

## AN ANIMAL MODEL OF COOPERATING DYADS: METHODOLOGICAL AND THEORETICAL ISSUES<sup>1</sup>

*UN MODELO ANIMAL DE DÍADAS COOPERATIVAS:  
PUNTOS CONCEPTUALES Y METODOLÓGICOS*

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### ABSTRACT

Probably the most widespread form of cooperation in animals occurs when individuals learn to coordinate behaviors for joint outcomes. Coordination also characterizes courtship and aggression in a variety of species. Yet the social significance of coordinated actions is often neglected in favor of an individual behavior perspective with respect to what is learned and by what processes. Learning theory has generally followed the suggestion of Skinner that the same "laws of learning," based on behavior-outcome contingencies, are sufficient whether individuals cooperate or behave alone. Support comes from laboratory models of cooperation with animal or human subjects that minimize social interaction. Participants are *physically isolated* in separate chambers and individually reinforced according to how both behave. Isolation models have also been used by game theorists and behavioral ecologists to analyze how subjects choose between individual behaviors representing the options of cooperating and defecting. Field studies of cooperative coordination in both animals and humans demonstrate that outcomes alone are insufficient to explain why and how cooperation occurs. Cooperative behaviors and allocation of outcomes are shown to arise from social influences both during the performance and from shared membership in

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social groups. In some cases, cooperation persists when participants benefit unequally or even when individual action seems to be more profitable. Research is described using a laboratory model to study social influences on cooperation. Pairs of laboratory rats are rewarded for coordinating back-and-forth shuttling within a shared chamber in which social interaction is unrestricted and pairs have considerable latitude in how the reinforcement contingency is satisfied. In addition, competition over outcomes can be evoked by periodic presentation of one or two reinforcements. Results are described showing that coordinated shuttling is a social behavior sensitive to the presence and type of partner and the reinforcement contingency. Pairs differ in levels of coordination and in the emergence of stable asymmetries in dimensions that include roles, aggressive dominance, and allocation of outcomes. Evidence is also presented that cooperation affects participants, modifying the preference between cooperative and individual options and increasing post-session consumption of the reinforcement.

Key words: Laws of learning, contingencies, physically isolated, cooperative behavior, defection, social groups, reinforcement, aggressive dominance, allocation, individual options.

### RESUMEN

Probablemente la forma de cooperación que más se ha expandido en animales ocurre cuando los individuos aprenden a coordinar conductas para obtener consecuencias comunes. En una variedad de especies la coordinación se caracteriza por el cortejo y la agresión. No obstante, se le ha restado importancia al significado de las acciones coordinadas favoreciendo así la perspectiva de la conducta individual con respecto a lo que se aprende y a lo que se procesa. Generalmente, la teoría del aprendizaje ha seguido la sugerencia de Skinner de que las mismas "leyes del aprendizaje" que se basan en consecuencias contingentes a la conducta son suficientes tanto para la cooperación como para la conducta individual. Esta sugerencia ha recibido apoyo de modelos de cooperación que minimizan la interacción social desarrollados en el laboratorio con sujetos animales o con humanos. A los participantes físicamente se les aísla y separa en cámaras para ser reforzados individualmente de acuerdo al comportamiento de ambos participantes. Los modelos de aislamiento también se han usado por los teóricos del juego y los ecologistas conductuales para analizar como los sujetos eligen entre conductas individuales que representan opciones de cooperación y deserción. Estudios de campo de coordinación cooperativa en animales y humanos demuestran que las consecuencias por si solas son insuficientes para explicar porque y como ocurre la cooperación. Se ha mostrado que las conductas cooperativas y la distribución de consecuencias surgen a partir de las influencias sociales durante la ejecución así como de una membresía compartida en grupos sociales. En algunos casos, la cooperación persiste cuando los

participantes se benefician por igual o cuando la acción individual es más remunerable. La investigación se describe usando un modelo de laboratorio para estudiar las influencias sociales en la cooperación. Pares de ratas de laboratorio son reforzadas por ir y venir en una cámara compartida en la cual no se restringe la interacción social y los pares tienen una latitud considerable en como la contingencia de reforzamiento debe ser satisfecha. Adicionalmente, se puede evocar una competencia sobre la ganancia si se presenta uno o dos reforzadores periódicamente. Los resultados se describen mostrando que en la cámara el ir y venir coordinado es una conducta social sensible a la presencia y tipo de compañero así como a la contingencia de reforzamiento. Los pares difieren en los niveles de coordinación y en el surgimiento de dimensiones asimétricas que incluyen roles, dominancia agresiva, y distribución de ganancias. También se presenta evidencia que indica que la cooperación afecta a los participantes, modifica las preferencias entre opciones individuales y cooperativas e incrementa el consumo de reforzamiento posterior a la sesión.

Palabras clave: Leyes de aprendizaje, contingencias, aislamiento, conducta de cooperación, deserción, grupo social, reforzamiento, dominancia agresiva, distribución. Opción individual.

Humans and animals often engage in highly coordinated actions by pairs or larger groups. Humans are probably unique in their predilection for precisely orchestrated actions performed by multitudes. These include highly ritualized ceremonies in diverse contexts such as religion, politics and sports, as well as in music or dance performed by pairs or larger groups (McNeill, 1995). Often exciting to watch, they are probably even more exciting for participants who are apt to feel rapport and cohesion with their fellow performers. Even without deliberate action, humans tend to "behaviorally match" the behaviors of others (e.g., LaFrance, M. 1979; Chartrand & Bargh, 1999; Meltzoff & Moore, 1977). This too can exert a positive influence on how others are judged.

Animals also engage in highly coordinated actions in ways that seem to affect the participants. In the context of courtship, some species select a mate for copulation or long-term pair bonding based on the level of coordination in songs, movements or aerobatic displays (Maynard Smith, 1978). Perhaps more surprising is the use of highly coordinated duetting in the context of aggression. Mated pairs use song "duets" to cooperatively advertise and defend their territory and perhaps also to strengthen their pair bond (e.g., Serpell, 1981; Todt, 1975; Hall, 2000). Aggressive duetting, however, is also known between rival males competing from adjacent territories, as in both the singing of birds (e.g., Todt, 1981; Beecher, Campbell & Nordby, 2000) and the "challenge rituals" of antelope (e.g., Schuster, 1976). Ritualized aggression between rivals has been interpreted as cooperative because rivals gain by both demarcating boundaries and minimizing the risk of serious injury through violence (Serpell, 1981; Todt, 1981; Krebs, 1982). This phenomenon has sometimes been described as "dear enemy." This

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captures the idea that aggression can become a shared strategy between competitors well known to one another through repeated interactions, e.g. within hierarchies or territorial networks (Krebs, 1982; Dugatkin, 1997:71-73).

Cooperative coordination (hereafter CC) is perhaps most obvious when there is a concrete, immediate, and measurable outcome obtained through conjoint action. Group hunting is a well-documented example in species as diverse as spotted hyenas *Crocuta crocuta* (Kruuk, 1972), lions *Panthera leo* (Packer & Rutan, 1988; Scheel & Packer, 1991), cheetahs *Acinonyx jubatus* (Caro, 1994), Harris' hawks *Parabuteo unicinctus* (Bednarz, 1988) and chimpanzees *Pan troglodytes* (Boesch & Boesch, 1989). The hawk and cheetah examples are interesting because CC has emerged in species usually characterized more by individual action. Cooperative hunting can even develop across unrelated species, between badgers *Taxidea taxus* and coyotes *Canis latrans* (Minta, Minta & Lott, 1992). Another context associated with CC is *inter-group aggression and defense* (e.g., in hyenas: Kruuk, 1972; in lions: Heinsohn & Packer, 1995; Grinnell, Packer & Pusey, 1995; in chimpanzees: Boehm, 1992). Within groups, *coalitions* or *alliances* form to contest and maintain high rank. The latter is well documented in nonhuman primates (de Waal, 1986; Harcourt, 1988; Noë & Sluiter, 1995).

In several respects, the expression of CC under free-ranging conditions can be a highly social phenomena (Roberts, 1997; Schuster, 2000). Among the social properties of CC are the following (Schuster, in press):

a) *Familiarity*. Participants may be well known to each other as members of a group and even as competitors within a hierarchy (e.g., in male chimpanzees: Boesch & Boesch, 1989). Familiarity also arises from repeated instances of cooperation. As a consequence of familiarity, cooperators sometimes have preferred partners, which in turn might influence the incentive to cooperate (Dugatkin & Wilson, 1991; Noë & Sluiter, 1995).

b) *Pre-cooperative congregation*. Cooperators will typically congregate together before launching their action (e.g., Kruuk, 1972; Boesch & Boesch, 1989).

c) *Absence of orchestrating stimuli*. Under free-ranging conditions, there are usually no external stimuli to guide the act of coordinating. Even when there is a shared goal such as a prey item at the end of a group hunt, the participants will often exhibit coordinated action before the prey is encountered. Without external stimuli, coordination becomes possible only if participants are somehow using each other's presence and behaviors.

d) *Roles*. Experienced cooperators sometimes adopt different and complementary roles, shown in both group hunting (lions: Stander, 1992a,b; chimpanzees: Boesch & Boesch, 1989) and inter-group aggression (lions: Heinsohn & Packer, 1995; Grinnell et al., 1995). Complementary roles also characterize group tasks in humans (Hutchins, 1995).

e) *Allocation of outcomes*. Under free-ranging conditions, social interaction does not always cease when the goal is achieved. To obtain a share, cooperators may then have to compete over allocations (Noë, 1990). These confrontations can

be violent when competing over access to single prey (e.g., in chimpanzees: Boesch & Boesch, 1989; in lions: Packer & Pusey, 1982). Outcome asymmetries mean that cooperation can be sustained when benefits for participants are far from equal. Some participants may actually gain little or nothing. Differential outcomes have led some investigators to query why certain individuals would choose to cooperate, especially if more could be gained by working alone (Scheel & Packer, 1991; Packer, Scheel & Pusey, 1990; Caro, 1994).

f) *Intrinsic rewards from cooperating.* To explain why cooperation is sustained even when not profitable, one hypothesis is that the very act of cooperating with others can be rewarding (Schuster, in press). The *motive* underlying an act of cooperation would then include not only the tangible individual gains but also the experience of working with others (Todt, 1981; Frank, 1988; Sober & Wilson, 1998; Schuster, in press). As yet, no physiological system has been specifically linked to participating in cooperation or to *variation* in levels of coordination. Endogenous opioids have been linked in a general way with social interaction (Panksepp et al., 1980; Panksepp, Siviy & Normansell, 1985) and *social rewards* (Panksepp, Nelson & Bekkedal, 1997; D'Amato & Pavone, 1993). The latter are hypothesized to provide reinforcement from social interactions based on systems that are behaviorally and physiologically distinct from other reward mechanisms.

