The Behavioral Ecology of Food Sharing

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Jeffrey Ross Stevens

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

David W. Stephens, Advisor

December 2002

Acknowledgments

A thesis has only one author but many contributors. Of course, the most outstanding contributor to this thesis is my advisor David W. Stephens. Dave has put a considerable amount of work into helping me, devoting time, allocating money, dispensing advice, cracking jokes, inflicting suffering (apparently “it builds character”). I am honored to have seen Dave evolve into an exceptional advisor that cares greatly about the success of his students. I have learned a enormous amount from him, and I feel that he has done a superb job preparing me for a bright future. Hopefully, I can take what he has taught me and aspire to become a rigorous scientist, an inspiring advisor, and an effective teacher.

In addition, I would like to acknowledge Dave’s direct role in this thesis. As a co-author of Chapter 2, he provided much of the inspiration for the design of the project, as well as financial and material support and editing of the manuscript. For Chapter 3, Dave guided my early attempts at a model and helped create the final version. In addition, he co-wrote the model’s description and edited the manuscript for publication in *Behavioral Ecology*. Thank you Dave, for all you have done for me.

I would also like to thank my other committee members for contributing to this thesis. In particular, Craig Packer stimulated my growth as a scientist by providing opportunities in a teaching context (EEB 5327: Behavioral Ecology) and a research context (analysis of lion hunting data). I truly appreciate all of his support of my thesis and career. In addition, I am thankful to Anne Pusey for including me in many of the primate-related activities in the department, as well as for allowing me the chance to be a teaching assistant for Biol 3411 (Animal Behavior) and EEB 5321 (Social Behavior). Also, I appreciate the careful comments on my research, including the inspiration for a follow-up experiment with the blue jays. Finally, I am indebted to Gail Peterson for kindling my interest in psychology. Those fantastic classes on learning taught me to approach psychological questions with a parsimonious eye.

During my time at the University of Minnesota, I was very lucky to have a colleague studying a similar topic from a different perspective. Ian Gilby studied the other side of the food sharing coin: sharing in natural populations. Verifying my theoretical and empirical results with data from natural sharing situations bolstered confidence in my results. I am very grateful to Ian for providing an insightful perspectives on food sharing. Our similar interests resulted in a collaborative review paper on food sharing (Chapter 1). Ian contributed to this chapter by reviewing innumerable articles, co-writing sections of text, and providing helpful comments on the remaining text.

I would like to thank many of the other students that influenced me as a graduate student over the years. Although I was in Nebraska for less than a year, James Anderson, Kari Benson, and Richard Bischoff helped me greatly in that time. In Minnesota I am especially thankful for my cohort and extended cohort members Eli Bridge, Anja Brunet, Ian Gilby, Stan Harpole, Eric Lonsdorf, and Michelle Solensky. The margaritas from Don Pablo's helped maintain my sanity. Other members of the Stephens lab including Esteban Fernández-Juricic, Ben Kerr, and Colleen McLinn provided fantastic colleagues during my tenure. I also appreciate the feedback and support from the many members of the Packer/Pusey lab including Annie Bosacker, Dawn Kitchen, Dan MacNulty, Jordan Price, Peyton West, Karyl Whitman, and Mike Wilson.

Maintaining captive colonies of happy animals is very difficult and time-consuming work. I am grateful to all of the blue jay colony staff that maintained the jays and helped with my experiments, including Dack Anderson, Jolene Ruf, and Claire Leung. I thank Linda Brent for supervising my work at the Southwest Foundation for Biomedical Research in San Antonio, Texas. Linda and the SFBR staff made my work with the chimpanzees as pleasant as is possible when working with apes. I also thank Larry

Williams, Christian Abee, and the staff at the Squirrel Monkey Breeding and Research Resource for their knowledge, generosity, and help with my project.

This project could not have been completed without funding from many sources. First, my advisor Dave Stephens fully funded the entire blue jay experiment (funding from National Science Foundation and University of Minnesota Graduate School). In addition, I am very grateful to the L.S.B. Leakey Foundation for funding the majority of the primate experiments. The Alexander P. and Lydia Anderson Foundation provided supplementary funding for the primate experiments. The Animal Behavior Society funded a pilot experiment on harassment in squirrel monkeys. The Department of Ecology, Evolution, and Behavior provided travels grants for me to attend meetings and present my work. I appreciate the the University of Minnesota Graduate School granting me the freedom to write my thesis without distraction by awarding me a Doctoral Dissertation Fellowship. Also, I am grateful summer support from the Alexander P. and Lydia Anderson Fellowship and the EEB summer fellowships. Finally, I thank the Dayton and Wilkie Natural History Funds for use of a digital video camera.

My family played an integral role in my decision to attend graduate school. Without their support and encouragement, I would probably be a rather wealthy but miserable attorney. In particular, I would like to thank my grandfather J.R. Stevens for encouraging me to pursue my dreams and focus on a career that I would enjoy. In addition, I am extremely grateful for the love and support of my parents Julie and Robert Stevens, as well as my brother Adam Stevens and my grandparents Adelene Stevens, Marcia Grant, and U.S. Grant. Witnessing the transition from "you want to play with animals for the rest of your life?" to "what cool stuff are you studying now?" proved very satisfying (although, there is still the occasional "monkey boy" comment).

Finally, for the person who kept me together for most of my graduate career, I would like to thank my colleague, my inspiration, my wife Alison Nicole Stevens for keeping

me sane. I truly appreciate the love, patience, and support she has offered me over the years. I only hope that I had the sense to reciprocate.

DEDICATED TO JR STEVENS

For encouraging me to follow my dreams

Abstract

Animal food sharing has puzzled biologists for decades. Why would an animal sacrifice potential survival and reproductive benefits to help another individual? This apparent altruism has been explained as benefiting kin or providing future benefits through reciprocation. Other explanations of sharing focus on selfish, immediate benefits of sharing. An experiment with unrelated blue jays (*Cyanocitta cristata*) tested cooperation in controlled-payoff games such as the Prisoner's Dilemma. Results indicated that the jays did not cooperate or reciprocate in the Prisoner's Dilemma. Instead, they only cooperated when it produced immediate benefits; that is, the cooperation was selfish rather than altruistic. These selfish benefits could arise in natural food sharing situations via harassment. By harassing, a beggar may inflict fitness costs on a food owner, making defending costly. The owner may "pay" the beggar with part of the food to avoid costly harassment. A game theoretical model of this situation predicted that harassment may profit a beggar when gaining other "non-contingent benefits" offsets costs of harassing. In the face of high harassment pressure, owners may benefit most by sharing with the beggar. A comparative experiment with captive chimpanzees (*Pan troglodytes*) and squirrel monkeys (*Saimiri boliviensis*) tested the model predictions. By varying food divisibility and the beggar's access to the owner, this experiment manipulated non-contingent benefits for the beggar and potential harassment costs for the owner. Results indicated that beggars did harass when they gained non-contingent benefits, and the owners shared more frequently when beggars harassed. Squirrel monkeys harassed more frequently than chimpanzees, but chimpanzees harassed for longer durations. Interestingly, both chimpanzees and squirrel monkeys shared equally often, and squirrel monkeys shared larger amounts. These experimental and comparative data indicate that harassment can elicit sharing in primates. Since harassment provides a simple, selfish explanation of some sharing situations, it must be considered before invoking complex explanations such as reciprocity.

Table of Contents

List of Tables

List of Figures

Introduction

ONLY AN HOUR BEFORE, *the elk calf suckled from his mother in the relative safety of the herd. Now, the weary calf notices a tingle in the air. His radar-like ears do not detect anything, but hearing is difficult over his loud panting. Suddenly, a grey flash races out of the brush, toppling him to the fresh snow. The wolf lunges and bites until she secures a firm grip on the calf's throat. After an exhaustive chase, the hunter can finally abandon her week-long fast. Only a few minutes into the feast, the soft crunch of snow signals the arrival of another female wolf, ready to eat. The newcomer trots over to the carcass and begins eating, side-by-side with the hunter.*

The hunter in this story appears to act altruistically towards the newcomer. That is, she pays a sizable cost—in terms of energy used and possible injuries—to capture the quarry. By allowing the newcomer to eat, the hunter forfeits the opportunity to consume all of the food and, in fact, helps the newcomer. These types of altruistic behavior, particularly in the social insects, troubled Charles Darwin and provided what he considered the most potent challenge to his theory of natural selection (Darwin, 1859). Why would an animal sacrifice potential survival and reproductive benefits (evolutionary fitness), while at the same time helping the fitness of a competitor? If fitness is indeed relative, altruism offers a true evolutionary paradox. Nevertheless, examples of deferred reproduction, cooperative breeding, alarm calling, cooperative hunting, and food sharing abound throughout the animal kingdom. Researchers have proposed a number of theories to account for altruism.

Group selection

Many students of animal behavior turned to group selection to explain altruistic behavior (Wright, 1945; Lewontin, 1962; Wynne-Edwards, 1962). Proponents of group selection argued that altruism that benefits the group allows those groups to outcompete selfish groups. Williams (1966) challenged this view by proposing that selection on individuals acts faster than selection on groups. Therefore, group selection may not be as important as individual selection. Despite a resurgence in group selection theory (Wilson, 1980; Wynne-Edwards, 1993; Sober and Wilson, 1998), many suggest that group selection adds nothing new to evolutionary biology (Maynard Smith, 1998; Reeve and Keller, 1999). Most recent research focuses on how altruism benefits the donor rather than the group.

Kin selection

Hamilton (1964) turned behavioral ecology on its head by proposing that, although costly to the donor, altruism may benefit kin. Because individuals share a proportion of their genes with relatives, helping relatives yields genetic benefits that may outweigh individual costs. Hamilton predicted that altruism could occur when the benefit to the recipient weighted by the recipient's relatedness to the donor exceeds the cost to donor. The formalization of kin selection suggested that selection may act the level of the gene rather than the individual (Dawkins, 1976). These ideas have inspired a wealth of theory and experiments demonstrating the importance of kinship in altruism. In particular, kin selection can put Darwin's concerns to rest by accounting for much of the altruism exhibited by social insects. Worker insects forego their own reproduction and tend to the queen's offspring because they share genetic material with the queen (reviewed in Bourke, 1997). Staying and helping with brood care propagates that genetic material at a faster rate than dispersing and reproducing outside of the colony. Many other examples of kin-selected altruism exist including alarm calling in ground squirrels (Sherman, 1977, 1985), food sharing in crows (Ha et al., 2003), and deferred reproduction in lions (Packer et al., 1991). Kin selection offers a parsimonious explanation of altruism because the mechanism maintaining altruism is relatively simple. Often animals do not even require special mechanisms to detect kinship. Natural selection can favor simple rules such as "help the individuals you grew up with". However, groups with mixed relatedness require more complicated means of recognizing kin, such as phenotypic matching (Sherman et al., 1997), to avoid cheaters. A potential drawback to the general application of kin selection is the limited set of individuals to interact with. When interacting with unrelated individuals, kin selection cannot promote altruism. Nevertheless, kin selection is probably the most ubiquitous type of altruism.

Reciprocity

To explain examples of non-kin altruism, Trivers (1971) proposed reciprocal altruism in which animals alternate donating and receiving help. By alternating these roles, animals recoup current costs in future interactions. Trivers' theory required that (1) the recipient's benefit exceed the donor's cost, (2) players recognize and interact with the same individuals repeatedly, and (3) players track debts owed and favors given. This theory, however, provides the temptation for cheaters to exploit the generosity of donors by not reciprocating. A cheater that avoids costs of donating but always receives benefits will have higher fitness than a reciprocal altruist. Axelrod and Hamilton (1981) approached this problem by integrating economic game theory (von Neumann and Morgenstern, 1944) with Triver's reciprocal altruism using the Prisoner's Dilemma (Rapoport and Chammah, 1965). The Prisoner's Dilemma is a two-player, non-zero sum game in which each player chooses to cooperate or defect. Originally, the payoffs associated with particular choice combinations represented utility in human economic games (von Neumann and Morgenstern, 1944). Maynard Smith (1982), however, demonstrated that traditional game theory could apply to evolutionary games of animal contests. Rather than economic utility, evolutionary biologists could measure payoffs in units of fitness. The payoffs for cooperating and defecting in the Prisoner's Dilemma are given by:

Against:

		Cooperate	Defect
Payoff to:	Cooperate	R	S
	Defect	T	P

in which T, R, P, and S represent the payoffs to the row player against the column player and $\mathsf{T} > \mathsf{R} > \mathsf{P} > \mathsf{S}$. Therefore, if both individuals cooperate, they both receive a "reward" R. If one player defects while the other cooperates, the defector receives the largest payoff T (the "temptation to cheat"), whereas the cooperator receives the lowest payoff S (the "sucker's payoff"). Mutual defection "punishes" both players with a relatively low payoff P. Given these payoffs, we can define cooperation economically as joint action for mutual benefit. Both players must cooperate in order for both players to benefit—if one player deviates, the other is worse off. For instance, if the wolves in the previous example hunted the elk simultaneously, both would benefit by splitting energetic and injury costs. In the example, however, one wolf avoided any hunting costs (thrusting them all on the hunter) and still gained the benefits of consuming the carcass. Therefore, the benefits of not hunting provide a temptation to cheat.

To solve the economic game, we must determine the Nash equilibrium (Nash, 1951)—a set of strategies such that each player's response is the optimum reply to its opponent's choice (similar to the Evolutionarily Stable Strategy proposed by Maynard Smith, 1982). The Nash equilibrium of a single Prisoner's Dilemma game is to defect. Regardless, of whether the opponent cooperates or defects, a player would benefit most by defecting ($\mathsf{T} > \mathsf{R}$ and $\mathsf{P} > \mathsf{S}$). This results in mutual defection and both players receiving the very low P payoff. However, if the players could forego the temptation to cheat and mutually cooperate, both players would benefit from obtaining R, hence the dilemma.

Axelrod and Hamilton (1981) proposed a strategy based on reciprocal altruism that maintains cooperation but requires repeated plays of the Prisoner's Dilemma (the Iterated Prisoner's Dilemma or IPD). The strategy tit-for-tat is defined as cooperating in the first game and copying the opponent's prior move in all subsequent games. Axelrod and Hamilton contended that tit-for-tat could stablize cooperation in the IPD if the players expected to play against each other repeatedly. Single games result in mutual defection, but repeated games may produce cooperation. A maelstrom of theory expanded upon the original model by including multiple players, a stochastic environment, spatial structure, mistakes, and many more nuances (reviewed in Dugatkin, 1997). A few researchers claimed to demonstrate tit-for-tat strategies in IPD situations in animal interactions (Milinski, 1987; Dugatkin, 1988; Fischer, 1988; Godard, 1993). However, validating that these situations conform to a true Prisoner's Dilemma proves difficult. Other researchers challenged the authenticity of these claims (Lazarus and Metcalfe, 1990; Connor, 1992; Stephens et al., 1997; Noë, 2001), presenting simpler explanations for the observed behavior. Until recently (Stephens et al., 2002), no evidence of cooperation existed in a verifiable Prisoner's Dilemma.

Why is there no evidence demonstrating reciprocity despite an abundance of supporting theory? Animals must overcome a number of obstacles for reciprocity to maintain altruism. The repeated interaction requirement restricts reciprocity to fairly social animals. Also, reciprocity requires individual recognition, which may involve complicated cognitive skills. The largest impediment, however, is the ability to track debts owed and favors given over a network of individuals. Detecting cheaters and remembering helpers may require complex cognitive mechanisms. These challenges may place reciprocity beyond the capabilities of most non-human animals.

Mutualism

In both kin selection and reciprocal altruism, donors act altruistically. Even though the act benefits relatives or is repaid in the future, the donor receives an immediate cost. In contrast, many examples of cooperation may appear altruistic, but upon closer inspection, the donor receives immediate benefits. In these cases of by-product mutualism (West-Eberhard, 1975; Brown, 1983), apparently altruistic cooperation behavior results from the by-product of selfish behavior. Therefore, cooperation benefits individuals regardless of the opponent's decision. Whereas benefits from kin selection depend on cooperating with kin and the benefits of reciprocal altruism depend on your opponent's reciprocation, the benefits of mutualistic cooperation are unconditional. No temptation to cheat exists, because any individual that deviates from cooperation does worse than if it cooperates. For example, 'cleaner' fish swim inside the mouths of larger 'client' fish to remove ectoparasites and dead tissue (Bshary, 2001). Why do cleaners remove parasites from the clients and why do clients not eat the cleaners? Mutual benefits for both parties maintain this interspecific cooperation. Cleaners benefit by consuming the parasites removed from clients; some consume up to 1200 parasites per day (Grutter, 1996). Clients avoid eating cleaners because of the health benefits of a reduced parasite load. If the clients consumed the cleaners, their parasite load could increase fourfold (Grutter, 1999). Therefore, both cleaners and clients increase their fitness by participating in this cooperative interaction.

Mutualism applies to a wide range of cooperative situations and probably explains many cases of apparent altruism (Clements and Stephens, 1995; Connor, 1995; Pusey and Packer, 1997). Its simplicity provides the primary advantage of mutualism as an explanation of cooperation. Mutualism does not require interaction with the same individuals (kin or reciprocating partners). Instead, any two individuals can meet and have a mutualistic interaction. Also, it does not require complicated cognitive mechanisms such as individual recognition or score-keeping. These simple requirements and the immediate benefits make mutualism a very parsimonious explanation of cooperation.

Thesis overview

Given the focus on kin selection and reciprocity, this thesis examines whether mutualistic alternatives can explain many instances of animal altruism. In particular, I focus on food sharing as an apparent altruistic behavior. By sharing food with another individual, a donor loses the potential fitness benefit of the shared food. Most investigations of food sharing cite kin selection and reciprocity as the functional explanation of sharing. I propose an alternative, mutualistic reason for sharing.

I begin this thesis (Chapter 1, co-authored with Ian Gilby) by reviewing the current food sharing literature in non-human animals. This chapter provides a conceptual framework for considering non-kin sharing. Chapter 2 (co-authored with David W. Stephens) describes an empirical examination of the economics of cooperation. We describe testing the costs and benefits of cooperation in blue jays (*Cyanocitta cristata*) facing repeated Prisoners Dilemma and other game theoretical situations. Originally, we designed this experiment to test food sharing in the jays. A follow-up experiment, however, indicated that the jays did not perceive the situation as sharing, and, thus, I generalized it to a cooperative rather than food sharing game. Chapter 3 (co-authored with David W. Stephens) proposes a game theoretical model of a mutualistic food sharing situation. The model formalizes the circumstances under which food beggars should harass owners and when food owners should share with beggars. Chapter 4 describes a set of comparative experiments designed to test the model proposed in Chapter 3. I provide empirical evidence of the effect of harassment on food sharing in two species of primate: chimpanzees (*Pan troglodytes*) and squirrel monkeys (*Saimiri boliviensis*). Finally, I conclude with a section speculating on the role of harassment as a general mechanism underlying both human and non-human food sharing. This thesis focuses on non-human sharing, but the literature in anthropology provides relevant theory and observations on human food sharing. In particular I would like to draw attention to contributions from Bliege Bird and Bird (1997), Blurton Jones (1984, 1986, 1987), Boyd and Richerson (1992), Hawkes (1991a,b, 1992a,b, 1993), Kaplan and Hill (1985), and Winterhalder (1986, 1996a,b, 1997).

Please note that I wrote the chapters in this thesis as independent publications. Therefore, the chapters may not contain an comprehensive review of background information or an exhaustive presentation of all data available as is common in most theses. Instead, the chapters are more concise and stand alone. I apologize in advance for any redundancy resulting from this format.

References

Axelrod, R. and Hamilton, W. D. 1981. The evolution of cooperation. *Science* 211:1390–1396.

Bliege Bird, R. L. and Bird, D. W. 1997. Delayed reciprocity and tolerated theft: the behavioral ecology of food-sharing strategies. *Current Anthropology* 38:49–78.

Blurton Jones, N. G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology* 5:1–3.

Blurton Jones, N. G. 1986. Fitness returns from resources and the outcome of contests: some implications for primatology and anthropology. *In* J. G. Else and P. C. Lee (eds.), Primate Ontogeny, Cognition, and Social Behavior. Cambridge University Press, Cambridge. pp. 393–406.

Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.

Bourke, A. F. G. 1997. Sociality and kin selection in insects. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology: An Evolutionary Approach, 4th ed. Blackwell Science, Oxford. pp. 203–227.

Boyd, R. and Richerson, P. J. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.

Brown, J. L. 1983. Cooperation—a biologist's dilemma. *In* J. S. Rosenblatt (ed.), Advances in the Study of Behaviour. Academic Press, New York. pp. 1–37.

Bshary, R. 2001. The cleaner fish market. *In* R. Noë, J. A. R. A. M. van Hooff, and P. Hammerstein (eds.), Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge University Press, Cambridge. pp. 146–172.

Clements, K. C. and Stephens, D. W. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour* 50:527–535.

Connor, R. C. 1992. Egg-trading in simultaneous hermaphrodites: an alternative to tit for tat. *Journal of Evolutionary Biology* 5:523–528.

Connor, R. C. 1995. The benefits of mutualism: a conceptual framework. *Biological Reviews* 70:427–457.

Darwin, C. 1859. On the Origin of Species. Murray, London.

Dawkins, R. 1976. The Selfish Gene. Oxford University Press, Oxford.

Dugatkin, L. A. 1988. Do guppies play tit for tat during predator inspection visits? *Behavioral Ecology and Sociobiology* 25:395–399.

Dugatkin, L. A. 1997. Cooperation Among Animals: An Evolutionary Perspective. Oxford University Press, New York.

Fischer, E. A. 1988. Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. *Ethology and Sociobiology* 9:119–136.

Godard, R. 1993. Tit-for-tat among neighboring hooded warblers. *Behavioral Ecology and Sociobiology* 33:45–50.

Grutter, A. S. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus. Marine Ecology Progress Series* 118:51–58.

Grutter, A. S. 1999. Cleaner fish really do clean. *Nature* 398:672–673.

Ha, R. R., Bentzen, P., Marsh, J., and Ha, J. C. 2003. Kinship and association in social foraging Northwestern crows (*Corvus caurinus*). *Bird Behavior* in press.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology* 7:1–52.

Hawkes, K. 1991a. Showing off: tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology* 12:29–54.

Hawkes, K. 1991b. Why do men hunt? Benefits for risky choices. *In* E. A. Cashdan (ed.), Risk and Uncertainty in Tribal and Peasant Communities. Westview Press, Boulder. pp. 145–166.

Hawkes, K. 1992a. On sharing and work. *Current Anthropology* 33:404–407.

Hawkes, K. 1992b. Sharing and collective action. *In* E. A. Smith and B. Winterhalder (eds.), Evolutionary Ecology and Human Behavior. Aldine de Gruyter, New York. pp. 269–300.

Hawkes, K. 1993. Why hunter-gatherers work: an ancient version of the problem of public goods. *Current Anthropology* 34:341–361.

Kaplan, H. and Hill, K. 1985. Food sharing among Ache foragers: tests of explanatory hypotheses. *Current Anthropology* 26:223–246.

Lazarus, J. and Metcalfe, N. B. 1990. Tit for tat cooperation in sticklebacks: a critique of Milinski. *Animal Behaviour* 39:987–989.

Lewontin, R. C. 1962. Interdeme selection controlling a polymorphism in the house mouse. *American Naturalist* 96:65–78.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith, J. 1998. The origin of altruism. *Nature* 393:639–640.

Milinski, M. 1987. Tit for tat and the evolution of cooperation in sticklebacks. *Animal Behaviour* 39:989–991.

Nash, J. 1951. Non-cooperative games. *Annals of Mathematics* 54:286–295.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. *In* R. Noë, J. A. R. A. M. van Hooff, and P. Hammerstein (eds.), Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge University Press, Cambridge. pp. 93–118.

Packer, C., Gilbert, D. A., Pusey, A. E., and O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562–565.

Pusey, A. E. and Packer, C. 1997. The ecology of relationships. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology: An Evolutionary Approach, 4th ed. Blackwell Science, Oxford. pp. 254–283.

Rapoport, A. and Chammah, A. N. 1965. Prisoner's Dilemma: A Study in Conflict and Cooperation. University of Michigan Press, Ann Arbor.

Reeve, H. K. and Keller, L. 1999. Levels of Selection in Evolution. Princeton University Press, Princeton.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science* 197:1246–1253.

Sherman, P. W. 1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology* 17:313–323.

Sherman, P. W., Reeve, H. K., and Pfennig, D. W. 1997. Recognition systems. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology: An Evolutionary Approach, 4th ed. Blackwell Science, Oxford. pp. 69–96.

Sober, E. and Wilson, D. S. 1998. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, Mass.

Stephens, D. W., Anderson, J. P., and Benson, K. E. 1997. On the spurious occurrence of tit for tat in pairs of predator-approaching fish. *Animal Behaviour* 53:113–131.

Stephens, D. W., McLinn, C. M., and Stevens, J. R. 2002. Discounting and reciprocity in an Iterated Prisoner's Dilemma. *Science* 298:2216–2218.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

von Neumann, J. and Morgenstern, O. 1944. Theory of Games and Economic Behavior. Princeton University Press, Princeton.

West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology* 10:1–33.

Williams, G. C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton.

Wilson, D. S. 1980. The Natural Selection of Populations and Communities. Benjamin/Cummings, Menlo Park, Calif.

Winterhalder, B. 1986. Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5:369–392.

Winterhalder, B. 1996a. A marginal model of tolerated theft. *Ethology and Socio-*

biology 17:37–53.

Winterhalder, B. 1996b. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology* 5:46–57.

Winterhalder, B. 1997. Gifts given, gifts taken: the behavioral ecology of nonmarket, intragroup exchange. *Journal of Archaeological Research* 5:121–168.

Wright, S. 1945. Tempo and mode of evolution: a critical review. *Ecology* 26:415–419.

Wynne-Edwards, V. C. 1962. Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, London.

Wynne-Edwards, V. C. 1993. A rationale for group selection. *Journal of Theoretical Biology* 162:1–22.

Chapter 1

Non-kin food sharing: a conceptual framework [1]

Abstract

Many animal species, from arthropods to apes, share food. This paper presents a new framework that categorized non-kin food sharing according to two dimensions: (1) the interval between sharing and receiving the benefits of sharing, and (2) the currency in which benefits accrue to the sharer (especially food vs. non-food). Sharers can obtain immediate benefits from increased foraging efficiency, predation avoidance, mate provisioning, or manipulative mutualism. Reciprocity, trade, status enhancement, and group augmentation can delay benefits. When benefits are delayed or when food is exchanged for non-food benefits, maintaining sharing can become more difficult because animals face discounting and currency conversion problems. Therefore, explanations that require delayed or non-food benefits are less parsimonious because few species possess the required cognitive mechanisms. The immediate, selfish fitness benefits that a sharer may gain through by-product or manipulative mutualism, however, apply to various food sharing situations across many species and provide a simpler, more general explanation of sharing.

---

[1] This chapter was co-authored with I.C. Gilby.

Sharing food appears to exemplify the paradox of altruism—a recipient gains fitness benefits at the expense of a donor. Despite this altruistic appearance, food sharing commonly occurs in non-human animals, including insects (Bolten et al., 1983; Boggs, 1995; Vahed, 1998), birds (Heinrich, 1988b; Stacey and Koenig, 1990; Thiollay, 1991; Evans and Marler, 1994), cetaceans (Johnson, 1982; Hoelzel, 1991), vampire bats (Wilkinson, 1984; Denault and McFarlane, 1995), and other small mammals (Judd and Sherman, 1996; Brotherton et al., 2001). Primates, in particular, have been well-studied (reviewed in Feistner and McGrew, 1989), including prosimians (Gurksy, 2000), New World monkeys (Starin, 1978; Ferrari, 1987; Feistner and Price, 1990; Perry and Rose, 1994; Pastor-Nieto, 2001), Old World monkeys (Kavanagh, 1972; Strum, 1975, 1981; Dittus, 1984), and apes (Kuroda, 1984; Goodall, 1986; Nettelbeck, 1998). Many of these and other authors have used different definitions of food sharing. Here, we adopt a relatively broad definition of sharing—joint use of monopolizable food items. That is, if an individual can defend a food item but allows another individual to consume part of the item, it is considered to be sharing. This definition includes both passive (tolerated theft) and active sharing (facilitated transfer, food recruitment). Regardless of the method of transfer, the food owner loses potential fitness benefits by sharing.

We propose this broad definition because sharing poses an important economic problem in animal societies. Though apparently altruistic, sharing typically yields benefits to the food donor either indirectly through kin selection (Hamilton, 1964) or directly through other mechanisms. Much of animal food sharing probably results from kin selection; mother-offspring sharing frequently occurs in nature, as does other kin-based sharing. Because this type of sharing is well understood, we focus on non-kin explanations of sharing involving direct fitness benefits to the donor.

Fitness benefits

Here we review non-kin sharing studies using a conceptual framework partially based on Brown's (1980) fitness components. We divide fitness benefits for non-kin sharing along two dimensions (Table 1.1). Our first dimension considers the time at which the donor receives its benefit: either immediately following sharing or after a delay. For example, a lioness that just captured a Thompson's gazelle has two options when another pride member approaches: she can defend the carcass or allow the intruding lioness to feed with her. By sharing, the owner may benefit by avoiding a contest, which would result in the loss of the entire carcass. In this case, the owner receives the immediate benefit of continuing to consume the food. Alternatively, sharing may provide delayed benefits by increasing the survival of the intruding female, thereby raising the chances that she remains in the group. If larger groups of females can better defend their cubs from infanticidal males, the lioness may reap future rewards for sharing.

Categorizing types of sharing by the time at which the fitness benefit accrues (immediate or delayed benefits) provides an important distinction. Deferring immediately obtainable benefits until the future has two primary difficulties. First, delaying benefits trades current fitness for future fitness. Animals can invest current resources into offspring, but by delaying benefits, they divert investment into future offspring. If this delays reproduction, it could reduce the lifetime reproductive success. Second, much can happen between the time that a food item is shared and the return benefit accrues. The donor or recipient could forget about the debt or even die. Because of this uncertainty, animals may discount the value of delayed benefits (Mazur, 1987; Rachlin, 2000), thus increasing the perceived value of immediate benefits. That is, animals may prefer smaller, immediate benefits to larger, delayed benefits. This preference may cause animals to devalue food up to 50% in the first second of delay (Mazur, 2000). Discounting plays an important role in food sharing since food items are often ephemeral (Stephens and

Krebs, 1986) . Explanations that rely on these delayed benefits may require complicated mechanisms to overcome the problem of discounting.

Our second dimension considers the fitness currency of the benefit received by the donor. The donor can either receive more food as a result of sharing or receive another type of benefit such as grooming, predation avoidance, or mating opportunities. In the lion example, the owner that shares to avoid the contest and possible loss of the carcass gives up part of her food to consume more food—the returned benefit currency is the same. Yet, the owner that shares to maintain a large group size exchanges food for another currency: increased cub survival.

Classifying fitness effects based on the currency of the received benefit allows us to consider whether the food donors must convert between fitness currencies (biological markets: Noë and Hammerstein, 1994, 1995; Noë et al., 2001). How much does one bite of food translate into decreasing predation risk, increasing the probability of mating, reducing harassment costs, lowering parasite load, increasing rank, or enlarging the group size? We do not suggest that animals consciously calculate these conversions; rather, natural selection favors individuals that make appropriate conversions. Nevertheless, variation in amounts of food donated and values of returned benefits may require flexible, complicated rules to convert between variable amounts of benefits. Some argue that the complexity of these trading networks may have driven the evolution of the human brain (La Cerra and Bingham, 1998).

Despite the importance of timing and currency on fitness, few studies have satisfactorily considered these aspects for food sharing. We argue that these factors influence the complexity of hypotheses used to explain sharing. Therefore, this framework can help us evaluate which hypotheses provide the most parsimonious explanations of sharing.

Immediate benefits

Immediate benefits accrue during or directly following the sharing event. Occasionally, classifying benefits as immediate or delayed proves difficult—some types of benefits can occur both immediately and after a delay. Nevertheless, a clear difference often distinguishes between benefits that accrue during or immediately following sharing and those that accrue after a time delay.

Food for food

Increased foraging efficiency

Although it may appear to be counterintuitive, individuals may actually increase their foraging efficiency by sharing food with other individuals. This occurs most often through recruitment calling. In some species, individuals that have information about the location of food give specific calls that attract nearby foragers. The callers do not necessarily possess food but alert others to the location of food, resulting in food sharing.

