waal, 2002; Roberts, 1997; Schuster, 2002; Schuster & Perelberg, 2004). In particular, this approach focuses on the social dimensions associated with cooperating as a factor that might predispose dolphins—or any species—to cooperate at levels that exceed predictions from economic factors alone. In human economic theory, decision-making that deviates from the prediction of outcome maximization has been explained by attributing "bounded rationality" to subjects (Kahneman, 2003; Simon, 1955), and Aumann suggested that rationality could still be claimed if subjects obey a predefined "rule" (Aumann, 1997). But how such rules develop in the first place, and how they can be applied to animals, remain to be explained.

Studying Cooperation: Integrating Proximate and Ultimate Explanations

The evidence for a cooperation bias in animals invites explanation that goes beyond rational decision-making and the economics of individual benefits to include more basic behavioral/psychological processes that influence the likelihood of engaging in the behavior when it is performed; that is, proximate processes. Moreover, assuming that the behavior of cooperating is nevertheless adaptive in an evolutionary sense, there ought to be a link between processes that generate excessive levels of cooperation in the short-term and benefits from cooperation in the long-term that influence natural selection. One approach is to integrate behavioral and evolutionary processes within a time-extended developmental framework (Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster & Perelberg, 2004; Thierry, 2007). This will be presented here as a brief outline that will be developed more extensively in Perelberg et al. (2008).

The cornerstone of the integration is a distinction between the currencies, economics, and timing of the short-term outcomes that influence levels of cooperating due to proximate behavioral processes such as the Law of Effect (Skinner, 1938; Thorndike, 1911) and the long-term material outcomes that elevate fitness due to natural selection (Krebs & Davies, 1993). Long-term outcomes are typically used to distinguish cooperation from other kinds of social behaviors by reference to the kinds of material outcomes—food, territory, mating partners, money—that are assumed a priori to elevate fitness and influence natural selection (e.g., Krebs & Davies, 1993; Trivers, 1985). According to evolutionary economics, cooperation is then defined as an individual act performed with others that leads to material outcomes that are accessed by all participants who then reap comparable fitness benefits.

The existence of a cooperation bias, however, highlights the influence of outcomes whose primary influence on cooperation is limited to the time that the behavior occurs. Short-term outcomes can then include not only material gains at the time of cooperating (if any), but also additional intrinsic outcomes linked to positive affective states associated with the social dimensions of cooperating (Boesch & Boesch, 1989; Perelberg & Schuster, 2008; Perelberg et al., 2008; Schuster & Berger, 2006; Schuster & Perelberg, 2004, 2008). The total sum of all immediate outcomes—material and/or affective—can then be used to explain the likelihood of engaging in cooperation and why cooperation might then be expressed at significant levels even when it appears to be uneconomic at the time of performance. Also explained is the ability to learn complex cooperative behaviors, such as cooperative hunting

with division of labor (Boesch & Boesch, 1989; Stander, 1992) that improve during repeated trials despite repeated failures.

The idea of behaviors influenced by intrinsic motivation, emotion, and reinforcement is hardly new (e.g., Harlow, 1953). A hedonic perspective on immediate reinforcement was implied by Thorndike (1911), who formulated the original Law of Effect based on outcomes that evoke "satisfaction" and was explicitly hypothesized by Cabanac (1992) who suggested that perhaps all immediate reinforcers—whether material or intrinsic—share a "common currency" of hedonic affect. The function of intrinsic motivation and reinforcement were also core concepts for ethologists such as Tinbergen (1951, 1963) who suggested that adaptive behaviors like hunting in cats and gnawing in rats have to be partly self-motivating as a means to evoke performance that is not completely dependent on immediate material benefits. Behavioral indices of hedonic affect are often observable and measurable in behaviors such as play that are characterized by excitement and prolonged performance with no obvious material benefit at the time of performance (Bekoff & Allen, 1998; Burghardt, 2005; Pellis & Pellis, 1998).

There is also a difference between the economics of short-term outcomes influencing proximate psychological processes and long-term outcomes influencing natural selection (Thierry, 2007). There is an "apparent economic rationality" underlying evolutionary processes that select for or against phenotypes according to how consequences influence fitness. Evolutionary theory also predicts that behavioral strategies will be "optimal" in terms of costs such as time, energy, and risk (Krebs & Davies, 1993). This kind of "evolutionary rationality," however, is not cognitive in the behavioral/psychological sense of an individual that intentionally and deliberately weighs alternatives before making a rational decision. Gene selection is inherently passive and nonpurposive: if left undisturbed, the proportions of genes linked in any way to increased fitness will eventually increase within a population. Evolutionary economics may therefore mimic rationality, but they are not rational in any sense relevant to psychology (Thierry, 2007).