### CC AS AN INDIVIDUAL BEHAVIOR

Despite evidence in favor of CC as a social strategy, current understanding all but ignores its social elements in favor of a perspective that focuses almost exclusively on CC as a collection of individual behaviors and their outcomes. The individual perspective has dominated our understanding of both the function of CC—the “Why?” question meant to explain its evolution, and the behavioral processes underlying CC—the “How?” question. In both cases, the analysis is always framed with reference to outcomes contingent upon the behavior of each individual cooperator.

#### *Learning theory*

Skinner, like other learning theorists, was concerned mainly with behavioral processes. For Skinner (1953, Chp. 19), the experimental analysis of cooperation required no more, in both method and theory, than the processes governing individual behavior. To model cooperation, two “Skinner boxes” were “yoked” together, physically isolating two animals in separate chambers. Reinforcements were delivered separately to both subjects contingent upon their emitting individual acts such as bar pressing or key pecking that were synchronized within a short time span such as 0.5 sec (Skinner, 1953, p. 306; Lindsley, 1966; for a review, Hake & Vukelich, 1972). Defined entirely by the outcome contingency, isolation

models of CC are classified as social and cooperative because outcomes are contingent on the behavior of *two* animals (Weingarten & Mechner, 1966).

Apart from the payoff contingency, other social processes are excluded from the analysis. With both behavior and reinforcement occurring in isolation, the influences of social factors are minimized. If the partition separating the partners is *transparent*, isolation models remain to some extent social since partners need to observe each other's behavior in order to obtain the timing cue for successful coordination. Interactions based on direct physical contact, however, are prevented, excluding behaviors such as touching, grooming, olfactory exploration or fighting. Isolation models thus remain faithful to a science dedicated to specifying the stimulus and reinforcement conditions that control individual behavior. Each animal is pre-assigned its own individual behavior, its own reinforcement, a defined discriminative stimulus and a latency limitation such as 0.5 sec, all guaranteed to generate a high level of consistency and coordination.

From the individual behavior perspective, social interaction is not even necessary. This becomes obvious from so-called "non-social" models of cooperation designed to generate comparable levels of coordination *in the complete absence of social interaction* (Hake & Vukelich, 1972). Separated by an *opaque* partition, partners can now coordinate only if the behavior of one partner causes the presentation of non-social lights or sounds that can be used by the other for satisfying the reinforcement contingency. Cooperation has now, in effect, become completely equated with individual behavior, with one minor exception. A so-called "social emergent" was identified and labeled as "leadership." This is expressed as a tendency for the behavior of one partner to consistently precede that of the other. (Skinner, 1953, p. 306; Lindsley, 1966). The social relevance of "precedence," however, is questionable. Since differences in precedence can arise without any social interaction, the most parsimonious explanation is the development of a pair of "superstitious" stereotypes (Herrnstein, 1966). For unknown reasons, one partner has learned to initiate an individual behavior without a cuing stimulus. This behavior then supplies the controlling stimulus used by the other partner to time its own individual actions. The design of the models made Skinner's conclusion inevitable (Skinner, 1953:298) "...a 'social law' must be generated by the behavior of individuals. It is always an individual who behaves, and he behaves with the same body and according to the same processes as in a non-social situation."

### *Behavioral ecology*

The selfish-gene school of evolutionary biology advocates a similar individual-behavior position regarding cooperation (Mesterton-Gibbons & Dugatkin, 1992; Dugatkin, 1997; Clements & Stephens, 1995; Stephens & Anderson, 1997). The expectation that all participants will benefit is clearly expressed in the label *mutualism* that has been widely adopted to identify cooperative coordination,

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including *by-product mutualism* and *mutual selfishness* (McFarland, 1985; Wilson & Dugatkin, 1992; Krebs & Davies, 1993; Alcock, 1998). The message is that one needs look no further than individual behaviors and their outcomes to account for the decision by every individual to work alone or with others. There is even an implication that an individual would behave in much the same way, and for the same reasons, whether operating alone or with others. If others happen to gain, this is an unintended "byproduct" (Dugatkin 1997:32).

The wholesale adoption of an individual perspective becomes clear from game theoretical models. These are used by both evolutionary theorists and social scientists interested in strategic decision-making under conditions of social conflict. In one way or another, games usually offer a choice between the options of cooperation or "defection" (non-cooperation), including the well-known Prisoner's Dilemma, or PD (Axelrod & Hamilton, 1980; Mesterton-Gibbons & Dugatkin, 1992; Dugatkin, 1997). As typically modeled, both options exclude social influence. Adapting the Skinnerian methodology to games based on choice, total strangers are isolated in separate cubicles where both behaviors and outcomes remain individual experiences. Each chamber now offers two options – pressing on two levers, computer keys, etc.–that arbitrarily represent "cooperation" and "defection". A "payoff matrix" determines the outcomes for each player according to how *both* players choose between the two options. Under these impoverished conditions, players behave in much the same way whether games are played between two live subjects or between one subject interacting with computer-generated "choices" (Rapoport & Mowshowitz, 1966). To some extent, human subjects can be made aware that their outcomes also depend on the behavior of another (e.g., Forsythe et al., 1994; Dugatkin, 1995), and there is evidence showing that choices in a Prisoner's Dilemma are sometimes based on more than individual gain (Palameta & Brown, 1999). But when animals are physically isolated and tested in a PD or other game, behavior is governed mainly by undiluted selfishness and immediate outcomes (e.g., Green & Price, 1995). In one example with pairs of blue jays *Cyanocitta cristata*, choices tended to follow whatever key led to the higher reinforcement rate (Clements & Stephens, 1995).

### STUDYING CC AS A SOCIAL BEHAVIOR

Based on the above, isolation models would seem a poor choice for analyzing both the *why* and *how* of cc. But this cannot be assumed *a priori*. A particular example of cooperation might be based entirely on individual outcomes. Inter-species mutualisms, for example, occur when different species engage in different behaviors for qualitatively different outcomes (Trivers, 1985). The cooperation between cleaners and their hosts is an example. Even if cooperation normally includes both social interaction and reinforcing outcomes, the validity of an isolation model would depend upon the degree to which a given species is

sensitive to both. If social influences are not salient, then isolation models would still offer a reasonable approximation to CC by focusing on the effects of outcomes for individual behaviors.

The problem for isolation models arises from species whose performance of CC is highly coordinated and strongly susceptible to social influences. Unfortunately, behavioral ecologists and game theorists have avoided the implications of the social behavior perspective with a sharp distinction between the *why* and *how* questions (Krebs & Davies, 1993; Roberts, 1997; Stevens & Anderson, 1997; Dugatkin, 1997). For them, analyses of coordination and all the other social elements of cooperation are only about behavioral processes, the *how* of cooperation. But to understand the *why* of cooperation, and therefore to explain its evolution, the focus has been almost exclusively on the economics of profit-and-loss for every individual choosing to cooperate. And for this, it is argued, isolation models are better at neutralizing all the bothersome and unpredictable social phenomena that might obscure the ultimate profitability from adopting a cooperative strategy. Moreover, priority is claimed for the individual economic approach by claiming that it addresses the fundamental question about cooperation, why it exists as a strategy. The social behavior perspective, in contrast, is relegated to the secondary and less interesting question of *how* cooperators actually do it (e.g., Dugatkin, 1997, p. 32; Stephens & Anderson, 1997).

As noted elsewhere (Schuster, in press), the tactic of separately analyzing *why* and *how* becomes problematical when CC is socially mediated. This is because the social influence may not be limited only to behaviors but also to modifying motives and outcomes. Some evidence suggests that socially mediated CC modifies the value of outcomes and/or the incentive to choose cooperation (McNeill, 1995; Todt, 1981; Frank, 1988; Sober & Wilson, 1998; Schuster, in press). These are not just abstract issues but testable questions that can be translated into experiments designed to show whether social interaction during cooperation makes any difference.

There are at least three issues amenable to experimental investigation:

1. *Behavior.* Regarding the behavior of cooperating, the first task is to determine whether or not a given instance of CC is actually socially mediated. Is the performance based on interactions and their consequences? Is behavior coordinated or are subjects acting independently? Are the stimuli controlling the behavior social or non-social? Does the identity of the subjects matter, i.e., are factors such as relationship, sex or kinship influential? Do cooperators adopt complementary roles, and are these acquired during repeated episodes of CC? Have subjects actually learned to work with others?

2. *Effects on cooperators.* If CC does prove to be socially mediated, how does this affect the cooperators? Does choice between cooperation and individual action vary only with outcomes or do social factors bias the preference? Would CC still be preferred when outcomes for cooperation and individual action are equal or when individual behavior is actually more profitable? Is preference

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influenced by dimensions of CC such as level of synchrony, social interaction, and competition over outcomes or dominance? Are there perceptual, emotional and/or reinforcing consequences arising just from the act of coordinating?

3. *States*. Is socially mediated CC associated with *underlying physiological states* such as altered levels of neurotransmitter functioning or gene expression? Do these states vary with levels of coordination? Are these states absent when reinforcements are contingent on individual behavior or on CC generated by an isolation model?

For addressing such questions, field conditions can pose almost insurmountable problems. Coordination is more often described than measured and the controlling stimuli are rarely specified. Apparent cooperation can be based on minimal social interaction not only when behaviors are uncoordinated but also when coordination is triggered by an event external to the group. The sudden appearance of prey, for example, might evoke a simultaneous attack from a group of predators without a concerted, coordinated strategy. Moreover, such non-social synchrony might be sufficient for increasing the likelihood of making a kill (Dugatkin, 1997). While interesting as a way to increase profits, non-social synchrony would be of marginal interest as a social phenomenon.

In the laboratory, an experimental model of CC should generate coordination that can be measured and analyzed for behavioral processes and consequences based on social interaction. Coordination can be linked to some kind of social interaction such as directed gazing or to an action by one subject that exerts a direct influence on the action of another. Chimpanzees and orangutans, for example, appeared to be using each other when reinforced for coordinated lever pulling (Chalmeau & Gallo, 1996; Chalmeau et al., 1997). And capuchin monkeys showed social influence when reinforced for pulling in a weighted tray that required the combined efforts of two animals (Mendres & de Waal, 2000). Socially mediated cooperation was also demonstrated with pairs of young rhesus monkeys when one animal had to provide a cue that guided the other to the correct option (Mason & Hollis, 1962). In this procedure, however, partners were both physically separated and pre-assigned their individual roles.

### **A MODEL OF CC WITH LABORATORY RATS: COORDINATED SHUTTLING**

Under free-ranging conditions, cooperators typically enjoy unrestricted interaction and the freedom to develop their own idiosyncratic ways of working together. This was modeled in a pioneering experiment with laboratory rats *Rattus norvegicus* (Daniel, 1942). Pairs, in a shared chamber, had to coordinate an exchange of locations in order to obtain reinforcements while also avoiding electric shocks. The experimental report included anecdotal descriptions of touching or tail pulling that appeared to facilitate the coordination.