Richner and Heeb (1995, 1996) proposed the recruitment center hypothesis as a selfish alternative to Ward and Zahavi's (1973) altruistic information center explanation of communal roosts. Richner and Heeb contended that recruitment calling actually benefits the caller by immediately increasing its capture rate. Brown et al. (1991) supported this claim by observing that cliff swallows (*Hirundo pyrrhonota*) attract conspecifics with food calls. Since individuals in a group have higher prey capture rates than singletons (Brown and Brown, 1996), callers may recruit group members to increase individual foraging efficiency. Larger group sizes may also lower individual vigilance for predators (Lima and Dill, 1990), thereby allowing more time for foraging.

In addition to increasing baseline capture rate, recruiting can allow individuals to form groups that displace food owners, thereby providing access to otherwise inaccessible food sources. Probably one of the most celebrated cases of this is raven (*Corvus corax*) recruitment calling at large carcasses. Heinrich and colleagues (Heinrich, 1988a,b, 1989; Heinrich and Marzluff, 1991, 1995) described situations in which juvenile ravens give recruitment calls before feeding at large carcasses. After eliminating reciprocal altruism and kin selection as possible explanations (Heinrich, 1988a; Marzluff and Heinrich, 1991; Parker et al., 1994), Heinrich and colleagues proposed that by-product mutualism (West-Eberhard, 1975; Brown, 1983) probably explains the sharing. By recruiting other ravens, juveniles can overwhelm the defenses of adult territory holders, thereby gaining access to the otherwise inaccessible carcass (Heinrich, 1988b, 1989).

Spotted hyenas (*Crocuta crocuta*) also appear to recruit others to take over a carcass, supplanting non-clan members as well as other species such as lions or leopards (East and Hofer, 1991). Both group size and call rate increase when approaching lions at a carcass, suggesting that the hyenas recruit other clan members (Holekamp et al., 2000). Although lions (*Panthera leo*) may not actively recruit other pride members when defending a carcass from hyenas (C. Packer, personal communication), sharing with pride members may allow them to defend their kill more effectively, thereby reducing their chances of losing the entire kill (Cooper, 1991).

Killer whales (*Orcinus orca*) may increase their foraging efficiency by sharing the carcasses of pinnipeds and other cetaceans (Hoelzel, 1991; Guinet et al., 2000). Guinet et al. (2000) hypothesized that they may share to maintain buoyancy of large carcasses. If a single killer whale feeds solitarily, the carcass may quickly sink in deep water. By sharing, multiple whales can keep the carcass afloat, allowing individual foragers more time to consume.

Food for non-food benefits

Predation avoidance

In addition to increasing capture rate, recruitment calling may yield immediate benefits in a currency other than food: reduced predation risk. By recruiting others, an individual feeds in a group rather than solitarily, potentially diluting predation risk, increasing predator detection, and confusing predators (Lima and Dill, 1990; Krause and Ruxton, 2002). Elgar (1986) found that house sparrows (*Passer domesticus*) give more recruitment calls in the presence of divisible food; however, call rate decreases dramatically as flock size increases. This suggests that the birds may recruit others to dilute their own predation risk only when food is sharable and individual risk is high.

Only empirical studies that vary predation risk provide a direct link between predation risk and sharing. Nevertheless, a few theoretical models predict that sharing/recruiting can immediately benefit individuals through predation avoidance. Newman and Caraco (1989) modeled recruitment calling situations in which risk of starvation and group predation risk vary. Recruiting is evolutionarily stable when predation risk decreases with group size; therefore, calling benefits solitary individuals by increasing group size and diluting risk. In another set of models, provisioning unrelated offspring at a nearby nest quiets begging calls, thereby reducing the chance of attracting predators. By sharing with unrelated offspring, an individual may decrease predation risk for its own young (Caraco and Brown, 1986; Giraldeau and Caraco, 2000).

Mate provisioning

In many species of insects, birds, and mammals, males acquire and donate food to females either before, during, or after copulation (termed mate provisioning, courtship feeding, nuptial gift giving, or meat-for-sex). Males may relinquish body parts, produce glandular secretions, or share prey or other food to gain immediate fitness benefits via natural and sexual selection (reviewed in Lack, 1940; Thornhill, 1976; Boggs, 1995; Gwynne, 1997; Vahed, 1998).

Naturally selected fitness benefits act primarily on the survival of the male and female. In several insect species, females cannibalize males during or after copulation. Provisioning the female may distract her from cannibalizing the male, thereby increasing his probability of survival and facilitating the transfer of sperm (Gwynne, 1997). Provisioning may also offer paternal investment by providing nutritional support for the female. Providing food directly affects female fecundity in many species by increasing egg number, egg size, and offspring weight (Nisbet, 1973; Newton, 1979; Gwynne, 1982; Lifjeld and Slagsvold, 1986; Moore et al., 2000).

Sexual selection may also maintain mate provisioning via sperm competition and female choice. Males of many insect species donate an edible gelatinous mass (spermatophylax) in addition to a sperm sac during mating. Sakaluk (1984) suggested that provisioning female crickets (*Gryllodes supplicans*) allows enough time for the ejaculate to transfer out of the sperm sac before she can feed on the sperm. Other researchers propose that the spermatophylax may prevent future matings by releasing refractory chemicals, plugging or filling the reproductive tract, or releasing chemicals that render foreign sperm inviable (Gwynne, 1986). Probably the most common explanation of mate provisioning is mate attraction. Males share food with females to entice them to mate, and sharing may signal the male's fitness and paternal investment. Feeding females often increases copulation rate (Tasker and Mills, 1981; Vahed, 1998; Mougeot, 2000; González-Sols et al., 2001) and mate retention (Tasker and Mills, 1981) in insects and birds.

In chimpanzees (*Pan troglodytes*), males capture monkeys and may give meat to females, some suggest in exchange for mating access (meat-for-sex hypothesis). Male chimpanzees occasionally withhold meat from a sexually receptive female until mating with her, after which he allows her to obtain a portion (Goodall, 1986; Stanford, 1998). Sexually receptive females may receive more meat from males than expected by chance (Teleki, 1973, 1981). Stanford and others (Stanford et al., 1994; Stanford, 1998) interpreted this as evidence that males trade meat for mating. However, Goodall (1986) and Teleki (1973, 1981) demonstrated that sexually receptive females are more persistent in their efforts to obtain meat (i.e., high harassment), possibly explaining their increased success. Kuroda (1984) showed that female bonobos (*Pan paniscus*) obtain more food from males if they first copulate with them.

Other studies of chimpanzees have failed to find a relationship between food and mating, instead finding no preferences for receptive females (I.C. Gilby, unpublished data) or, more importantly, no effect of sharing on male reproductive success (Hemelrijk et al., 1992, 1999; Mitani and Watts, 2001). Rather than sharing in return for an immediate copulation, a male chimpanzee may share in order to establish an affiliative relationship with a female, increasing the chances of mating later. In the chimpanzees at Gombe National Park, Tanzania, a male's frequency of involvement in consortships (exclusive mating relationships) positively correlates with the frequency with which a male shares food with females (Tutin, 1979). However, it remains unknown whether sharing with a particular female increases the chances of consorting with that individual.

Harassment and manipulative mutualism

Sharing may occur because begging and harassment reduce the fitness of the owner. Owners can gain immediate benefits by sharing part of the food with the beggar to avoid injury and energetic or opportunity costs. Blurton Jones (1984, 1986, 1987) proposed the tolerated theft hypothesis for sharing, contending that if the fitness benefit of consuming a packet of food follows a diminishing returns function, later bites of food provide less fitness benefit than earlier bites. Therefore, if a hungry beggar encounters a partially satiated owner, an asymmetry in hunger level exists. Parker's (1974) model predicted that individuals that gain more from a resource should fight more vigorously, forcing the partially satiated owner to acquiesce and share with the beggar. Other theoretical (Winterhalder, 1996) and observational (Kuroda, 1984; Goodall, 1986; Perry and Rose, 1994) studies support the effect of satiation on sharing. However, an empirical study manipulating satiation level found no increase in begging or sharing with hungry beggars (Nissen and Crawford, 1936).

Blurton Jones' model only considered what happens in the presence of an asymmetry in satiation between the players. The tolerated theft model does not explain sharing that occurs when both players are equally hungry. Harassment can influence sharing in the presence or absence of a satiation asymmetry. Wrangham (1975) first emphasized the importance of harassment (or sharing under pressure) when studying the Gombe chimpanzees. He suggested that a food possessor "may use the parts which he does not need to reduce the costs of possession by 'paying' other individuals to go away" (p. 4.57). Moore (1984) proposed that this threat of attack from a beggar may be very costly for an owner and offered a graphical model of how costs of harassment (both physical and social) can influence sharing. Stevens and Stephens (2002, Chapter 3) formalized the first mathematical model of the effects of harassment on sharing using game theory. They predicted that the defensibility of a food source may influence harassment by beggars—if beggars can obtain scraps, harassment may payoff. If beggars harass intensely enough, they may inflict such costs on owners that sharing becomes the best strategy (manipulative mutualism).

To demonstrate the viability of harassment as an explanation of food sharing, two predictions must hold: (1) harassment must cost the owner and (2) increasing harassment should increase the probability of the beggar accessing food. Harassment can include extending a hand toward an owner, vocalizing, slapping the ground, grabbing at food, or attacking the owner (Nissen and Crawford, 1936; Schessler and Nash, 1977; Goodall, 1986; Perry and Rose, 1994; Westergaard et al., 1998). These high levels of aggression may injure the owner or force it to expend energy by retaliating or moving away (Wrangham, 1975; Fragaszy and Mason, 1983; Goodall, 1986). Harassment may also impose opportunity costs associated with a reduced intake rate and the potential to lose all of the resource to the beggars. Hauser (1992) revealed that rhesus macaques (*Macaca mulatta*) that give recruitment calls experience less aggression and consume more food than those that do not recruit. Therefore, the harassment associated with not recruiting is more costly (in terms of food consumed) than the food shared after recruiting.

For food sharing to occur, the costs of harassment to the owner must outweigh the potential benefit lost by sharing (Stevens and Stephens, 2002); therefore, more intense harassment should elicit more sharing. Many observational studies suggest that begging more intensely increase sharing (Nissen and Crawford, 1936; Teleki, 1973; Wrangham, 1975; Kuroda, 1984; Takahata et al., 1984; Boesch and Boesch, 1989, I.C. Gilby, unpublished data) and more beggars elicit more sharing (Fruth and Hohmann, 2002). In addition, an empirical study indicates that squirrel monkey (*Saimiri boliviensis*) and chimpanzee food owners share four times more often with a beggar that harasses (see Chapter 4).

Delayed benefits

Animals may recoup the benefits of sharing following the sharing event. This benefit can accrue after several seconds or potentially after several months. The amount of time between sharing and recouping the benefit plays an important role in the evolution of sharing, especially in short-lived animals. The bias towards primates presented here reflects the status of the literature for delayed-benefit hypotheses of sharing.

Food for food

Reciprocity

One of the more popular explanations of food sharing is reciprocal altruism (or reciprocity), which states that an animal may perform a costly act that benefits another if the recipient returns the favor later (Trivers, 1971). Computer models suggest that reciprocity is evolutionarily stable (Axelrod and Hamilton, 1981) but proves difficult to test directly, chiefly because of the difficulty in measuring the fitness costs and benefits (Seyfarth and Cheney, 1988). Relatively few studies test reciprocal altruism in a food-sharing context, and most fail to establish its importance in sharing. Some demonstrate a reciprocal sharing pattern but fail to consider that such patterns can emerge as by-products of other mechanisms. For instance, if two individuals demonstrate symmetrical attraction or aversion to each other, and such positive or negative association affects food sharing behavior, then a reciprocal distribution of sharing will result, even though reciprocal altruism does not explain why they share food ('symmetry-based reciprocity': de Waal and Luttrell, 1988; de Waal, 2000; Brosnan and de Waal, 2002). As an example, consider a pair of unrelated male chimpanzees that are inseparable. When potential food sharing situations arise, both members of the pair tend to share because the other harasses. Because these two individuals spend more time with each other than with other individuals, their mutualistic sharing will appear reciprocal. This symmetry-based reciprocity may explain food sharing in wild chimpanzees (Mitani and Watts, 1999, 2001), vampire bats (*Desmodus rotundus*: Wilkinson, 1984; Denault and McFarlane, 1995), and captive tufted capuchins (*Cebus apella*: de Waal et al., 1993; de Waal, 1997b). Although symmetry-based reciprocity implies reciprocal sharing, it does not necessarily involve precise accounting of costs and benefits required in traditional or 'calculated' reciprocity.

Other examples of reciprocal sharing adjust for symmetry-based reciprocity. For instance, captive chimpanzees exhibited a reciprocal sharing pattern, even after statistically adjusting for association patterns (de Waal, 1989). Nevertheless, this correlational study found long-term reciprocal relationships (over all trials, A tended to share with B and vice versa) rather than manipulating ownership and assessing the effects of sharing in the next trial. In an experiment with captive capuchins, de Waal (2000) found that if individual A shared frequently with individual B in one particular trial, then B tended to share frequently with A in the next trial. De Waal concluded that the events of the first stage "set the tone" for the second—if A was nice, then B would be nice too. Unlike traditional reciprocity, such 'attitudinal reciprocity' does not require "strict contingency between given and received services" and therefore proves less cognitively demanding (de Waal, 2000, p. 260). The general relevance of attitudinal reciprocity remains unclear. No studies have convincingly documented traditional reciprocity.

Negative reciprocity Another variation on reciprocal altruism is negative reciprocity or punishment. In this case, an animal punishes by inflicting a fitness cost on a defecting (non-cooperative) opponent, discouraging future defection (Boyd and Richerson, 1992; Clutton-Brock and Parker, 1995a). Punishment differs from harassment because punishment requires delayed rather than immediate benefits. Benefits accrue in future interactions when opponents learn the contingencies of punishment and switch to cooperation. Although common in contexts such as mate guarding (Clutton-Brock and Parker, 1995b), the effect of aggression on future food sharing is not well studied in non-human animals.

Food for non-food benefits

Trade

Strict reciprocal altruism, as discussed above, assumes that reciprocation occurs in the same fitness currency as the original act. The trade hypothesis also assumes reciprocal exchange, but reciprocation occurs in a different currency. For example, players may exchange food for social favors such as grooming or support in a dominance conflict. As with reciprocity, this concept proves challenging to test directly because of the difficulty in measuring the relative fitness value of different currencies. Is grooming actually costly to perform? However, a few studies indicate that trade may elicit food sharing behavior for some species.

Blood sharing among vampire bats may depend on grooming. Wilkinson (1986) found that grooming positively correlates with blood sharing frequency. However, grooming may also allow the bats to assess whether an individual has recently fed, determining the likelihood of receiving a regurgitated meal (Wilkinson, 1986).

Studies of captive monkeys demonstrate that some species may trade food for other currencies. In one experiment with captive tufted capuchins, subjects in one group transferred stones to subjects in a second group, who used the stones as tools to access food (Westergaard and Suomi, 1997). Subjects in the second group then transferred food to subjects in the first group. Despite the appearance of trading tools for food, food transfer occurred at a similar rate whether or not tools were needed, indicating that trade did not explain the sharing. De Waal and Berger (2002) demonstrated trade in captive capuchins, suggesting that food owners that receive help in a cooperative task will share food more frequently. In a study with captive spider monkeys (*Ateles geoffroyi*), the frequency of dyadic grooming positively correlated with co-feeding at a monopolizable feeder, suggesting that grooming influenced tolerance at the feeding site (Pastor-Nieto, 2001).

In a study with captive chimpanzees, food possessors tolerated frequent grooming partners more often, allowing them to passively acquire food (Koyama and Dunbar, 1996). In another study, individual A shared more frequently with B if B had groomed A earlier in the day, but not after A had groomed B (de Waal, 1989, 1997a). After food sharing trials, possessors rarely groomed individuals with which they had shared (de Waal, 1997a). This supplies the strongest evidence that chimpanzees may trade food for grooming, because the temporal pattern of taking turns exchanging grooming and food prevents one individual from gaining all of the benefits (de Waal, 1989).

Some studies of wild chimpanzees also support the idea of trade. Nishida et al. (1992) demonstrated that the frequency with which chimpanzees obtains meat from the alpha male positively correlates with the total amount of time spent grooming with the alpha. Additionally, the alpha male tends to support males that he frequently shares with when they participate in dominance conflicts with other males. The authors concluded that chimpanzees use meat sharing to maintain coalitions, with the alpha male effectively trading meat for grooming and dominance support. While suggestive, this study does not rule out symmetry-based reciprocity, because an index of proximity positively correlates with the frequency with which individuals obtained meat from the alpha male.

Others argue that chimpanzees utilize meat as a social or political tool to build coalitionary support (Mitani and Watts, 2001) and “reward allies and snub rivals” (Stanford, 1998, 1999). Several researchers have suggested that chimpanzees hunt to provide highly prized items to trade (Stanford et al., 1994; Mitani and Watts, 2001). These authors, however, have provided no data concerning the opportunity to receive meat. Perhaps only grooming partners or allies attempt to get meat from a possessor, and possessors share meat because of other mechanisms, such as harassment.

Show-off/status enhancement

Food sharing may serve as a costly display that advertises an animal's social status. For example, meat is energetically costly and risky for chimpanzees to acquire (Boesch, 1994), so sharing with others may advertise an individual's strength and health. Such a signal may intimidate rivals or attract mates. When seen begging, an individual appears weak, in essence giving up a unit of social status for a nutritional benefit (Moore, 1984). Also, simply possessing a desirable food item may draw positive attention to an individual (Teleki, 1973; Rijksen, 1978), thus raising its social status.

As with the other cognitively complex hypotheses, the status enhancement hypothesis proves difficult to test. Proper assessment of this hypothesis requires a long-term study that tracks changes in both an individual's social status and sharing patterns (de Waal, 1989). Apart from anecdotes (Boesch and Boesch, 1989), little evidence supports meat sharing to enhance status in chimpanzees (de Waal, 1989); however, some support comes from work with Arabian babblers (*Turdoides squamiceps*). These birds maintain a strict dominance hierarchy, in which dominant individuals feed insects to subordinates. Adults appear to compete to feed each other and interfere when subordinates try to feed others (Zahavi, 1990). When fed by a subordinate, a dominant male usually responds with aggression. Typically, the alpha male seeks out and feeds the beta male. Zahavi interpreted this sharing as a display, and the acceptance of food decreases the social status of the recipient.

Group augmentation

The cooperative breeding literature first introduced the concept of group augmentation (Woolfenden and Fitzpatrick, 1978; Brown, 1980; Wiley and Rabenold, 1984; Brown, 1987), although Kropotkin (1908) and Trivers (1971) alluded to these ideas earlier. By helping raise non-descendent offspring, a helper increases the group size, which may aid it in acquiring a nearby territory in the future. Group augmentation can explain many examples in which cooperation increases the group size, thereby providing some future benefit to the cooperator (e.g., group territory defense in lions: Grinnell et al., 1995; Heinsohn and Packer, 1995). Because the cooperator gains future benefits, this type of delayed mutualism resists cheaters, since they have smaller group sizes and therefore reduced future fitness (Kokko et al., 2001; Packer et al., 2001; Clutton-Brock, 2002).

Lima (1989) modeled a similar situation of this 'mutual dependence' in which an individual's fitness depends on the presence of another group member which, in turn, depends on the actions of the individual. If an individual defects in an iterated Prisoner's Dilemma, its partner will probably not survive to the next round. If the probability of finding another partner is low, the defector could face a much higher predation risk as a singleton. Therefore, by cooperating an individual increases its group size and reduces the future risk of predation.

Most examples of group augmentation still come from the cooperative breeding literature (reviewed in Clutton-Brock, 2002). Although helping in cooperative breeders frequently involves group territory defense, predator vigilance, and babysitting, offspring provisioning plays a large role. Often the helpers are closely related to the offspring but not always (Stacey and Koenig, 1990; Cockburn, 1998). Because of the frequency of helping unrelated offspring in meerkats (*Suricata suricatta*), Clutton-Brock and colleagues proposed group augmentation as a possible explanation for such cooperativeness. Provisioning increases pup growth and survival thereby increasing group size (Clutton-Brock et al., 2001). Large group sizes offer direct benefits to helpers such as lower predation risk (Clutton-Brock et al., 1999) and a pool of potential helpers when the current helpers begin to breed (Brotherton et al., 2001). A similar increase in offspring number and adult survival associated with larger group size occurs in dwarf mongooses (*Helogale parvula*: Rood, 1990).

Wilkinson (1992) suggested that communal nursing in evening bats (*Nycticeius humeralis*) may increase colony size and reduce predation risk. However, this 'milk dumping' could also have the immediate effect of reducing weight and decreasing energetic costs for foraging (Roulin, 2002). Extreme forms of group augmentation may include adopting or even kidnapping unrelated offspring to increase the group size (Woolfenden and Fitzpatrick, 1984; Zahavi, 1990; Heinsohn, 1991), possibly to ensure the presence of helpers for future breeding attempts (Connor and Curry, 1995).

Discussion

Several interesting patterns emerge from our organization of the food sharing data. First, only long-lived species (birds and mammals) reap delayed benefits. The short-lived insects only received immediate benefits for their sharing. This could be attributed to differing discounting rates in food sharing situations among species. Although little data exists on discounting rate for species other than pigeons (Mazur, 2000), rats (Richards et al., 1997), and humans (Green et al., 1994), discounting should negatively correlate with expected life span—why would an animal defer benefits to the future, when it may soon die? Tobin and Logue (1994) proposed a similar relationship between discounting and metabolic rate (a correlate of life-span). Recent evidence, however, demonstrated low discounting in the honey bee (Cheng et al., 2002), indicating possible context-specific discounting (Logue, 1988; Stephens and Anderson, 2001).

The second pattern emerging from the data is that most examples of collecting return benefits in different currencies occur in highly social species (e.g., babblers, meerkats, and primates). This proves important because repeated interactions involving multiple types of fitness currencies may facilitate exchange between currencies. That is, species that repeatedly groom, eat with, mate with, or avoid predation with others, may exchange these currencies more frequently than species that interact only when feeding.

Combining these patterns allows us to predict which types of explanations of food sharing are viable for which species. Most species can gain immediate benefits of exchanging food for food; however, once benefits are delayed and/or in a different currency, the number of potential species for which these hypotheses apply decreases dramatically. Therefore, this framework would predict that delayed, different currency explanations of food sharing may apply only to long-lived, low discounting, highly social species. The apparent bias towards primates in these studies probably results from the fact that they possess all of these characteristics. Investigating other species that share these attributes can test these predictions.

Reciprocity

Historically, research on sharing and cooperation has primarily focused on explanations involving delayed benefits. In particular, many theoretical studies have investigated the role of reciprocity in the evolution of cooperation (reviewed in Dugatkin, 1997); however, little empirical support exists for non-human animals (Noë, 1990; Connor, 1995; Pusey and Packer, 1997; Stephens et al., 1997). Timing of benefits could eliminate reciprocity as a general explanation of cooperation. Axelrod and Hamilton (1981) appreciated the importance of repeated interactions by incorporating a "shadow of the future" or probability of future encounter. They did not consider, however, the timing of benefits. May (1981) applied this timing problem to Axelrod and Hamilton's reciprocity theory, suggesting that discounting can devalue future reciprocated acts. Studies on humans and non-human animals verify the effect of discounting on cooperation (Green et al., 1995; Baker and Rachlin, 2001; Stephens et al., 2002). Trivers (1971) emphasized the importance of timing in his original model:

> The time lag is the crucial factor, for it means that only under highly specialized circumstances can the altruist be reasonably guaranteed that the causal

> chain he initiates with his altruistic act will eventually return to him and confer, directly or indirectly, its benefit (p. 39).

Therefore, animals may require ‘interest’ to compensate for discounted future rewards, much like Trivers (1971) suggested for humans. Reciprocity theory must account for some form of discounting future benefits.

Although theoretically intriguing, reciprocity does not offer the most parsimonious explanation of food sharing. In addition to requiring multiple interactions and individual recognition, reciprocity requires a low discounting rate and complex cognitive skills to track debts owed and favors given. Some species of primates may possess the skills necessary to reciprocate, but these explanations probably do not account for cooperative behavior in most animals. Despite Trivers’ (1971) and Axelrod and Hamilton’s (1981) claims of its generality and the deluge of theory that followed, reciprocity does not appear to be a broadly applicable explanation of non-human cooperation. In fact, reciprocity appears to occur in only a few very celebrated examples such as vampire bats and primates. These instances, however, probably occur via symmetry-based reciprocity rather than traditional reciprocity. Due to the dearth of empirical evidence, we reiterate the need to focus both theory and empirical tests on alternatives to reciprocity (Dugatkin et al., 1992; Connor, 1995; Pusey and Packer, 1997; Clutton-Brock, 2002; Stevens and Stephens, 2002).

Future directions

The rule of parsimony requires the elimination of simpler explanations before invoking more elaborate ones. The explanations focusing on immediate benefits (e.g., mutualism) offer simple, selfish descriptions of benefits that apply to general cooperative situations. We feel that mutualism provides a simple but frequently ignored explanation of cooperation (and specifically food sharing) despite mounting evidence that it often offers the most parsimonious explanation (Elgar, 1986; Heinrich and Marzluff, 1991; Grinnell et al., 1995). Manipulative mutualism—altering the payoffs of an opponent such that cooperation becomes beneficial—may also supply an often overlooked explanation of cooperation (e.g., harassment: Stevens and Stephens, 2002). Several studies of food sharing describe harassment during sharing bouts but dismiss its relevance. For instance, de Waal (1989) and Mitani and Watts (2001) invoke complex explanations such as reciprocity and trade; however, they do not exclude harassment as a contributing factor in reciprocal sharing.

Although group augmentation requires delayed benefits in different currencies, it too may provide a fertile area of exploration as an explanation of cooperation. Recent theoretical and empirical investigations by Clutton-Brock and colleagues (Clutton-Brock et al., 2000; Kokko et al., 2001; Clutton-Brock, 2002) suggest that group augmentation may explain much of meerkat cooperation. Because of the profound benefits of being in a group (Krause and Ruxton, 2002), natural selection favors individuals that recruit and maintain more group members. Unlike reciprocity and trade, group augmentation does not require special cognitive mechanisms.

The framework presented here indicates that a complete study of food sharing requires synthesizing the current functional explanations with potential cognitive mechanisms. Therefore, evaluating the underlying psychological constraints on animals can provide important insights into the applicability of certain hypotheses. In particular, this framework suggests that reciprocity and trade may require complex cognitive mechanisms that many animals may not possess. In addition, future studies should include comparative components—most studies to date have only considered a single species. Comparing food sharing in multiple species allows us to examine the ecological and cognitive attributes that lead to different types of sharing.

Acknowledgments

We would like to thank Esteban Fernández-Juricic, Craig Packer, Anne Pusey, Dave Stephens, and Mike Wilson for helpful comments on the manuscript.

References

Axelrod, R. and Hamilton, W. D. 1981. The evolution of cooperation. *Science* 211:1390–1396.

Baker, F. and Rachlin, H. 2001. Probability of reciprocation in repeated prisoner's dilemma games. *Journal of Behavioral Decision Making* 14:51–67.

Blurton Jones, N. G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology* 5:1–3.

Blurton Jones, N. G. 1986. Fitness returns from resources and the outcome of contests: some implications for primatology and anthropology. *In* J. G. Else and P. C. Lee (eds.), Primate Ontogeny, Cognition, and Social Behavior. Cambridge University Press, Cambridge. pp. 393–406.

Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.

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

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

Boggs, C. L. 1995. Male nuptial gifts: phenotypic consequences and evolutionary implications. *In* S. R. Leather and J. Hardie (eds.), Insect Reproduction. CRC Press, New York. pp. 215–242.

Bolten, A. B., Robinson, F. A., Nation, J. L., and Yu, S. J. 1983. Food sharing between honeybee (*Apis mellifera*) colonies in flight cages. *Journal of Apicultural Research* 22:90–100.

Boyd, R. and Richerson, P. J. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.

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

Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R., and McIlrath, G. M. 2001. Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology* 12:590–599.

Brown, C. R. and Brown, M. B. 1996. Coloniality in the Cliff Swallow: The Effect of Group Size on Social Behavior. University of Chicago Press, Chicago.

Brown, C. R., Brown, M. B., and Shaffer, M. L. 1991. Food-sharing signals among social foraging cliff swallows. *Animal Behaviour* 42:551–564.

Brown, J. L. 1980. Fitness in complex avian social systems. *In* H. Markl (ed.), Evolution of Social Behaviour: Hypotheses and Empirical Tests. Verlag Chemie, Weinheim. pp. 115–128.

Brown, J. L. 1983. Cooperation—a biologist's dilemma. *In* J. S. Rosenblatt (ed.), Advances in the Study of Behaviour. Academic Press, New York. pp. 1–37.

Brown, J. L. 1987. Helping and Communal Breeding in Birds. Princeton University Press, Princeton.

Caraco, T. and Brown, J. L. 1986. A game between communal breeders: when is food sharing stable? *Journal of Theoretical Biology* 118:379–393.

Cheng, K., Penea, J., Porter, M. A., and Irwin, J. D. 2002. Self-control in honeybees. *Psychonomic Bulletin and Review* 9:259–263.

Clutton-Brock, T. H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.

Clutton-Brock, T. H., Brotherton, P. N. M., O'Riain, M. J., Griffin, A. S., Gaynor, D., Sharpe, L., Kansky, R., Manser, M. B., and McIlrath, G. M. 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta. Proceedings of the Royal Society of London, Series B* 267:301–305.

Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., MacColl, A. D. C., Kansky, R., Chadwick, P., Manser, M. B., Skinner, J. D., and Brotherton, P. N. M. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta. Journal of Animal Ecology* 68:672–683.

Clutton-Brock, T. H. and Parker, G. A. 1995a. Punishment in animal societies. *Nature* 373:209–216.

Clutton-Brock, T. H. and Parker, G. A. 1995b. Sexual coercion in animal societies. *Animal Behaviour* 49:1345–1365.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S., and Cameron, E. Z. 2001. Effects of helpers on juvenile development and survival in meerkats. *Science* 293:2446–2449.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29:141–177.

Connor, R. C. 1995. Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends in Ecology and Evolution* 10:84–86.

Connor, R. C. and Curry, R. L. 1995. Helping non-relatives: a role for deceit? *Animal Behaviour* 49:389–393.

Cooper, S. M. 1991. Optimal hunting groups size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology* 29:130–136.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution* 18:433–459.

de Waal, F. B. M. 1997a. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior* 18:375–386.

de Waal, F. B. M. 1997b. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology* 111:370–378.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour* 60:253–261.

de Waal, F. B. M. and Berger, M. L. 2000. Payment for labour in monkeys. *Nature* 404:563.

de Waal, F. B. M. and Luttrell, L. M. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethology and Sociobiology* 9:101–118.

de Waal, F. B. M., Luttrell, L. M., and Canfield, M. E. 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. *American Journal of Primatology* 29:73–78.

Denault, L. K. and McFarlane, D. A. 1995. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Animal Behaviour* 49:855–856.

Dittus, W. P. J. 1984. Toque macaque (*Macaca sinica*) food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour* 32:470–477.

Dugatkin, L. A. 1997. Cooperation Among Animals: An Evolutionary Perspective. Oxford University Press, New York.

Dugatkin, L. A., Mesterton-Gibbons, M., and Houston, A. I. 1992. Beyond the Prisoner's Dilemma: toward models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology and Evolution* 7:202–205.

East, M. L. and Hofer, H. 1991. Loud calling in a female-dominated mammalian society: I. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour* 42:651–669.

Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour* 34:169–174.

Evans, C. S. and Marler, P. 1994. Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Animal Behaviour* 47:1159–1170.

Feistner, A. T. C. and McGrew, W. C. 1989. Food-sharing in primates: a critical review. *In* P. K. Seth and S. Seth (eds.), Perspectives in Primate Biology, vol. 3. Today & Tomorrow's Printers and Publishers, New Delhi. pp. 21–36.

Feistner, A. T. C. and Price, E. C. 1990. Food-sharing in cotton-top tamarins (*Saguinus oedipus*). *Folia Primatologica* 54:34–45.

Ferrari, S. F. 1987. Food transfer in a wild marmoset group. *Folia Primatologica* 48:203–206.

Fragaszy, D. M. and Mason, W. A. 1983. Comparisons of feeding behavior in captive squirrel and titi monkeys (*Saimiri sciureus* and *Callicebus moloch*). *Journal of Comparative Psychology* 97:310–326.

Fruth, B. and Hohmann, G. 2002. How bonobos handle hunts and harvests: why share food? *In* C. Boesch, G. Hohmann, and L. F. Marchant (eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge. pp. 231–243.

Giraldeau, L.-A. and Caraco, T. 2000. Social Foraging Theory. Princeton University Press, Princeton.