The influence of short-term outcomes, in contrast, is primarily behavioral/psychological, based on the kinds of proximate processes that underlie the emotions, motivations and reinforcements that influence the likelihood of performance and decision-making. Actions and decisions also have the potential to be purposive in species such as dolphins whose cognitive functioning presumably includes prediction of future reinforcements and awareness of the influence that behaviors have on gaining access to those reinforcements, that is, intentionality (Herman, 2002; Schusterman, Thomas, & Wood, 1986). Such behavioral processes would be favored by natural selection if they increase the likelihood of behaving in a way that eventually elevates fitness. But it seems unlikely that natural selection would have a direct influence on the economics of proximate processes—for example, limiting the intensity of pleasure or the attractiveness of rewards—beyond selecting for processes sufficient to guarantee that the adaptive behaviors will emerge. Affective pleasure is the kind of commodity that—like the overeating of tasty carbohydrates in junk food or the over indulgence in sex—is not obviously subject to regulation with regard to amount or frequency. It seems then that a behavior such as cooperation, when expressed as familiar individuals working together for shared outcomes, may be the kind of phenomenon whose expression is not tightly regulated by considerations of immediate cost/benefit, but more by intrinsic emotions linked to its expression.

A corollary of the economic difference between short- and long-term outcomes is how behavioral and evolutionary processes are differentially influenced by the time-delay between behaviors and outcomes. Natural selection is a life span process that can be influenced by access to material outcomes at any time (Krebs & Davies, 1993). A behavior performed by juveniles can undergo natural selection as long as there is any future influence on fitness, no matter how long the time delay or how indirect the influence. A good example is that of play behavior with the long-term potential to hone the skilled performance of older adults in ways that elevate fitness (Bekoff & Allen, 1998; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Pellis & Pellis, 1998; but, see also Burghardt, 2005). For example, Kuczaj et al. (2006) suggested that play in juvenile dolphins may contribute to their cognitive flexibility in future problem solving under unfamiliar circumstances. But the long-term adaptive consequences of play cannot by themselves explain why juveniles expend so much time and energy in play without also considering the role of proximate behavioral/psychological mechanisms in providing the motivation, emotion, and reinforcement at the time that the behavior is performed (Burghardt, 2005). This is because the influence of reinforcements on the Law of Effect is acutely sensitive to the time-delay between performance and reinforcement. If the performance of a behavior leads to positive reinforcement, the strongest influence will be immediately following the behavior because of sharp discounting as time elapses (Kagel et al., 1986; Stephens et al., 1995). Immediate intrinsic reinforcement would thereby offer a mechanism for bridging the substantial time gaps between performance and future long-term outcomes that influence fitness and for allowing cooperation to be learned when immediate material reinforcements are minimal or absent (Perelberg & Schuster, 2008; Schuster & Perelberg, 2004).

The behavior of cooperating also illustrates the advantages of adopting an explanatory framework that separates short- from long-term outcomes. Analyses of cooperation are often at pains to identify the currency and amounts of immediate material outcomes that explain both the behavior and evolution of cooperation (e.g., Packer & Ruttan, 1988; Scheel & Packer, 1991; Watts & Mitani, 2002). By focusing on the intrinsic influence of social dimensions, it becomes possible to understand why lionesses and common chimpanzees might continue to cooperate in hunting despite greater individual success as solitary hunters (Boesch, 1994; Boesch & Boesch, 1989; Packer et al., 1990). In one population of chimpanzees, for example, the best predictors of hunting were neither nutritional shortage nor meat exchange for sex, but the social and political relations among group members (Mitani & Watts, 2001). Indo-Pacific bottlenose dolphins exhibit a particularly clear case supporting intrinsic reinforcement. Adolescent males form alliances with no evidence of any immediate material gain (Connor et al., 1992). In the long run, however, cooperation would become adaptive if social bonds develop with the potential to modify access to the kinds of material outcomes that influence natural selection. It seems that in dolphins, the alliances of adolescent males pay-off years later when the same males, as adults, cooperate in herding and guarding females for mating, even though only one male will usually sire all offspring (Krützen et al., 2004).