In our laboratory, pairs of rats are positively reinforced for coordinated shuttling in a shared chamber (Berger, Mesch & Schuster, 1980; Schuster, Rachlin, Rom & Berger, 1982; Schuster, Berger & Swanson, 1988, 1993; Schuster, in press). The general procedure is outlined here and in Schuster (in press). Details can be found in Schuster et al. (1993).

In contrast with isolation models, three elements of the learning situation are probably significant: the *reinforcement contingency*, *social cues* and *unrestricted social interaction*:

Operational  $D \rightarrow N$  Contingency of Coordination

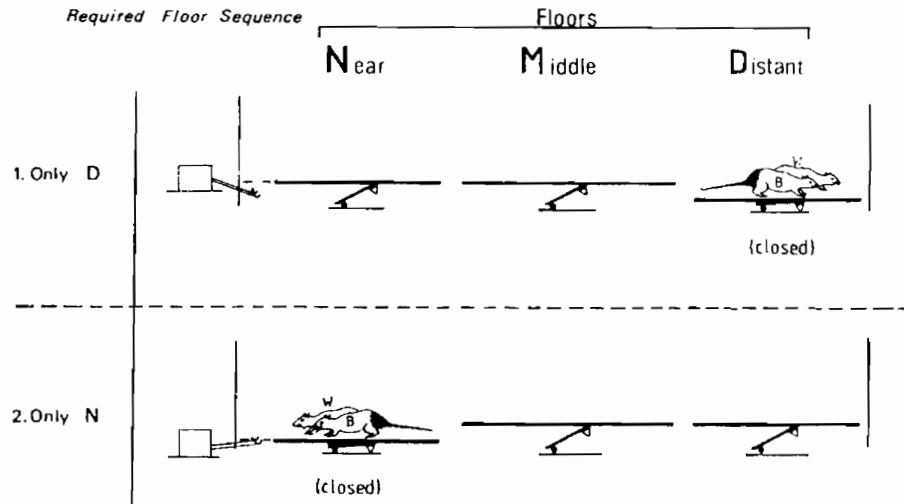


Figure 1.

*The reinforcement contingency*

Reinforcement for cooperating pairs is contingent upon coordinating back-and-forth shuttling so that pairs are together in two locations at opposite ends of a chamber. The chamber is 94 x 24 x 30 cm, with three separate, contiguous grid floors. An opaque partition with two rectangular passages divides the chamber into two compartments, the smaller (25 x 24 cm) enclosing only the **D** floor (*D*istant with respect to reward cups) and the larger (42 x 24 cm) enclosing both the **M**

(*M*iddle) and *N* (*N*ear) floors. The actual reinforcement contingency is sketched in Figure 1. Whether animals are run individually or in pairs, reinforcement (3 ml saccharine solution) is contingent upon shuttling between floor *D*, most distant from the cups, and floor *N*, nearest to the cups. In addition, animals must remain *only* on floor *D* for a minimum of 0.5 sec and then *only* on floor *N* for a minimum of 0.5 sec. For *pairs* of cooperating rats, the **Floor D→N** contingency (hereafter **D→N**) requires that the two partners coordinate shuttling so that *both* are simultaneously located for a minimum 0.5 sec *only* first on floor *D* and then *only* on floor *N*. Working together within a large area, almost 1 meter in length, the contingency can be met by arriving either simultaneously or sequentially onto each floor. In the latter case, a correct performance requires the first animal reaching a floor to remain until the arrival of its partner, and then both have to remain together for at least 0.5 sec.

#### *Social cues*

Sensory feedback while shuttling is limited to social cues provided by the animals themselves from their locations, movements, and social interactions. There are no additional non-social stimuli such as lights or sounds to facilitate coordination. Nonsocial stimuli are limited to a light above the cups providing immediate feedback that a coordinated shuttle has been completed. Another light over the *M* floor signals the end of a session.

#### *Unrestricted social interaction*

Animals are run together in a single chamber without partitions or any other restrictions on social interaction. Access to reinforcement also depends upon social interaction. Delivery of reinforcement is from two cups, each holding 0.06 cc. Depending on the aims of a particular experiment, the two cups can be presented together, providing reinforcement for both cooperators, or either cup can be presented independently. In the latter case, cooperation can evoke competition over single outcomes.

Taken together, the three conditions outlined above leave pairs free to develop their own styles and levels of coordination based not only on outcomes but also on how they interact and influence each other. This kind of model therefore exemplifies a social interaction or *dyadic* perspective on cooperation. Strict control over individual behavior is relaxed in favor of a laboratory context within which the partners themselves, and their relationship, become more influential. The result is considerable variation across pairs in coordination success and coordination strategy (see, e.g., Schuster et al., 1993). Relationships also vary in their degree of aggressive dominance, competitive dominance and/or control.

### Measures

Measures of CC include: *rate*; *social interaction*; and *coordination performance*:

- *Rate* is measured by the *number of completed coordinations*, the *total time* to complete that number, or the *rate of completing coordinations* (coordinations/unit time). Acquisition is shown by improvement (if any) over sessions.
- *Social interactions* are species-typical behaviors and their outcomes scored by trained observers, including touch, ano-genital investigation, allo-grooming, mount, sideways threat, defensive upright (“boxing”), clinch fight, and freeze.
- *Coordination performance* refers to how pairs work together, based on separate measures of *coordination*, *proximity* and *precedence*:
  1. Coordination is measured by the proportion of completed *coordinations with or without errors*. An error is scored when the first animal arriving to a floor fails to remain until the arrival of its partner. The percent of completed coordinations with (or without) errors provides an *index of coordination* that reflects the extent to which partners are utilizing their partners.
  2. Proximity is measured indirectly by “*separation*” events, when partners are maximally separated in the chamber. These are operationally defined as **N∩D**, the simultaneous closures of micro-switches under the **N** and **D** floors at opposite ends of the chamber, without closure of switches under the **M** floor. Increased proximity is therefore demonstrated by decreases in both the cumulative *number* of separation events per completed coordination and the cumulative *total time* of separation events per completed coordination.
  3. Precedence is based on measuring *leading* and *lagging* within coordinating pairs. This provides information about roles and stability within pairs, based on the proportion of completed coordinations in which one partner either leads or lags.

### Procedures

The typical experiment includes three stages: *preparation*; *pre-training in individual shuttling*; and *cooperation*. These are outlined below:

- *Preparation*. Subjects in most experiments have been intact males at least 90 days of age. Both Sprague Dawley and Wistar strains have been used. During experimentation, animals are usually housed in same-sex pairs, either with their cooperation partners or with another male. In more recent experiments, the other male has been castrated to roughly equate the social conditions of housing across all subjects. During this stage, subjects undergo daily handling, weighing, and water deprivation of 1-hr (two days) and then 30-min access per day with food available *ad libitum*.

- *Learning to shuttle individually.* All cooperating partners are initially pre-trained to shuttle individually. This continues until subjects attain a pre-determined criterion of  $x$  completed shuttles (e.g., 30) within  $y$  time (e.g., 30 minutes). This training occurs within the same chamber in which they are later to cooperate. Pre-training guarantees that all subjects have reached comparable levels of individual shuttling so that subsequent variation in the acquisition and performance of CC can be attributed to social influences. Pre-training begins with c. 5 min of *exploration* when the apparatus is inoperative and the reinforcer is made accessible by maintaining the reinforcement cups in the raised position. Exploration thus provides preliminary learning about the reinforcer, where it is located, and its availability after leaving and returning to the vicinity of the cups. Exploration is followed immediately by *self-shaping*. The apparatus is now activated and all completed individual **D→N** shuttles automatically reinforced. Any rat failing to meet the criterion within a specified number of sessions is discarded. If pairs are housed together, both partners are discarded.
- *Learning to cooperate.* When two subjects have both satisfied the criterion for individual shuttling, they are paired together and now required to coordinate **D→N** shuttling in order to be reinforced. This stage is always continued for a fixed number of sessions regardless of whether or not cooperation is developing. Every session is automatically terminated either by completing a pre-determined number of coordinations, e.g. 30, or a maximum total time, e.g., ½ hr, if the coordination limit is not reached.

### IS COORDINATED SHUTTLING SOCIAL?

In this section, experiments are briefly described whose aim was to validate coordinated shuttling in laboratory rats as a social model of cooperation. Specifically, each experiment tested some aspect of whether or how partners learn to use each other when coordinating. Among the issues examined below are the following: whether coordination is better when partners share a chamber; whether social stimuli and the reinforcement contingency are controlling behavior; whether partners have actually learned to work together; and whether the behavior is sensitive to factors such as sex, strain, housing and kinship. Some of the following experiments were also reported in Schuster (in press) and are to be published elsewhere in more detail. All results reported below were tested for statistical significance at the level of at least 0.05.

These experiments also address the issue of social criteria that has rarely been applied to cooperation models in the laboratory. In contrast, animal models of "imitation" have been extensively analyzed for underlying social processes (e.g., Galef, 1988; Whiten & Ham, 1992; Heyes & Dawson, 1990). But the social relevance of cooperation models has rarely been addressed. For example, Skin-

ner (1953) and others (e.g., Hake & Vukelich, 1972), coming from the individual-behavior perspective, were not concerned that isolation models generated comparable levels of coordination whether partitions were transparent or opaque. Before studying whether coordinated shuttling affects the cooperators, the first task was therefore to confirm that coordinated shuttling is a social behavior.

1. Does the presence of the partner influence CC?

If coordinated shuttling is a social behavior, the physical presence of the partner should make a difference. This was tested by reinforcing pairs for coordinated **D**→**N** shuttling either when *together*, within a single chamber (the “*paired*” condition), or when isolated in two separate chambers located in different cubicles (the “*yoked*” condition). The results showed that partners in the paired condition were using each other in some unspecified way. Paired coordination was markedly superior to yoked coordination on all relevant measures: number of completed coordinations, rate of coordinating and “separations” (Schuster, in press). This result was confirmed by *switching* the social conditions after pairs had completed 20 sessions of either paired or yoked coordinating: yoked were switched to paired, and paired were switched to yoked. Figure 2 shows that, on the rate measure of total time to complete 50 coordinations, asymptotic rates of coordinated shuttling were facilitated by partner presence. This finding supports a role for social interaction in coordinated shuttling.

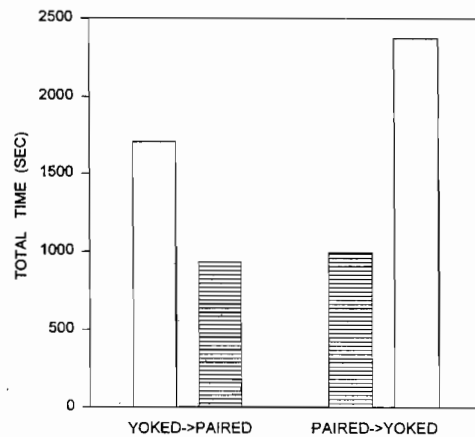


Figure 2.