González-Sols, J., Sokolov, E., and Becker, P. H. 2001. Courtship feedings, copulations, and paternity in common terns, *Sterna hirundo. Animal Behaviour* 61:1125–1132.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, Mass.

Green, L., Fry, A. F., and Myerson, J. 1994. Discounting of delayed rewards: a life-span comparison. *Psychological Science* 5:33–36.

Green, L., Price, P. C., and Hamburger, M. E. 1995. Prisoner's Dilemma and the pigeon: control by immediate consequences. *Journal of the Experimental Analysis of Behavior* 64:1–17.

Grinnell, J., Packer, C., and Pusey, A. E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour* 49:95–105.

Guinet, C., Barrett-Lennard, L. G., and Loyer, B. 2000. Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: strategies for feeding on negatively-buoyant prey. *Marine Mammal Science* 16:829–834.

Gurksy, S. 2000. Allocare in a nocturnal primate: data on the spectral tarsier, *Tarsius spectrum. Folia Primatologica* 71:39–54.

Gwynne, D. T. 1982. Courtship feeding increases female reproductive success in bushcrickets. *Nature* 307:361–363.

Gwynne, D. T. 1986. Courtship feeding in katydids (Orthoptera: Tettigoniidae): investment in offspring or in obtaining fertilizations? *American Naturalist* 128:342–352.

Gwynne, D. T. 1997. The evolution of edible 'sperm sacs' and other forms of courtship feeding in crickets, katydids and their kin (Orthoptera: Ensifera). *In* J. C. Choe and B. J. Crepi (eds.), The Evolution of Mating Systems in Insects and Arachnids. Cambridge University Press, Cambridge. pp. 110–129.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology* 7:1–52.

Hauser, M. D. 1992. Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences (USA)* 89:12137–12139.

Heinrich, B. 1988a. Food sharing in the raven, *Corvus corax. In* C. N. Slobodchikoff (ed.), The Ecology of Social Behavior. Academic Press, San Diego. pp. 285–311.

Heinrich, B. 1988b. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by ravens, *Corvus corvax. Behavioral Ecology and Sociobiology* 23:141–156.

Heinrich, B. 1989. Ravens in Winter. Simon and Schuster, New York.

Heinrich, B. and Marzluff, J. M. 1991. Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology* 28:13–22.

Heinrich, B. and Marzluff, J. M. 1995. Why ravens share. *American Scientist* 83:342–349.

Heinsohn, R. G. 1991. Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Animal Behaviour* 41:1097–1100.

Heinsohn, R. G. and Packer, C. 1995. Complex cooperative strategies in group-territorial African lions. *Science* 269:1260–1262.

Hemelrijk, C. K., Meier, C., and Martin, R. D. 1999. 'Friendship' for fitness in chimpanzees? *Animal Behaviour* 58:1223–1229.

Hemelrijk, C. K., van Laere, G. J., and van Hooff, J. A. R. A. M. 1992. Sexual exchange relationships in captive chimpanzees? *Behavioral Ecology and Sociobiology* 30:269–275.

Hoelzel, A. R. 1991. Killer whale predation on marine mammals at Punta Norte, Argentina: food sharing, provisioning, and foraging strategy. *Behavioral Ecology and Sociobiology* 29:197–204.

Holekamp, K. E., Boydston, E. E., and Smale, L. 2000. Group travel in social carnivores. *In* S. Boinski and P. A. Garber (eds.), On the Move: How and Why Animals Travel in Groups. University of Chicago Press, Chicago. pp. 587–627.

Johnson, R. H. 1982. Food-sharing behavior in captive Amazon River dolphins (*Inia geoffrensis*). *Cetology* 43:1–3.

Judd, T. M. and Sherman, P. W. 1996. Naked mole-rats recruit colony mates to food sources. *Animal Behaviour* 52:957–969.

Kavanagh, M. 1972. Food-sharing behaviour within a group of douc monkeys (*Pygathrix nemaeus nemaeus*). *Nature* 239:406–407.

Kokko, H., Johnstone, R. A., and Clutton-Brock, T. H. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London, Series B* 268:187–196.

Koyama, N. F. and Dunbar, R. I. M. 1996. Anticipation of conflict by chimpanzees. *Primates* 37:79–86.

Krause, J. and Ruxton, G. D. 2002. Living in Groups. Oxford University Press, Oxford.

Kropotkin, P. 1908. Mutual Aid: A Factor of Evolution. Alfred A. Knopf, New York.

Kuroda, S. 1984. Interaction over food among pygmy chimpanzees. *In* R. Sussman (ed.), The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Plenum Press, New York. pp. 301–324.

La Cerra, P. and Bingham, R. 1998. The adaptive nature of the human neurocognitive architecture: an alternative model. *Proceedings of the National Academy of Sciences (USA)* 95:11290–11294.

Lack, D. 1940. Courtship feeding in birds. *Auk* 57:169–178.

Lifjeld, J. T. and Slagsvold, T. 1986. The function of courtship feeding during incubation in the pied flycatcher, *Ficedula hypoleuca. Animal Behaviour* 34:1441–1453.

Lima, S. L. 1989. Iterated prisoner's dilemma: an approach to evolutionarily stable cooperation. *American Naturalist* 134:828–834.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.

Logue, A. W. 1988. Research on self-control: an integrating framework. *Behavioral and Brain Sciences* 11:665–709.

Marzluff, J. M. and Heinrich, B. 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Animal*

Behaviour 42:755–770.

May, R. M. 1981. The evolution of cooperation. *Nature* 292:291–292.

Mazur, J. E. 1987. An adjusting procedure for studying delayed reinforcement. *In* M. L. Commons, J. E. Mazur, J. A. Nevin, and H. Rachlin (eds.), Quantitative Analyses of Behavior: The Effect of Delay and of Intervening Events on Reinforcement Value, vol. 5. Lawrence Erlbaum Associates, Hillsdale, NJ. pp. 55–73.

Mazur, J. E. 2000. Tradeoffs among delay, rate, and amount of reinforcement. *Behavioural Processes* 49:1–10.

Mitani, J. C. and Watts, D. P. 1999. Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology* 109:439–454.

Mitani, J. C. and Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* 61:915–924.

Moore, D. J., Williams, T. D., and Morris, R. D. 2000. Mate provisioning, nutritional requirements for egg production, and primary reproductive effort of female Common Terns, *Sterna hirundo*. *Journal of Avian Biology* 31:183–196.

Moore, J. 1984. The evolution of reciprocal sharing. *Ethology and Sociobiology* 5:5–14.

Mougeot, F. 2000. Territorial intrusions and copulation patterns in red kites, *Milvus milvus*, in relation to breeding density. *Animal Behaviour* 59:633–642.

Nettelbeck, A. R. 1998. Observations on food sharing in wild lar gibbons (*Hylobates lar*). *Folia Primatologica* 69:386–391.

Newman, J. A. and Caraco, T. 1989. Co-operative and non-co-operative bases of food-calling. *Journal of Theoretical Biology* 141:197–209.

Newton, I. 1979. Population Ecology of Raptors. T&AD Poyser, London.

Nisbet, I. C. T. 1973. Courtship feeding, egg size and breeding success in Common Terns. *Nature* 241:141–142.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., and Uehara, S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? *In* T. Nishida, W. C. McGrew, P. Marler, M. Pickford, and F. B. M. de Waal (eds.), Topics in Primatology, vol. 1. University of Tokyo Press, Tokyo. pp. 159–174.

Nissen, H. W. and Crawford, M. P. 1936. A preliminary study of food-sharing behaviour in young chimpanzees. *Journal of Comparative Psychology* 22:383–419.

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* 39:79–90.

Noë, R. and Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology* 35:1–11.

Noë, R. and Hammerstein, P. 1995. Biological markets. *Trends in Ecology and Evolution* 10:336–339.

Noë, R., van Hooff, J. A. R. A. M., and Hammerstein, P. 2001. Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge University Press, Cambridge.

Packer, C., Pusey, A. E., and Eberly, L. E. 2001. Egalitarianism in female African lions. *Science* 293:690–693.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology* 47:223–243.

Parker, P. G., Waite, T. A., Heinrich, B., and Marzluff, J. M. 1994. Do common ravens share ephemeral food resources with kin? DNA fingerprinting evidence. *Animal Behaviour* 48:1085–1093.

Pastor-Nieto, R. 2001. Grooming, kinship and co-feeding in captive spider monkeys (*Ateles geoffroyi*). *Zoo Biology* 20:293–303.

Perry, S. and Rose, L. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capuchinus*. *Primates* 35:409–415.

Pusey, A. E. and Packer, C. 1997. The ecology of relationships. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology: An Evolutionary Approach, 4th ed. Blackwell Science, Oxford. pp. 254–283.

Rachlin, H. 2000. The Science of Self-Control. Harvard University Press, Cambridge, Mass.

Richards, J. B., Mitchell, S. H., de Wit, H., and Seiden, L. S. 1997. Determination of discount functions in rats with an adjusting-amount procedure. *Journal of the Experimental Analysis of Behavior* 67:353–366.

Richner, H. and Heeb, P. 1995. Is the information center hypothesis a flop? *In* P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and M. Milinski (eds.), Advances in the Study of Behavior, vol. 24. Academic Press, San Diego. pp. 1–45.

Richner, H. and Heeb, P. 1996. Communal life: honest signaling and the recruitment center hypothesis. *Behavioral Ecology* 7:115–118.

Rijksen, H. 1978. Hunting behavior in hominids: some ethological aspects. *In* D. Chivers and K. Joysey (eds.), Recent Advances in Primatology, vol. III. Academic Press, London. pp. 499–502.

Rood, J. P. 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour* 39:566–572.

Roulin, A. 2002. Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour* 63:201–208.

Sakaluk, S. K. 1984. Male crickets feed females to ensure complete sperm transfer. *Science* 223:609–610.

Schessler, T. and Nash, L. T. 1977. Food sharing among captive gibbons (*Hylobaytes lar*). *Primates* 18:677–689.

Seyfarth, R. M. and Cheney, D. L. 1988. Empirical tests of reciprocity theory: problems in assessment. *Ethology and Sociobiology* 9:181–187.

Stacey, P. B. and Koenig, W. D. 1990. Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior. Cambridge University Press, Cambridge.

Stanford, C. B. 1998. Chimpanzee and Red Colobus. Harvard University Press, Cambridge, Mass.

Stanford, C. B. 1999. The Hunting Apes: Meat Eating and the Origins of Human Behavior. Princeton University Press, Princeton.

Stanford, C. B., Wallis, J., Mpongo, E., and Goodall, J. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1–18.

Starin, E. D. 1978. Food transfer by wild titi monkeys (*Callicebus torquatus torquatus*). *Folia Primatologica* 30:145–151.

Stephens, D. W. and Anderson, D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behavioral Ecology* 12:330–339.

Stephens, D. W., Anderson, J. P., and Benson, K. E. 1997. On the spurious occurrence of tit for tat in pairs of predator-approaching fish. *Animal Behaviour* 53:113–131.

Stephens, D. W. and Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton.

Stephens, D. W., McLinn, C. M., and Stevens, J. R. 2002. Discounting and reciprocity in an Iterated Prisoner's Dilemma. *Science* 298:2216–2218.

Stevens, J. R. and Stephens, D. W. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology* 13:393–400.

Strum, S. C. 1975. Primate predation: interim report on the development of a tradition in a troop of olive baboons. *Science* 187:755–757.

Strum, S. C. 1981. Processes and products of change: baboon predatory behavior in Gilgil, Kenya. *In* R. S. O. Harding and G. Teleki (eds.), Omnivorous Primates: Gathering and Hunting in Human Evolution. Columbia University Press, New York. pp. 255–302.

Takahata, Y., Hasegawa, T., and Nishida, T. 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *International Journal of Primatology* 5:213–233.

Tasker, C. R. and Mills, J. A. 1981. A functional analysis of courtship feeding in the red-billed gull. *Behaviour* 77:222–241.

Teleki, G. 1973. The Predatory Behavior of Wild Chimpanzees. Bucknell University Press, Lewisburg.

Teleki, G. 1981. The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania. *In* R. S. O. Harding and G. Teleki (eds.), Omnivorous Primates. Gathering and Hunting in Human Evolution. Columbia University Press, New York. pp. 303–343.

Thiollay, J. M. 1991. Foraging home range use and social behaviour of a group-living rainforest raptor, the red-throated caracara, *Daptrius americanus*. *Ibis* 133:382–393.

Thornhill, R. 1976. Sexual selection and parental investment in insects. *American Naturalist* 110:153–163.

Tobin, H. and Logue, A. W. 1994. Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *Journal of Comparative Psychology* 108:126–133.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology* 6:29–38.

Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews* 73:43–78.

Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as "information centers" for food-finding. *Ibis* 115:517–534.

West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology* 10:1–33.

Westergaard, G. C., Kuhn, H. E., Babitz, M. A., and Suomi, S. J. 1998. Aimed throwing as a means of food transfer between tufted capuchins (*Cebus apella*). *International Journal of Primatology* 19:123–131.

Westergaard, G. C. and Suomi, S. J. 1997. Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). *American Journal of Primatology* 43:33–41.

Wiley, R. H. and Rabenold, K. N. 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* 38:609–621.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308:181–184.

Wilkinson, G. S. 1986. Social grooming in the vampire bat, *Desmodus rotundus*. *Animal Behaviour* 34:1880–1889.

Wilkinson, G. S. 1992. Communal nursing in the evening bat, *Nycticeius humeralis*. *Behavioral Ecology and Sociobiology* 31:225–235.

Winterhalder, B. 1996. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology* 5:46–57.

Woolfenden, G. E. and Fitzpatrick, J. W. 1978. The inheritance of territory in group breeding birds. *Bioscience* 28:104–108.

Woolfenden, G. E. and Fitzpatrick, J. W. 1984. The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird. Princeton University Press, Princeton.

Wrangham, R. W. 1975. The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, Cambridge University.

Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. *In* P. B. Stacey and W. D. Koenig (eds.), Cooperative Breeding in Birds: Long-Term Studies of Ecology and Behavior. Cambridge University Press, Cambridge. pp. 103–130.

Table 1.1: Summary of hypotheses and examples of food sharing categorized by timing and currency of benefits.

	Immediate benefits			**Delayed benefits**		
	Explanation	*Species*	*Studies*	*Explanation*	*Species*	*Studies*
Food for food	*Increased foraging*	Ravens	Heinrich 1988 a,b, 1989	*Reciprocity*	Vampire bats	Wilkinson 1984; Denault & MacFarlane 1995
		Hyenas	East & Hofer 1991		Capuchin monkeys	de Waal 1997b, 2000
		Killer whales	Hoelzel 1991; Guinet et al. 2000		Chimpanzees	de Waal 1989, Mitani & Watts 1999, 2000
Food for non-food benefits	*Predation avoidance*	House sparrows	Elgar 1986	*Trade*	Vampire bats	Wilkinson 1986
	Mate provisioning	Insects	Boggs 1995; Gwynne 1997; Vahed 1998		Capuchin monkeys	Westergaard & Suomi 1997
		Chimpanzees	Hemelrijk et al. 1992, Stanford 1998		Chimpanzees	de Waal 1989, 1997a, Koyama & Dunbar 1996
	Harassment	Rhesus monkeys	Hauser 1992	*Status enhancement*	Arabian babblers	Zahavi 1990
		Chimpanzees	Wrangham 1975, Goodall 1986		Chimpanzees	Boesch & Boesch 1989
				Group augmentation	Scrub jays	Woolfenden & Fitzpatrick 1978; Brown 1980, 1987
					Meerkats	Clutton-Brock 2002

Chapter 2

The economic basis of cooperation: experimental tests using a novel procedure[1]

Abstract

This study examined the economics of cooperation in controlled-payoff games using captive blue jays, *Cyanocitta cristata*. This investigation used a special feeding apparatus to test for the stability of cooperative choice in a series of iterated games. At the beginning of each trial food was dispensed into a series of bins in a feeding table. The actions of the players determined the destination of the food in each bin, sometimes sending it to their own food cup, and sometimes sending it to their opponent's food cup. The jays experienced experimentally determined game theoretical payoff matrices, which determined the distribution of food to themselves and their opponent, depending on their decision to cooperate or defect. The experiment tested four game matrices, called the 'Cooperate Only', 'Defect Only', 'Prisoner's Dilemma', and 'Opponent Control' treatments. This study found little cooperation in the Defect Only and Prisoner's Dilemma treatments. Cooperation occurred significantly more often in the Opponent Control treatment. These findings suggest that the jays attend to short-term consequences; they cooperate when an immediate benefit exists (Cooperate Only treatment) but not in the absence of that benefit (Defect Only), even if a long term benefit may exist (Prisoner's Dilemma). The Opponent Control treatment suggests that, although unstable, cooperation can occur when an individual's benefits depend completely on the actions of others. This study, therefore, agrees with recent studies in concluding that simpler, selfish models should be considered before invoking more complex explanations such as reciprocal altruism.

---

[1] This chapter was co-authored with D.W. Stephens.

During the last 20 years the central paradigm of non-kin cooperation in non-human animals has been reciprocal altruism. Trivers (1971) formulated the concept of reciprocal altruism as an investigation of altruism via turn-taking. Axelrod and Hamilton (1981) spurred the economic examination of reciprocal altruism by championing the concept of tit-for-tat—a strategy of copying your opponent's last choice—in a Prisoner's Dilemma game. Despite a massive theoretical effort investigating the evolutionary stability of the tit-for-tat strategy (reviewed in Dugatkin, 1997), there is little empirical evidence supporting tit-for-tat or reciprocal altruism as a primary explanation for cooperation or altruism, suggesting the need to examine alternative models (Dugatkin et al., 1992; Connor, 1995; Pusey and Packer, 1997; Stevens and Stephens, 2002, Chapter 3). Critics of reciprocal altruism argue that it is unnecessarily complex. For example, the inherent time delay between cooperation and repayment in reciprocal altruism makes it difficult to implement. In addition, tracking debts owed and favors given requires complex score-keeping that may exceed the cognitive capabilities of many animal species. This study is part of a larger effort to understand the behavioral constraints on cooperation, and use this understanding to develop more plausible alternative models.

This study replicates and extends the study of Clements and Stephens (1995), which found that blue jays (*Cyanocitta cristata*), placed in an iterated Prisoner's Dilemma (IPD) situation, did not cooperate. They did, however, readily cooperate in a simpler mutualistic situation in which there was no temptation to cheat. The highly controlled conditions used by Clements and Stephens have both advantages and disadvantages. The key advantage of their laboratory approach is the ability to create and precisely control game matrices which are, after all, the main causal variables in game theoretical hypotheses. On the negative side, several reviewers (Dugatkin, 1997; Pusey and Packer, 1997; Roberts, 1997) have expressed reservations about the artificiality of these controlled situations. More broadly one might question the generality of these results: do they apply to other situations, and if not what sets the limits of their applicability?

This study represents an attempt to explore these concerns, while maintaining the precise control over game matrices that we see as the central advantage of the laboratory approach. We continue to use blue jays as a model system. In an effort to determine whether we can replicate the results in a different context, we designed a novel feeding apparatus. Figure 2.1 shows our design. At the beginning of each 'play' food was distributed to six bins in view of, but inaccessible to, the players. Each player controlled three of the bins, in the sense that one option shifted the three bins to the left, and another shifted them to the right. When the bins slid to the left or right, the food within them was drawn over openings that distributed the food to one of three destinations (Figure 2.1a). Food in bin number 1 distributed food either to 'self' or to 'other'; food in bin number two distributed food to 'other' or to no one ('trash'); while food in bin number three distributed food either to 'self' or to no one. We could, therefore, control the nature of the game by varying the amounts of food distributed to each bin. To clarify this let A_1, A_2 and A_3 be the amounts in bins 1, 2 and 3 respectively. The design of the feeding apparatus means that subjects must choose between delivering amount A_1 or A_3 to itself, yet if it chooses A_3, it also delivers amounts A_1 and A_2 to its opponent. This creates a game matrix shown in Table 2.1.

Consider, for example, a situation in which $A_1 = 2$, $A_2 = 1$, $A_3 = 0$. If both players choose 'C' each delivers three units to its opponent, but if both choose 'D', they both deliver the two units to themselves. The amount A_2, therefore, represents a 'cooperative premium', that is, the additional value of a cooperative act. On the other hand, if the focal player chooses D when its opponent chooses C, it obtains 5 units, while its opponent gets nothing. This is, of course, the traditional Prisoner's Dilemma game.

This design provides the opportunity to explore several important conceptual issues in cooperation. First, the amount in bin 1 (A_1) represents the classic conflict between selfishness and generosity: should I keep A_1 for myself or give it to another? The amounts in bins 2 & 3 represent two different ways of modifying the value of generosity, by making the generous act more valuable to the recipient (increasing A_2) or more valuable to the actor (increasing A_3). Therefore, animals' choices in this situation give us insight into the importance of generosity vs. selfishness. Also, with this design we directly test the significance of the cooperative premium. By comparing situations with similar payoffs except for the presence (Prisoner's Dilemma) or absence (Defect Only) of the cooperative premium, we examine the value animals place on the cooperative premium. Finally, our novel apparatus allows us to test an 'Opponent Control' matrix that represents an extreme situation in which cooperative action is the only way to obtain food. Because the birds' choices determine their opponents' payoffs and not their own, this treatment permits us to study a case of generosity with minimal direct costs to the donor.

In addition to methodological advances, this study provides different analytical techniques to investigate the presence of higher level strategies such as tit-for-tat and Pavlov (Nowak and Sigmund, 1993). With these new aspects of our study we attempt to expand the external validity (Campbell and Stanley, 1963; Kamil, 1988a,b) of earlier studies, and ask what kinds of manipulations make a difference.

Materials and Methods

Subjects

We used four pairs of blue jays (*Cyanocitta cristata*) of unknown sex and varied age in the experiment (birds 3 & 140, 70 & 85, 4 & 122, 130 & 208). The within-subjects design of this experiment controls for any differences in sex and age. Prior to the experiment, we maintained the jays on a diet of mealworms and Lafeber's cockatiel food, housing them in individual cages (measuring 38×38×61 cm) in a colony of 25. The housing room had an average temperature of 23^{o}C with lights on between 0600-2000 hours. See Clements and Stephens (1995) for further housing information.

Apparatus

We used two operant boxes consisting of two adjoining chambers constructed of galvanized sheet metal (61×124×51 cm, Figure 2.1b). We separated the chambers with transparent plexi-glass partitions. We attached the table apparatus (Figure 2.1a) to both sides of the central partition. Each table had a static acrylic base with six 1 cm holes to which we connected flexible, transparent Tygon tubing (10 mm inner diameter, 13 mm outer diameter). Each tube led to (1) the feeding cup on the same side of the partition, (2) the feeding cup on the other side of the partition (by passing through a hole in the partition), or (3) an inaccessible but visible plexi-glass 'trash bin' at the bottom of the partition (Figure 2.1a). We constructed the top portion of the table from a transparent acrylic 'slide' with three 2 cm holes (bins) that were offset from the six holes in the base. We connected the slide to a cam attached to a motor. One revolution of the motor/cam moved the slide to the right 2.5 cm, back past the center to the left 2.5 cm, stopping back at the center of the table. Tygon tubes (13 mm inner diameter, 16 mm outer diameter) connected three Med Associates 20 mg pellet dispensers to the holes on top of the slide. Transparent plexi-glass partitions separated the jays from the table, motor, tubes, and feeders. This design allowed each bird to dispense food to itself, its partner, or the trash, depending on its choice. Varying the number of pellets dispensed to the bins allowed us to create different payoff matrices.

Each chamber contained three perches (one back and two front perches) with microswitches under the crossbars that activated when the birds occupied the perches. We attached light emitting diodes (LEDs) to the perches (two orange LEDs for the back perches and one either red or green LED for the front perches).

A C++ computer program recorded all inputs (microswitches on perches) and controlled all outputs (LEDs, pellet dispensers, slide motors) via an Alpha Products input/output computer interface system. The program controlled the timing of all aspects of the experimental trials.

General procedure

In this experiment we created a closed economy system in which all of the food the jays received resulted from successfully completing the experimental trials. Therefore, the jays remained in the operant boxes for 23h a day, 7 days a week. They were maintained at 80% of their normal weight (measured daily) by ensuring a minimum of 7 g and a maximum of 10 g of food per day.

At 0600 hours the room lights turned on, and at 0700 hours the computer program initiated the day's trials. The trials repeated until 1100 hours, when we removed the jays from the operant boxes and placed them in their home cages for an hour while we cleaned the operant boxes and replenished fresh water. At 1200 hours we returned the jays to the experimental boxes, and the trials resumed until 1600 hours when the program terminated the trials. Overhead lights extinguished at 2000 hours.

Trials

To initiate a trial, the back perch lights (LEDs) for both subjects illuminated to signal the start of a trial. After both players occupied the back perches, the lights extinguished, and the feeders dispensed pellets into the appropriate table bins. After a 1 sec delay, the lights on both subjects' front perches illuminated. When both players concurrently occupied one of their front perches, the lights extinguished, and both tables simultaneously slid in the direction of the chosen perch (independently for each player). For example, if player

1 occupied the right or 'Cooperate' perch, the slide on that side of the partition slid to the right, so that pellets in bins 1 and 2 went to the other player, and pellets in bin 3 went to its own food cup (Figure 2.1a). If player 2 occupied the left perch, the table slid to the left, delivering the pellets in bin 1 to itself and the pellets in bins 2 and 3 to the trash bin. Distributing the pellets completed a trial and initiated the 45 sec inter-trial interval.

We used forced, or no choice, trials to ensure that the jays experienced the consequences of all possible choice combinations. We randomly assigned 20% of the trials as forced trials, in which we forced both birds to make a pre-determined choice between C and D. We illuminated only one of the two front lights for each of the players and required them to land only on the perch with the illuminated light, thereby forcing them to face a specific choice combination. This ensured that the birds faced all choice combinations, thus reducing the possibility of an arbitrary choice. Since no other signals indicated a change in treatment, forced trials also accelerated the process of learning a new set of payoffs.

Experimental design

This experiment follows a three by three repeated measures design, using payoff-matrix treatment and time block as factors. For the payoff treatments, we subjected the jays to three test treatments and a baseline treatment before each test treatment. Each test treatment lasted for 1700 trials (about 11 days), and the baseline treatment lasted until the jays mutually cooperated on at least 75% of the trials for three consecutive days.

Payoff matrices

We used a 'Cooperate Only' treatment as the baseline treatment. In this treatment, three pellets dropped in bin 3, allowing the jays to receive the pellets if they cooperated and dropping the pellets into the trash if they defected, creating the payoff combination in Table 2.2a. Because the Nash equilibrium (Nash, 1951) is mutual cooperation, we used this procedure to establish cooperative behavior before subjecting pairs to any of the test matrices. Game theoretical solutions are stability solutions, so by establishing cooperative action before a test situation begins, we tested whether cooperation persists in a given test situation, as the game theoretical models predict. This procedure also minimizes any effects that might 'carry-over' from one test matrix to the next.

The test matrices (treatments) included Defect Only, Prisoner's Dilemma, and Opponent Control payoffs (Table 2.2).

1. In the Defect Only treatment, two pellets dropped only in bin 1 ($A_1 = 2$, $A_2 = 0$, $A_3 = 0$), so cooperation dispensed all pellets to the opponent and defection allowed the player to keep all pellets (Table 2.2b). All defection is both the single game and repeated game equilibrium.

2. Our Prisoner's Dilemma treatment was similar to the Defect Only scenario, except one pellet also dropped into bin 2 (i.e. $A_1 = 2$, $A_2 = 1$, $A_3 = 0$), where it was dispensed to the opponent if the player cooperated or fell into the trash bin if the player defected. The single game Nash equilibrium is mutual defection, but tit-for-tat, Pavlov, and all defection have been proposed as stable for repeated games.

3. Finally, in the Opponent Control treatment three pellets dropped into bin 2 ($A_1 = 0$, $A_2 = 3$, $A_3 = 0$) which distributed all pellets to the opponent when cooperating and to the trash bin when defecting (Table 2.2d). In this treatment, a player could not dispense food to itself, but was forced to rely on its partner. The single game Nash equilibrium is all pairs of mixed strategies, and virtually any strategy is stable in repeated games.

We randomized the order of treatment matrices for each pair of birds. In addition, a baseline treatment preceded each test matrix, so each pair experienced a series of treatments such as Cooperate Only → Opponent Control → Cooperate Only → Prisoner's Dilemma → Cooperate Only → Defect Only.

Time block

We divided the total trials per treatment into three blocks of time. We expected a 'time block' effect because it takes time to adjust to a new treatment matrix. Therefore, choice behavior in the later trials provided a better estimate of the jays' preferences.

Data analysis

Using the S-PLUS statistical package we conducted a repeated measures ANOVA using the arcsine, square root transformation (to normalize the data) of the mean proportion of mutual cooperation (CC) as our response variable. We included payoff matrix (Defect Only, Prisoner's Dilemma, Opponent Control) and time block (1-3) as within-pair treatment factors. We then conducted Tukey paired comparisons to contrast treatment differences.

Results

Figure 2.2 gives an overview of the data, showing that defection quickly replaced cooperation in the Prisoner's Dilemma and Defect Only conditions. In contrast, mutual cooperation was maintained at a relatively high level in the Opponent Control treatment. Confirming these observations, a two-factor repeated measures ANOVA (Table 2.3) on the proportion mutual cooperation indicates highly significant treatment effects (ANOVA: $F_{2,6} = 166.09$, $p < 0.0001$) and block effects (ANOVA: $F_{2,6} = 11.75$,

$p = 0.0084$) but no interaction between treatment and block (ANOVA: $F_{4,12} = 1.60$, $p = 0.2387$, Figure 2.3). A Tukey paired comparison on treatments shows no difference between the proportion mutual cooperation in the Prisoner's Dilemma and Defect Only treatments, but the birds cooperated significantly more in the Opponent Control treatment than in the Prisoner's Dilemma and Defect Only treatments (Defect Only: $\bar{X} \pm SE = 0.1609 \pm 0.0354$; Prisoner's Dilemma: $\bar{X} \pm SE = 0.2259 \pm 0.0373$; Opponent Control: $\bar{X} \pm SE = 0.5734 \pm 0.0374$). A paired comparison on block suggests that significantly less cooperation occurred in the last block compared to the first block pooled over all treatments (Block 1: $\bar{X} \pm SE = 0.4511 \pm 0.0463$; Block 2: $\bar{X} \pm SE = 0.3106 \pm 0.0434$; Block 3: $\bar{X} \pm SE = 0.2233 \pm 0.0407$). Due to the 75% mutual cooperation criteria for the Cooperate Only baseline treatment, the birds began all test treatments with a high level of cooperation. Therefore, the block effect suggests that the birds began each treatment cooperating, but quickly defected as they learned the Defect Only and Prisoner's Dilemma payoff structure.

In both Defect Only and Prisoner's Dilemma treatments, the jays cooperated less often than expected by chance (25% is the chance expectation for mutual cooperation, because if both birds choose C 50% of the time, we have $0.5 \times 0.5 = 0.25$) in the last third of the trials (Defect Only: $\bar{X} \pm SE = 0.0646 \pm 0.0295$; one-sample t-test: $\mu = 0.25$, $t = -3.56$, $p = 0.0379$; Prisoner's Dilemma: $\bar{X} \pm SE = 0.0531 \pm 0.0273$; one-sample t-test: $\mu = 0.25$, $t = -5.79$, $p = 0.0103$). The jays cooperated above chance levels during the last third of the Opponent Control treatment ($\bar{X} \pm SE = 0.5428 \pm 0.0610$; one-sample t-test: $\mu = 0.25$, $t = 3.23$, $p = 0.0481$, Figures 2.2 and 2.3).

Strategic analysis

We calculated strategy vectors to explore the finer-scale properties of the blue jay's decision rules (Stephens et al., 1997). These vectors represent the probability of cooperating following a previous payoff. For example, t represents the probability of cooperating in the trial following a payoff of T (player defects, opponent cooperates). Table 2.4 illustrates the theoretical strategy vector for a pair of tit-for-tat or Pavlov strategists. If two players played tit-for-tat, we would expect high t and r values and low p and s values. That is, cooperation should follow previous opponent cooperation (T and R trials). Pavlov predicts the "win-stay, lose-shift" strategy in which players will repeat a rewarding choice and switch after a punishing choice (Kraines and Kraines, 1989; Nowak and Sigmund, 1993). Therefore, we would expect high r and p values and low t and s. The blue jays, however, diverge from both theoretical strategies. In all three treatments the jays showed high r and s values but low t and p values (Table 2.4). Rather than following their opponent's previous choice or shifting choices based on reward/punishment contingencies, our results demonstrate the maintenance of cooperation following cooperation and defection following defection. The jays focused on the short term benefits by reaping the temptation to cheat, T.