In lions and chimpanzees as well, cooperative hunting may turn out to be a necessary precursor to future cooperation in the contexts of group aggression and territoriality with direct implications for reproductive success (Schuster & Perelberg, 2004; Watts & Mitani, 2001).

The above analysis concerning cooperation is preliminary and potentially controversial. It has been hindered by a tendency to overemphasize the role of evolutionary economics by reducing psychological economics to the secondary issue of "how" cooperation is performed in comparison with the core question of "why" it is performed (e.g., Dugatkin, 1997; Sigmund, Fehr, & Nowak, 2002; Stephens & Anderson, 1997). It has also been hindered by the relative ease of documenting material outcomes by amounts and frequency of access, for example, caloric intake from food, whereas emotional concomitants of behaviors are typically expressed in less tangible forms. But measures of hedonic affect can be applied to the analysis of cooperation, such as the bias when choosing between cooperation and noncooperation (Schuster & Perelberg, 2004, 2008), the preference for particular partners when cooperating or the evidence for excitement shown by social interactions, hyperactivity or vocalizations, including the kinds of ultrasonic calls studied by Panksepp and Burgdorf (2003). The problem of explaining the kind of cooperation bias reported here in dolphins, like the bias to play, will not be resolved by exclusive appeals to rationality and evolutionary economics without considering the behavioral/psychological processes of emotion, motivation and reinforcement that better predict the likelihood that an individual will behave cooperatively.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49,* 227–265.

Animal & Plant Health Inspection Service. (2001). Section 3.111 Swim-with-the-dolphin programs. In *Title 9: Animals and animal products/Pt. 3: Standards.* Retrieved July 18, 2007, from http://www.aphis.usda.gov/ac/publications/AWR/9cfr3.111.txt

Aumann, R. J. (1997). Rationality and bounded rationality. *Games and Economic Behavior, 21,* 2–14.

Bekoff, M., & Allen, C. (1998). Intentional communication and social play: How and why animals negotiate and agree to play. In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 97–114). Cambridge, United Kingdom: Cambridge University Press.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour, 48,* 653–667.

Boesch, C. (2002). Cooperative hunting roles among Taï chimpanzees. *Human Nature, 13,* 27–46.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology, 78,* 547–573.

Brensing, K., & Linke, K. (2004). Behavior of dolphins *Tursiops truncatus* towards adults and children during swim-with-dolphin programs and towards children with disabilities during therapy sessions. *Anthrozoös, 16,* 315–330.

Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature, 13,* 129–152.

Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits.* Cambridge, MA: MIT Press.

Busnel, R. G. (1973). Symbiotic relationship between man and dolphins. *Transactions of the New York Academy of Science, 35,* 112–131.

Cabanac, M. (1992). Pleasure: The common currency. *Journal of Theoretical Biology, 155,* 173–200.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76,* 893–910.

Clements, K. C., & Stephens, D. W. (1995). Testing models of non-kin cooperation: Mutualism and the prisoner's dilemma. *Animal Behaviour, 50,* 527–535.

Colman, A. M. (2003). Cooperation, psychological game theory, and limitations of rationality in social interaction. *Behavioral and Brain Sciences, 26,* 139–198.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Dolphin alliances and coalitions. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415–443). Oxford: Oxford University Press.

Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91–126). Chicago: University of Chicago Press.

de Waal, F. B. M., & Berger, M. L. (2000). Payment for labour in monkeys. *Nature, 404,* 563.

Dill, L. M., Dill, E. S., & Charles, D. (2003). Feeding preferences of the Monkey Mia dolphins: Results from a simultaneous choice protocol. *Marine Mammal Science, 19,* 650–660.

Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals, 24,* 129–142.

Dudzinski, K. M., Frohoff, T. G., & Crane, N. L. (1995). Behavior of a lone female bottlenose dolphin (*Tursiops truncatus*) with humans off the coast of Belize. *Aquatic Mammals, 21,* 149–153.

Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective.* New York: Oxford University Press.

Fehr, E., Fischbacher, U., & Gächter, S. (2002). Strong reciprocity, human cooperation, and the enforcement of social norms. *Human Nature, 13,* 1–25.