2. *Is CC controlled by the cooperative D→N contingency of reinforcement?*

If proximity and coordination increase when animals are reinforced in a shared chamber, it was necessary to demonstrate that this improvement arose from the contingency linking **D**→**N** coordination and reinforcement. Since rats will spontaneously approach each other (Latané, Cappell, & Joy, 1970; Taylor, 1976), increases in coordination might arise only from placing two animals in the same chamber and reinforcing them independently for individual shuttles. Levels of coordination were therefore compared between two groups run together in one chamber. In one group, reinforcement was contingent on the **D**→**N** cooperative contingency; in the second group, subjects were *independently reinforced* for individual **D**→**N** shuttling without regard to the shuttling and obtained reinforcements of the other. Both groups were otherwise matched in the proportions of reinforced individual shuttles. Although *rates* of shuttling increased in both groups, *an increase in coordination was obtained only in the group whose reinforcement depended on cooperation* (Schuster, in press).

3. *Do partners learn to work together?*

To demonstrate that coordinated shuttling is based on subjects that learn to work together, an experiment was run to test how readily experienced cooperators are able learn to coordinate with new, naive partners. In a two-stage experiment, two groups were initially reinforced either for coordinated or for individual shuttling over 10 sessions. During each session, every subject shuttling individually was matched to a cooperator in the proportions of reinforced shuttles. All of the above subjects were then reinforced for coordinating in new pairs in which the other partner was experienced only in individual shuttling but not in cooperating. When compared with the original coordination learning of the five naive/ naive pairs, *prior cooperation experience facilitated learning to coordinate with new partners. In contrast, prior individual experience markedly interfered with subsequent coordination learning* (Schuster, in press).

4. *Do partners learn complementary "roles?"*

As noted above, coordination based on social interaction is supported by roles that arise between experienced partners (Stander, 1992a,b; Boesch & Boesch, 1989; Hutchins, 1995). Although coordinated shuttling within a rectangular space offers limited scope for role-taking, one example has emerged. In some pairs, one partner was observed to reliably initiate a social behavior such as touching or allo-grooming that then triggered shuttling in the other partner (see Schuster et al., 1993). From the precedence measure, the initiator of social interactions usually emerged as the *follower* that lagged when shuttling from the **D** floor to the

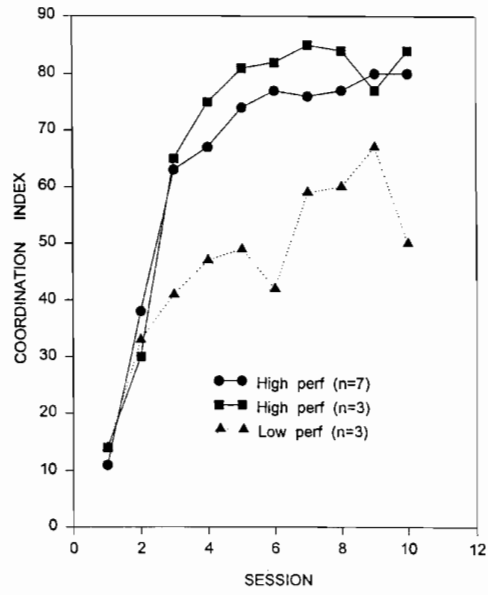


Figure 3.

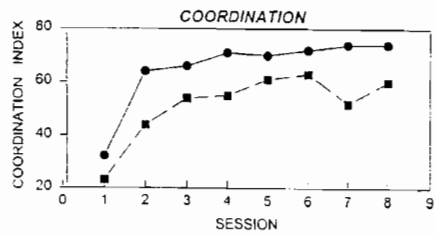
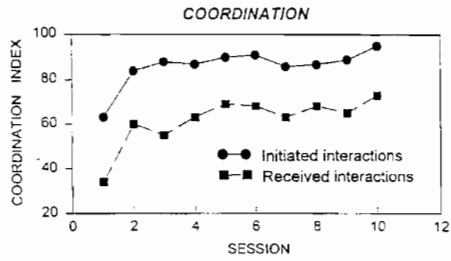


Figure 4.



N floor for reinforcement. In this model, the behaviors of "leading" and "lagging" therefore arose from social interactions.

The difference between leading and lagging, however, was not only about which partner happened to run first. In pairs with a marked asymmetry in precedence, the partner initiating social interactions also appeared to function as a "controller" whose role was to supply cues that would trigger shuttling by the partner that was the target of the interaction. In effect, the partner initiating social interactions was influencing when, how, and at what rate coordination was performed by the pair. This phenomenon was first observed serendipitously in the experiment described above in "3." Although the ten new pairs with one experienced cooperator were better overall in learning to coordinate, three of these new pairs were markedly inferior to the remaining seven. Moreover, the experienced partners in these three pairs came from three different original pairs. In all cases, their former partners performed much better in their new pairs. This result is shown in Figure 3. This result was unexpected because the five original pairs had been comparable in their levels of coordinating.

To test whether the asymmetry in initiating social behaviors was responsible for the difference in subsequent learning of CC, eight experienced pairs were selected from experiments that had recently ended. The pairs were chosen based on ratings by two independent observers that they exhibited a marked asymmetry in initiating social behaviors. The experiment included two subgroups of new pairs that differed in their composition. One was based on *switched partners*. Randomly choosing three of the original asymmetric pairs, the partners were interchanged so that two initiators or two recipients were now together in new pairs. The other group consisted of *experienced/naive partners*, duplicating the procedure in 3, above. All subjects from the remaining five pairs, initiators and recipients, were each given a new partner naive in cooperating.

The results shown in Figure 4 were similar in the two subgroups: *new pairs learned better when the experienced partners had been initiators of social interactions in their original pairs*. There were also two pairs in the experienced/naive subgroup whose data were not included in the lower half of Figure 4: the experienced partners had been *recipients* of social behaviors and did not learn at all.

The results described above are potentially significant for understanding the origins of some intra-pair role differences. The impression gained from isolation models is that "leaders" and "laggers" are arbitrary, arising by chance as equivalent individual strategies. But the above data suggest that when leading and laggings are consequences of social interaction, the difference in behavior is an expression of intra-pair asymmetries with relevance to dominance, control and outcomes. It is tempting, therefore, to take another look at field data on "leading" and "lagging" in cooperative relationships. Under some conditions, the difference can have serious implications for outcomes and even for survival. In our own species, the leading attacker in an army unit is more at risk. The same is known in lion predation when certain animals regularly "rush the prey" while others lag behind

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(Scheel & Packer, 1991). The lion making the initial attack on a large prey animal also runs a greater risk of injury from flying hooves, horns, or falling. In lions, similar risks arise from "leading" and "lagging" in inter-group fights (Heinsohn & Packer, 1995; Grinnell et al., 1995).

Even without risk, payoff asymmetries can be related to ranks and roles among members engaged in group-level tasks. In chimpanzee hunting, dominant males usually appropriate larger shares of the kill (Boesch & Boesch, 1989). In human groups, the individual organizing and/or giving instructions is likely to be treated as a dominant over others, with consequences for assigned rank, privileges and financial compensation. For leaders and followers, therefore, roles have consequences not only for control but also for net payoffs.

##### *5. The type of partner*

If cc is socially mediated, the behavior ought to be sensitive to characteristics of the partners that have to work together. Four examples are briefly described in which coordinated shuttling was sensitive to the partners.

*a. Isolated housing.* Isolated housing of male rats selectively impaired coordinated shuttling, with no effect on individual shuttling (Schuster et al., 1982). The impairment was associated with extreme dominant-subordinate asymmetries in which one animal attacked violently, causing the other to freeze for extended periods.

*b. Sex and strain.* The deleterious effects of isolated housing reported above were also shown to be sex and strain specific (Schuster et al., 1988, 1993). Males and females of strains differing in aggressiveness were housed either in pairs or in isolation. Whereas all socially-housed pairs learned to cooperate, isolated housing again led to severe impairment. But this was limited to males and only in the two more aggressive strains ((Schuster et al., 1993). Sex-specificity was confirmed by linking the deficit to testosterone (Swanson & Schuster, 1987).

*c. Live vs. inanimate "partner."* Another way to show the model's sensitivity to social interaction is to compare two-animal cooperation with single-animal "cooperation" in which the other "partner" is a non-living object. As Zentall (1988) warned for studies of imitation, a valid model of social behavior ought to be sensitive to substituting a live, behaving partner with an inanimate object. This was tested by comparing the effects of isolated housing on the coordinated shuttling of two-rat pairs and rat-light "pairs" (Berger & Schuster, unpublished). In the latter, the live partner had to coordinate with a sequence of lights presented above the **D-floor** and **N-floor** whose timing mimicked the shuttling of a live rat. Both kinds of pairs first learned to coordinate shuttling when socially housed. (Since live rats in rat-light "pairs" are not housed with their non-living partners, meeting only when cooperating, two-rat pairs were also not housed with their partners.) After both groups learned to coordinate, half the pairs in each group were switched to isolated housing while the remainder continued to live in pairs.

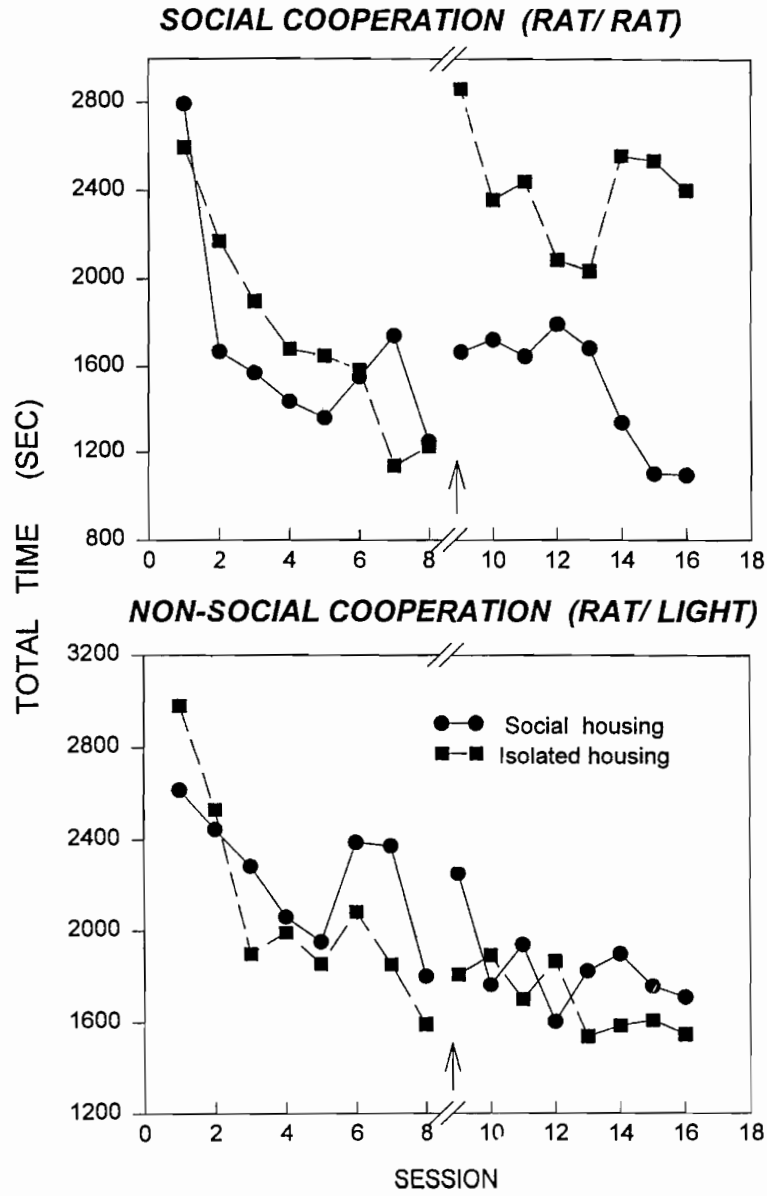


Figure 5.