Order effects

Because the jays could see each other's choices, the second bird to choose had the advantage of reacting to its opponent's choice, making this a sequential rather than simultaneous game. To examine this phenomenon, we calculated the probability that each choice was made by the second bird after a given choice was made by the first bird using the last third of the data (Table 2.5). In the Defect Only treatment cooperation and defection were equally likely to follow cooperation (Chi-square test: $\chi^2_1 = 0.34$, $p = 0.5588$), but defection was more likely to follow defection (Chi-square test: $\chi^2_1 = 497.3$, $p < 0.0001$). In the Prisoner's Dilemma, defection followed both cooperation and defection (cooperation—Chi-square test: $\chi^2_1 = 59.65$, $p < 0.0001$, defection—Chi-square test: $\chi^2_1 = 956.75$, $p < 0.0001$). We found the opposite in the Opponent Control treatment, in which cooperation followed both cooperation and defection (cooperation—Chi-square test: $\chi^2_1 = 664.51$, $p < 0.0001$, defection—Chi-square test: $\chi^2_1 = 119.15$, $p < 0.0001$).

Time of day

An eight hour work day for the jays provided the potential for satiation. To explore the possibility of satiation influencing cooperation, we used a repeated measures ANOVA to examine the arcsine, square root transformed proportion of cooperative choices divided into eight, hour-long intervals per day. There was a significant effect of time of day (ANOVA: $F_{7,21} = 5.33$, $p = 0.0419$) with more cooperation in the last hour, but there was no interaction between time of day and treatment (ANOVA: $F_{14,38} = 1.44$, $p = 0.3631$).

Discussion

Our experiment replicates and extends the findings of Clements and Stephens (1995) by suggesting that the blue jays do not cooperate in the Prisoner's Dilemma despite ample opportunity. In addition, we show that the jays perform no differently than when no premium for cooperating exists (Defect Only treatment). Nevertheless, when cooperation benefits the jays (Cooperate Only treatment), they consistently choose the C response. In addition, the jays do not use tit-for-tat or Pavlov strategies in any of the treatments. They tend to repeat previous choices rather than change their behavior. Any reciprocity that may occur, must occur over a longer time scale than individual trials.

New methodology

Our novel apparatus replicates Clements and Stephens (1995) in a different context. Here information about the contingencies is more visible and accessible to the blue jays. How they attend to these contingencies is a cognitive question beyond the scope of this experiment. Nevertheless, the manner in which subjects obtain food is quite different. Therefore, if the inability to see the consequences was a problem in the Clements and Stephens (1995) study, then we might expect different results using this more elaborate apparatus.

Our study also differs from Clements and Stephens's earlier work, because it includes two additional test matrices—the Defect Only and Opponent Control matrices. We selected these test situations to address specific game theoretical issues, and we discuss the implications of our results for each situation below.

Defect Only treatment

The Defect Only treatment is important because it provides a temptation to defect without a cooperative premium (Table 2.2b): T=4, R=2, P=2,S=0. Mutual defection is the Nash equilibrium. Both the Prisoner's Dilemma and Defect Only treatments involve a temptation to defect; however, the Prisoner's Dilemma also includes a cooperative premium (Table 2.2c): T=5, R=3, P=2, S=0. Recall that the cooperative premium is simply the additional value of cooperation; in our case, one extra food pellet. Therefore, the single-game Nash equilibrium for the Prisoner's Dilemma is again defection; however, the cooperative premium has made mutual cooperation more profitable than mutual defection.

This additional unit of benefit has profound theoretical effects on choice behavior. Many theorists suggest that the presence of the cooperative premium can allow higher level strategies (tit-for-tat, Pavlov, etc.) to permit stable cooperation (Axelrod and

Hamilton, 1981; Nowak and Sigmund, 1993; Dugatkin, 1997). They would predict stable defection in our Defect Only treatment and stable cooperation in our Prisoner's Dilemma treatment. Our laboratory investigation of the treatments, however, indicates that the animals do not consider these two treatments to be fundamentally different. That is, despite its theoretical significance, the cooperative premium is not functionally important in our experiments. Similar experiments on rats and pigeons also show very low levels of cooperation in these controlled-payoff games (Flood et al., 1983; Gardner et al., 1984; Green et al., 1995). In fact, the generality of this phenomenon is evident by extremely low levels of cooperation in humans, one of the most cooperative animals (Andreoni and Miller, 1993; Baker and Rachlin, 2001; Rilling et al., 2002).

One of the primary reasons that animals may ignore the cooperative premium is because they discount the future rewards of playing the game and focus on immediate benefits. Theoretical and empirical evidence reveals that animals may prefer an immediate reward despite higher long term payoffs for a delayed reward (McDiarmid and Rilling, 1965; Benson and Stephens, 1996). This preference may be caused by discounting the value of future rewards that may not materialize (Kagel et al., 1986; McNamara and Houston, 1987; Stephens et al., 1995; Stephens, 2000), although this discounting effect can be overcome (Stephens et al., 2002). If the jays do discount steeply, they may ignore future interactions and play each trial like a one-shot game.

Opponent Control treatment

The Opponent Control treatment offers an interesting conflict for the jays because the players control the payoffs to their partner rather than to themselves. Reboreda and Kacelnik (1993) conducted experiments on starlings (*Sturnus vulgaris*) using a similar matrix (T=food, R=not available, P=0, S=0). In their study, however, the birds were only rewarded with food when the opponent cooperated and the player defected. Therefore, a cost to cooperating existed because cooperators never received food. The only way to gain food was to defect in the presence of cooperation. For both birds to accumulate food over time, they had to alternately take the 'temptation to cheat'. Yet, cooperation occurred in only 26% of the last third of their trials.

Cheap generosity and tit-for-tat

Our Opponent Control treatment differs from the Reboreda and Kacelnik matrix because both individuals are allowed to cooperate. Also, generosity is cheap because players do not pay a cost for cooperating (there is no temptation to defect), but they can increase their opponents' fitness. In the absence of costs, generosity should be more likely. We do find that the jays cooperate more frequently in the Opponent Control treatment than in the Prisoner's Dilemma and Defect Only treatments. Whereas mutual defection is the Nash equilibrium in the Defect Only and Prisoner's Dilemma treatments, in the Opponent Control treatment the equilibrium is all mixed strategies. Nash actually described a similar matrix in the original formulation of his equilibrium, describing the solution as "all pairs of mixed strategies" (Nash, 1951, pp. 291). This means that there is a mixed ESS (Maynard Smith, 1982) in which all ratios of cooperation to defection are equilibria—no frequency dependence exists. Therefore, initial probabilities of cooperation will remain neutrally stable. For example, individuals that already cooperate with kin may maintain cooperation with non-kin because of the initial bias. Consequently, our results confirm this mixed strategy because individuals demonstrate about 72% cooperation. The high levels of cooperation in this treatment could be attributed to carry-over from the initial high levels of cooperation in the preceding Cooperate Only treatment. The strong effect of initial conditions suggests further experiments in which either Cooperate Only or Defect Only treatments precede the Opponent Control treatment to determine the effect of initially high or low levels of cooperation. We would predict lower levels of cooperation following the Defect Only treatment.

Another possible explanation for the elevated levels of cooperation depends on psychological constraints on animal decision-making. Standard animal learning models propose an important psychological difference between zero and non-zero payoffs. Animals avoid making choices resulting in no reward when the alternate choice yields any positive reward. This inherent motivation to avoid zero choices could inflate the levels of cooperation in our Opponent Control treatment. Again, we predict that a study comparing the current Opponent Control treatment with one in which we substitute one pellet for the zero pellet payoffs would show a decrease in overall cooperation in the non-zero treatment. Stephens and Clements (1998) presented jays with a similar matrix (T=5, R=5, P=1, S=1) and found lower levels of cooperation.

Pavlov

Nowak and Sigmund (1993) advocated a win-stay/lose shift strategy called Pavlov (Kraines and Kraines, 1989) in which the player repeats rewarding choices but switches choices following punishing results. Nowak and Sigmund suggest that Pavlov provides a strategy that outcompetes tit-for-tat because it responds better to mistakes and is resistant to obligate cooperators. In addition, they offer this strategy as a psychologically sound strategy founded on the law of effect (Thorndike, 1911). In the Prisoner's Dilemma, Nowak and Sigmund's Pavlov strategy considers T and R as 'wins' and P and S as 'losses'. Our opponent control situation represents a strong test of the Pavlov strategy, because T and R produce identical wins, while P and S produce unambiguous and identical losses (no food).

Consequently, if Pavlov is a viable mechanism of cooperation, it should be employed in our Opponent Control treatment because the players are rewarded for T and R choices and punished for P and S choices. Table 2.4 illustrates the theoretical strategy vector for a Pavlov strategist. Examining the strategy vector for our Prisoner's Dilemma and Opponent Control treatments indicates low probabilities of cooperating following T and high probabilities of cooperating following S. These results agree with Clements and Stephens' critique of the Pavlov strategy, in questioning its importance, even in this situation where it is most likely to apply.

Behavioral inertia and order effects

Despite the absence of tit-for-tat in this experiment, the jays did tend to maintain similar patterns of cooperation and defection over repeated trials. The strategy vectors in Table 2.4 illustrate this behavioral inertia because the probabilities of following cooperation with cooperation (r and s) and defection with defection ($1-\mathsf{t}$ and $1-\mathsf{p}$) are high in most treatments (also seen in humans: Rilling et al., 2002).

Our experimental design violates assumptions of game theoretical models for the sake of realism by allowing individuals to witness their opponent's decisions as they make their own. The second bird to make a decision can see its opponent's choice and, therefore, react accordingly. We will call the decision made by the first bird to choose 'primary' cooperation or defection and the choice by the second bird 'secondary' cooperation or defection. The second bird's advantage could inflate the levels of mutual defection in the Prisoner's Dilemma by allowing a bird to avoid the Sucker's payoff (S) when its opponent has already chosen to defect. Our data agree because the second birds defect in 86% of the choices (Table 2.5). Also, this advantage allows a player to reap the Temptation to cheat (T) when its opponent has already chosen to cooperate. Our results concur in that after primary cooperation, secondary defection occurs 69% of the time (Table 2.5).

The probabilities of repeating previous behavioral choices (r and s) are high despite potential costs involved. The most costly form of this 'behavioral inertia' occurs when one player repeatedly cooperates while the other defects, and the cooperator receives no reward (S). This inertia could be caused by a psychological bias that favors repeating rather than switching behaviors. Motivational state could also have influenced the behavioral inertia. If individuals were no longer food motivated, they may not try to maximize food intake and, therefore, they might choose arbitrarily or repeat their previous move. Time of day (a proxy for satiation) influences cooperation, resulting in the jays cooperating more the last hour of the day than in the morning, particularly in the Prisoner's Dilemma treatment (Figure 2.4). This result contrasts with Axelrod and Hamilton's (1981) contention that cooperation should unravel given a finite number of games. While motivation may play a small role in our results, the cause of the time of day and inertia effects remains unclear.

Species justification

We feel that blue jays are an appropriate model species for this type of study for a number of reasons. First, both Trivers (1971) and Axelrod and Hamilton (1981) made broad claims about the generality of reciprocity biological systems. These two seminal papers apply reciprocity to bacteria, cancer cells, cleaner fish symbioses, multi-species bird flocks, and of course humans.

Second, much work has explored how equilibrium behavior can be learned in game theoretical situations (Harley, 1981; Maynard Smith, 1982; Fudenberg and Levine, 1998; Stephens and Clements, 1998). That is, although many animals may not meet some of the assumptions of game theory such as rationality, they may learn the equilibrium strategy through repetition. One of the most recent developments in the Prisoner's Dilemma explicitly emphasizes the role of learning in cooperation. The Pavlov or 'win-stay/lose-shift' strategy (Kraines and Kraines, 1989; Nowak and Sigmund, 1993) proposes that simple instrumental learning could outcompete tit-for-tat in the iterated Prisoner's Dilemma. Consequently, even though animals may not be specifically adapted to respond to a Prisoner's Dilemma, they may be able to respond to the contingencies of the game and act accordingly via the law of effect (Clements and Stephens, 1995).

Finally, although blue jays probably do not experience these exact games in the wild, they may have ample opportunities to face Prisoner's Dilemma-like situations in nature. Little is known about the social behavior of blue jays, but the apparent social unit is the pair, although the pairs often join small, stable flocks (Racine and Thompson, 1983; Tarvin and Woolfenden, 1999). Possible cooperative behaviors include predator mobbing (Fitch, 1958; Taylor, 1972; Cohen, 1976; Tarvin and Woolfenden, 1999), biparental care (Laine, 1981, 1983; Tarvin and Woolfenden, 1999), and cooperative breeding (Gross, 1982; Cox, 1984; Kuenning, 1994). In fact, cooperative breeding is so common in the corvids that some researchers suggest that it is the ancestral condition for the family (Arnold and Owens, 1998, 1999; Baglione et al., 2002). These and other social interactions suggest that blue jays may very well be adapted to cooperative and even Prisoner's Dilemma-like situations.

Conclusion

These results reinforce the conclusions of others, who have argued that the role of the Prisoner's Dilemma's as the basic paradigm of non-kin cooperation should be reevaluated despite the wealth of theoretical interest (Dugatkin et al., 1992; Connor, 1995; Pusey and Packer, 1997; Stevens and Stephens, 2002). This study improved on the designed used by Clements and Stephens (1995), but we still find no evidence of stable cooperation in a foraging situation using a Prisoner's Dilemma game matrix. Instead, we demonstrate stable defection levels that do not differ from a game theoretical matrix in which defection is the Nash equilibrium. Additionally, we find no evidence of tit-for-tat or Pavlov strategies occurring in any of our treatments. These findings suggest that animals may emphasize the immediate economic benefits of decision making rather than long-term benefits. The dearth of empirical evidence for reciprocal altruism indicates that it may be too complicated of an explanation for the evolution of cooperation. Reciprocal altruism requires complex cognitive skills (self-control, mental record keeping, etc.) that many animals may not possess. Perhaps we should focus on more parsimonious explanations of cooperation such as kin selection, mutualism, and group augmentation before resorting to complex ones. In addition, we should investigate alternative models of cooperation such as the Opponent Control model presented here.

Acknowledgments

We would like to thank Ben Kerr, Alison Pearce, and Mike Wilson for reviewing the manuscript; the Packer/Pusey/Stephens behavior group for stimulating discussions and helpful criticism of the project; and Dack Anderson, Jolene Ruf, Claire Leung, and Geoff Harms for assistance in completing the project. This project was funded with support from the National Science Foundation (IBN-9896102 to D.W.S.) and the Graduate School at the University of Minnesota. This project was approved by the Institutional Animal Care and Use Committee at the University of Minnesota (Animal Subjects Code 0008A614181).

References

Andreoni, J. A. and Miller, J. H. 1993. Rational cooperation in the finitely repeated Prisoner's Dilemma: experimental evidence. *Economic Journal* 103:570–85.

Arnold, K. E. and Owens, I. P. F. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London, Series B* 265:739–745.

Arnold, K. E. and Owens, I. P. F. 1999. Cooperative breeding in birds: the role of ecology. *Behavioral Ecology* 10:465–471.

Axelrod, R. and Hamilton, W. D. 1981. The evolution of cooperation. *Science* 211:1390–1396.

Baglione, V., Canestrari, D., Marcos, J. M., Griesser, M., and Ekman, J. 2002. History, environment and social behaviour: experimentally induced cooperative breeding in the carrion crow. *Proceedings of the Royal Society of London, Series B* 269:1247–1251.

Baker, F. and Rachlin, H. 2001. Probability of reciprocation in repeated prisoner's dilemma games. *Journal of Behavioral Decision Making* 14:51–67.

Benson, K. E. and Stephens, D. W. 1996. Interruptions, tradeoffs, and temporal discounting. *American Zoologist* 36:506–517.

Campbell, D. T. and Stanley, J. C. 1963. Experimental and Quasiexperimental Designs for Research. Rand McNally, Chicago.

Clements, K. C. and Stephens, D. W. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour* 50:527–535.

Cohen, S. M. 1976. Blue Jay Vocal Behavior. Ph.D. dissertation, University of Michigan.

Connor, R. C. 1995. Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends in Ecology and Evolution* 10:84–86.

Cox, J. A. 1984. Distribution, Habitat, and Social Organization of the Florida Scrub Jay, with a Discussion of the Evolution of Cooperative Breeding in New World Jays. Ph.D. dissertation, University of Florida.

Dugatkin, L. A. 1997. Cooperation Among Animals: An Evolutionary Perspective. Oxford University Press, New York.

Dugatkin, L. A., Mesterton-Gibbons, M., and Houston, A. I. 1992. Beyond the Prisoner's Dilemma: toward models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology and Evolution* 7:202–205.

Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the natural history reservation. *University of Kansas Publications of the Museum of Natural History* 11:63–326.

Flood, M., Lendenmann, K., and Rapoport, A. 1983. 2x2 games played by rats: different delays of reinforcement as payoffs. *Behavioral Science* 28:65–78.

Fudenberg, D. and Levine, D. K. 1998. Theory of Learning in Games. MIT Press, Cambridge, Mass.

Gardner, R. M., Corbin, T. L., Beltramo, J. S., and Nickell, G. S. 1984. The prisoner's dilemma game and cooperation in the rat. *Psychological Reports* 55:687–696.

Green, L., Price, P. C., and Hamburger, M. E. 1995. Prisoner's Dilemma and the pigeon: control by immediate consequences. *Journal of the Experimental Analysis of Behavior* 64:1–17.

Gross, D. A. 1982. Residential Status and Occurrence of Helpers at the Nest in the Blue Jay (*Cyanocitta cristata* Linnaeus: Corvidae) near Bloomsburg, Pennsylvania. M.S. thesis, Bloomsburg State College.

Harley, C. B. 1981. Learning and the evolutionarily stable strategy. *Journal of Theoretical Biology* 89:611–633.

Kagel, J. H., Green, L., and Caraco, T. 1986. When foragers discount the future: constraint or adaptation? *Animal Behaviour* 34:271–283.

KAMIL, A. C. 1988a. Experimental design in ornithology. *In* R. F. Johnston (ed.), Current Ornithology, vol. 5. Plenum Press, New York. pp. 313–346.

KAMIL, A. C. 1988b. A synthetic approach to the study of animal intelligence. *In* D. L. Leger (ed.), Nebraska Symposium on Motivation, vol. 35. University of Nebraska Press, Lincoln. pp. 257–308.

KRAINES, D. AND KRAINES, V. 1989. Pavlov and the prisoner's dilemma. *Theory and Decision* 26:47–79.

KUENNING, R. R. 1994. Observations on Blue Jay cooperative breeding May through July 1993. *Colorado Field Ornithologists Journal* 28:29–33.

LAINE, H. 1981. Male participation in incubation and brooding in the blue jay. *Auk* 98:622–623.

LAINE, H. 1983. Parental chores distribution in the monogamous blue jay. *American Zoologist* 23:930.

MAYNARD SMITH, J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

MCDIARMID, C. G. AND RILLING, M. E. 1965. Reinforcement delay and reinforcement rate as determinants of schedule preference. *Psychonomic Science* 2:195–196.

MCNAMARA, J. M. AND HOUSTON, A. I. 1987. A general framework for understanding the effects of variability and interruptions on foraging behaviour. *Acta Biotheoretica* 36:3–22.

NASH, J. 1951. Non-cooperative games. *Annals of Mathematics* 54:286–295.

NOWAK, M. A. AND SIGMUND, K. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* 364:56–58.

PUSEY, A. E. AND PACKER, C. 1997. The ecology of relationships. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology: An Evolutionary Approach, 4th ed. Blackwell Science, Oxford. pp. 254–283.

RACINE, R. N. AND THOMPSON, N. S. 1983. Social organization of wintering blue jays. *Behaviour* 87:237–255.

REBOREDA, J. C. AND KACELNIK, A. 1993. The role of autoshaping in cooperative two-player games between starlings. *Journal of the Experimental Analysis of Behavior* 60:67–83.

RILLING, J., GUTMAN, D., ZEH, T., PAGNONI, G., BERNS, G., AND KILTS, C. 2002. A neural basis for social cooperation. *Neuron* 35:395–405.

ROBERTS, G. 1997. Testing mutualism: a commentary on Clements & Stephens. *Animal Behaviour* 53:1361–1362.

STEPHENS, D. W. 2000. Cumulative benefit games: achieving cooperation when players discount the future. *Journal of Theoretical Biology* 205:1–16.

STEPHENS, D. W., ANDERSON, J. P., AND BENSON, K. E. 1997. On the spurious occurrence of tit for tat in pairs of predator-approaching fish. *Animal Behaviour* 53:113–131.

STEPHENS, D. W. AND CLEMENTS, K. C. 1998. Game theory and learning. *In* L. A. Dugatkin and H. K. Reeve (eds.), Game Theory and Animal Behavior. Oxford University Press, Oxford. pp. 239–260.

Stephens, D. W., McLinn, C. M., and Stevens, J. R. 2002. Discounting and reciprocity in an Iterated Prisoner's Dilemma. *Science* 298:2216–2218.

Stephens, D. W., Nishimura, K., and Toyer, K. B. 1995. Error and discounting in the Iterated Prisoner's Dilemma. *Journal of Theoretical Biology* 176:457–469.

Stevens, J. R. and Stephens, D. W. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology* 13:393–400.

Tarvin, K. A. and Woolfenden, G. E. 1999. Blue Jay (*Cyannocitta cristata*). *In* A. Poole and F. Gill (eds.), The Birds of North America, vol. 469. The Birds of North America, Inc., Philadelphia. pp. 1–32.

Taylor, W. K. 1972. Mobbing of a Fish crow by passerines. *Wilson Bulletin* 84:98.

Thorndike, E. L. 1911. Animal Intelligence. Macmillan, New York.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Table 2.1: Payoffs to focal player resulting from opponent's choice

		Opponent			
		C (slide table right)		D (slide table left)	
Focal player	C	From Self:	A_3	From Self:	A_3
		From Other:	$A_1 + A_2$	From Other:	0
		Total:	$A_1 + A_2 + A_3$	**Total:**	A_3
	D	From Self:	A_1	From Self:	A_1
		From Other:	$A_1 + A_2$	From Other:	0
		Total:	$2A_1 + A_2$	**Total:**	A_1

Table 2.2: Payoff matrices used as treatment levels (includes number of pellets in each bin of table apparatus)

(a) Cooperate Only

	Cooperate	Defect	$A_1=0$
Cooperate	$\mathsf{R}=3$	$\mathsf{S}=3$	$A_2=0$
Defect	$\mathsf{T}=0$	$\mathsf{P}=0$	$A_3=3$

(b) Defect Only

	Cooperate	Defect	$A_1=2$
Cooperate	$\mathsf{R}=2$	$\mathsf{S}=0$	$A_2=0$
Defect	$\mathsf{T}=4$	$\mathsf{P}=2$	$A_3=0$

(c) Prisoner's Dilemma

	Cooperate	Defect	$A_1=2$
Cooperate	$\mathsf{R}=3$	$\mathsf{S}=0$	$A_2=1$
Defect	$\mathsf{T}=5$	$\mathsf{P}=2$	$A_3=0$

(d) Opponent Control

	Cooperate	Defect	$A_1=0$
Cooperate	$\mathsf{R}=3$	$\mathsf{S}=0$	$A_2=3$
Defect	$\mathsf{T}=3$	$\mathsf{P}=0$	$A_3=0$

Table 2.3: Analysis of variance table for arcsine, square root transformed proportion mutual cooperation as a function of payoff-matrix treatment and time block

Source of variation	*df*	*Mean Square*	*F*	*p*
Payoff-matrix	2	0.7063	166.09	5.6×10^{-6}
Error(Pair × matrix)	6	0.0043		
Time block	2	0.2552	11.75	0.0084
Error (Pair × block)	6	0.0217		
Matrix x block	4	0.0492	1.60	NS
Error (Pair × matrix × block)	12	0.0309		

Table 2.4: Transition vectors describing probability of cooperating following previous payoffs for tit-for-tat and Pavlov (theoretical predictions) and Defect Only, Prisoner's Dilemma, and Opponent Control (observed data)

	t	r	p	s
Tit-for-tat	1	1	0	0
Pavlov	0	1	1	0
Defect Only	0.204	0.863	0.084	0.582
Prisoner's Dilemma	0.231	0.809	0.118	0.670
Opponent Control	0.313	0.879	0.392	0.825

Table 2.5: Probabilities and number of times that the second bird to occupy a perch copies the choice the first bird made (using last third of data)

		Defect Only		Prisoner's Dilemma		Opponent Control	
First Choice	Second Choice	No.	Prob.	No.	Prob.	No.	Prob.
C	C	123	0.519	126	0.309	1156	0.850
C	D	114	0.481	282	0.691	205	0.150
D	C	513	0.253	263	0.141	666	0.734
D	D	1518	0.727	1597	0.859	241	0.266

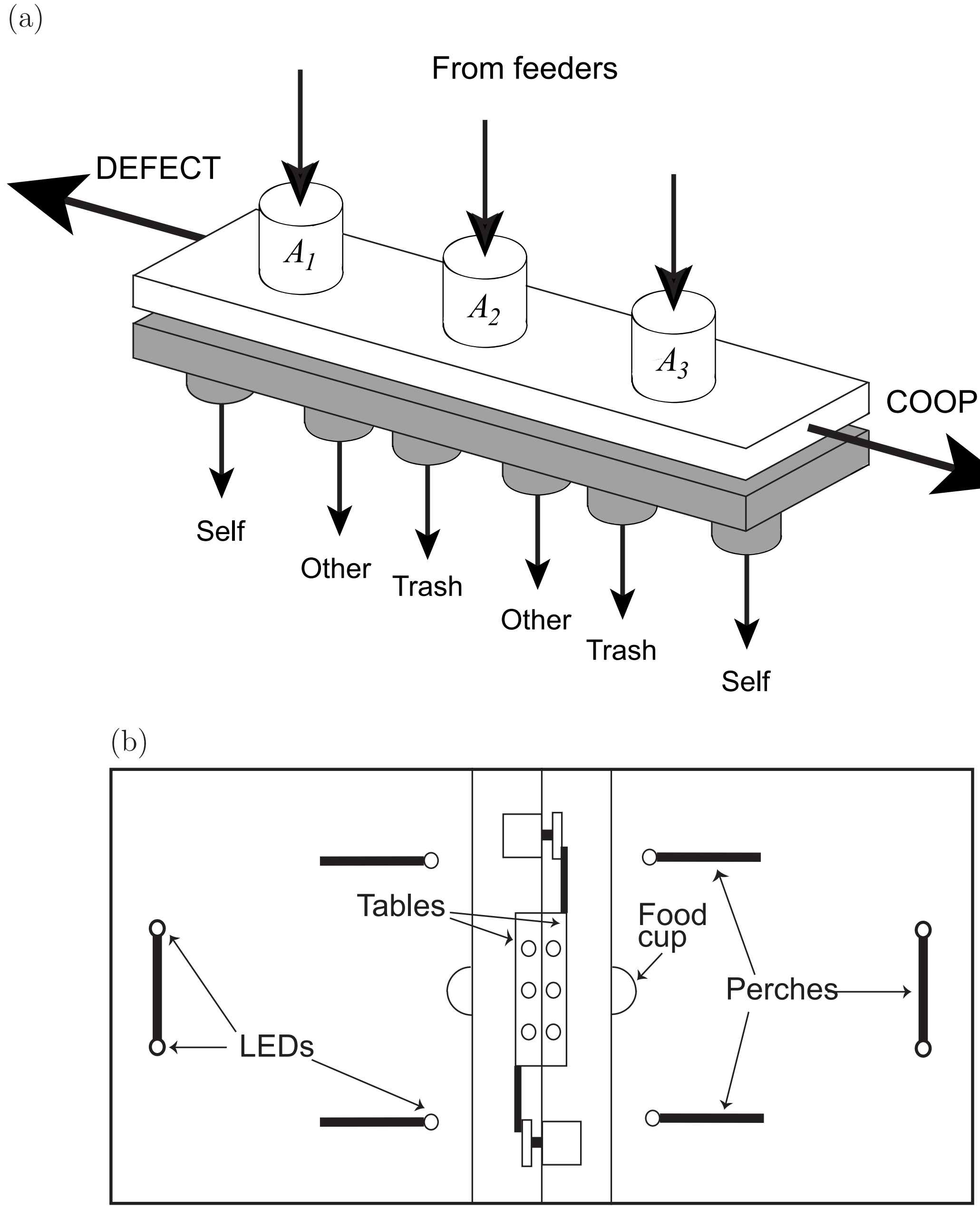


Figure 2.1: (a) Diagram of table apparatus. Pellets from three feeders drop into the three transparent food bins. Depending on which perch the blue jay occupied, the top piece slides to the right or left (lower, dark piece remains stationary), dropping the pellets into transparent tubes that lead to subject's own food cup (self), the opponent's food cup (other), or an inaccessible trash bin (trash). (b) Diagram of operant conditioning chamber (top view). We placed one jay on each side of the box that was separated by a transparent partition.

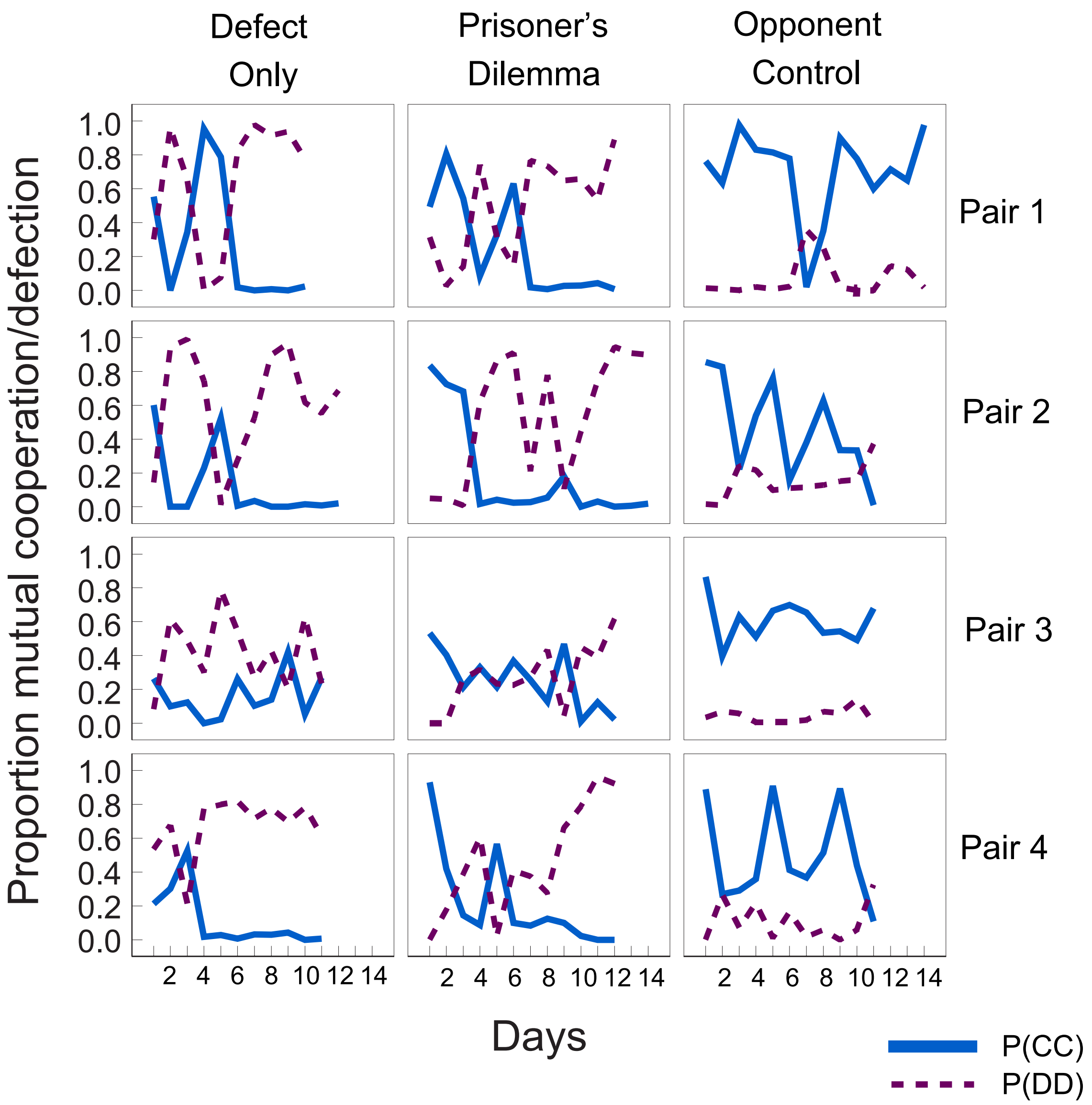


Figure 2.2: Graph of each pair's proportion mutual cooperation (CC) and mutual defection (DD) per day as a function of treatment matrix (▬ mutual cooperation, ▬ ▬ ▬ ▬ mutual defection). Stable mutual defection occurs in Defect Only and Prisoner's Dilemma treatments, where as the Opponent Control treatment indicates higher but unstable levels of mutual cooperation.