Fehr, E., & Gächter, S. (2002). Altruistic punishment in humans. *Nature, 415,* 137–140.

Fehr, E., & Rockenbach, B. (2004). Human altruism: Economic, neural, and evolutionary perspectives. *Current Opinion in Neurobiology, 14,* 784–790.

Frohoff, T. G., & Packard, J. M. (1995). Human interactions with free-ranging and captive bottlenose dolphins. *Anthrozoös, 8,* 44–53.

Goffman, O. (2005). Changes in behavioral patterns towards humans, of a solitary but social female bottlenose dolphin: *Tursiops aduncus,* from Nuweiba, Sinai, Egypt over a period of 5.5 years. Unpublished doctoral dissertation, University of Haifa, Israel.

Hake, D. F., & Vukelich, R. (1972). A classification and review of cooperation procedures. *Journal of the Experimental Analysis of Behavior, 18,* 333–343.

Harlow, H. F. (1953). Mice, monkeys, men and motives. *Psychological Review, 60,* 23–32.

Herman, L. M. (2002). Exploring the cognitive world of the bottlenosed dolphin. In M. Bekoff, C. Allen, & G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 275–283). Cambridge, MA: MIT Press.

Hutchins, E. (1995). *Cognition in the wild.* Cambridge, MA: MIT Press.

Kagel, J. H., Green, L., & Caraco, T. (1986). When foragers discount the future: Constraint or adaptation? *Animal Behaviour, 36,* 271–283.

Kahneman, D. (2003). A perspective on judgment and choice: Mapping bounded rationality. *American Psychologist, 58,* 697–720.

Killeen, P. R. (2005). An alternative to null hypothesis significance tests. *Psychological Science, 16,* 345–353.

Krebs, J. R., & Davies, N. B. (1993). *An introduction to behavioral ecology* (3rd ed.). London: Blackwell.

Krützen, M., Barré, L. M., Connor, R. C., Mann, J., & Sherwin, W. B. (2004). "O father: Where art thou?" Paternity assessment in an open fission-fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology, 13,* 1975–1990.

Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology, 19,* 223–240.

Lockyer, C. (1990). Review of incidents involving wild, sociable dolphins, worldwide. In S. Leatherwood, & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 337–353). San Diego, CA: Academic Press.

Lockyer, C., & Morris, R. (1986). The history and behaviour of a wild, sociable bottlenose dolphin (*Tursiops truncatus*) off the north coast of Cornwall. *Aquatic Mammals, 12,* 3–16.

Maynard-Smith, J. (1982). *Evolution and the theory of games.* Cambridge, United Kingdom: Cambridge University Press.

McNeill, W. H. (1995). *Keeping together in time: Dance and drill in human history.* Cambridge, MA: Harvard University Press.

Mesterton-Gibbons, M., & Dugatkin, L. A. (1992). Cooperation among unrelated individuals: Evolutionary factors. *The Quarterly Review of Biology, 67,* 267–281.

Mitani, J. C., & Watts, D. (2001). Why do chimpanzees hunt and share meet? *Animal Behaviour, 61,* 915–924.

Müller, M., Battersby, M. Z., Buurman, D., Bossley, M., & Doak, W. (1998). Range and sociability of a solitary bottlenose dolphin *Tursiops truncatus* in New Zealand. *Aquatic Mammals, 24,* 93–104.

Müller, M., & Bossley, M. (2002). Solitary bottlenose dolphins in comparative perspective. *Aquatic Mammals, 28,* 298–307.

Neil, D. T. (2002). Cooperative fishing interactions between Aboriginal Australians and dolphins in eastern Australia. *Anthrozoös, 15,* 3–18.

Noë, R. (1990). A veto game played by baboons: A challenge to the use of the prisoner's dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour, 39,* 78–90.

Orams, M. B. (1997). Historical accounts of human-dolphin interaction and recent developments in wild dolphin based tourism in Australasia. *Tourism Management, 18,* 317–326.

Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *The American Naturalist, 132,* 159–194.

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: Food is not enough. *American Naturalist, 136,* 1–19.

Palameta, B., & Brown, W. M. (1999). Human cooperation is more than by-product mutualism. *Animal Behaviour, 57,* F1–F3.

Panksepp, J., & Burgdorf, J. (2003). "Laughing" rats and the evolutionary antecedents of human joy? *Physiology and Behavior, 79,* 533–547.