The result, shown in Figure 5, was a selective impairment in rat/rat pairs after the switch to isolated housing, whereas rat-light pairs were unaffected. In essence, this result replicates the earlier finding that isolated housing had a selective influence on the coordination of pairs, leaving individual shuttling unaffected (Schuster et al., 1982). The insensitivity of rat-light "pairs" to social isolation demonstrates the obvious, namely that rat/light coordination is not social in any meaningful sense. The same conclusion can be extended to "non-social cooperation models" in which the coordination of two live subjects is based entirely on using non-social cues (Hake & Vukelich, 1972).

*d. Kin vs. non-kin.* When an individual engages in cooperative coordination, outcomes and fitness can also accrue to others. CC, like altruism and reciprocity, should therefore show sensitivity to genetic relatedness (e.g., Trivers, 1985; McFarland, 1985; Dugatkin, 1997). In lions, for example, coalitions formed for the purpose of territorial fighting are influenced by kinship (Packer et al., 1991). In a preliminary study, coordinated shuttling was compared between pairs of former littermates and pairs of non-kin (Hareli, Katzir & Schuster, 1996; Schuster, in press).

The model proved sensitive to kinship in two ways. When 100 percent of all coordinations were reinforced with two cups, kin pairs learned more rapidly and more kin pairs reached the daily maximum of 50 coordinations. Kinship also influenced levels of competition when reinforcement conditions were changed. Coordinations were now followed by intermittent, quasi-random presentation of double cups, left cup, right cup, or no cups. Since the animals were now in a shared space, the potential for reinforcement competition was created whenever either of the single cups was presented alone. Results showed that, overall, *kin pairs were less competitive*. This conclusion was based on which partner, the "owner" or the "invader," gained access to single cups. "Ownership" over the left and right cup was assigned to the partner that regularly drank from that cup when *both* were presented. The other partner was then a potential "invader" if it attempted to gain access to a single cup that "belonged" to the other. When single cups were presented, the modal behavior in kin pairs was for the more dominant partner to drink from the same cup that was selected when *both* cups were presented, i.e., a tendency towards sharing. In contrast, dominants in non-kin pairs were most likely to compete over the cup "owned" by their partners.

#### HOW DOES COMPETITION OVER OUTCOMES AFFECT COOPERATION?

A recently completed study with Peter Killeen focused in more detail on how coordinated shuttling is influenced by competition over reinforcement outcomes. The experiment modeled a well-documented feature of CC under free-ranging conditions, namely that cooperation and competition can become sequentially

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linked when cooperation is followed by competition over single outcomes (Packer & Pusey, 1982; Boesch & Boesch, 1989; Caro, 1994; Noë et al., 1991). The experiment is complex and will be published in its entirety elsewhere. Excerpts will be reported here that illustrate additional consequences of social interaction on coordinated shuttling. Some results also address the issue of how participants are affected by engaging in CC.

As in the experiment on kinship reported in **5d**, above, this study focused on how competition affected cooperation that had already been acquired. Before introducing competition, animals were first trained to shuttle alone and then to coordinate while separated by a partition of vertical bars, both to a criterion. The partition was then removed and coordinated **D→N** shuttling was reinforced according to conditions that included sequences of single and double reinforcements.

The experiment was run in five successive stages:

*Stage 1: pre-learning.* Housing with *castrated cage-mates*, daily handling and water deprivation.

*Stage 2: learning individual shuttling.* Reinforcing 100% of individual **D→N** shuttling to a criterion.

*Stage 3: Cooperation with dividing partition.* Reinforcing 100% of coordinated **D→N** shuttling to a criterion. Partners were physically separated by a partition of vertical metal bars running the entire length of the chamber.

*Stage 4: cooperation without partition.* Reinforcing coordinated **D→N** shuttling with unrestricted social interaction for 12 sessions. The conditions of reinforcement differed as follows:

- a) *100% reinforcement:* two cups as in Stage 3;
- b) *Competition:* intermittent presentation of one or two cups;
- c) *Non-competition:* intermittent presentation of two cups or no cups.

*Stage 5: individual shuttling, post cooperation:* individual **D→N** shuttling as in Stage 2.

#### *Reinforcement conditions for competition*

The competition condition included four groups reinforced following every coordination with intermittent presentations of three events: a single left cup, a single right cup, or two cups. The numbers of single left and right cups were always equal. The groups, identified as C-25, C-50, C-75 and C-100, were distinguished by decreasing proportions of double cups and increasing proportions of single cups. The group labels refer to the *maximum percent increase* in numbers of reinforcement that one partner could have obtained by successfully competing over every single outcome. For example, for the C-50 sub-group, one partner could potentially gain a maximum 50% increase in its total number of reinforcements by gaining access to *all single reinforcements*. This increase would be at the expense of the partner that would suffer a corresponding 50% decrease in its

reinforcements. Both the increase and decrease are relative to the number of reinforcements obtainable by each partner without engaging in competition, i.e., the number obtained by each partner if it only drinks from its own cup whether presented alone or together with the other cup ("sharing."). For the C-100 group, all coordinations were reinforced only with single cups. One partner, by gaining access to all single cups, could double its outcomes, i.e., a 100% increase. The other partner would then obtain no reinforcements.

#### *Reinforcement conditions for non-competition*

The effects of competition on coordination were compared with four groups reinforced with the *same total numbers of reinforcements* obtainable by each of the competition groups but without the competition evoked by single cups. Reinforcements were instead presented intermittently *only as double cups* or no cups. The four groups are identified as NC-25, NC-50, NC-75 and NC-100. Feedback for all completed coordinations was provided by illuminating the light above the cup locations whether or not the primary saccharine reinforcement was presented.

## RESULTS

### *Coordination*

The data have not yet been analyzed in detail but some trends are emerging. During Stage 4, when pairs had full social interaction, there was wide variation in coordination. Of 106 pairs across all groups, 81 (76%) were classified as "cooperators" These attained the maximum number of completed coordinations during *at least one of the 12 sessions*. The remaining 25 pairs (24%) were "non-cooperators" that failed to reach the session maximum. Non-cooperators were characterized by higher levels of violent fighting and freezing, as described in **5a** and **b** above.

Among the cooperators, there was also wide variation. Pairs differed in their session-to-session improvement in coordinating, measured by the slope of the linear trend line linking coordination rates over sessions. Using the mean slope of 2.01 ( $z = 0$ ), pairs are classified as "good cooperators", with slopes above 2.01, and "bad cooperators" with slopes below 2.01 (Schuster, in press). The difference between "good" and "bad" cooperators was not only in rate but also in other measures such as proximity (Figure 6) and coordination (Figure 7).

The data outlined above provide yet another demonstration that cooperation is not the same phenomenon when performed with or without full social interaction. Stage 3 was essentially an isolation model of cooperation in which all pairs were run to the same criterion while physically separated. Yet cooperation by the

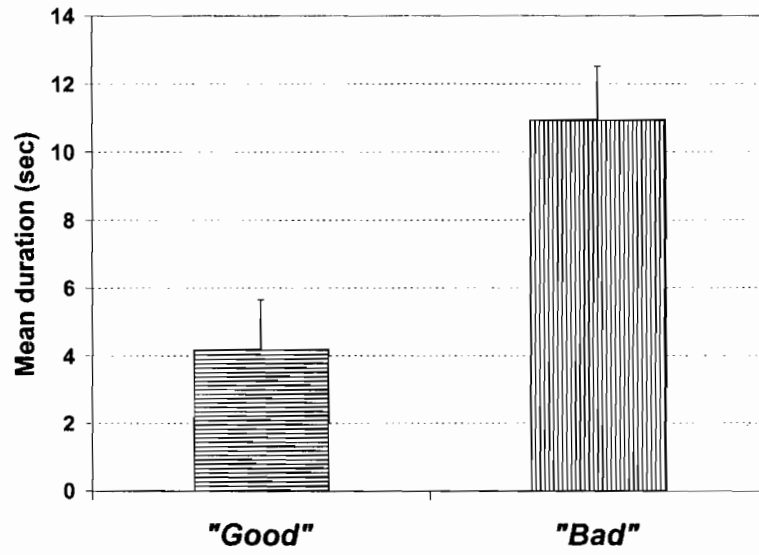


Figure 6.

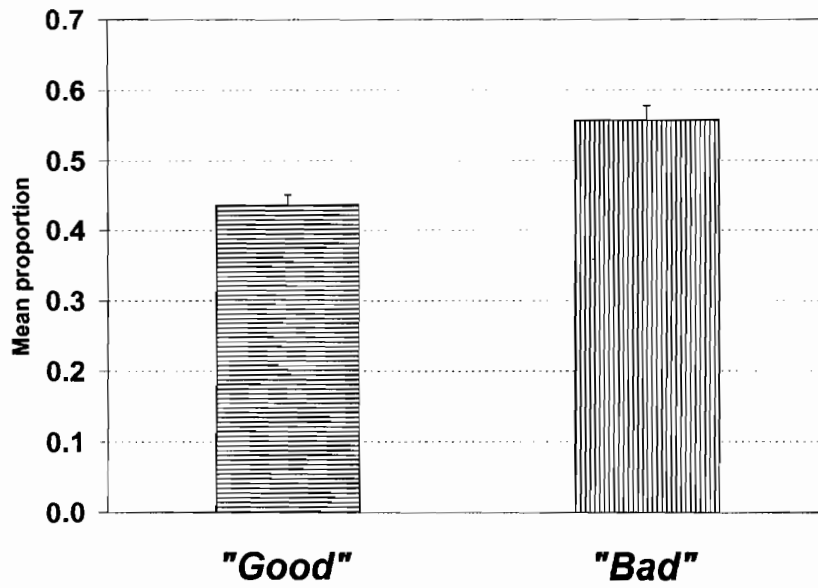


Figure 7.