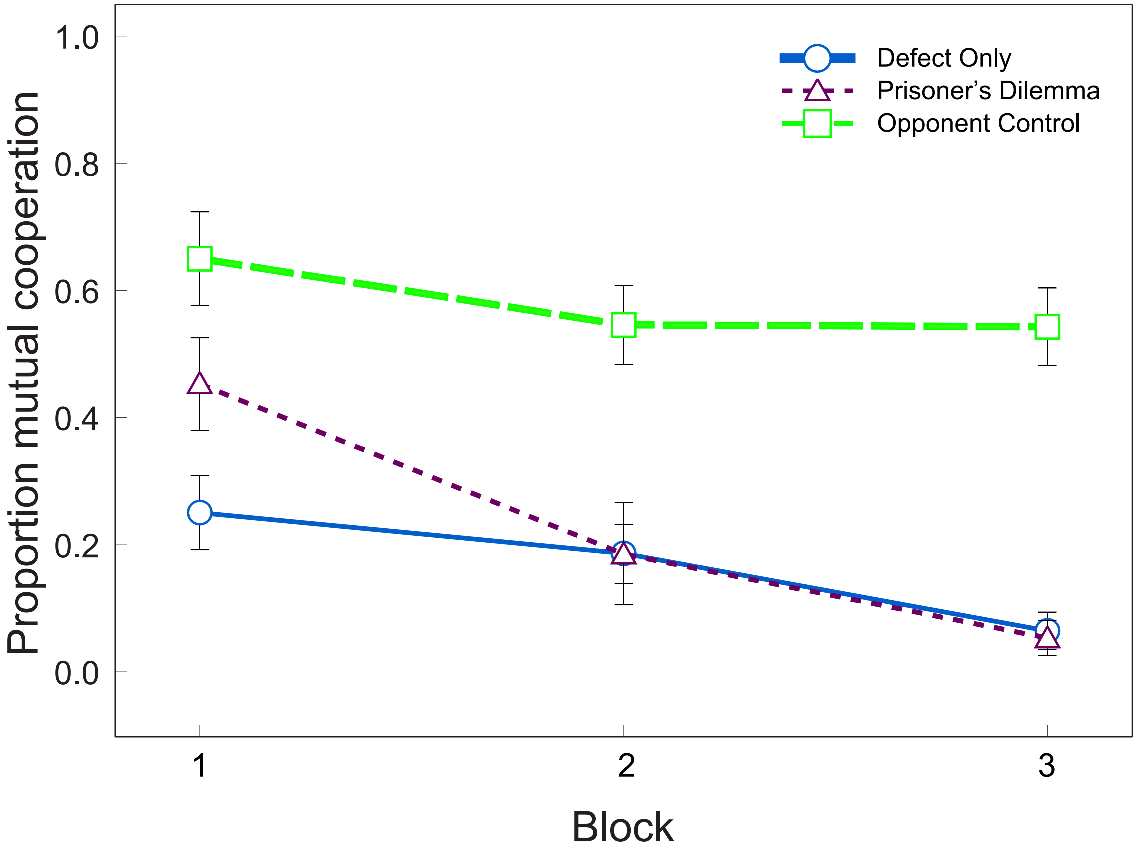


Figure 2.3: Graph of mean proportion mutual cooperation (CC) pooled over all pairs but separated by payoff-matrix treatment and time block (error bars represent standard error; ▪▪▪△▪▪▪ Prisoner's Dilemma, —○— Defect Only, — —□— — Opponent Control). In both Defect Only and Prisoner's Dilemma treatments, the jays mutually cooperate significantly less often than by chance in the last third of the trials. In the Opponent Control treatment, they cooperate more often than by chance (25%).

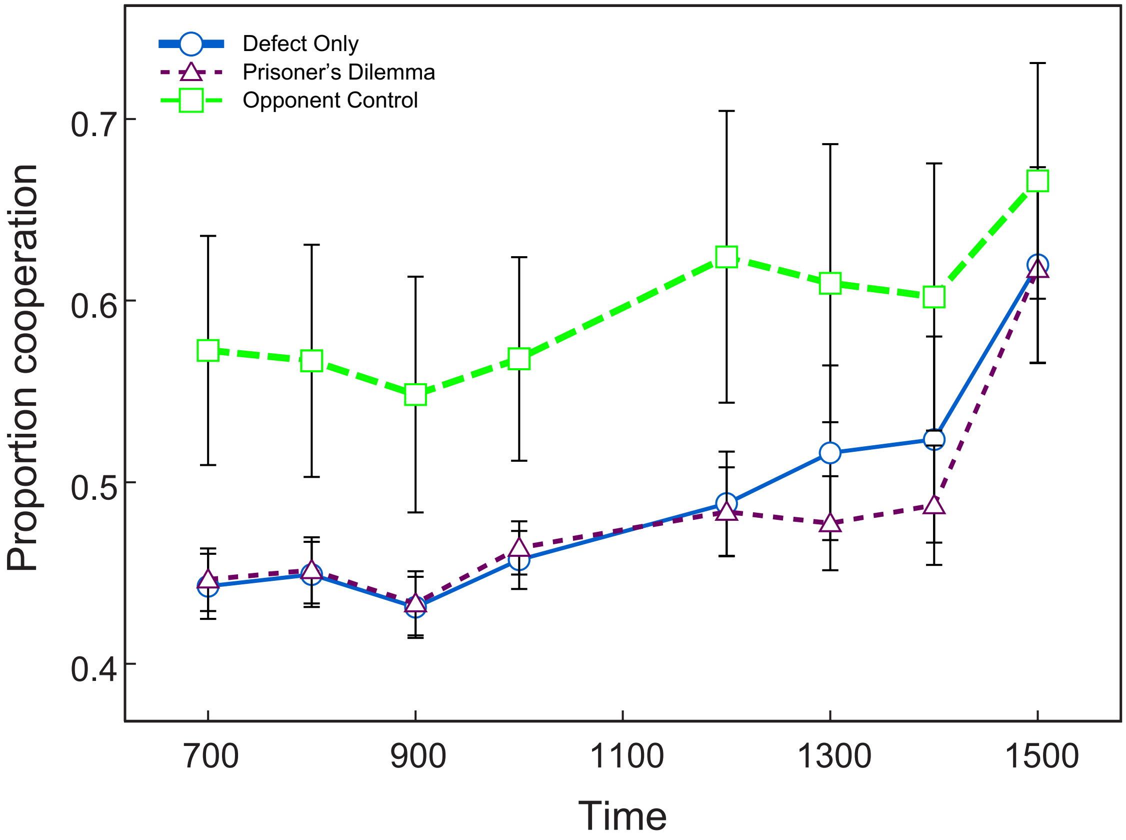


Figure 2.4: Graph of mean proportion individual cooperation (C) pooled over all birds as a function of time of day and treatment matrix (- - -△- - - Prisoner's Dilemma, —○— Defect Only, — —□— — Opponent Control). The jays cooperated significantly more in the last hour of the day than in the morning hours.

Chapter 3

Food sharing: a model of manipulation by harassment[1]

Abstract

Most analyses of food sharing behavior invoke complex explanations such as indirect and delayed benefits for sharing via kin selection and reciprocal altruism. However, food sharing can be a more general phenomenon accounted for by more parsimonious, mutualistic explanations. We propose a game theoretical model of a general sharing situation in which food owners share because it is in their own self-interest—they avoid high costs associated with beggar harassment. When beggars harass, owners may benefit from sharing part of the food if their consumption rate is low relative to the rate of cost accrual. Our model predicts that harassment can be a profitable strategy for beggars if they reap some direct benefits from harassing other than shared food (such as picking up scraps). Therefore, beggars may manipulate the owner's fitness payoffs in such a way as to make sharing mutualistic.

---

[1] This chapter has been previously published as Stevens, J.R. & Stephens, D.W. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology* 13(3):393-400. Please see Appendix for a letter of permission from the publisher. ©Oxford University Press

Red colobus monkeys (*Colobus badius*) are an important and desirable source of protein for chimpanzees (*Pan troglodytes*: Goodall, 1986). A monkey kill attracts beggars that sidle up to the carcass owner, extending their hands, vocalizing, and sometimes grabbing a scrap of meat. In some situations, the carcass owner may share with the beggar, breaking off a piece of meat and handing it to a beggar. Why would the owner give away food that it could consume?

Food sharing, defined here as joint use of a monopolizable food source, can be as active as this chimpanzee example or as passive as a lioness allowing another lioness to feed on her gazelle carcass. Either way, sharing appears to exemplify animal altruism because one individual accepts a fitness cost while another receives a fitness benefit. Although sharing may be altruistic at the time of the sharing event, mechanisms such as kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971) may provide indirect or delayed benefits to the sharer (de Waal, 1989; Perry and Rose, 1994; Mitani and Watts, 2001). In the case of reciprocal altruism, the food is recouped in the future; thereby making sharing altruistic in the short term but selfish in the long term. The complicated cognitive machinery necessary for reciprocal altruism and the presence of relatives necessary for kin selection, make these explanations limited in the contexts in which they apply. If, however, sharing leads to an immediate gain for the owner, the situation becomes much more general, and the more complex, long term accounts are unnecessary. Applying resource defense theory (Brown, 1964; Ydenberg et al., 1986) to our general concept of sharing allows us to consider unexplored explanations of sharing: non-food owners may harass or interfere with the owner's feeding, thereby making it uneconomical to defend the food. In our chimpanzee example, a beggar may harass the owner for food by screaming, grabbing at the carcass, or stealing the entire carcass. Often the owner defends its carcass, thus risking injury and incurring energetic costs, opportunity costs of slowing feeding rate, and other costs such as attracting more beggars. The beggar faces similar but probably reduced costs of its own when harassing. Therefore, the beggar can influence the net payoffs to the owner by inflicting or withholding the costs of harassment. If the costs of harassment are large, sharing might yield a higher net benefit to the owner than defending. If the beggar alters the owner's net benefits enough to change the owner's optimal strategy, the beggar has manipulated the payoffs in a way which makes sharing in the owner's immediate self-interest (i.e., sharing becomes mutualistic). This 'manipulative mutualism' may occur commonly in situations in which an actor's behavior manipulates the net payoffs for another individual's cooperative behavior, making cooperation mutualistic rather than altruistic.

Harassment is a particularly interesting factor that may influence sharing across many situations and taxa because the beggar's actions rather than extrinsic forces (such as patch profitability or travel time) determine the owner's payoffs and optimal decision. To analyze the effect of harassment on food sharing explicitly, we consider an asymmetric game theoretical model. This model is one of only a few models of food sharing and, more importantly, one of the first to analyze the potential immediate fitness benefits associated with food sharing. This model examines the circumstances under which harassment and sharing should occur as well as optimal amounts of harassment and sharing.

Model

Elements of the sharing/harassment game

Consider two animals: a resource owner, who possesses a valuable food item of size A (for amount), and a beggar, who has nothing but is aware of the owner's food item. Both individuals may forage elsewhere, but this food item offers a much more valuable fitness benefit per unit time. The owner may choose to share a portion of its food, say

A_s (for amount shared). The beggar can choose to harass the owner or leave him alone. We express the beggar's harassment intensity as a rate c (e.g., measured in calories per second). If the beggar harasses the owner for time t, this costs the beggar ct, and it costs the owner γct (where γ represents a conversion factor that captures how the beggar's harassment affects the owner). We assume that the beggar harasses at intensity c when it is not busy eating; that is, while the beggar consumes shared food, it does not or cannot harass.

Consumption and time available for harassment

We base our model on time in the sense that we calculate the costs and benefits in terms of the time engaged in various activities and corresponding rates of expenditure during these activities. We assume that both players consume food at rate r, so a single animal consuming the entire resource (amount A) will spend time $\frac{A}{r}$ eating. Next, we express the time available for harassment (T_h) in the form

$$T_h = \frac{A}{r}\pi(p) \tag{1}$$

where p represents the proportion of A that the owner shares (i.e., $p = \frac{A_s}{A}$). The function $\pi(p)$ gives the proportion of the maximum consumption time ($\frac{A}{r}$) that is available for harassment. If the owner shares nothing, the beggar has the entire time available for harassment, so we expect that $\pi(0) = 1$. Similarly, if the owner gave everything away, the beggar would have no time available to harass, so we expect that $\pi(1) = 0$. More generally, we expect that the time available for harassment will decrease as the proportion shared increases.

In this game, then, the owner influences the cost and duration of harassment by controlling A_s, while the beggar influences the cost of harassment by controlling the harassment intensity c.

The simplest game

Using these assumptions, we can write down the benefits to the owner (B_o) as a function of the proportion of A shared (denoted by p) and intensity of harassment c:

$$\begin{aligned} B_o(p,c) &= A - pA - \frac{c\gamma A}{r}\pi(p) \\ &= A\left[1 - p - \frac{c\gamma}{r}\pi(p)\right] \end{aligned} \tag{2}$$

The benefits obtained by the beggar B_b also depend on the proportion shared and the intensity of harassment

$$\begin{aligned} B_b(p,c) &= pA - \frac{cA}{r}\pi(p) \\ &= A\left[p - \frac{c}{r}\pi(p)\right] \end{aligned} \tag{3}$$

In the next step in finding a solution to the game, we ask how the owner's choice of p affects the beggar's optimal c and vice-versa.

No share/No harass

The simple structure of $B_b(p,c)$ leads us to a simple conclusion. 'No sharing' ($p = 0$) and 'No harassment' ($c = 0$) is the only Nash equilibrium of the game as presently constituted (a strong Nash equilibrium is equivalent to an evolutionarily stable strategy—ESS: Maynard Smith, 1982). The beggar's benefits can only decrease with increasing harassment intensity ($\frac{dB_b}{dc} = -\frac{\pi(p)}{r}$), meaning that $c = 0$ is the beggar's best option regardless of the owner's behavior. A non-zero harassment intensity cannot persist, because, according to equation 3, a beggar that reduces it's harassment intensity always increases the benefits it obtains. In turn, this means that $p = 0$ represents the owner's best choice, because $B_o(p,0) = A(1-p)$ can only decrease with increasing p. This result may seem disappointing because no sharing and no harassment makes for an uneventful interaction. We feel, however, that it reflects a common natural situation: when an owner possesses a completely defendable resource, a harasser only incurs costs by harassing, and it only benefits by recognizing the possessor's ownership and moving on to some other possibility.

Non-contingent benefits of harassment

This situation can change if harassment has some direct benefits that accrue even if the owner does not share. A harasser may, for example, collect scraps, cause a distracted owner to spill, or actively steal parts of the resource. We call these gains the 'non-contingent benefits' of harassment because they do not depend on the owner's sharing.

Modeling non-contingent benefits

We suppose that these non-contingent benefits should increase with the intensity of harassment c and with the time available for harassment $\frac{A}{r}\pi(p)$. With these in mind we can re-write our benefit functions as

$$\begin{aligned} B_o(p,c) &= A - pA - \frac{c\gamma A}{r}\pi(p) - \frac{ckA}{r}\pi(p) \\ &= A\left[1 - p - \frac{c(\gamma+k)}{r}\pi(p)\right] \end{aligned} \tag{4}$$

for the owner, and

$$\begin{aligned} B_b(p,c) &= Ap - \frac{cA}{r}\pi(p) + \frac{ckA}{r}\pi(p) \\ &= A\left[p + \frac{c(k-1)}{r}\pi(p)\right] \end{aligned} \tag{5}$$

for the beggar, where k represents a factor that measures the non-contingent benefits of harassment. We assume that the non-contingent benefits depend on the intensity of harassment (more harassment yields more benefits), thus k is proportional to c. Notice that we subtract the non-contingent gains from the owner's benefits, because we assume that any benefit that the beggar derives from resource (A) comes at the owner's expense.

A non-contingent benefit factor k can destabilize the 'No Share/No Harass' equilibrium by making harassment worthwhile in its own right. Generally speaking, if $k > 1$ the beggar can benefit from harassment regardless of the owner's behavior, and the beggar's optimal harassment level ($\hat{c}$) should be the maximum intensity, say c^*. If, however, $k < 1$ the beggar should not harass and 'No Share/No Harass' is the only equilibrium.

The owner's problem and the $\pi(p)$ function

We expect that the beggar should either not harass ($\hat{c} = 0$) or harass at the maximal intensity ($\hat{c} = c^*$). To study whether the owner should share when harassed, and if so, how much, we need to know more about the function $\pi(p)$ that specifies the proportion of the maximum consumption time available for harassment. In the Appendix we derive a $\pi(p)$ function using a stochastic model of the sharing process. This model assumes that the resource is subdivided into n discrete pieces with the owner deciding whether to share each chunk with probability p. Notice that this subtle re-interpretation of p means that we should think of p as the average proportion shared, rather than the realized proportion shared (technically, we now have $Ap = E(A_s)$, instead of $Ap = A_s$). If the resource is not divisible ($n = 1$), $\pi(p)$ decreases linearly with p with a slope of -1 ($\pi'(p) = -1$; Figure 3.1). For divisible resources ($n > 1$), the $\pi(p)$ function has a slope of -2 at $p = 0$, increases in slope around $p = \frac{1}{2}$, and has a slope of 0 at $p = 1$ (Figure 3.1). Regardless of divisibility, $\pi(p)$ always decreases with p.

Optimal sharing when harassed

With the basic properties of $\pi(p)$ in hand, we can now show how harassment should affect the owner's willingness to share (p). To begin, we differentiate the owner's benefit function (equation (4)):

$$\frac{dB_o}{dp} = A\left[-1 - \frac{c(\gamma+k)}{r}\pi'(p)\right] \tag{6}$$

For indivisible resources ($n = 1$), $\pi'(p) = -1$, and

$$\frac{dB_o}{dp} = A\left[-1 + \frac{c(\gamma+k)}{r}\right] \tag{7}$$

We predict, therefore, that the owner should defend an indivisible resource (set $p = 0$) when

$$\frac{r}{c(\gamma+k)} > 1$$

and abandon it (set $p = 1$) when

$$\frac{r}{c(\gamma+k)} < 1$$

The dimensionless term $\frac{r}{c(\gamma+k)}$ plays an important role in our model. The numerator includes the food consumption rate, and the denominator expresses the rate at which costs accrue during harassment. It represents, therefore, an efficiency—a quotient of rate of benefit gain over rate of cost accrual, and we call it the 'efficiency of consumption when harassed' (or ECH).

A divisible resource, however, complicates the analysis. Since $\pi'(0) = -2$, we know that the owner maximizes its benefits at $p = 0$ (no sharing) when

$$-1 + \frac{2c(\gamma+k)}{r} \leq 0 \tag{8}$$

$$\text{or} \qquad \frac{r}{c(\gamma+k)} \geq 2 \tag{9}$$

That is, the owner should share a divisible resource only when the ECH is less than 2.

Optimal amount to share If, however, $2 > \frac{r}{c(\gamma+k)} \geq 0$, then we expect the owner to share some portion of a divisible resource (Figure 3.2). Although the complexity of $\pi(p)$ prevents a general algebraic specification of the optimal p (or $\hat{p}$), a graphical method gives a relatively complete characterization. The $\hat{p}$ value is the solution of

$$\frac{r}{c(\gamma+k)} = -\pi'(p) \tag{10}$$

Because $\pi'(p)$ is an increasing sigmoid function of p, $-\pi'(p)$ is a sigmoid function that decreases from 2 at $p = 0$ to 0 at $p = 1$. Figure 3.3 shows how $\hat{p}$ is related to the term $\frac{r}{c(\gamma+k)}$. To find $\hat{p}$ corresponding to a given $\frac{r}{c(\gamma+k)}$, we locate $\frac{r}{c(\gamma+k)}$ on the vertical axis and trace a horizontal line to the sigmoid $-\pi(p)$ curve, next we trace a vertical line to p axis to the find $\hat{p}$.

This graphical solution gives a relatively complete picture of the economics of sharing: (1) $\hat{p}$ increases as $\frac{r}{c(\gamma+k)}$ decreases; (2) if $\frac{r}{c(\gamma+k)} \geq 2$, $\hat{p} = 0$; (3) if $2 > \frac{r}{c(\gamma+k)} \geq 1$ then $\frac{1}{2} \geq \hat{p} > 0$; (4) if $1 > \frac{r}{c(\gamma+k)} \geq 0$ then $1 \geq \hat{p} > \frac{1}{2}$

In addition, this graphical solution shows the effect of resource divisibility. For a more divisible resource (higher n), the sigmoid function will be more abrupt and step-like (Figure 3.3b), shifting optimal sharing proportions closer to one-half.

Assembling the pieces

Now that we have a reasonably complete picture of the owner's and beggar's options, we assemble these pieces into a game theoretical analysis. The simple form of the beggar's problem makes this job easier, because we only have to consider $\hat{c} = 0$ and $\hat{c} = c^*$ (where c^* is the maximal intensity). This simplifies things because we only need to consider two possibilities for the owner as well: the best reply to zero harassment, and the best reply to maximal harassment. As discussed above, the owner's best reply to no harassment is no sharing ($\hat{p} = 0$). We denote the best reply to maximal harassment as p^* and remark that this is given by:

$$p^* = 0 \qquad \text{if} \quad \frac{r}{c(\gamma + k)} \geq 2 \tag{11}$$

$$\frac{r}{c(\gamma + k)} = -\pi'(p^*) \qquad \text{otherwise} \tag{12}$$

Since we have two alternatives for each player ($\hat{c} = 0$ or $\hat{c} = c^*$ for the beggar and $\hat{p} = 0$ or $\hat{p} = p^* \neq 0$ for the owner) we can gain some intuition about the game using the familiar tool of the two-by-two game matrix as shown in Table 3.1.

We can now characterize all possible Nash equilibria ('Share/No Harass'is never an equilibrium; Figure 3.4):

No Share/No Harass If $k < 1$, the non-contingent benefits of harassment are too small, so the beggar should not harass, and as a consequence the owner should not share.

No Share/Harass If $k > 1$ and $\frac{r}{c^*(\gamma+k)} \geq 2$, non-contingent benefits make harassment worthwhile for the beggar, but sharing does not benefit the owner because of the high ECH. That is, harassment has little effect on the owner's consumption rate.

Share/Harass If $k > 1$ and $\frac{r}{c^*(\gamma+k)} < 2$, again non-contingent benefits make harassment worthwhile for the beggar, but now sharing benefits the owner because of high costs of harassment relative to the rate of food consumption (low ECH).

Model discussion and conclusions

This section reviews and highlights several key features of the model. First, notice that adopting the maximum harassment intensity c^* doesn't necessarily mean that the beggar will spend much time harassing the owner. Our model assumes that beggars harass only when not consuming shared food. Considering the three equilibria listed above then we would expect the most harassment in the 'No Share/Harass' case, the least harassment in the 'No Share/No Harass' case, and an intermediate amount in the 'Share/Harass' case.

Second, we review the key variables in the model. The parameter k measures the non-contingent benefits of harassment and is probably the most important variable in the model. The condition $k > 1$ simply means that the benefits of harassment must outweigh the costs even if the owner does not share. An animal that harasses when $k < 1$ simply burns his/her own resources (and an owner's best strategy is to let him do so!). Our model's second key parameter, the efficiency of consumption when harassed or ECH ($\frac{r}{c^*(\gamma+k)}$), measures the speed of food intake relative to the cost rate of harassment. The role of intake rate (r) agrees with intuition, for we don't expect sharing of small or easily processed resources.

Given that the resource is divisible ($n > 1$), the amount of divisibility does not affect the equilibria outlined above, but it should affect the proportion shared when sharing occurs. Our model predicts that the amount shared should approach one-half as resource divisibility increases (Figure 3.3). One-half is special in our model because we assume that both player's feed at the same rate. It follows that if the owner wants to eat the maximum amount in peace (keeping the beggar occupied while it eats), then a 50:50 split will achieve this goal.

Discussion

Our model explores the effects of harassment on food sharing. For harassment to be profitable, the beggar must receive benefits for harassing (high k) whether or not the owner shares (e.g., gathering scraps, stealing small pieces). In the face of this harassment, an owner may share if harassment sufficiently reduces its feeding efficiency ($\frac{r}{c^*(\gamma+k)}$).

Importance and implications

Harassment and manipulation

As one of the first models to examine explicitly immediate benefits of food sharing, we set the stage for more general or parsimonious explanations of sharing than kin selection and reciprocal altruism (de Waal, 1989; Perry and Rose, 1994). Clutton-Brock and Parker (1995) reviewed general forms of manipulation and punishment in animal societies, but only two studies provide evidence that harassment does influence animal sharing. First, Wrangham (1975) suggested that harassment may play a large role in chimpanzee sharing of colobus monkey meat after kills. These kills often attracted beggars that vocalized, used begging hand gestures, and even attacked the owner (Wrangham, 1975; Goodall, 1986). If the owner shared part of the food, the recipient usually left, followed by a small band of beggars. Wrangham (1975) hypothesized that the owners 'paid' the beggars with pieces of food to avoid harassment. More recent evidence indicates that chimpanzees that harass intensely receive more food than those that harass less intensely (I.C. Gilby, unpublished data).

Hauser and Marler (Hauser, 1992; Hauser and Marler, 1993) described an extreme example of harassment affecting food sharing. In experiments involving rhesus macaques (*Macaca mulatta*), Hauser and colleagues provided food to individual monkeys that were out of view of other monkeys. They found that, when detected by others, monkeys that did not give food recruitment calls experienced more aggression than monkeys that called. Interestingly, calling females consumed more food than silent females because silent females dropped food while being chased (Hauser, 1992). The increase in callers' consumption indicates that calling may be immediately mutualistic.

Non-contingent benefits

Our model emphasizes benefits that beggars receive even if the owner defends the food; that is, the owner cannot unilaterally defend the entire food source, so harassing the owner to gather scraps or steal pieces of food may benefit the beggar. Without these incentives to remain close to the owner, harassment is not profitable, and in the absence of harassment, the owner has no incentive to share.

Kummer and Cords (1991) conducted experiments on captive long-tailed macaques (*Macaca fascicularis*), varying non-contingent benefits for non-food owners. They found that non-food owners tended to harass more (via stealing, steal attempts, and food manipulation) when the owner could not completely control the food than when it could control the food. Unfortunately, the authors did not present data on the non-food owner's success rate for obtaining food.

Resource divisibility

Our finding that resource divisibility does not affect the owner's decision to share is a bit curious. Although it does not directly influence sharing, divisibility may indirectly influence the decision to share if it affects the non-contingent benefits of harassment. We do find, however, that divisibility determines the proportion of the food source that the owner should share if it does share: owners should share about one-half of highly divisible food.

Consider a lioness consuming a freshly killed gazelle. A single lioness can defend an intact carcass, but when the carcass begins to disintegrate, the lioness may have difficulty defending the entire carcass, and she may allow others to take small pieces. Elgar (1986) suggested that, upon discovery of a food source, house sparrows (*Passer domesticus*) sparrows gave 'chirrup' calls, thereby attracting conspecifics and decreasing individual predation risk. Interestingly, the sparrows called more frequently after discovering a divisible food source than a solid source. Hauser et al. (1993) reported similar results with chimpanzees—individuals gave more food-associated calls when consuming a divided watermelon than an intact watermelon. Perhaps frequent sharing of a divisible food source is simply a question of sheer monopolizability. Defending multiple food sources may prove much more difficult than defending a single source.

Latent harassment

In natural situations in which owners defend food before sharing (such as in chimpanzees), harassment is obvious. In situations in which the owner shares immediately, however, blatant harassment may not appear even if the ever-present threat of harassment maintains the sharing. Of course, latent harassment may prove difficult to observe in nature, necessitating empirical manipulations of sharing and potential for harassment. In a related vein, the overt harassment and food defense may be an information-gathering ritual for both the owner and beggar; each one gauging the other's motivation and resolve (see Ydenberg et al., 1986, for applications of the war of attrition to resource defense).

Related models

Although few models directly focus on the immediate benefits of food sharing (but see Mesterton-Gibbons and Dugatkin, 1999; Giraldeau and Caraco, 2000), several classes of models lay the foundation for theoretically exploring the evolution of food sharing.

Resource defense

Whereas the term 'sharing' often evokes thoughts of one individual actively donating food to another, sharing can be much more generally defined in terms of two or more individuals consuming a resource that one can monopolize. This broader concept of sharing encompasses many instances of resource defense. Brown (1964) originally described the ‘economic defendability’ of territory defense as the circumstances under which an individual should accept the costs involved in defending a territory. Others have extended this work to the defense of food sources. Ydenberg et al. (1986) have modeled the defense of food sources in a way relevant to this model by considering the effects of interference (analogous to our harassment) on foraging decisions. Their model predicted that interference will slow intake rate, thereby making defense uneconomical for individuals that are far from their home and for those with richer food patches in their home range. The combined effect of interference and the asymmetries in home range distance and richness may allow subordinate individuals to feed in patches with dominant individuals or even interfere with and exclude dominant individuals from patches.

Tolerated theft

In important early papers, Blurton Jones (1984, 1986, 1987) argued that an asymmetry of value based on satiety might be important in ‘tolerated theft’ situations. Although the next morsel of food is not very important to the sated owner, it may be very valuable to the hungry beggar. Because of this decrease in the marginal value of food during consumption, the owner should tolerate theft of food by the beggar.

Although this idea provided a valuable foundation for modeling food sharing, the important aspect of behavior in game theory is the relative value of an individual’s options, not the value difference between individuals. Blurton Jones mentioned that owners must weigh the costs of defending food but never incorporated this idea into the model. Without this key inclusion, the analysis ignores strategy stability. Winterhalder (1996a,b) continued the marginal analysis of tolerated theft, but still did not apply a game theoretical approach.

Producer/scrounger games

Our model examines the conditions under which a non-food owner benefits by harassing an owner and an owner benefits by sharing with the beggar. The producer-scrounger game (Barnard and Sibly, 1981; Vickery et al., 1991) addresses whether individuals specialize in either searching for food individually (producing) or avoiding costs of foraging by parasitizing the finds of the producers (scrounging); thereby assuming that harassing and sharing occur. Keep in mind, however, that individuals can choose between the two strategies; that is, for any given foraging bout, an individual is either a producer or scrounger, but it can choose either strategy in a future bout. Giraldeau and colleagues have experimentally investigated theory based predictions on the effects of dominance, resource divisibility, role specialization, patch departure time, and competition intensity in a producer-scrounger situation (Giraldeau et al., 1990; Beauchamp and Giraldeau, 1997).

Extensions

Destabilizing the 'No Share/No Harass'equilibrium

In our model harassment can only persist when harassing produces non-contingent benefits for the harasser, and this result has lead us to hypothesize that phenomena such as stealing and scrap collecting are prerequisites to harassment induced sharing. We do not, of course, claim that this is the only way to destabilize the 'No Share/No Harass'equilibrium, but it does seem to be a plausible and parsimonious approach. This result arises in our model because we assume that the beggar's gains change linearly with harassment intensity, so that the optimal harassment intensity must be either the minimum level (0) or the maximum level (c^*). Future work, ideally guided by empirical results, might explore non-linear benefit functions which can (in theory) destabilize the

'No Share/No Harass'equilibrium without non-contingent benefits.

Food consumption rate

Food consumption rate (r) is an important parameter in our model. We assume that the players have similar consumption rates, which means that the amount required to keep a harasser busy is similar to the amount the owner will be able to eat in peace. In natural situations consumption rates may be quite different, because of differences in sex, age, or levels of satiety. Systematic variation in individual consumption rates may provide an interesting avenue to explore both theoretically and empirically. An informal application of our model's logic suggests that differential consumption rates may influence the beggar's decision to harass and the owner's decision to share and how much to share. For example, owners may be more willing to share with 'slow eaters' (for example, juveniles who have not learning efficient food handling techniques) because they can be kept busy at minimal cost.

N-player game

Our model considers only two players to simplify the problem and to conform to a standard two-by-two game matrix. In natural situations, however, multiple beggars often surround an owner. We speculate that including multiple beggars in our model increases the overall intensity of harassment, thereby forcing the owner to share more frequently (any parent knows it is easier to tolerate harassment from one child than from several children). Chapman and Kramer (1996) found experimentally that as the number of food competitors increased, the owner's intake rate decreased, guarding success decreased, and total number of chases peaked at intermediate competitor numbers. The difficulty in analyzing the effects of beggar number on sharing lies in how to distribute the food in such a way to minimize harassment costs when facing multiple beggars. Further analysis is necessary to explore optimal amounts of food that an owner should share with multiple beggars: should the owner share one large piece to draw some of the beggars away or should it share small pieces with every beggar?