Pellis, S. M., & Pellis, V. C. (1998). Structure-function interface in the analysis of play fighting. In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 115–140). Cambridge, United Kingdom: Cambridge University Press.

Perelberg, A. (2005). Coordinated cooperation of the bottlenose dolphin (*Tursiops truncatus*) from an integrated social-economic perspective. Unpublished doctoral dissertation, University of Haifa, Israel.

Perelberg, A., & Schuster, R. (2008). Coordinated breathing in bottlenose dolphins (*Tursiops truncatus*) as cooperation: Integrating proximate and ultimate explanations. *Journal of Comparative Psychology, 122,* 109–120.

Perelberg, A., Schuster, R., & Motro, U. (2008). An integrated social-economic approach to cooperation: A formal model incorporating psychological and evolutionary explanations. Manuscript in preparation.

Pryor, K., Lindbergh, J., Lindbergh, S., & Milano, R. (1990). A dolphin-human fishing cooperative in Brazil. *Marine Mammal Science, 6,* 77–82.

Rapoport, A., & Chammah, A. M. (1965). *Prisoner's dilemma: A study in conflict and cooperation.* Ann Arbor, MI: University of Michigan Press.

Roberts, G. (1997). Testing mutualism: A commentary on Clements & Stephens. *Animal Behaviour, 53,* 1361–1362.

Sakai, M., Hishi, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science, 22,* 966–978.

Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: A search for cooperation. *Animal Behaviour, 41,* 697–709.

Schmitt, D. R., & Marwell, G. (1968). Stimulus control in experimental study of cooperation. *Journal of the Experimental Analysis of Behavior, 11,* 571–574.

Schuster, R. (2002). Cooperative coordination as a social behavior: Experiments with an animal model. *Human Nature, 13,* 47–83.

Schuster, R., & Berger, B. D. (2006). An animal model for studying the behavior of cooperating. In M. J. Anderson (Ed.), *Tasks and techniques: A sampling of the methodologies for the investigation of animal learning, behavior and cognition* (pp. 189–208). Hauppauge, NY: Nova Science.

Schuster, R., & Perelberg, A. (2004). Why cooperate? An economic perspective is not enough. *Behavioural Processes, 66,* 261–277.

Schuster, R., & Perelberg, A. (2008). *On the experimental analysis of cooperative behavior.* Manuscript in preparation.

Schusterman, R. J., Thomas, J. A., & Wood, F. G. (1986). *Dolphin cognition and behavior: A comparative approach.* Hillsdale, NJ: Erlbaum.

Sigmund, K., Fehr, E., & Nowak, M. A. (2002). The economics of fair play. *Scientific American, 286,* 83–87.

Simon, H. A. (1955). A behavioral model of rational choice. *Quarterly Journal of Economics, 64,* 99–118.

Skinner, B. F. (1938). *The behavior of organisms.* New York: Appleton-Century-Crofts.

Skinner, B. F. (1953). *Science and human behavior.* New York: Macmillan.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The principles and practice of statistics in biological research.* New York: Freeman.

Stander, P. E. (1992). Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology, 29,* 445–454.

Stephens, D. W., & Anderson, J. P. (1997). Reply to Roberts: Cooperation is an outcome, not a mechanism. *Animal Behaviour, 53,* 1363–1364.

Stephens, D. W., Nishimura, K., & Toyer, K. B. (1995). Error and discounting in the iterated prisoners dilemma. *Journal of Theoretical Biology, 76,* 457–469.

Thierry, B. (2007). Behaviorology divided: Shall we continue? *Behaviour, 144,* 861–878.

Thorndike, E. L. (1911). *Animal intelligence: Experimental studies.* New York: Macmillan.

Tinbergen, N. (1951). *The study of instinct.* Oxford, United Kingdom: Clarendon.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20,* 410–433.

Trivers, R. (1985). *Social evolution.* Menlo Park, CA: Benjamin/Cummings.

Watts, D., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour, 138,* 299–327.

Watts, D., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology, 23,* 1–28.

Webb, N. G. (1978). Women and children abducted by a wild, but sociable adult male bottlenose dolphin. *Carnivore, 1,* 89–94.

Whitehead, H. (2004). Programs for analyzing social structure. SOCPROG2.2 [Computer software and manual]. Retrieved August 27, 2008, from http://myweb.dal.ca/hwhitehe/social.htm