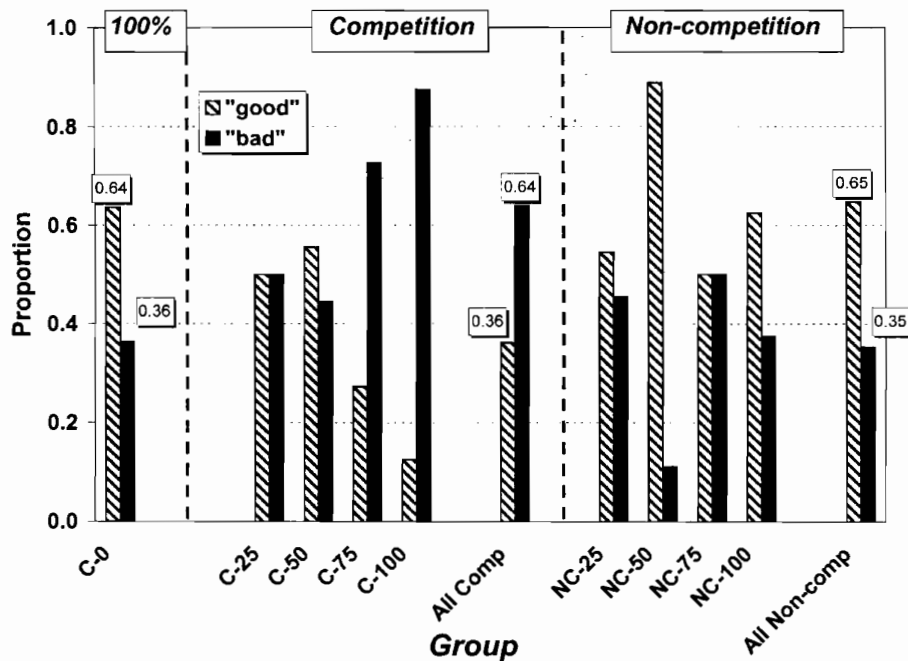


Figure 8.

same pairs was highly variable during Stage 4 when social interaction was unrestricted.

#### Competition

Competition over reinforcements during Stage 4 is emerging as a factor with a negative influence on cooperation. This is shown by comparing the proportions of "good" and "bad" cooperators in the 100% group and the four competition groups C25, ..., C100. These represent a set of conditions designed to evoke increasing levels of competition over reinforcement, from *no* competition in the 100% group to maximum competition in C100. Figure 8 shows that, across these five groups, the proportions of "good" cooperators steadily declined. In contrast, a similar trend did not emerge among the four groups NC25...NC100. Without competition, there was no obvious tendency for "good" cooperators to decline with decreasing reinforcement frequency. Overall, about 2/3 of the pairs in the 100% group and



the four non-competition groups were "good" cooperators, as defined above. In contrast, only about 1/3 of all pairs in the four competition groups were "good" cooperators.

### *Dominance*

Another dimension of behavior that varied widely in the four competition groups was the level of competitive dominance over single cups. As reported in 5d, above, dominance was based on first establishing cup ownership. Dominance was then measured on an ordinal scale of 0-7, with 0 indicating no attempt at invasion and 7 indicating that one partner gained access to all single cups, both its own and those of its partner. Figure 9 shows a wide range of dominance scores from cooperators. These were obtained from all groups. Also shown is that the level of competitive dominance was unrelated to performance levels as measured by the numbers of sessions that a pair completed the maximum number of coordinations. The majority of pairs developed marked asymmetries in dominance between 4 and 6, i.e., there were many pairs in which partners differed considerably in numbers of obtained reinforcements. Yet many of these pairs were able to cooperate at high levels.

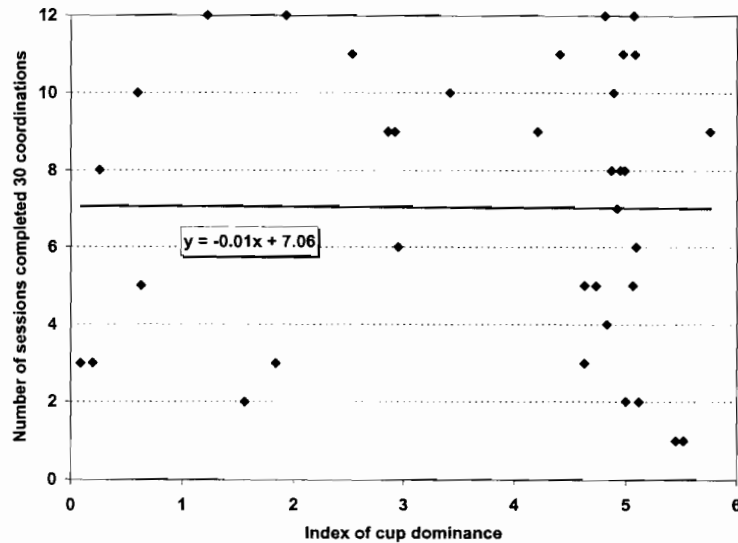


Figure 9.

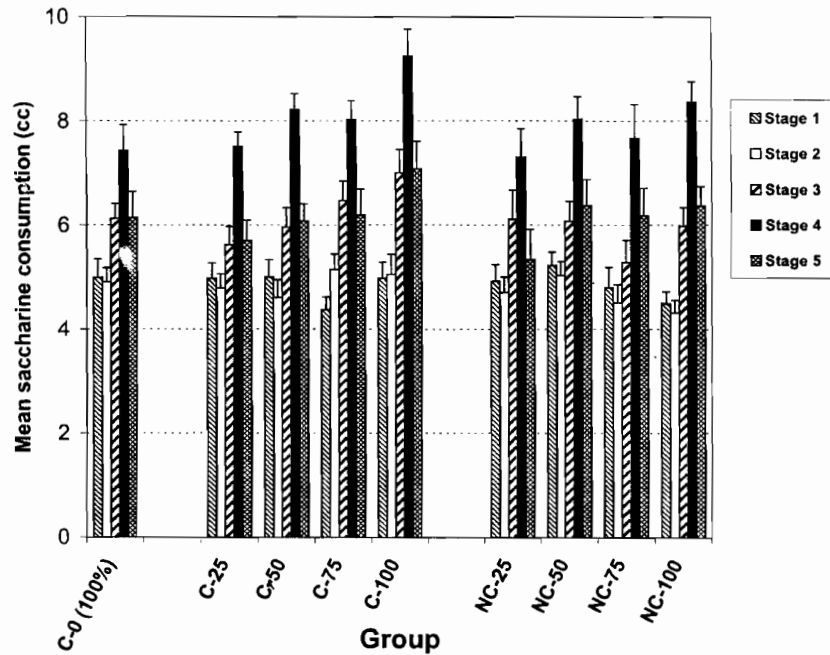


Figure 10.

#### *Post-session consumption of the reinforcer*

There was also evidence that animals were selectively affected by cooperating with unrestricted social interaction. The evidence comes from measuring post-session consumption of the reinforcing saccharine solution. Consumption was measured by transferring subjects from the experimental chambers directly to individual drinking cages following the end of every session. Testing was conducted in isolation to eliminate social influences while drinking. For 5 minutes, subjects chose between two calibrated drinking burettes, one containing the reinforcing saccharine solution and the other water. Tests were conducted throughout all five stages described above: during the last 7 days of Stage 1 (pre-learning) and following the end of every session during Stages 2-5.

The most prominent feature of the data on post-session consumption is a selective increase during Stage 4, cooperation with unlimited social interaction (Figure 10). The higher level during Stage 4 contrasts with the level during Stage 3 when subjects were also cooperating while separated by the partition. In addition, consumption during Stage 3 was not markedly different from levels during Stages 2 and 5 when the same animals were reinforced for individual

shuttling. Post-session consumption is thus providing yet another indication that CC with full social interaction is qualitatively different from both individual shuttling and coordinated shuttling with physical isolation. The explanation for the increased consumption is unclear, since it could arise either from increased need or increased hedonic affect (Berridge, 2000). Either way, the data suggest that motivation for the reinforcer may have been elevated by cooperating with social interaction.

### CHOICE BETWEEN COOPERATION AND INDIVIDUAL ACTION

Evidence for states evoked by CC is also being obtained from experiments in which subjects choose between cooperation or individual behavior. This experiment models the situation under free-ranging conditions when potential cooperators have the luxury of choosing whether to gain outcomes through coordinated or individual action, as in hunting lions (Packer, Scheel & Pusey, 1991).

The issue of choice between cooperative and individual action touches upon most of the issues discussed above. According to an individual behavior perspective, the choice is between two individual behaviors and should therefore be governed mainly by outcomes such as numbers or rates of reinforcement. In contrast, the social interaction perspective states that the choice is not only between outcomes but also between two qualitatively different situations. One is a real social option, working with a known partner, whereas the other option, defection, is abandoning the relationship and all of its concomitants in favor of individual action. Moreover, the social option incorporates all of the emergents discussed above—coordination, roles, aggressive dominance, control, hedonic attractiveness of the reinforcer, competition over outcomes, etc.—as well as their physiological concomitants. To the extent that these emergents evoke positive or negative affect, they should also bias subjects in their choice of cooperation or individual action.

The methodology for studying preference uses a T-maze connecting two cooperative learning chambers. Different floor surfaces in the T-maze aid in distinguishing the routes to the goal boxes. A three-stage procedure is used: 1) learning the two tasks; 2) forced choice; and 3) free choice. In the learning stage, subjects are reinforced for CC in one chamber and for individual shuttling in the second chamber. In the second stage, subjects continue as in "1" while learning the routes to the two options by means of *forced choices* within the T-maze. When entering the cooperation chamber, its partner is immediately inserted from above. During the third stage, subjects can choose freely between the two options.

One experiment was reported in Schuster (in press) and will be published elsewhere in detail. It was based on matching reinforcement probabilities for cooperation and individual behavior, without any competition over outcomes following cooperation. The results were that relative rates of reinforcement for

cooperating [cooperative reinforcement rate / (cooperative reinforcement rate + individual reinforcement rate)] were initially lower during Stages 1 and 2, and then almost equal during Stage 3. Nevertheless, *cooperation was the strongly preferred option*: 74% of all choices by 28 subjects (14 pairs) were to cooperate. There was also a significant correlation between preference and levels of cooperation during Stage 1. "Good" cooperators, as defined above from the experiment on competition, were also more likely to prefer cooperating.

Choice was also examined in a preliminary experiment with four pairs in which the cooperation option included competition over single reinforcements. Competition was evoked by programming four possible outcomes following successful coordination, each occurring with a probability of 0.25: both cups, the left cup, the right cup or no cup. All outcomes were signaled by a light over the cups. "Dominants" and "subordinates" were identified in all pairs based on differences in access to single cups, as described above. There was no reinforcement advantage, however, from choosing to cooperate or to shuttle alone. For both dominants and subordinates, reinforcement conditions for every subject were matched with respect to the proportions of reinforced shuttles when cooperating or shuttling alone.