The optimal strategy of the beggars offers a challenge as well. One can imagine multiple beggars in a situation similar to that of a group of vigilant prey. Like the concept of 'corporate vigilance' (Bertram, 1980), a beggar would probably benefit more from having additional beggars around to increase chances of sharing. Packer and Abrams (1990) modeled vigilance situations and found that Nash equilibrium vigilance levels were often lower than Pareto equilibrium (or cooperative optimum) vigilance levels. Similarly, food beggars are tempted to 'cheat' or not harass by relying on harassment by others, thereby avoiding their own costs of harassment.

Summary

Using a game theoretical approach, we modeled the effects of harassment on food sharing. Our model predicts that a non-food owner should harass an owner when the non-owner can gain benefits even in the absence of sharing. These non-contingent benefits (such as gathering dropped scraps) can recoup energetic costs of harassing. An owner should only share when a beggar harasses, significantly reducing its consumption rate. Therefore, if an owner consumes the food slowly, a beggar can harass for large periods of time, so the owner pays high costs of defending. Experimentally manipulating parameters such as feeding rate, non-contingent benefits, resource divisibility, and number of beggars in a sharing context could provide rigorous tests of our model.

Appendix

The $\pi(p)$ function and time available for harassment

Here we determine how the amount shared A_s influences the time available for harassment. Since we assume that both players feed at rate r, the owner consumes for time

$$\frac{A - A_s}{r}$$

while the beggar consumes for time

$$\frac{A_s}{r}$$

The difference

$$\frac{A - A_s}{r} - \frac{A_s}{r} = \frac{A - 2A_s}{r}$$

represents the time available for harassment with the proviso that a negative value means zero time available for harassment (because the beggar spends longer eating than the owner). If we let T_h represent the time available for harassment then we have

$$T_h = \begin{cases} \frac{A-2A_s}{r} & \text{if} \quad A_s \leq \frac{A}{2} \\ 0 & \text{otherwise} \end{cases}$$

Substituting this into equation (1) suggests a $\pi(p)$ function of the form

$$\pi(p) = \begin{cases} 1 - 2p & \text{if} \quad p \leq \frac{1}{2} \\ 0 & \text{otherwise} \end{cases} \tag{A-1}$$

so that $T_h = \frac{A}{r}\pi(p)$ as required. Figure 3.1 uses equation (A-1) to plot $\pi(p)$ as a function of the proportion shared p. Although one might construct a model based on the 'kinked'

$\pi(p)$ function (Figure 3.1) discussed above, it is both inconvenient and implausible. It is inconvenient because the discontinuity at $p = \frac{1}{2}$ means that all remaining calculations must also take account of this condition. It is implausible because stochastic variation in consumption rates (r) and the amount shared (A_s) will combine to create smooth expected harassment time curve ($E(T_h)$). The next few paragraphs discuss one simple way to incorporate this stochasticity.

Resource divisibility and binomial sharing.

Some resources divide easily into parts, whereas others cannot. Suppose that the resource in question can be divided into n equal parts of size $\frac{A}{n}$. Now, suppose that when the owner chooses the proportion to share p, it determines the probability of sharing each part. In this scenario the number of parts shared is a random variable drawn from a binomial distribution with parameters p and n; where p represents the owner's willingness to share ($p = \frac{A_s}{A}$) and the n represents the divisibility of the resource.

The assumption that a binomial process governs sharing allows us to specify completely the expected time available for harassment given the owner's willingness to share p. If the owner shares m of the n parts, the owner retains amount

$$\frac{(n-m)A}{n}$$

and the beggar obtains amount

$$\frac{mA}{n}$$

Since we assume that both animals feed at the same rate (r), the time available for harassment is the difference

$$T_h = \frac{(n-m)A}{rn} - \frac{mA}{rn} = \frac{A(n-2m)}{rn}$$

as long as $n - 2m$ is positive. If not, the beggar has more food than the owner and it will continue eating even after the owner has finished. So there is no time available for harassment ($T_h = 0$) if $m \geq \frac{n}{2}$. To find the expected time available for harassment ($E(T_h)$) we calculate the product of the time available (T_h) and the probability of m pieces being shared, summed over every possible m. We use $\binom{n}{m} p^m (1-p)^{n-m}$ as the binomial probability of sharing m pieces (Zar, 1996).

$$E(T_h) = \frac{A}{r} \underbrace{\sum_{m=0}^{m<\frac{n}{2}} \frac{(n-2m)}{n} \binom{n}{m} p^m (1-p)^{n-m}}_{\pi(p)} \tag{A-2}$$

where the indicated portion of this expression is the $\pi(p)$ function that we seek. Figure 3.1 shows this $\pi(p)$ function for a range of resource divisibilities (n's). The figure compares this family of $\pi(p)$ functions to the piecewise function (equation A-1) obtained when we assume infinite divisibility and error-free sharing. For indivisible resources ($n = 1$), $\pi(p)$ is a straight line ($\pi(p) = 1 - p$, Figure 3.1). As resource divisibility increases, $\pi(p)$ approaches the piecewise function derived earlier (equation (A-1); see Figure 3.1).

Although we cannot express $\pi(p)$ in an algebraically convenient closed form, we can easily state the important properties of $\pi(p)$. The most important feature of $\pi(p)$ is its derivative at zero ($\pi'(0)$). Direct differentiation shows

$$\pi'(0) = \begin{cases} -1 & \text{if} \quad n = 1 \\ -2 & \text{if} \quad n \geq 2 \end{cases} \tag{A-3}$$

that is, the derivative at zero is -1 for indivisible resources and -2 otherwise. Moreover, for divisible resources, the derivative at $p = 1$ is zero ($\pi'(1) = 0$). In the indivisible case, $\pi(p) = 1 - p$, so $\pi'(p) = -1$ for all p. Finally, we observe that $\pi(p)$ decreases with p

(technically, it is non-increasing with p).

Index of variables

A	entire resource amount
A_s	amount owner shares with beggar
B_b	fitness benefits received by beggar
B_o	fitness benefits received by owner
c	intensity of harassment
c^*	maximum intensity of harassment
$\hat{c}$	optimal intensity of harassment
ECH	efficiency of consumption when harassed
k	non-contingent benefits factor
m	number of discrete parts of resource shared by owner
n	total number of discrete parts of resource
p	proportion of total amount shared
p^*	proportion of total amount shared that is optimal reply to c^*
$\hat{p}$	optimal proportion of total amount shared
r	consumption rate
t	total harassment time
T_h	time available for harassment
γ	effect of beggar's harassment intensity on owner's fitness
$\pi(p)$	proportion of maximum consumption time that is available for harassment when owner shares p proportion of food

Acknowledgments

We thank Ian Gilby, Craig Packer, Alison Pearce, and two anonymous referees for reviewing the manuscript. We thank the Packer/Pusey/Stephens lab group at the University of Minnesota for stimulating discussions on this topic. This project was funded by the National Science Foundation grant IBN-9896102 (to D.W.S.).

References

Barnard, C. J. and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.

Beauchamp, G. and Giraldeau, L.-A. 1997. Patch exploitation in a producer-scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behavioral Ecology* 8:54–59.

Bertram, B. C. R. 1980. Vigilance and group size in ostriches. *Animal Behaviour* 28:278–286.

Blurton Jones, N. G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology* 5:1–3.

Blurton Jones, N. G. 1986. Fitness returns from resources and the outcome of contests: some implications for primatology and anthropology. *In* J. G. Else and P. C. Lee (eds.), Primate Ontogeny, Cognition, and Social Behavior. Cambridge University Press, Cambridge. pp. 393–406.

Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.

Chapman, M. R. and Kramer, D. L. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* 52:83–94.

Clutton-Brock, T. H. and Parker, G. A. 1995. Punishment in animal societies. *Nature* 373:209–216.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution* 18:433–459.

Elgar, M. A. 1986. House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour* 34:169–174.

Giraldeau, L.-A. and Caraco, T. 2000. Social Foraging Theory. Princeton University Press, Princeton.

Giraldeau, L.-A., Hogan, J. A., and Clinchy, M. J. 1990. The payoffs to producing and scrounging: what happens when patches are divisible? *Ethology* 85:132–146.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, Mass.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology* 7:1–52.

Hauser, M. D. 1992. Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences (USA)* 89:12137–12139.

Hauser, M. D. and Marler, P. 1993. Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology* 4:206–212.

Hauser, M. D., Teixidor, P., Fields, L., and Flaherty, R. 1993. Food-elicited calls in chimpanzees: effects of food quantity and divisibility. *Animal Behaviour* 45:817–819.

Kummer, H. and Cords, M. 1991. Cues of ownership in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour* 42:529–549.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Mesterton-Gibbons, M. and Dugatkin, L. A. 1999. On the evolution of delayed recruitment to food bonanzas. *Behavioral Ecology* 10:377–390.

Mitani, J. C. and Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* 61:915–924.

Packer, C. and Abrams, P. 1990. Should co-operative groups be more vigilant than selfish groups? *Journal of Theoretical Biology* 142:341–357.

Perry, S. and Rose, L. 1994. Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capuchinus*. *Primates* 35:409–415.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. 1991. Producers, scroungers, and group foraging. *American Naturalist* 137:847–863.

Winterhalder, B. 1996a. A marginal model of tolerated theft. *Ethology and Sociobiology* 17:37–53.

Winterhalder, B. 1996b. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology* 5:46–57.

Wrangham, R. W. 1975. The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, Cambridge University.

Ydenberg, R. C., Giraldeau, L.-A., and Kramer, D. L. 1986. Interference competition, payoff asymmetries, and the social relationships of central place foragers. *Theoretical Population Biology* 30:26–44.

Zar, J. H. 1996. Biostatistical Analysis, 3rd ed. Princeton Hall, Upper Saddle River, NJ.

Table 3.1: Two-by-two game matrix representing the harassment game.

	BEGGAR	
	No Harass	*Harass*
OWNER	$\hat{c} = 0$	$\hat{c} = c^*$
No Share $\hat{p} = 0$	0 1	$\frac{c^*(k-1)}{r}$ $1 - \frac{c^*(\gamma+k)}{r}$
Share $\hat{p} = p^* \neq 0$	p^* $1 - p^*$	$p^* + \frac{c^*(k-1)}{r}\pi(p^*)$ $1 - p^* + \frac{c^*(\gamma+k)}{r}\pi(p^*)$

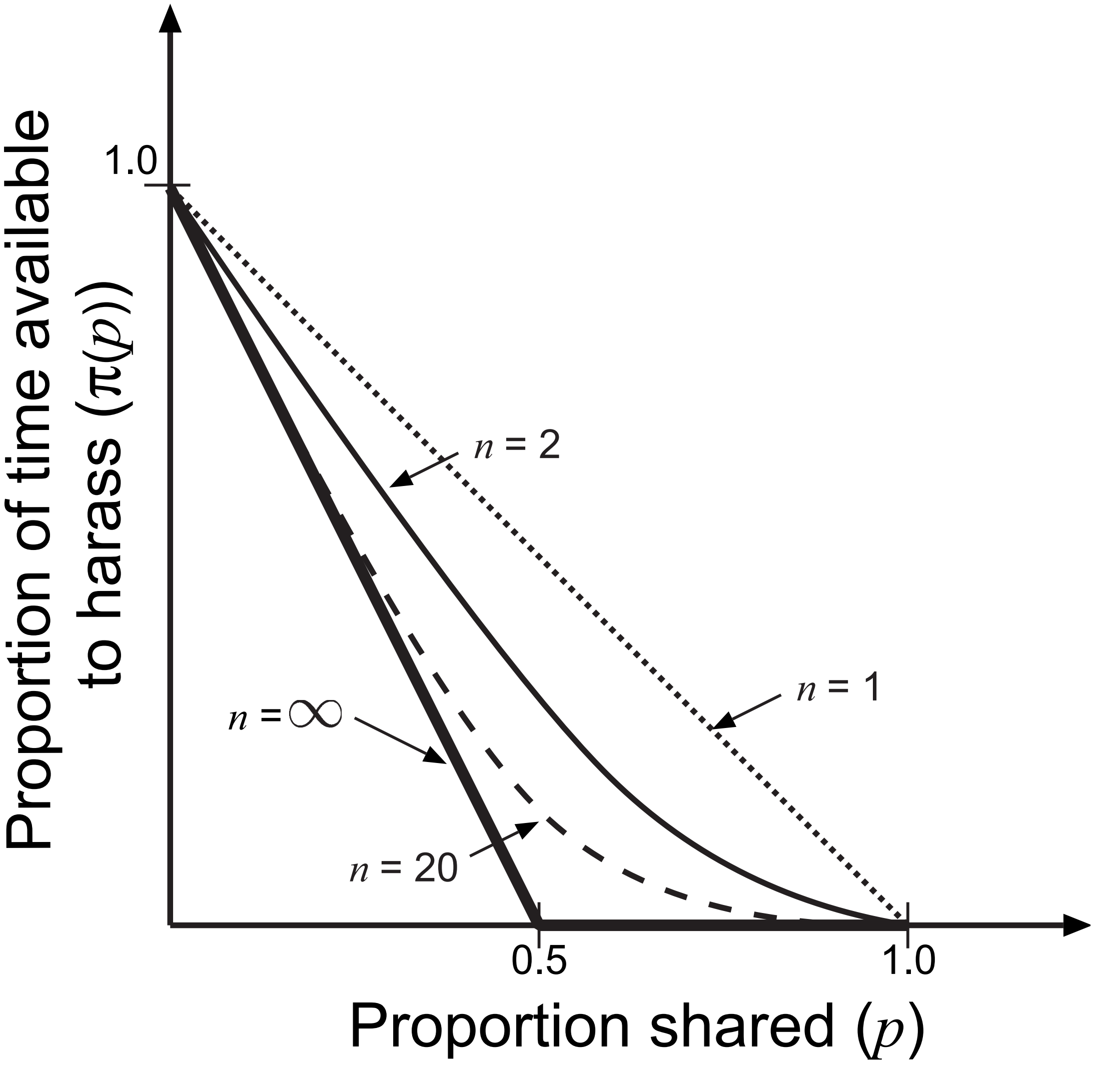


Figure 3.1: The proportion of time available to harass always decreases with the proportion shared. In the simplest case (equation (A-1)), the time available to harass decreases linearly to zero as the owner shares up to half of the resource, and if the owner shares over half of the resource, the beggar never has the opportunity to harass (thick line). By incorporating resource divisibility or n (equation (A-2)), we smooth the 'kinked' property of the function (all other lines). Increasing divisibility (n) approaches the simpler 'kinked' function.

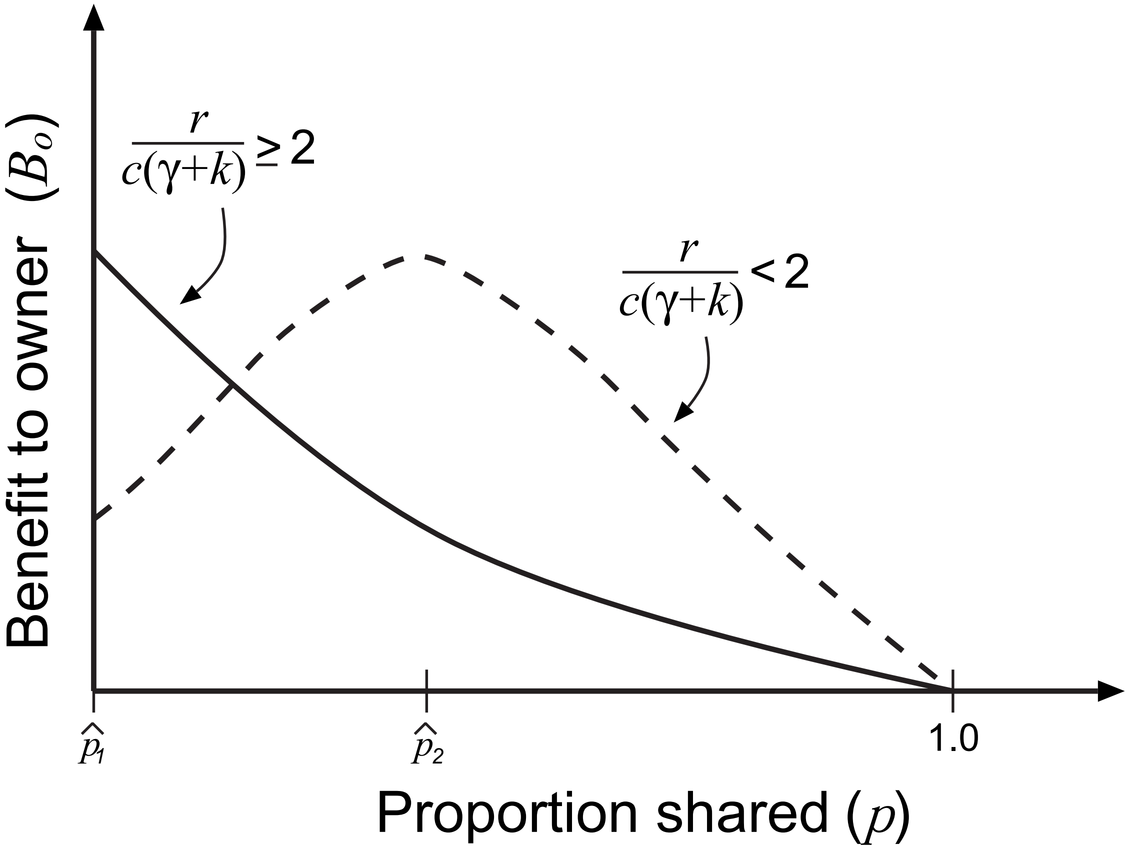


Figure 3.2: To determine the optimal proportion to share, we maximize the owner's benefit (B_o) as a function of proportion shared (p). If this maximum is less than or equal to zero (negative derivative at $p = 0$), the owner should not share ($\hat{p}_1 = 0$). If this maximum is greater than zero, the owner should share an intermediate amount ($\hat{p}_2 > 0$; equation (10)).

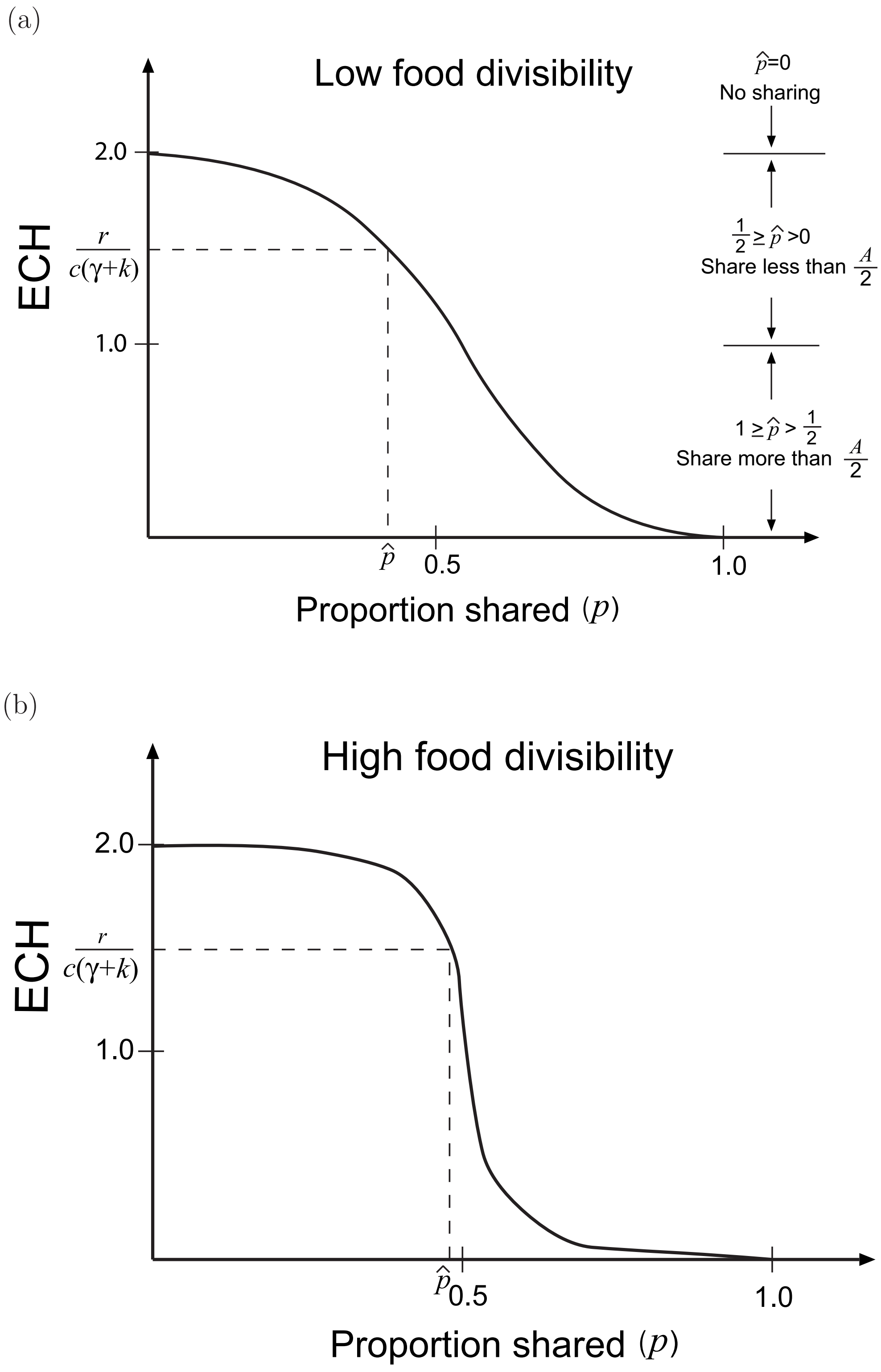


Figure 3.3: With low resource divisibility (**A**), the optimal proportion to share ($\hat{p}$) is relatively low for a given efficiency of consumption when harassed (ECH). With high resource divisibility (**B**), $\hat{p}$ approaches one-half for the same ECH.

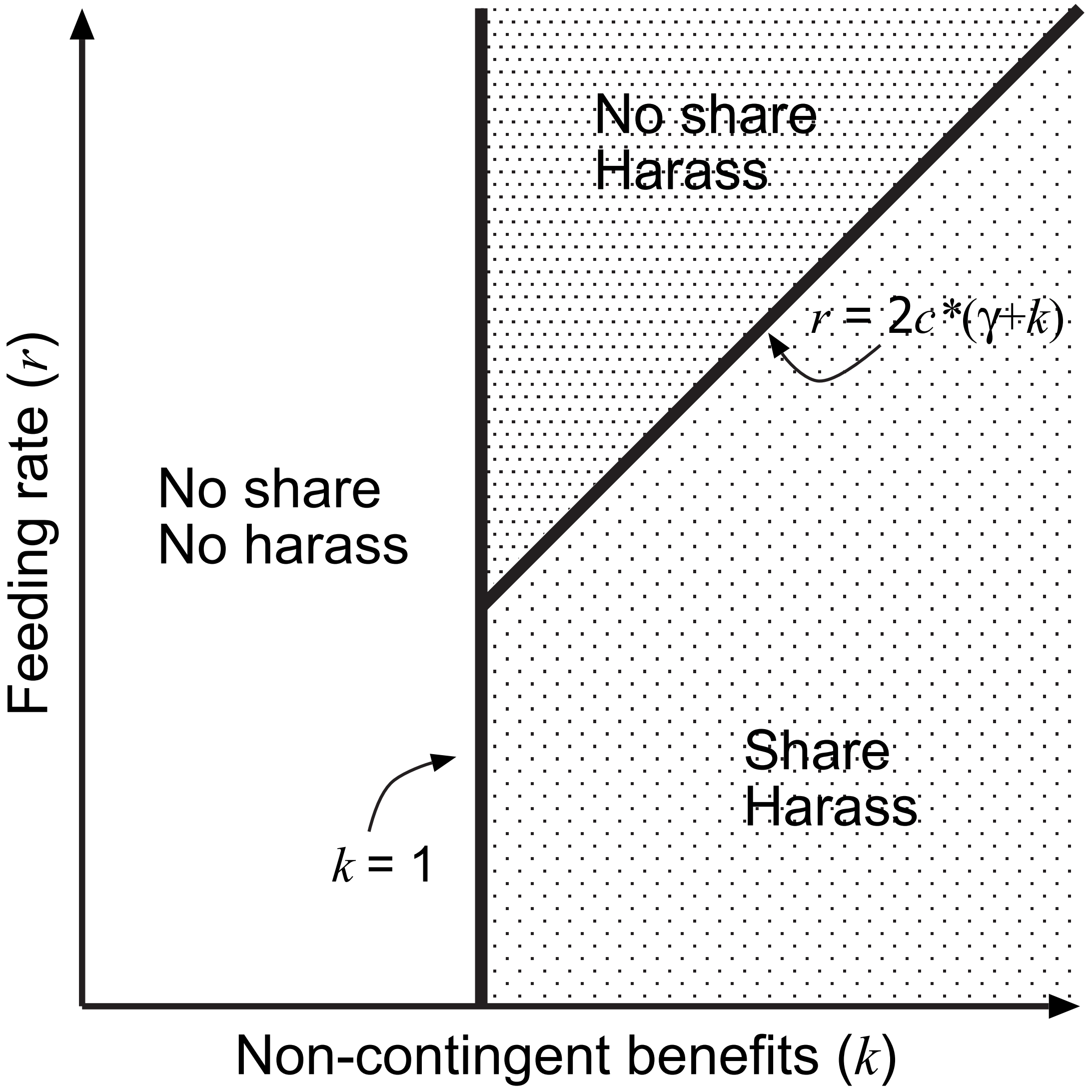


Figure 3.4: The three possible Nash equilibria depend on non-contingent benefits (k) and feeding rate (r).

Chapter 4

Selfish generosity: harassment increases food sharing in primates

Abstract

Animals share food to gain either immediate or delayed fitness benefits. This study provides an empirical analysis of the immediate benefits of a food owner sharing to avoid costly harassment from a beggar. Experiments were conducted on two species of primate: chimpanzees (*Pan troglodytes*) and squirrel monkeys (*Saimiri boliviensis*). Comparing these species test the effects of harassment on species that share frequently (chimpanzees) and rarely (squirrel monkeys). In these experiments two subjects were placed in a cage separated by a mesh partition. Food was provided to a randomly chosen owner and instances of food sharing by the owner and harassment by the beggar were recorded. Each experiment varied harassment potential (mesh partition present or absent) and food divisibility (food solid or partially divided). For both squirrel monkeys and chimpanzees, the absence of the partition (allowing the beggar full access to the owner) significantly increased both beggar harassment and sharing by the owner. The divisibility treatment did not affect harassment or sharing. Interestingly, squirrel monkeys and chimpanzees shared equally frequently despite differences in natural sharing rates. These results suggest that harassment can play a significant role in primate food sharing. The selfish nature of harassment emphasizes the importance of considering simple explanations of cooperative behavior before invoking complex explanations.

Work on food sharing typically has focused on the delayed benefits of sharing. Researchers have examined kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971), and trade as potential delayed advantages of sharing. Few studies, however, have examined immediate benefits of sharing. Field observations of chimpanzees suggest that persistent begging can force food owners to avoid beggars or cause them to share food (Teleki, 1973). Wrangham (1975) predicted that the energetic and opportunity costs of defending a food source may force owners to 'pay' beggars with part of the resource to avoid harassment (the sharing-under-pressure hypothesis). Blurton Jones (1984, 1986, 1987) proposed the 'tolerated theft' model of sharing, predicting that satiation decreases the marginal fitness value of the remaining resource. The owner should share to avoid costs associated with defending the food, because the owner values the remaining resource less than a hungry newcomer. In Chapter 3 (Stevens and Stephens, 2002), I have extended this idea by considering how beggar harassment may impose a cost on food owners. The model predicts that beggars should harass only when they can gain benefits other than shared food (non-contingent benefits). When the owner defends the food, the beggar must gather or steal scraps to offset its cost of harassing. Thus, harassment is profitable only when the owner can not completely defend the food. If the harassment costs to the owner are high enough, it may benefit more by sharing part of the food rather than accepting the costs. Therefore, sharing may provide selfish, immediate benefits to the sharer by reducing the costs of defense.

This study tests the following predictions from the model:

1. Beggars should preferentially harass when they can gain non-contingent benefits.
2. Owners should share food only when harassment imposes costs.

To test these predictions, I manipulated food divisibility and the beggar's harassment potential. By manipulating food divisibility, I could control the owner's ability to defend the food and vary the presence of non-contingent benefits. I controlled the harassment costs inflicted on the owner by allowing the beggar to harass or preventing harassment with a mesh partition. Table 4.1 summarizes the predicted behavior for both owners and beggars in each of the experimental treatments.

To evaluate the generality of harassment, I conducted experiments on two species of captive primates: common chimpanzees (*Pan troglodytes*) and squirrel monkeys (*Saimiri boliviensis*). I used these two species because they differ in their natural sharing rates. Chimpanzees frequently share in both natural and captive situations (Goodall, 1986; Nishida et al., 1992; Hemelrijk et al., 1999), whereas squirrel monkeys do not often share food (Fragaszy and Mason, 1983). If both species exhibit effects of harassment on sharing, this strongly supports the importance of selfish explanations of food sharing.

Materials and Methods

Subjects

I worked with common chimpanzees (*Pan troglodytes*) at the Southwest Foundation for Biomedical Research in San Antonio, Texas from May to August 2001. The subjects were 12 adult females (ages ranged from 17 to 41 years old), paired within their social groups (3 to 5 members). I paired unrelated individuals of similar age, dominance rank, and food motivation to minimize competitive asymmetries. The pairs remained constant throughout the experiment. Subjects lived in indoor/outdoor cages with other group members prior to testing. I tested subjects in the outdoor section of their home cages, while other group members remained indoors.

I worked with Bolivian squirrel monkeys (*Saimiri boliviensis*) at the Squirrel Monkey Breeding and Research Resource at the University of South Alabama in Mobile, Alabama from September to November 2001. Again, the subjects were 12 unrelated adult females (ages ranged from 4 to 9 years old), paired within their social groups (20 to 37 members). Subjects lived in indoor cages with all group members before testing. Lab technicians removed subjects from their home cages and placed them in an experimental cage in a separate room for testing.

For both species, some subjects had participated in previous behavioral experiments, but none had experienced sharing experiments.

Experimental apparatus and treatments

I tested the chimpanzees in adjacent outdoor cages, each measuring 3.15×4.56×2.88 m (Figure 4.1a). Metal fencing (4.8×4.8 cm square holes) enclosed most of the cage, except for the concrete floor and back wall. Hardware cloth covered the fencing separating the two adjacent experimental cages (1.4×1.4 cm square holes). A 142×50 cm section of the 4.8×4.8 cm square hole fencing (Figure 4.1a) was exposed.

For the squirrel monkeys I used a 155×64×77 cm Allentown cage (Figure 4.1b), composed of stainless steal mesh (2.3×4.3 cm rectangular holes) on all sides. A plexiglass sheet provided a solid floor for the cage. The 65×71 cm partition separating the two chambers consisted of Gard'n Fence plastic mesh (3.5×5.5 cm rectangular holes).

The experimental treatments followed a 2×2 repeated measures design with two factors: partition and food divisibility. Partition treatments manipulated the subjects' potential to harass each other with the presence or absence of a mesh partition. When present the mesh partition prevented full access between the subjects by separating them in adjacent cages. When absent the subjects had access to both cages and to one another.

The second treatment factor varied the defensibility of the food source by manipulating whether the food was either solid or partially divided (Divisibility treatment). Owners could defend solid food because it remained intact as the owner consumed it.

Partially divided food (food that was cut multiple times but not completely through) disintegrated as the owner consumed it, thereby preventing the owner from defending every piece of dropped food. I used three bananas (weighing about 600 g) as food for chimpanzees and a 20 g cube of cantaloupe for squirrel monkeys. I fed the squirrel monkeys cantaloupe because their consumption duration was comparable to that of the chimpanzees consuming bananas.

Each individual experienced the factorial combination of these four treatment levels as both owner and beggar (non-owner). I replicated these randomly ordered treatment combinations four times for a total of 32 trials per pair (2 partition levels×2 divisibility levels×2 ownership levels×4 replicates). Each pair experienced one trial per day until completing all trials.

Experimental procedure

Trials ran slightly differently for the two species. For chimpanzees, I placed the solid or partially divided bananas on the floor about 20 cm from the large mesh partition. I transferred the randomly chosen owner into the cage with food and the beggar into the cage without food. For Partition Absent trials, I opened the door separating the two experimental cages when the owners possessed the food. The door remained closed for Partition Present trials.

For squirrel monkeys, I placed the randomly chosen owner into the left chamber of the experimental cage and the beggar in the right chamber. I placed the solid or partially divided cantaloupe in the owner's food dish. This configuration placed the food near the beggar but out of her reach (10 cm from partition; Figure 4.1b). I removed the entire partition separating the chambers upon possession of the cantaloupe in Partition Absent trials and left the partition in place for Partition Present trials.

I video taped (using Sony DCR-TRV8 mini-DV camera) the trials from food delivery until 30 sec after the subjects consumed all of the food or abandoned the food. In addition, I recorded all interactions between the subjects, including instances of sharing, harassment, stealing, and attacking. I operationally defined sharing and harassment loosely based on de Waal et al. (1993) and de Waal (1997).

Types of sharing

- collect near—recover food from within arm's reach of owner
- co-feeding—beggar and owner feed on food source concurrently
- relaxed claim—beggar takes part of food that owner possesses without resistance from owner
- food giving—owner facilitates transfer of food to beggar

Types of harassment

- forced claim—beggar forcefully takes food from owner; owner attempts to avoid theft
- unsuccessful forced claim—beggar attempts but fails to take food from owner
- passive begging—beggar sits within arm's reach of the owner and stares but does not physically contact owner or food
- active begging—beggar physically contacts owner or food
- attacking—beggar aggressively interacts with owner

From the video tape, I quantified the frequency and time spent harassing by the beggar, frequency and proportion shared by the owner, proportion of food consumed by each subject, and time spent consuming for each subject.

Data analyses

I used repeated measures analyses of variance to test Partition and Divisibility treatment effects on several measures of harassment and sharing. I calculated *harassment frequency* as the total number of harassment events per trial and *harassment duration* as the total amount of time spent harassing per trial. I also analyzed *active harassment frequency* and *active harassment duration*. Active harassment included forced claims, unsuccessful forced claims, active begging, and attacking. I calculated *sharing frequency* as total number of sharing events per trial and *sharing amount* as amount of total food shared per trial. I estimated *sharing amount* by multiplying the proportion shared and the average total mass of all food (600 g for chimpanzees and 20 g for squirrel monkeys). I define *active sharing frequency* as the number of active sharing events (co-feeding, relaxed claim, and food giving) per trial. Because active sharing rarely occurred, I did not analyze active sharing amount.

To examine the direct effects of harassment on sharing, I conducted multiple regression analyses on sharing frequency, sharing amount, and active sharing frequency using harassment frequency, harassment duration, active harassment frequency, and active harassment duration as predictors. Because harassment and sharing rarely occurred in the Partition Present trials, I have restricted this analysis to the Partition Absent trials. Due to the large scale of these regressions, I have reported only trends and significant results—complete analyses can be found in Tables 4.4 and 4.7.

I tested whether harassment benefits beggars in the absence of sharing (non-contingent benefits). For this, I examined the beggar's amount consumed as a function of harassment only in the Partition Absent treatments in which no sharing occurred.

Finally, I combined the data for both species to test for species differences in sharing and harassment. All harassment and sharing measures remained the same as stated above except for amount shared. Because the two species received very different amounts of food (20 g vs. 600 g), I used an arcsine, square root transformation of proportion shared.

Results

Chimpanzees

Out of 192 trials, I observed 142 harassment events (3 forced claims, 3 unsuccessful forced claims, 120 passive begs, 14 active begs, and 2 attacks, Figure 4.2a) by the chimpanzees in 70 trials (36% of all trials). I observed 60 sharing events (39 collect near, 0 co-feed, 14 relaxed claim, and 7 food giving, Figure 4.2b) in 30 trials (16% of all trials).

Prediction 1: Non-contingent benefits increase harassment

A repeated measures analysis of variance indicates that the Divisibility treatment significantly influenced chimpanzee harassment frequency (ANOVA: $F_{1,11} = 7.17$, $p = 0.0215$) and tended to influence active harassment duration (ANOVA: $F_{1,11} = 3.33$, $p = 0.0951$). Divisibility influenced neither harassment duration nor active harassment frequency. Therefore, the beggars responded to less defensible food by increasing their harassment (Table 4.2, Figure 4.3a). However, beggars did not consume more food when they harassed.

Prediction 2: Owners share when harassed

Because the Partition treatment manipulated the potential for beggar harassment and not actual harassment, I verified that more harassment occurred in the No Partition treatment (Table 4.2, Figure 4.3a). As predicted, the chimpanzees harassed more frequently (ANOVA: $F_{1,11} = 11.24$, $p = 0.0064$) and for longer durations (ANOVA: $F_{1,11} = 12.09$, $p = 0.0052$) in the absence of a partition. The subjects also tended to actively harass for longer durations in the No Partition treatment (ANOVA: Partition: $F_{1,11} = 3.77$, $p = 0.0781$). The presence of the partition did not affect active harassment frequency.

Given that the Partition treatment did manipulate beggar harassment levels, I tested whether this treatment influenced sharing by the owner. The Partition treatment did affect sharing frequency (ANOVA: $F_{1,11} = 10.43$, $p = 0.0080$) and sharing amount(ANOVA: $F_{1,11} = 5.38$, $p = 0.0406$) but not active sharing. Thus, more sharing occurred in the absence of the partition and in the face of more harassment (Table 4.3, Figure 4.4a).

To ensure that harassment itself influenced sharing, I examined harassment and sharing in the absence of a partition. Sharing occurred more frequently when beggars harassed than when they did not (t-test: $t_{94} = 3.80$, $p = 0.0003$, Figure 4.5a). These results indicate that harassment from the beggar did increase its chance of receiving food. Sharing also increased with continuous measures of harassment such as harassment duration (Multiple regression: $F_{1,91} = 3.52$, $p = 0.0637$) and active harassment frequency (Multiple regression: $F_{1,91} = 18.62$, $p < 0.0001$; Table 4.4). These results confirm the effectiveness of harassment—more harassment resulted in more sharing.

Summary

The non-contingent benefits of gathering scraps from divisible food did increase harassment, but harassment did not increase the beggar's food intake. The absence of the partition increased harassment by beggars, which increased sharing by owners. Sharing increased in presence of direct harassment by the beggars. In general, these results support the model predictions. The only deviation from the predictions was that the Divisibility treatment did not influence owner sharing (Table 4.1).

Squirrel monkeys

In 192 total trials, I observed 346 harassment events (15 forced claims, 87 unsuccessful forced claims, 211 passive begs, 30 active begs, and 3 attacks, Figure 4.2a) by the squirrel monkeys in 114 trials (59% of all trials). I observed 65 sharing events (47 collect near, 0 co-feed, 18 relaxed claim, and 0 food giving, Figure 4.2b) in 43 trials (22% of all trials).

Prediction 1: Non-contingent benefits increase harassment

Repeated measures ANOVAs indicate no Divisibility treatment effect on harassment in squirrel monkeys (Harassment frequency: $F_{1,11} = 0.75$, $p = 0.4036$, Harassment duration: $F_{1,11} = 0.37$, $p = 0.5547$; Active harassment frequency: $F_{1,11} = 0.70$,p=0.4210; Active harassment duration: $F_{1,11} = 0.50$, $p = 0.4926$). Therefore, beggars did not harass more often around divisible resources (Table 4.5, Figure 4.3b). However, harassment did provide non-contingent benefits in another way: beggars consumed more food when they actively harassed more frequently (Multiple regression: $F_{1,53} = 5.68$, $p = 0.0208$).

Prediction 2: Owners share when harassed

A strong effect of Partition on harassment (Harassment frequency: $F_{1,11} = 24.43$, $p = 0.0004$; Harassment duration: $F_{1,11} = 12.74$, $p = 0.0044$; Active harassment frequency: $F_{1,11} = 9.62$, $p = 0.0100$; Active harassment duration: $F_{1,11} = 20.98$, $p = 0.0008$) indicated that subjects harassed significantly more in the absence of a partition (Table 4.5, Figure 4.3b).

The Partition treatment effect on harassment translated to an effect on sharing. The absence of the partition increased sharing frequency (ANOVA: $F_{1,11} = 15.96$, $p = 0.0021$), sharing amount (ANOVA: $F_{1,11} = 13.63$, $p = 0.0035$), and active sharing frequency (ANOVA: $F_{1,11} = 17.47$, $p = 0.0015$; Table 4.6, Figure 4.4b). In addition, when beggars harassed in the No Partition treatment, owners shared food more frequently (t-test: $t_{94} = 2.95$, $p = 0.0040$, Figure 4.5b). In addition, sharing amount tended to increase with harassment frequency (Multiple regression: $F_{1,91} = 3.12$, $p = 0.0805$), harassment duration (Multiple regression: $F_{1,91} = 3.54$, $p = 0.0632$), and active harassment duration (Multiple regression: $F_{1,91} = 3.03$, $p = 0.0850$; Table 4.7).

Summary

Squirrel monkey harassment and sharing did not respond to the Divisibility treatment. Nevertheless, beggars did receive non-contingent benefits by consuming more when harassing. The Partition treatment effectively manipulated harassment and sharing, because both increased with the partition absent. Owners shared more frequently as beggar intensity increased. In summary, harassment and sharing in squirrel monkeys supports the model predictions; however, the Divisibility treatment did not effectively manipulate food divisibility (Table 4.1).

Comparative analysis

Despite the similarity between these two experiments, they were not identical. I attempted to scale body size with cage size and food amount, but I could not scale them perfectly. Also, chimpanzees had only a small window of mesh partition available, whereas squirrel monkeys had an entire wall (Figure 4.1). Given these and other more subtle differences, we must interpret these results with caution. Nevertheless, striking similarities and differences between chimpanzees and squirrel monkeys emerged. First, the species differed in harassment frequency (ANOVA: $F_{1,6} = 20.69$, $p = 0.0039$) and active harassment frequency (ANOVA: $F_{1,6} = 23.23$, $p = 0.0029$), with squirrel monkeys harassing three times more frequently than chimpanzees. Chimpanzees, however, tended to harass for longer durations (ANOVA: $F_{1,6} = 4.05$, $p = 0.0909$).

The most important result involves sharing. Chimpanzees and squirrel monkeys showed no difference in sharing frequency (ANOVA: $F_{1,6} = 0.04$, $p = 0.8448$) or active sharing frequency (ANOVA: $F_{1,6} = 0.06$, $p = 0.8126$). Surprisingly, squirrel monkeys shared larger proportions of food than chimpanzees (ANOVA: $F_{1,6} = 6.35$, $p = 0.0453$). In summary, these two species share equally frequently, but squirrel monkeys share more of their food with beggars (Table 4.9, Figure 4.6b).

Discussion

These experimental results generally agree with the harassment model predictions (Stevens and Stephens, 2002). In particular, this study provides two striking results: (1) beggar harassment substantially increases food sharing in primates (Figures 4.4 & 4.5) and (2) very little difference in sharing rates exists between squirrel monkeys and chimpanzees (Figure 4.6b).

Although several studies have suggested a relationship between harassment and food sharing (Teleki, 1973; Wrangham, 1975; Goodall, 1986), this study offers the first empirical test that manipulates harassment and determines effects on sharing. Both squirrel monkey and chimpanzee food owners shared more often when beggars harassed. In addition, sharing frequency and amount increased as harassment intensity increased. Therefore, the immediate, selfish benefits of reducing the costs of harassment directly influenced sharing. Beggars manipulate the fitness benefits of defending a resource by imposing costs. To avoid these costs food owners must relinquish part of the food that they possess.

Chimpanzees are the premiere food sharers in the animal kingdom, sharing in both natural and captive settings (Goodall, 1986; Nishida et al., 1992; Hemelrijk et al., 1999). In some populations of chimpanzees, food owners almost always share part of a carcass with others following hunts (I.C. Gilby, unpublished data). In contrast, squirrel monkeys rarely share food in the wild or captivity (Fragaszy and Mason, 1983). Despite these apparent differences in sharing rates, chimpanzees and squirrel monkeys share equally often, and squirrel monkeys actually share larger proportions of food in this experimental situation (Figure 4.6b).

Model predictions

Stevens and Stephens (2002) described a game theoretical model which predicts the circumstances under which harassment can influence sharing. This model is similar to previous models of punishment (Boyd and Richerson, 1992; Clutton-Brock and Parker, 1995) because the beggar faces an enforcement cost associated with harassing the owner. In the punishment models, punishers do not offset these enforcement costs until they receive benefits in the subsequent interaction; punishment only influences future behavior and fitness. In the harassment model, however, the beggar recoups the cost immediately rather than in the future. By harassing a beggar increases its current probability of obtaining food. For harassment to persist against an owner that unilaterally defends its food, Stevens and Stephens hypothesized that the beggar must reap 'non-contingent benefits' of harassment. Harassing must provide benefits to the beggar in the absence of sharing, such as gathering dropped scraps and stealing pieces of food. To probe for these benefits in the current experiment, I examined harassment intensity and amount of food consumed by the beggar in No Partition trials in which the owner did not share. Squirrel monkeys gained more food as beggars when they harassed more intensely, even in the absence of sharing. Therefore, non-contingent benefits could maintain harassment in squirrel monkeys. Chimpanzees, in contrast, showed no increase in consumption with harassment. They did, however, harass more often when the food was divisible and possibly less defensible.

These empirical results support theoretical predictions regarding the importance of harassment in food sharing situations (Table 4.1). This is significant because few theoretical investigations predict circumstances under which food sharing should occur (but see Valone, 1996; Mesterton-Gibbons and Dugatkin, 1999; Giraldeau and Caraco, 2000; Dall, 2002). Even fewer empirical studies test model-based predictions. Other classes of models make similar predictions. Both resource defense theory (Brown, 1964) and producer-scrounger theory (Barnard and Sibly, 1981; Vickery et al., 1991) predict that increasing interference competition or harassment reduces an individual's intake rate and increases sharing of the resource (Ydenberg et al., 1986; Giraldeau and Beauchamp, 1999). Experimental tests of the theory support predictions that interference reduces resource defense (Chapman and Kramer, 1996; Beauchamp and Giraldeau, 1997). These experimental verifications of the harassment model indicate that modeling complex social behavior can provide fruitful predictions.

Implications of harassment effects

Because harassment elicited sharing in both chimpanzees and squirrel monkeys, it provides a general explanation of sharing. Several characteristics contribute to its general application. First, sharing provides immediate, selfish benefits for the owner by avoiding costly harassment. Unlike reciprocity, the owner does not act altruistically in the short term and wait for future repayment. These findings support a growing body of mutualistic explanations of cooperation (Heinrich, 1988; Clements and Stephens, 1995; Grinnell et al., 1995). Second, responses to harassment do not require complex cognitive skills. Individuals need not track debts owed, favors given, or the likelihood of reciprocation. Instead, natural selection simply favors individuals that donate food in such a way to avoid net costs. Finally, harassment does not require special relationships between owner and beggar. For instances of kin-selected food sharing, sharing only occurs within a limited set of related individuals. In reciprocal altruism, individuals must recognize and interact with the same individuals to track reciprocation. In the harassment paradigm, however, individuals need not recognize each other, much less interact repeatedly. Indeed, individuals that have never met and will never meet again may share food.

Harassment may explain many instances of sharing in a number of species. Thus far, researchers have reported harassment and sharing in only a few species, most notably chimpanzees. Its role in chimpanzee food sharing, however, has probably been vastly underestimated. A number of studies have described examples of harassment during chimpanzee food sharing events (Nissen and Crawford, 1936; Teleki, 1973; Wrangham, 1975; Kuroda, 1984; Takahata et al., 1984; Goodall, 1986; Boesch and Boesch, 1989), but few have considered it a major force in sharing. For example, de Waal (1989) and Mitani and Watts (2001) both discounted the effects of observed harassment and concluded that reciprocity and trade maintained sharing. In addition, Stanford et al. (1994) proposed correlational evidence that males may trade food for sex by sharing more frequently with sexually receptive females. Previously, however, Teleki (1973) provided an alternative explanation of Stanford's results by demonstrating that receptive females harass food owners more often. By underestimating harassment, studies of sharing may ignore a potentially basic mechanism of sharing. Neglecting harassment may confound results, generating spurious reciprocal sharing patterns. Harassment must be eliminated as a possible explanation of sharing before invoking more complex explanations such as reciprocity, trade, and meat-for-sex.

Potential challenges

Is 'collecting near' truly sharing? Most instances of sharing in this experiment occurred when the beggar collected food near the owner. Some researchers argue that this is not true food sharing because the owners do not actively donate the food. I contend that, like cooperation in general (Clements and Stephens, 1995; Stephens and Anderson, 1997), food sharing is an economic outcome not a behavioral mechanism. Sharing should be defined by the lost opportunity of consuming food regardless of whether animals share passively or actively. These experiments support this economic definition. Separate analyses that exclude 'collect near' sharing demonstrated similar patterns as analyses that included 'collect near' sharing.

How might multiple beggars affect harassment? This study simplified potential food sharing situations by using only pairwise interactions, although sharing often involves multiple owners and beggars. The data from this study probably generalize to multiple players rather easily. Specifically, more beggars should increase the total harassment intensity faced by the owner, thereby increasing the probability of sharing (Beauchamp and Giraldeau, 1997). Fruth and Hohmann (2002) observed that larger groups of beggars in bonobos resulted in more sharing events. By sharing, the owner creates other owners that beggars can harass, potentially reducing its own harassment levels. The more interesting question remains how will beggars behave in the presence of competition? A 'cheater' beggar that lets other beggars harass but reaps the benefits may avoid costs of harassing. This system, however, resists cheaters because sharing depends on harassment intensity. Only beggars that inflict costs on owners will receive food.

Does this experiment with captive primates generalize to natural food sharing situations? The multiple beggar issue represents a specific aspect of the more general problem of external validity. For chimpanzees, many studies of wild populations have verified the frequency of harassment (Teleki, 1973; Wrangham, 1975; Takahata et al., 1984; Goodall, 1986; Boesch and Boesch, 1989). Recently, a study focused on harassment and sharing in wild chimpanzees corroborated these experimental results (I.C. Gilby, unpublished data). Gilby found that harassment predicted sharing better than grooming frequency, association levels, and female sexual receptivity. No evidence of sharing exists for wild populations of squirrel monkeys. Evidence from another primate species, however, validates the importance of harassment in natural sharing situations. Hauser (1992) described scenarios in which rhesus macaques (*Macaca mulatta*) discovered food sources and could either withhold or give recruitment calls. If other monkeys discovered an individual that did not call, they chased and attacked the non-caller. If the individual called, others shared the food in relative peace. Interestingly, callers consumed more food on average than non-callers, suggesting that calling (and thereby sharing) offered higher benefits than not calling. These examples support the harassment hypothesis in natural primate populations.

Future studies

The results presented here indicate that harassment could provide a fertile area to explore in studies of food sharing. Harassment could modulate other important factors affecting sharing. For instance, as predicted by Blurton Jones (1984, 1986, 1987), hunger and food motivation may affect harassment and thereby sharing behavior. Asymmetries in motivation may result in increased harassment and sharing in the presence of hunger. Early attempts to manipulate hunger levels found no effect on sharing in chimpanzees (Nissen and Crawford, 1936). More thorough studies are needed to clarify the effects of food motivation on harassment and sharing.

Another factor potentially modulating harassment is relatedness. Kinship decreases aggressive behavior in a number of species (Holmes and Sherman, 1982; Gompper et al., 1997; Olsen and Jarvi, 1997), presumably due to inclusive fitness benefits (Hamilton, 1964). In addition, individuals tend to share food more often with kin (Fragaszy et al., 1997; Belisle and Chapais, 2001; Ha et al., 2003). These factors suggest that kinship could decrease harassment and increase sharing. Therefore, less harassment may elicit more sharing when interacting with kin.

Finally, I contend that harassment is a general explanation of sharing that can apply to many different species. Comparative studies provide critical information on the general applicability of hypotheses. Given that harassment only requires a divisible food source, it could influence sharing in a number of species. Primate food sharing has been well studied, yet researchers have examined harassment in only a handful of primate species. Other species that share food, such as vampire bats (Wilkinson, 1984; Denault and McFarlane, 1995), should also be examined for the presence of harassment. In addition, co-feeding in many social carnivores such as lions and hyenas could result from avoiding harassment costs associated with food defense. By defining the concept of sharing in terms of economics rather than behavior, we can apply sharing theory to many more instances of animal social foraging.

Acknowledgments

I would like to thank Linda Brent and the staff of the Southwest Foundation for Biomedical Research for assistance in working with chimpanzees. I would also like to thank Larry Williams, Christian Abee, and the staff of the Squirrel Monkey Breeding Research and Resource for assistance with the squirrel monkeys. Dave Stephens offered helpful comments on the manuscript. This project was funded with support from the L.S.B. Leakey Foundation, Alexander P. and Lydia Anderson Fellowship, Animal Behavior Society, Dayton and Wilkie Natural History Funds, Department of Ecology, Evolution, and Behavior, and the University of Minnesota Graduate School. This project was approved by the Institutional Animal Care and Use Committee at the University of Minnesota (Animal Subjects Code 0010A67581).

References

Barnard, C. J. and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.

Beauchamp, G. and Giraldeau, L.-A. 1997. Patch exploitation in a producer-scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behavioral Ecology* 8:54–59.

Belisle, P. and Chapais, B. 2001. Tolerated co-feeding in relation to degree of kinship in Japanese macaques. *Behaviour* 138:487–509.

Blurton Jones, N. G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology* 5:1–3.

Blurton Jones, N. G. 1986. Fitness returns from resources and the outcome of contests: some implications for primatology and anthropology. *In* J. G. Else and P. C. Lee (eds.), Primate Ontogeny, Cognition, and Social Behavior. Cambridge University Press, Cambridge. pp. 393–406.

Blurton Jones, N. G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.

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

Boyd, R. and Richerson, P. J. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.

Chapman, M. R. and Kramer, D. L. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* 52:83–94.

Clements, K. C. and Stephens, D. W. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour* 50:527–535.

Clutton-Brock, T. H. and Parker, G. A. 1995. Punishment in animal societies. *Nature* 373:209–216.

Dall, S. R. X. 2002. Can information sharing explain recruitment to food from communal roosts? *Behavioral Ecology* 13:42–51.

de Waal, F. B. M. 1989. Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution* 18:433–459.

de Waal, F. B. M. 1997. Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology* 111:370–378.

de Waal, F. B. M., Luttrell, L. M., and Canfield, M. E. 1993. Preliminary data on voluntary food sharing in brown capuchin monkeys. *American Journal of Primatology* 29:73–78.

Denault, L. K. and McFarlane, D. A. 1995. Reciprocal altruism between male vampire bats, *Desmodus rotundus*. *Animal Behaviour* 49:855–856.

Fragaszy, D. M., Feuerstein, J. M., and Mitra, D. 1997. Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). *Journal of Comparative*

Psychology 111:194–200.

Fragaszy, D. M. and Mason, W. A. 1983. Comparisons of feeding behavior in captive squirrel and titi monkeys (*Saimiri sciureus* and *Callicebus moloch*). *Journal of Comparative Psychology* 97:310–326.

Fruth, B. and Hohmann, G. 2002. How bonobos handle hunts and harvests: why share food? *In* C. Boesch, G. Hohmann, and L. F. Marchant (eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge. pp. 231–243.

Giraldeau, L.-A. and Beauchamp, G. 1999. Food exploitation: searching for the optimal joining policy. *Trends in Ecology and Evolution* 14:102–106.

Giraldeau, L.-A. and Caraco, T. 2000. Social Foraging Theory. Princeton University Press, Princeton.

Gompper, M. E., Gittleman, J. L., and Wayne, R. K. 1997. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Animal Behaviour* 53:781–797.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge, Mass.

Grinnell, J., Packer, C., and Pusey, A. E. 1995. Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour* 49:95–105.

Ha, R. R., Bentzen, P., Marsh, J., and Ha, J. C. 2003. Kinship and association in social foraging Northwestern crows (*Corvus caurinus*). *Bird Behavior* in press.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. *Journal of Theoretical Biology* 7:1–52.

Hauser, M. D. 1992. Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences (USA)* 89:12137–12139.

Heinrich, B. 1988. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by ravens, *Corvus corvax*. *Behavioral Ecology and Sociobiology* 23:141–156.

Hemelrijk, C. K., Meier, C., and Martin, R. D. 1999. 'Friendship' for fitness in chimpanzees? *Animal Behaviour* 58:1223–1229.

Holmes, W. G. and Sherman, P. W. 1982. The ontogeny of kin recognition in two species of ground squirrels. *American Zoologist* 22:491–517.

Kuroda, S. 1984. Interaction over food among pygmy chimpanzees. *In* R. Sussman (ed.), The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Plenum Press, New York. pp. 301–324.

Mesterton-Gibbons, M. and Dugatkin, L. A. 1999. On the evolution of delayed recruitment to food bonanzas. *Behavioral Ecology* 10:377–390.

Mitani, J. C. and Watts, D. P. 2001. Why do chimpanzees hunt and share meat? *Animal Behaviour* 61:915–924.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., and Uehara, S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? *In* T. Nishida, W. C. McGrew, P. Marler, M. Pickford, and F. B. M. de Waal (eds.), Topics in

Primatology, vol. 1. University of Tokyo Press, Tokyo. pp. 159–174.

Nissen, H. W. and Crawford, M. P. 1936. A preliminary study of food-sharing behaviour in young chimpanzees. *Journal of Comparative Psychology* 22:383–419.

Olsen, K. H. and Jarvi, T. 1997. Effects of kinship on aggression and RNA content in juvenile arctic charr. *Journal of Fish Biology* 51:422–435.

Stanford, C. B., Wallis, J., Matama, H., and Goodall, J. 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. *American Journal of Physical Anthropology* 94:213–228.

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

Stevens, J. R. and Stephens, D. W. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology* 13:393–400.

Takahata, Y., Hasegawa, T., and Nishida, T. 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *International Journal of Primatology* 5:213–233.

Teleki, G. 1973. The Predatory Behavior of Wild Chimpanzees. Bucknell University Press, Lewisburg.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Valone, T. J. 1996. Food-associated calls as public information about patch quality. *Oikos* 77:153–157.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. 1991. Producers, scroungers, and group foraging. *American Naturalist* 137:847–863.

Wilkinson, G. S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308:181–184.

Wrangham, R. W. 1975. The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, Cambridge University.

Ydenberg, R. C., Giraldeau, L.-A., and Kramer, D. L. 1986. Interference competition, payoff asymmetries, and the social relationships of central place foragers. *Theoretical Population Biology* 30:26–44.

Table 4.1: Predicted and observed responses by food owners and beggars to partition and divisibility treatments.

	Solid food			**Divided food**		
	Predicted	Chimpanzees	Squirrel Monkeys	Predicted	Chimpanzees	Squirrel Monkeys
Partition present	*Beggar: Not Harass*	Y	Y	*Beggar: Harass*	Y	N
	Owner: Defend	Y	Y	*Owner: Defend*	Y	Y
Partition absent	*Beggar: Not Harass*	Y	N	*Beggar: Harass*	Y	Y
	Owner: Defend	N	N	*Owner: Share*	Y	Y

Table 4.2: Effects of Partition and Divisibility treatments on harassment measures in chimpanzees (repeated measures ANOVA).

(a) Harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	22.69	11.25	0.0064
Error(Partition)	11	2.02		
Divisibility	1	4.69	7.17	0.0215
Error(Divisibility)	11	0.65		
Partition×Divisibility	1	0.02	0.01	NS
Error(Partition×Divisibility)	11	2.19		
Remaining Error	144	0.97		

(b) Harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	32007.5	12.09	0.0052
Error(Partition)	11	2647.7		
Divisibility	1	1185.0	1.68	NS
Error(Divisibility)	11	704.9		
Partition×Divisibility	1	0.3	0.00	NS
Error(Partition×Divisibility)	11	802.5		
Remaining Error	144	1606.4		

(c) Active harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	1.69	2.58	NS
Error(Partition)	11	0.65		
Divisibility	1	0.08	0.4490	NS
Error(Divisibility)	11	0.19		
Partition×Divisibility	1	0.08	0.4490	NS
Error(Partition×Divisibility)	11	0.19		
Remaining Error	144	0.07		

continued on next page

Table 4.2: *continued from previous page*

(d) Active harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	1180.08	3.77	0.0781
Error(Partition)	11	312.78		
Divisibility	1	391.02	3.33	0.0951
Error(Divisibility)	11	117.31		
Partition×Divisibility	1	481.33	4.83	0.0501
Error(Partition×Divisibility)	11	99.48		
Remaining Error	144	182.91		

Table 4.3: Effects of Partition and Divisibility treatments on sharing measures in chimpanzees (repeated measures ANOVA).

(a) Sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	17.52	10.43	0.0080
Error(Partition)	11	1.70		
Divisibility	1	0.08	0.27	NS
Error(Divisibility)	11	0.31		
Partition×Divisibility	1	0.19	0.62	NS
Error(Partition×Divisibility)	11	0.30		
Remaining Error	144	0.56		

(b) Sharing amount

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	15123.00	5.38	0.0406
Error(Partition)	11	2810.18		
Divisibility	1	60.75	0.16	NS
Error(Divisibility)	11	382.30		
Partition×Divisibility	1	36.75	0.09	NS
Error(Partition×Divisibility)	11	405.75		
Remaining Error	144	590.13		

(c) Active sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	1.88	1.27	NS
Error(Partition)	11	1.48		
Divisibility	1	0.05	3.67	0.0819
Error(Divisibility)	11	0.01		
Partition×Divisibility	1	0.13	2.57	NS
Error(Partition×Divisibility)	11	0.05		
Remaining Error	144	0.13		

Table 4.4: Effects of harassment measures on sharing amount in chimpanzees (multiple regression).

Source of variation	*df*	*Mean Square*	*F*	*p*
Harassment freq.	1	81.67	0.06	NS
Harassment duration	1	4439.75	3.52	0.0637
Active harassment freq.	1	23459.93	18.62	4×10^{-5}
Active harassment duration	1	574.45	0.46	NS
Error	91	1259.68		

Table 4.5: Effects of Partition and Divisibility treatments on harassment measures in squirrel monkeys (repeated measures ANOVA).

(a) Harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	162.05	24.43	0.0004
Error(Partition)	11	6.63		
Divisibility	1	0.87	0.75	NS
Error(Divisibility)	11	1.16		
Partition×Divisibility	1	1.16	0.31	NS
Error(Partition×Divisibility)	11	3.77		
Remaining Error	144	3.73		

(b) Harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	8146.68	12.74	0.0044
Error(Partition)	11	639.64		
Divisibility	1	70.81	0.37	NS
Error(Divisibility)	11	190.71		
Partition×Divisibility	1	114.83	0.59	NS
Error(Partition×Divisibility)	11	193.86		
Remaining Error	144	342.02		

(c) Active harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	20.67	9.61	0.0101
Error(Partition)	11	2.15		
Divisibility	1	0.42	0.70	NS
Error(Divisibility)	11	0.60		
Partition×Divisibility	1	0.42	0.32	NS
Error(Partition×Divisibility)	11	1.31		
Remaining Error	144	1.47		

continued on next page

Table 4.5: *continued from previous page*

(d) Active harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	1255.63	20.98	0.0008
Error(Partition)	11	59.86		
Divisibility	1	45.05	0.50	NS
Error(Divisibility)	11	89.41		
Partition×Divisibility	1	30.88	0.38	NS
Error(Partition×Divisibility)	11	82.15		
Remaining Error	144	90.23		

Table 4.6: Effects of Partition and Divisibility treatments on sharing measures in squirrel monkeys (repeated measures ANOVA).

(a) Sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	11.26	15.96	0.0021
Error(Partition)	11	0.71		
Divisibility	1	0.06	0.11	NS
Error(Divisibility)	11	0.51		
Partition×Divisibility	1	0.11	0.26	NS
Error(Partition×Divisibility)	11	0.43		
Remaining Error	144	0.40		

(b) Sharing amount

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	493.97	13.64	0.0035
Error(Partition)	11	36.23		
Divisibility	1	25.37	1.72	NS
Error(Divisibility)	11	14.73		
Partition×Divisibility	1	19.99	1.83	NS
Error(Partition×Divisibility)	11	10.94		
Remaining Error	144	16.96		

(c) Active sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Partition	1	1.69	17.47	0.0015
Error(Partition)	11	0.10		
Divisibility	1	0.00	0.00	NS
Error(Divisibility)	11	0.07		
Partition×Divisibility	1	0.00	0.00	NS
Error(Partition×Divisibility)	11	0.07		
Remaining Error	144	0.08		

Table 4.7: Effects of harassment measures on sharing amount in squirrel monkeys (multiple regression).