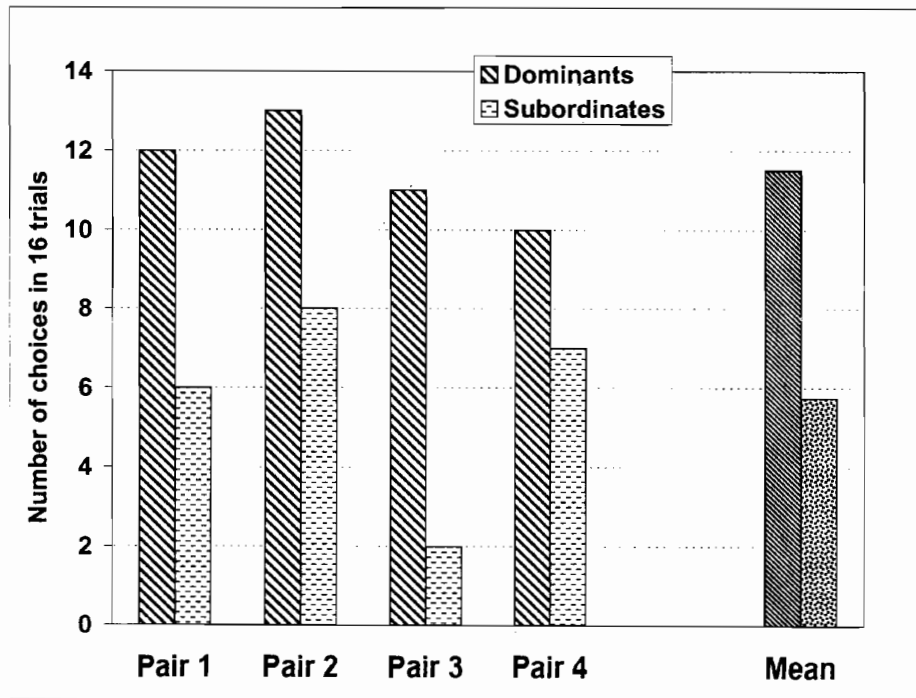


Figure 11.

Stage 3 (free choice) included sixteen trials over four sessions. The result, shown in Figure 11, was that competitive dominance affected preference. Dominants preferred the cooperation option in all pairs. Among subordinates, however, only one subject (in Pair 2) chose equally between the two options; the remainder clearly preferred the individual option. Overall, in both choice experiments, the data on preference demonstrate that choice between cooperation and individual behavior is determined not only by individual outcomes but by social influences when coordinating.

## DISCUSSION AND SUMMARY

To summarize, two contrasting perspectives have been used to explain why and how cooperation occurs (Roberts, 1997; Stephens & Anderson, 1997; Schuster, 2000, in press). The individual behavior perspective ignores the social context of cooperative behaviors under free-ranging conditions. CC, like any other form of cooperation, is predicted from the outcomes obtained by each participant for its individual behavior. If behaviors happen to be synchronized, this perspective is indifferent to whether the controlling cues are social or non-social. The second, social interaction perspective, lays stress on how CC emerges from the combined behaviors of two or more individuals. These coalesce in ways that depend upon how participants interact and influence each other while cooperating and on social relationships that may already exist.

The two perspectives have also given rise to very different ways of measuring cooperation in laboratory models. These closely mirror the respective theoretical perspectives that the models were designed to support. The individual perspective is supported by models that physically isolate subjects both when cooperating and when obtaining reinforcements. The social behavior perspective, in contrast, is focused on demonstrating how individuals influence each other by their presence and behaviors. Evidence for social influences from field studies includes coordination, roles, and allocation of outcomes (e.g., Boesch & Boesch, 1989; Stander, 1992a,b). In some laboratory models, coordination has been shown, at least informally, to depend upon social interaction (e.g., Daniel, 1942; Chalmeau & Gallo, 1996; Chalmeau et al., 1997; Mendres & de Waal, 2000).

Coordinated shuttling in rats was offered as a model of cooperation sensitive to the presence and behaviors of the participants. Within the limited confines of a laboratory, the model generates cooperative behaviors analogous to those observed under free-ranging conditions, e.g., variation in rates and levels of coordination, roles, dominance, and allocation of outcomes. Socially mediated coordination is also supported by its sensitivity to sex, strain, and housing. Perhaps most important is the model's demonstrated sensitivity to manipulating partner interaction. Coordination levels, preference, and post-session reward consumption were all affected by whether animals were run alone or together, or whether partners

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were physically separated by a partition. Many design features of this particular model were specially adapted for the rat—back-and-forth shuttling, for example. But the sensitivity of the model to social factors suggests a general approach to the problem of understanding socially mediated cooperation that can be adapted to research on any species including our own.

There can be little doubt, therefore, that models of cooperation generate different behaviors and different incentives depending upon how much subjects can interact. So what is the preferred model for studying cooperation? The answer probably depends upon the relative importance of individual outcomes vs. social factors for understanding cooperation. Outcomes clearly influence why individuals are specially adapted for cooperating. The majority of birds, for example, are apparently monogamous because females, working alone, would be less successful in rearing chicks (Krebs & Davies, 1993). But reproductive cooperation in birds is usually embedded in pair bonds that follow intense periods of courtship. And both males and females can exploit their partners by engaging in extra-pair copulations (e.g., Gowaty, 1996). Perhaps isolation models are therefore most relevant when social factors have little or no effect on the participants. In *inter*-species mutualisms, such as those between cleaners and their hosts, cooperators exchange favors based on qualitatively different behaviors for qualitatively different outcomes. There would be little temptation to dominate or compete over outcomes, and these generally seem to be minimal. With a relationship mainly beneficial to both, the term “no-cost cooperation” probably applies (Dugatkin, 1997, but see Bshary & Grutter, 1999).

But no-cost cooperation may be far less likely *within* species when individuals are familiar to each other and sensitive to each other's social behaviors. Competition, whether over ranks or direct access to the same resources, is also more likely in intra-species cooperation. By minimizing the influence of social factors on intra-specific cooperation, isolation models risk generating and analyzing behaviors that do not adequately represent cooperation under free-ranging conditions.

This essay has emphasized three limitations of isolation models. One concerns the act of cooperating. Data were shown that illustrate the extent to which the act of cooperation is shaped by underlying *behavioral processes* that depend upon interaction. Partners learned to work together, developing conjoint strategies with roles, ranks, etc.

Isolation models also limit the impact that social influences can have on the *net benefits* from cooperating. This can happen in at least two ways. One is when roles affect the costs and net benefits from cooperating, as in lion cooperation (Scheel & Packer, 1991; Heinsohn & Packer, 1995; Grinnell et al., 1995). Social influences also affect how outcomes are allocated, as reported for social hunters (Packer & Pusey, 1982; Boesch & Boesch, 1989). The data reported here on cooperation with competition over outcomes showed that many pairs could cooperate well despite marked differences within pairs in access to single reinforcements. Overall, the individual-outcome perspective is challenged by examples of

stable cooperation in which some participants acquiesce to lowered benefits and/or higher risks as a result of social influence.

The third limitation of isolation models concerns how cooperation with social interaction affects the participants. Supporting evidence was obtained from measuring both post-session consumption of the reward and preference for cooperative over individual shuttling. These data reinforce reports from humans of rapport, cohesion and pleasure associated with participation in coordinated actions (e.g., McNeill, 1995; Chartrand and Bargh, 1999). Perhaps one can speak of a motive from nothing more than the act of coordinating with others. This would help to explain the roles of intense coordination in both mate selection (Maynard Smith, 1978) and the aggressive restraint that characterizes the "dear enemy" phenomenon (Krebs, 1982; Dugatkin, 1997).

The only way to explain cooperation under such circumstances is to appeal to *how* the cooperation is performed, and with whom. In other words, if the individual perspective can predict the optimum strategies expected without effects of interaction, the social behavior perspective can explain the deviations from optimality that often characterize cooperation in the real world. If individuals appear to lose by staying and working with others, their motivation for cooperating could still be explained by the states and social rewards arising from the act of coordinating. Motivation would also be affected by increases in the incentive value of outcomes obtained by cooperating.

Given these phenomena, the individual perspective could be salvaged if cooperators gain from additional benefits not directly related to their current of cooperation (Noë, 1990; Noë et al., 1991, 1995; Packer, Scheel & Pusey, 1990). The idea seems to be that cooperators benefit from maintaining relationships that will be adaptive in the future, even if engaging in cooperation is not immediately profitable. But this idea begs the question of how lions, baboons or other animals might know this. Long-range strategizing, and the underlying cognitive processes, is human traits. Humans, however, also resort to revenge tactics and use of force that suggest some limitations. Animals, in contrast, seem to be governed mainly by immediate consequences (e.g., Green & Price, 1995). Proximate mechanisms are therefore needed to explain how cooperation can be used when it is not immediately profitable. Also needing explanation is the ability of individuals remains in highly asymmetric relationships despite significant differences in outcomes.

The point of all this is that we need to understand cooperation not only as a means to maximize outcomes but also as a means to maintain relationships when they are less than optimal. Reliable optimization may therefore be more likely when behavioral processes evolve for *individual* actions such as searching alone for food or mates (Krebs & Davies, 1993). But what works well for individual strategies may not apply to dynamic social situations based on interactions and asymmetries. Like dominance hierarchies, coordinated behaviors arise from interactions and their consequences. Yet social structures remain stable because

individuals adopt conditional strategies for remaining in their groups or relationships, often at some cost. A glib evolutionary explanation is that, to maximize fitness, any kind of social situation is better than none. But little research has been devoted to the processes that compensate individuals for enduring less than ideal relationships. This perspective introduces phenomena such as the level of cohesion, "rapport," "dear enemy," social rewards, and altered physiological states that seem to influence the choice between cooperating and acting alone. This chapter has suggested that a more complete understanding of cooperation can only emerge from combining the study of both why and how cooperation occurs. And for this, experimental models based on a social interaction perspective are needed.

## REFERENCES

- Alcock, J. 1998. *Animal Behavior: An Evolutionary Perspective, Sixth Edition*. Sunderland, Mass.:Sinauer.
- Axelrod, R. & Hamilton, W.D. 1980. The evolution of cooperation. *Science*, 211, 1390-1396.
- Bednarz, J.C. 1988. Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). *Science*, 239, 1525-1527.
- Beecher, M.D., Campbell, S.E. & Nordby, J.C. 2000. Territory tenure in song sparrows is related to song sharing with neighbors, but not to repertoire size. *Animal Behaviour*, 59, 29-37.
- Berridge, K.C. 2000. Measuring hedonic impact in animals and infants: microstructure of affective taste reactivity patterns. *Neuroscience and Biobehavioral Reviews*, 24, 173-198.
- Boehm, C. 1992. Segmentary warfare and management of conflict: a comparison of East African chimpanzees and patrilineal-patrilocal humans. In A. Harcourt and F.B.M. de Waal (Eds.), *Coalitions and Alliances in Humans and Other Animals* (pp. 137-173). Oxford: Oxford University Press.
- Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78, 547-573.
- Bshary, R. & Grutter, A.S. 1999. Asymmetric cheating opportunities and partner control in the cleaner fish-client mutualism. In S. Shakunthala (Ed.), *Advances in Ethology 34: Contributions to the XXVI International Ethological Conference, Bangalore, India* (p. 155).
- Caro, T.M. 1994. *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. Chicago: University of Chicago Press.
- Chalmeau, R. & Gallo, A. 1996. What chimpanzees (*Pan troglodytes*) learn in a cooperative task. *Primates*, 37, 39-47.
- Chalmeau, R., Lardeux, K, Brandibas, P & Gallo, A. 1997. Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, 18, 23-32.
- 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 Behavior*, 50, 527-535.
- D'Amato, F.R. & Pavone, F. 1993. Endogenous opioids: a proximate reward mechanism for kin selection? *Behavioral and Neural Biology*, 60, 79-83.
- Daniel, Daniel, W.J. (1942). Cooperative problem solving in rats. *Journal of Comparative Psychology*, 34, 361-368.
- Dugatkin, L.A. 1995. Partner choice, game theory and social behavior. *Journal of Quantitative Anthropology*, 5, 3-14.
- Dugatkin, L.A. 1997. *Cooperation Among Animals: An Evolutionary Perspective*. Oxford: Oxford University Press.
- Dugatkin, L.A. & Wilson, D.S. 1992. Rover: A strategy for exploiting cooperators in a patchy environment. *American Naturalist*, 138, 687-701.
- Forsythe, R., Horowitz, J., Savin, N. & Sefton, M. 1994. Replicability, fairness and play in experiments with simple bargaining games. *Games and Economic Behavior*, 6, 347-369.
- Frank R.H. 1988. *Passions Within Reason: The Strategic Role of the Emotions*. New York: W.W. Norton.
- Galef, B.G. Jr. 1988. Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In T.R. Zentall & B.G. Galef (Eds.), *Social Learning: Psychological and Biological Perspectives* (pp. 3-28). Hillsdale, N.J.: Erlbaum.
- Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. In J.L. Black (Ed.), *Partnerships in Birds* (pp. 21-52). Oxford Series in Ecology and Evolution. Oxford University Press: Oxford.
- Green, L., P. C. Price, et al. 1995. Prisoners-Dilemma and the Pigeon - Control by Immediate Consequences. *Journal of the Experimental Analysis of Behavior*, 64, 1-17.
- Grinnell, J., Packer, C. & Pusey, A.E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*, 49, 95-105.
- Hake, D.F., & Vukelich, R. 1972. A classification and review of cooperation procedures. *Journal of the Experimental Analysis of Behavior*, 18, 333-343.
- Hall, M.L. 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Animal Behaviour*, 60, 667-677.
- Harcourt, A.H. 1988. Alliances in contests and social intelligence. In R.W. Byrne and A. Whiten (Eds.), *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 132-152). Oxford: Clarendon Press..
- Hareli, S., Katzir, G. & Schuster, R. 1996. Effect of genetic relatedness and rearing conditions on cooperation, competition and dominance in laboratory rats. *Abstracts of the 1996 Annual Meeting of the Animal Behavior Society, Northern Arizona University, Flagstaff, AZ*.
- Heinsohn, R. & Packer, C. 1995. Complex cooperative strategies in group-territorial African lions. *Science*, 269, 1260-1262.
- Herrnstein, R.J. 1966. Superstition. In W.K. Honig (Ed.), *Operant Behavior: Areas of Research and Application* (pp. 33-51). New York: Appleton-Century-Crofts.
- Heyes, C.M. & Dawson, G.R. 1990. A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology*, 42B, 59-71.

- Hutchins, E. 1995. *Cognition in the Wild*. Cambridge, Mass.: The MIT Press.
- Krebs, J.R. 1982. Territorial defense in the great tit (*Parus major*): do residents always win? *Behavioral Ecology and Sociobiology*, 11, 185-194.
- Krebs, J.R. & Davies, N.B. 1993. *An Introduction to Behavioural Ecology, Third Ed.* London: Blackwell.
- Kruuk, H. 1972. *The Spotted Hyena*. Chicago: University of Chicago Press.
- LaFrance, M. 1979. Nonverbal synchrony and rapport: analysis by the cross-lag panel technique. *Social Psychology Quarterly*, 42, 66-70.
- Latané, B., Cappell, H. & Joy, V. 1970. Social deprivation, housing density, and gregariousness in rats. *Journal of Comparative and Physiological Psychology*, 70, 221-227.
- Lindsley, O.R. 1966. Experimental analysis of cooperation and competition. In T. Verhave (Ed.), *The Experimental Analysis of Behavior*, pp. 470-501. New York: Appleton-Century-Crofts.
- Mason, W.A. & Hollis, J.H. 1962. Communication between young rhesus monkeys. *Animal Behaviour*, 10, 211-221.
- Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge: Cambridge University Press.
- McFarland, D. 1985. *Animal Behavior: Psychobiology, Ethology and Evolution*. Manly Park, CA: Benjamin/Cummings.
- McNeill, W.H. 1995. *Keeping Together in Time: Dance and Drill in Human History*. Cambridge, Mass.: Harvard University Press.
- Meltzoff, A.N. & Moore, M.K. 1977. Imitation of facial and manual gestures by human neonates. *Science*, 198, 75-78.
- Mendres, K.A. & de Waal, F.B.M. 2000. Capuchins do cooperate: the advantage of an intuitive task. *Animal Behaviour*, 60, 523-529.
- Mesterton-Gibbons, M. & Dugatkin, L.A. 1992. Cooperation among unrelated individuals: evolutionary factors. *The Quarterly Review of Biology*, 67, 267-281.
- Minta, S.C., Minta, K.A. & Lott, D.F. 1992. Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). *Journal of Mammalogy*, 73, 814-820.
- 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.
- Noë, R., van Schaik, C.P., & van Hooff, J.A.R.A.M. 1991. The marketing effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, 87, 97-118.
- Noë, R. & Sluifjter, A.A. 1995. Which adult male savanna baboons form coalitions? *International Journal of Primatology*, 16, 77-105.
- Packer, C., Gilbert, D.A., Pusey, A.E. & O'Brien, S.J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, 351, 562-565.
- Packer, C. & Pusey, A.E. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature*, 296, 740-742.
- Packer, C. & Rutten, L. 1988. The evolution of cooperative hunting. *American Naturalist*, 132, 159-198.
- 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., Herman, B.H., Vilberg, T., Bishop, P. & DeEsquinazi, F.G. 1980. Endogenous opioids and social behavior. *Neuroscience and Biobehavioral Reviews*, 4, 473-487.
- Panksepp, J., Nelson, E. & Bekkedal, M. 1997. Brain systems for the mediation of social separation-distress and social-reward. In C.S. Carter, I. Lederhendler and B. Kirkpatrick (Eds.), *The Integrative Neurobiology of Affiliation* (pp. 78-100). New York: New York Academy of Sciences.
- Panksepp, J., Siviy, S.M. & Normansell, L.A. 1985. Brain opioids and social emotions. In M. Reite and T. Fields (Eds.), *The Psychobiology of Attachment and Separation* (pp. 3-49). New York: Academic Press.
- Rapoport, A. & Mowshowitz, A. 1966. Experimental studies of stochastic models for the Prisoner's Dilemma. *Behavioral Science*, 11, 444-458.
- Roberts, G. 1997. Testing mutualism: a commentary on Clements & Stephens. *Animal Behaviour*, 53, 1361-1362.
- Scheel, D. & Packer, C. 1991. Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour*, 41, 697-709.
- Schuster, R. 1976. Lekking behavior in Kafue lechwe. *Science*, 192, 1240-1242.
- Schuster, R. 2000. How useful is an individual perspective for explaining the control of social behavior? A commentary on M. Domjan, B.Cusato & R.Villarreal, Pavlovian feed-forward mechanisms in the control of social behavior. *Behavioral and Brain Sciences*, 23, 263-264.
- Schuster, R. In press. Cooperative coordination as a social behavior: experiments with an animal model. *Human Nature*.
- Schuster, R., Berger, B.D. & Swanson, H.H. 1988. Cooperative social coordination and aggression: sex and strain differences in the effects of housing on gonadectomized rats with hormone replacement. *Aggressive Behavior*, 14, 275-290.
- Schuster, R., Berger, B.D. & Swanson, H.H. 1993. Cooperative social coordination and aggression. II. Effects of sex and housing among three strains of intact laboratory rats differing in aggressiveness. *Quarterly Journal of Experimental Psychology*, 46B, 367-390.
- Schuster, R., Rachlin, H., Rom, M., & Berger, B.D. 1982. An animal model of dyadic social interaction: Influence of isolation, competition and shock-induced aggression. *Aggressive Behavior*, 8, 116-121.
- Serpell, J.A. 1981. Duets, greetings and triumph ceremonies: analogous displays in the parrot genus *Trichoglossus*. *Zeitschrift für Tierpsychologie*, 55, 268-283.
- Skinner, B.F. 1953. *Science and Human Behavior*. New York: Macmillan.
- Sober, E. & Wilson, D.S. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, Mass.: Harvard University Press.
- Stander, P.E. 1992a. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology*, 29, 445-454.
- Stander, P.E. 1992b. Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology*, 70, 8-21.
- Stephens, D.W. & Anderson, J.P. 1997. Reply to Roberts: cooperation is an outcome, not a mechanism. *Animal Behaviour*, 53, 1363-1364.

- Swanson, H.H. & Schuster, R. 1987. Cooperative social coordination and aggression in male laboratory rats: effects of housing and testosterone. *Hormones and Behavior*, 21, 310-330.
- Taylor, G.T. 1976. Affiliation and aggression in rats. *Animal Learning and Behavior*, 4, 139-144.
- Todt, D. 1975. Effect of territorial conditions on the maintenance of pair contact in duetting birds. *Experientia*, 31, 648-649.
- Todt, D. 1981. On functions of vocal matching: effect of counter-replies on song post choice and singing. *Zeitschrift für Tierpsychologie*, 57, 73-93.
- Trivers, R. 1985. *Social Evolution*. Menlo Park, California: Benjamin/Cummings.
- de Waal, F.B.M. 1986. The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, 61, 459-479.
- Weingarten, K., & Mechner, F. 1966. The contingency as an independent variable of social interaction. In T. Verhave (Ed.), *The Experimental Analysis of Behavior* (pp. 447-459). New York: Appleton-Century-Crofts.
- Whiten, A. & Ham, R. 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, 21, 239-283.
- Wilson, D.S. & Dugatkin, L.A. 1992. Altruism: contemporary debates. In E.F. Keller and E.A. Lloyd (Eds.), *Keywords in Evolutionary Biology* (pp. 29-33). Cambridge, Mass.: Harvard University Press.
- Zentall, T.R. 1988. Experimentally manipulated imitative behavior in rats and pigeons. In T.R. Zentall and B.G. Galef, Jr. (Eds.), *Social Learning: Psychological and Biological Perspectives* (pp. 191-206). Hillsdale, N.J.: Erlbaum.