Source of variation	*df*	*Mean Square*	*F*	*p*
Harassment freq.	1	109.20	3.12	0.0805
Harassment duration	1	106.02	3.03	0.0850
Active harassment freq.	1	123.66	3.52	0.0632
Active harassment duration	1	0.73	0.02	NS
Error	91	34.96		

Table 4.8: Effects of species (chimpanzee and squirrel monkey) on harassment measures (repeated measures ANOVA).

(a) Harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	110.07	20.69	0.0039
Error(Species)	6	31.92		
Partition	1	156.01	24.14	0.0005
Error(Partition)	11	6.46		
Divisibility	1	4.39	7.03	0.0226
Error(Divisibility)	11	0.62		
Remaining Error	288	2.35		

(b) Harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	8678.6	4.05	0.0909
Error(Species)	6	2143.0		
Partition	1	36742.1	25.82	0.0004
Error(Partition)	11	1423.1		
Divisibility	1	292.2	0.59	NS
Error(Divisibility)	11	494.7		
Remaining Error	288	972.7		

(c) Active harassment frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	33.60	23.24	0.0029
Error(Species)	6	1.45		
Partition	1	17.34	13.34	0.0038
Error(Partition)	11	1.30		
Divisibility	1	0.08	0.22	NS
Error(Divisibility)	11	0.39		
Remaining Error	288	0.77		

continued on next page

Table 4.8: *continued from previous page*

(d) Active harassment duration

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	157.80	0.78	NS
Error(Species)	6	203.45		
Partition	1	2438.46	10.19	0.0086
Error(Partition)	11	239.28		
Divisibility	1	352.82	3.14	NS
Error(Divisibility)	11	112.29		
Remaining Error	288	136.57		

Table 4.9: Effects of species (chimpanzee and squirrel monkey) on sharing measures (repeated measures ANOVA).

(a) Sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	0.03	0.04	NS
Error(Species)	6	0.64		
Partition	1	28.56	29.64	0.0002
Error(Partition)	11	0.96		
Divisibility	1	0.13	0.43	NS
Error(Divisibility)	11	0.31		
Remaining Error	288	0.48		

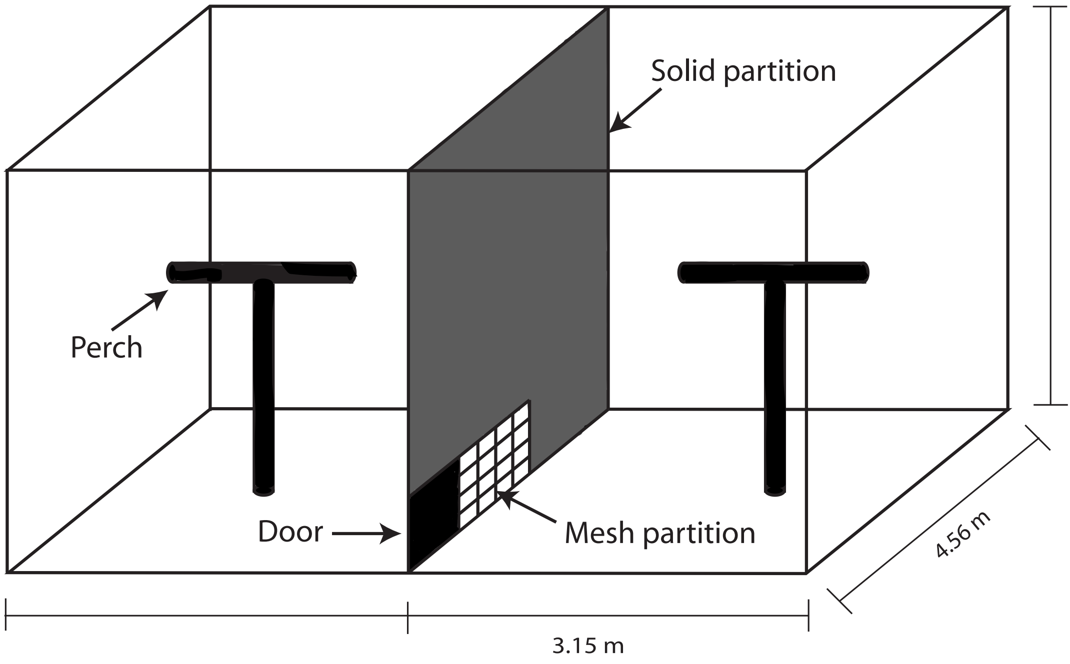
(b) Sharing amount

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	0.89	6.35	0.0453
Error(Species)	6	0.14		
Partition	1	3.08	28.98	0.0002
Error(Partition)	11	0.11		
Divisibility	1	0.04	0.90	NS
Error(Divisibility)	11	0.04		
Remaining Error	288	0.05		

(c) Active sharing frequency

Source of variation	*df*	*Mean Square*	*F*	*p*
Species	1	0.06	0.06	NS
Error(Species)	6	0.98		
Partition	1	3.52	4.64	0.0542
Error(Partition)	11	0.76		
Divisibility	1	0.03	0.57	NS
Error(Divisibility)	11	0.05		
Remaining Error	288	0.11		

(a) Chimpanzee



(b) Squirrel monkey

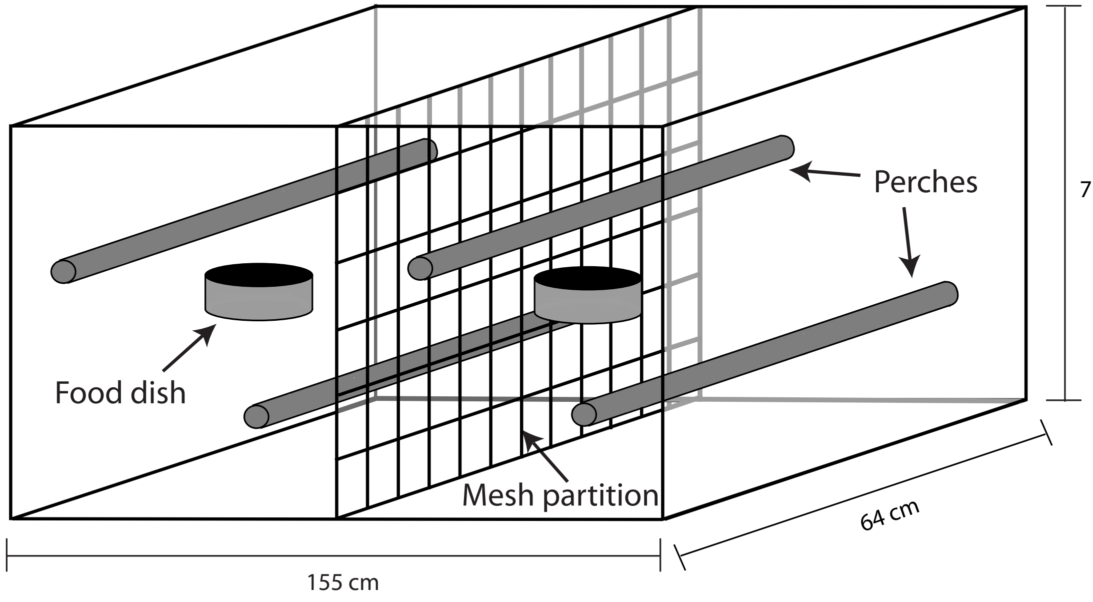
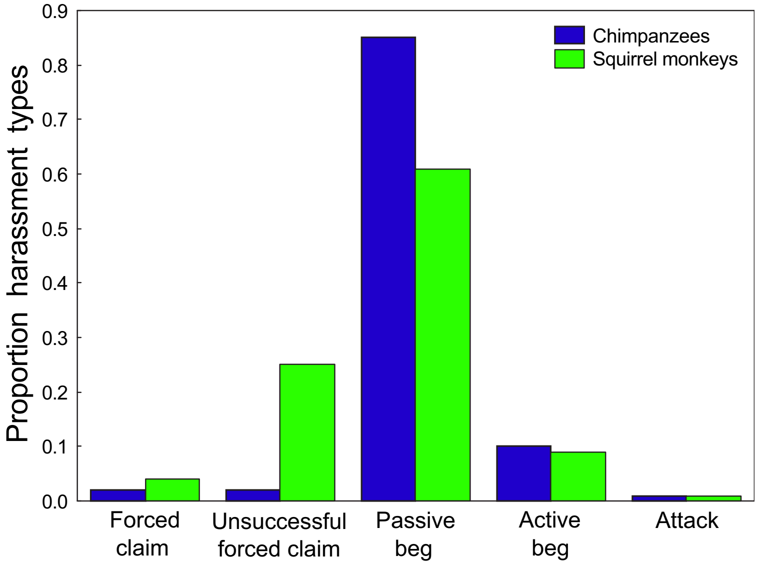


Figure 4.1: Experimental apparatus. (a) The chimpanzees were tested in their outdoor cages, one subject on either side of the partition. The partition was solid except for a 142×50 cm section of mesh. The door was opened during the No Partition treatment. (b) The squirrel monkeys were tested in Allentown cages, separated by a plastic mesh partition. The entire partition was removed for the No Partition treatment.

(a) Harassment



(b) Sharing

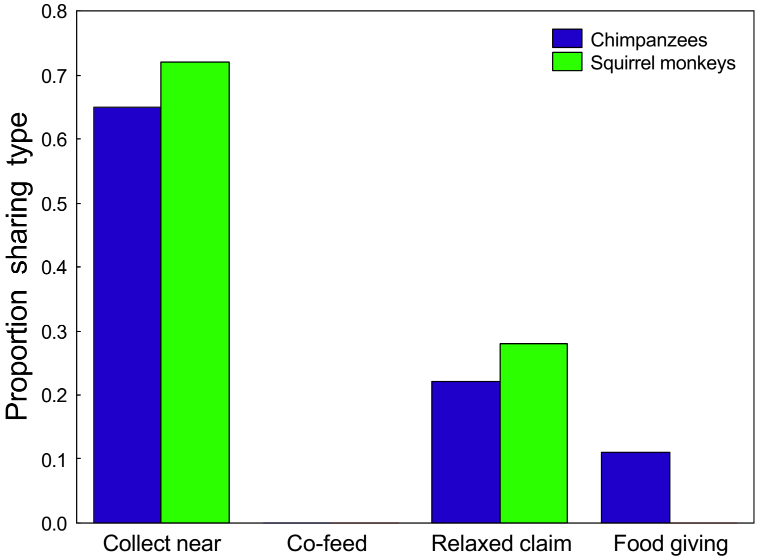
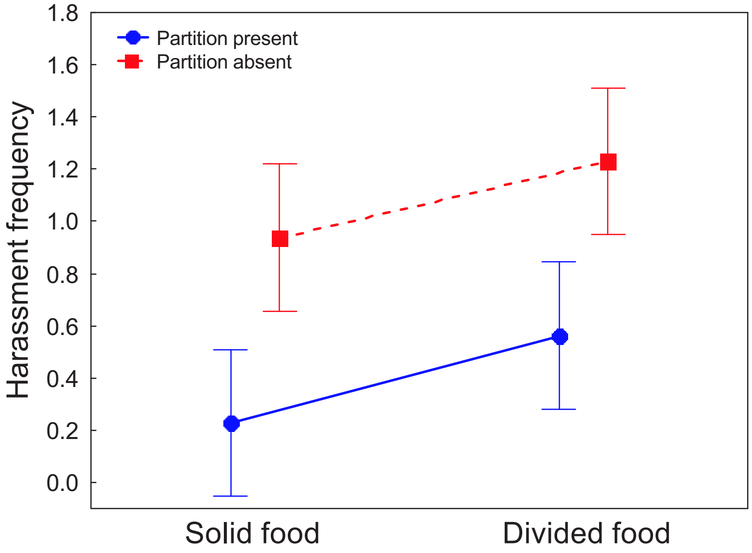


Figure 4.2: Behavior frequencies. (a) Chimpanzees and squirrel monkeys have similar frequencies of each of the harassment types. Chimpanzees harassed 142 times, whereas squirrel monkeys harassed 192 times. (b) Both species also have similar frequencies of the different sharing types. Chimpanzees shared 60 times, and squirrel monkeys shared 65 times.

(a) Chimpanzees



(b) Squirrel monkeys

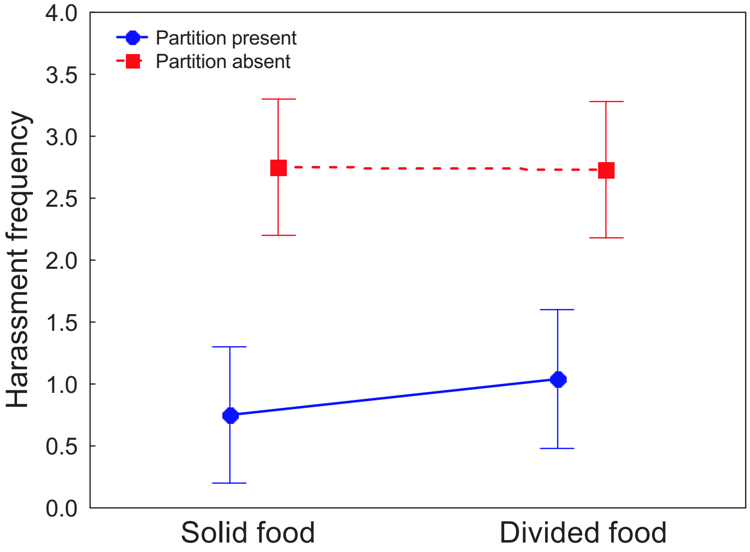
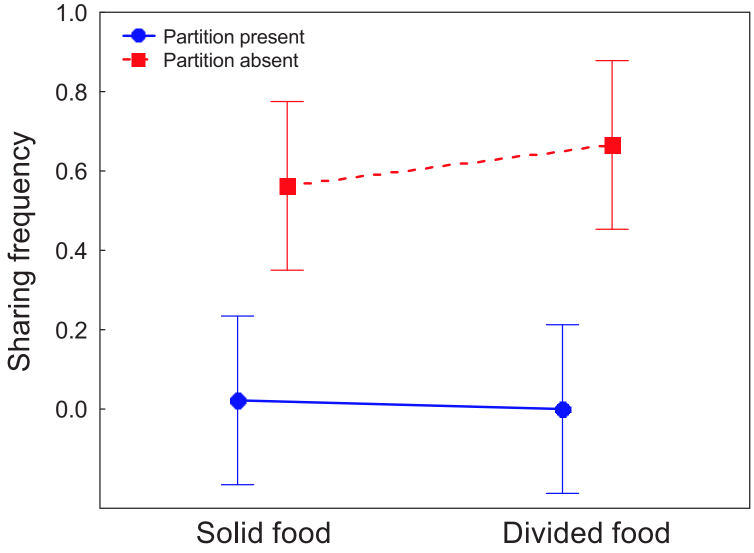


Figure 4.3: Effects of Partition and Divisibility treatments on harassment frequency (number of harassment events per trial). (a) Chimpanzees showed an effect of both Partition and Divisibility treatments on harassment. Subjects harassed more in the absence of the partition and when food was divisible. (b) Squirrel monkeys only showed an effect of Partition treatment, harassing more in the absence of the partition. Symbols and error bars represent least-squares means and 95% confidence intervals.

(a) Chimpanzees



(b) Squirrel monkeys

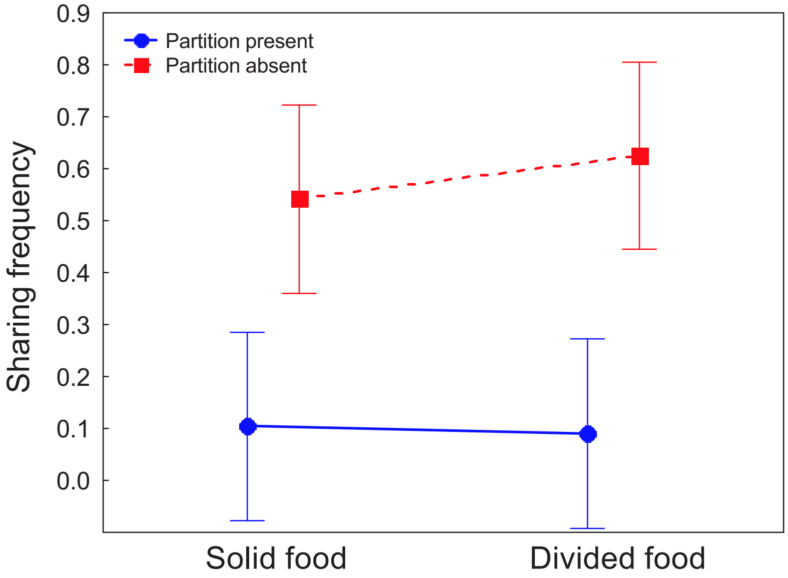
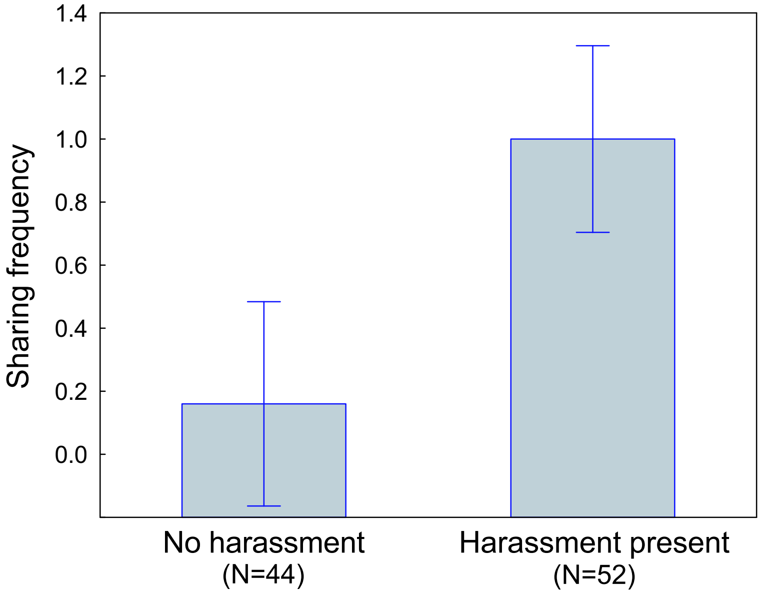


Figure 4.4: Effects of Partition and Divisibility treatments on sharing frequency (number of sharing events per trial). (a) Chimpanzees showed only an effect of Partition treatment on sharing. Subjects shared more in the absence of the partition. (b) Squirrel monkeys also only showed an effect of Partition treatment, sharing more in the absence of the partition. Symbols and error bars represent least-squares means and 95% confidence intervals.

(a) Chimpanzees



(b) Squirrel monkeys

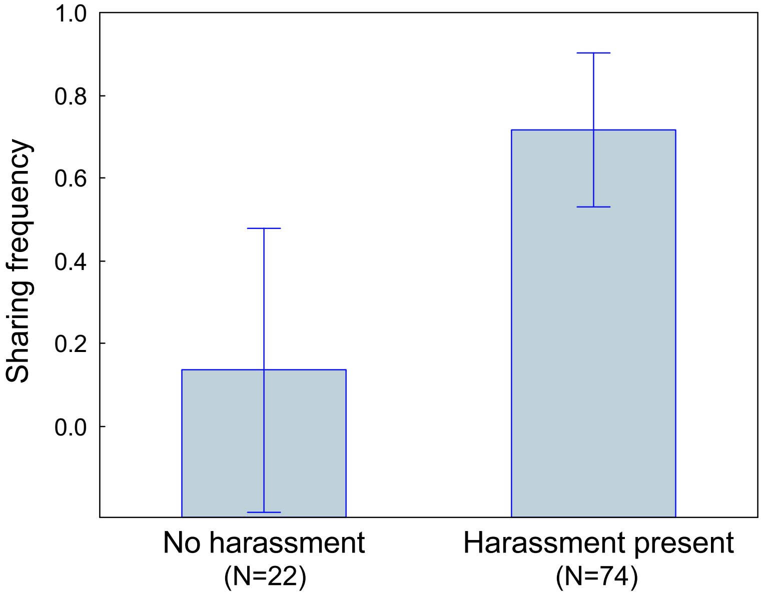
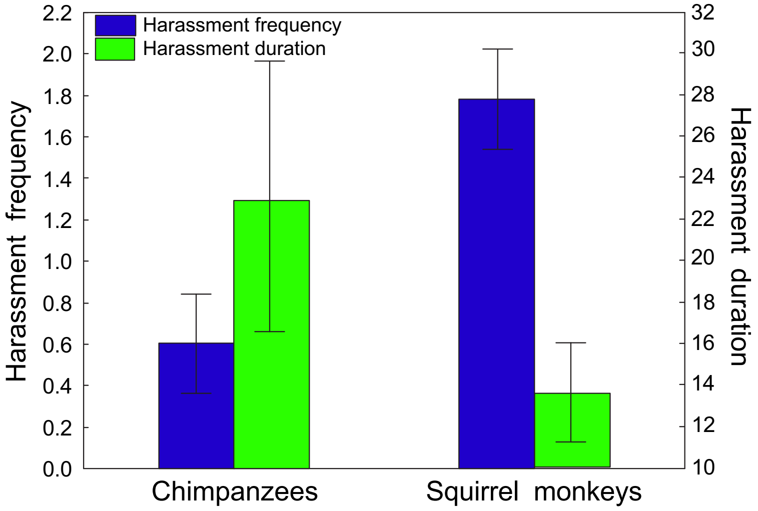


Figure 4.5: Effects of harassment on sharing. In the absence of a partition, both (a) chimpanzees and (b) squirrel monkeys shared more frequently in trials with harassment present. Error bars represent 95% confidence intervals.

(a) Harassment



(b) Sharing

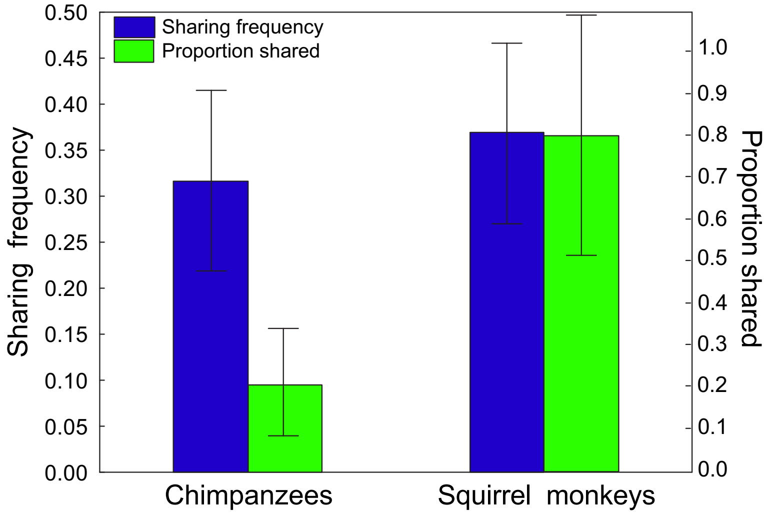


Figure 4.6: Comparison of harassment and sharing between chimpanzees and squirrel monkeys. (a) Squirrel monkeys harassed more frequently than chimpanzees (dark bars), but chimpanzees harassed for longer durations (light bars). (b) Surprisingly, both shared equally frequently (dark bars), and squirrel monkeys shared larger amounts (light bars). Error bars represent 95% confidence intervals.

Conclusion

This thesis integrates theoretical, empirical, and comparative analyses of food sharing to underscore the importance of harassment. The only line of evidence lacking is observational evidence from natural populations of animals. My colleague Ian Gilby has examined these issues in a wild population of chimpanzees. His results support the significance of harassment influencing food sharing. He has found that individuals that harass more intensely receive more food from food owners (unpublished data). In addition, harassment predicts sharing better than sexual receptivity, grooming frequency, and association levels. Multiple lines of evidence suggest that apparently altruistic food sharing may, in fact, provide selfish benefits to the donor. Therefore, we must address harassment in future investigations of sharing.

Harassment as a general explanation of sharing

The advantage of harassment as an explanation of sharing is its simplicity. With this simplicity comes general applicability to different sharing contexts in many species. Harassment requires no special relationships or cognitive skills to trigger sharing. Rather, any animal can harass to gain access to resources. Despite this generality, harassment probably remains unnoticed in many animal species.

Similar models of animal interaction indicate that harassment-like behavior occurs in many species. Resource defense, producer-scrounger, and kleptoparasitism theory predict that interference competition may reduce the defensibility of a resource and elicit sharing (Barnard, 1984; Giraldeau and Caraco, 2000). Researchers have recorded this effect in invertebrates (Iyengar, 2000; Miyashita, 2001), fish (Chapman and Kramer, 1996; Nilsson, 2000), birds (Brockmann and Barnard, 1979; Goss-Custard et al., 1998; Amat, 2000), and mammals (Durant, 2000; Di Bitetti and Janson, 2001; MacNulty et al., 2001). Therefore, harassment may occur more frequently than originally thought.

Harassment is such a general explanation that it may apply in other cooperative contexts. Harassment and punishment play a role in sexual coercion (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995a,b), reproductive suppression (Reeve and Gamboa, 1987; Emlen and Wrege, 1992; Reeve, 1992), and helping-at-the-nest (Mulder and Langmore, 1993). Drawing these diverse topics into a unified theory of harassment may help produce a more general model of manipulative mutualism.

Learning, harassment, and cooperation

The influence of harassment on sharing may owe its effectiveness to its close association with the general principles of learning. Although this thesis focuses on ultimate consequences of how harassment affects sharing (that is, how harassment and sharing affect fitness), the proximate consequences of harassment on animal behavior also influence sharing. Thus far, I have contended that harassment imposes fitness costs on food owners, making sharing beneficial because it avoids harassment. However, harassment may have more direct, immediate effects on behavior. If harassment is an unfavorable stimulus to the food owner, simple instrumental learning via the law of effect (e.g., Thorndike, 1911; Skinner, 1938, and the rich tradition of research that follows them) may account for the increase in sharing. Specifically, Thorndike's law of effect predicts that behaviors eliciting "satisfaction" tend to increase in frequency, while those that elicit "discomfort" tend to decrease in frequency (Thorndike, 1911, p. 245). By sharing, a food owner experiences the satisfaction of alleviating the discomfort resulting from defending the food. However, owners could prevent the negative stimulus altogether if they could detect a signal that precedes harassment and preemptively share before harassment occurs. Learning theory predicts that this type of 'avoidance conditioning' can occur through a combination of classical and instrumental conditioning (Mowrer, 1956).

Learning plays an important role in cooperative behaviors besides food sharing. One of the most relevant examples in the Prisoner's Dilemma literature is the Pavlov strategy (Kraines and Kraines, 1989; Nowak and Sigmund, 1993). Pavlov or 'win-stay/lose-shift' is a strategy in the Iterated Prisoner's Dilemma (IPD) based on principles of learning (although mistakenly named after Pavlov instead of Thorndike). In this strategy, players repeat choices that result in 'wins' and switch behaviors following 'losses'. Although based on psychological principles, the Pavlov strategy arbitrarily assigns CC and DC as wins and CD and DD as losses rather than explicitly considering the reinforcement value of the payoffs. Nowak and Sigmund (1993) contended that this strategy outperforms tit-for-tat and can maintain cooperation in the IPD. No experimental evidence corroborates these predictions in non-human animals (but see Wedekind and Milinski, 1996; Baker and Rachlin, 2002, for experiments with humans). Other researchers have utilized linear operator models to directly examine how animals learn to cooperate or defect in the IPD (Rapoport and Chammah, 1965; Stephens and Clements, 1998; Macy and Flache, 2002). These models explicitly investigate the role of a reinforcer 'standard' that distinguishes between rewarding and punishing payoffs. These and other models of the psychology of cooperation provide important perspectives to the study of the evolution of cooperation.

Extensions

Some researchers suggest that harassment and punishment may have played a pivotal role in the evolution of human cooperation. Economists, anthropologists, and behavioral ecologists have investigated punishment and cooperation in human public goods games (Boyd and Richerson, 1992; Frank, 1996; Henrich and Boyd, 2001; Sigmund et al., 2001). In public goods games, individuals contribute to a common pool and divide the spoils. For example, a group of hunters cooperate to capture a large prey item and share the carcass. What prevents an individual from avoiding the costs of hunting but reaping the benefits? Cooperation may stabilize by inflicting costs on cheaters via punishment. However, this shifts the temptation to cheat to a different level: who pays the costs of punishment? Although some argue that punishment may cost the punisher nothing (Hirshleifer and Rasmusen, 1989), others contend that this is an unrealistic assumption (Hammerstein, 1995). Boyd and Richerson (1992) proposed that punishment may occur if non-punishers are punished. That is, individuals that fail to pay the cost of punishing a defector receive a costly punishment from others. Unfortunately, this scenario falls into an infinite regress of punishers punishing those that do not punish those that do not punish defectors, *ad infinitum*. Henrich and Boyd (2001) avoided this problem by speculating that transmission of conformity may perpetuate punishment. If individuals adopt similar behaviors, punishment may stabilize, assuming that cooperation occurs regularly. This model, however, requires relatively high levels of initial cooperation and punishment to sustain cooperation. Regardless of theoretical limitations, empirical work demonstrates the effectiveness of punishment. In experimental public goods games, punishment substantially increases cooperation even though it decreases both players' payoffs and the subjects only play against each opponent once (Fehr and Gachter, 2002; Andreoni et al., 2003). Therefore, the ubiquity of harassment and punishment indicates their significance in the evolution of complex cooperative systems in humans.

Summary

Harassment and punishment may play a crucial role in cooperation for both human and non-human animals. By reducing the fitness of defectors, harassment favors selfish cooperation. This type of manipulative mutualism emphasizes the role of selfishness in apparently altruistic situations.

References

Amat, J. A. 2000. Courtship feeding, food sharing, or tolerated theft among paired red-crested pochards (*Netta rufina*)? *Journal Fur Ornithologie* 141:327–334.

Andreoni, J. A., Harbaugh, W., and Vesterlund, L. 2003. The carrot or the stick: rewards, punishments and cooperation. *American Economic Review* in press.

Baker, F. and Rachlin, H. 2002. Teaching and learning in a probabilistic prisoner's dilemma. *Behavioural Processes* 57:211–226.

Barnard, C. J. 1984. Producers and Scroungers: Strategics of Exploitation and Parasitism. Chapman and Hall, New York.

Boyd, R. and Richerson, P. J. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171–195.

Brockmann, H. J. and Barnard, C. J. 1979. Kleptoparasitism in birds. *Animal Behaviour* 27:487–514.

Chapman, M. R. and Kramer, D. L. 1996. Guarded resources: the effect of intruder number on the tactics and success of defenders and intruders. *Animal Behaviour* 52:83–94.

Clutton-Brock, T. H. and Parker, G. A. 1995a. Punishment in animal societies. *Nature* 373:209–216.

Clutton-Brock, T. H. and Parker, G. A. 1995b. Sexual coercion in animal societies. *Animal Behaviour* 49:1345–1365.

Di Bitetti, M. S. and Janson, C. H. 2001. Social foraging and the finder's share in capuchin monkeys. *Animal Behaviour* 62:47–56.

Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* 11:624–632.

Emlen, S. E. and Wrege, P. H. 1992. Parent-offspring conflict and the recruitment of helpers among bee-eaters. *Nature* 356:331–333.

Fehr, E. and Gachter, S. 2002. Altruistic punishment in humans. *Nature* 415:137–140.

Frank, S. A. 1996. Policing and group cohesion when resources vary. *Animal Behaviour* 52:1163–1169.

Giraldeau, L.-A. and Caraco, T. 2000. Social Foraging Theory. Princeton University Press, Princeton.

Goss-Custard, J. D., Cayford, J. T., and Lea, S. E. G. 1998. The changing trade-off between food finding and food stealing in juvenile oystercatchers. *Animal Behaviour* 55:745–760.

Hammerstein, P. 1995. A twofold tragedy unfolds. *Nature* 377:478.

Henrich, J. and Boyd, R. 2001. Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology* 208:79–89.

Hirshleifer, D. and Rasmusen, E. 1989. Cooperation in a repeated prisoner's dilemma with ostracism. *Journal of Economic Behavior and Organization* 12:87–106.

Iyengar, E. V. 2000. To steal or not to steal? That is the question. Suspension feeding versus kleptoparasitism in a marine snail. *American Zoologist* 40:1073.

Kraines, D. and Kraines, V. 1989. Pavlov and the prisoner's dilemma. *Theory and Decision* 26:47–79.

MacNulty, D. R., Varley, N., and Smith, D. W. 2001. Grizzly bear, *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. *Canadian Field-Naturalist* 115:495–498.

Macy, M. W. and Flache, A. 2002. Learning dynamics in social dilemmas. *Proceedings of the National Academy of Sciences (USA)* 99:7229–7236.

Miyashita, T. 2001. Competition for a limited space in kleptoparasitic Argyrodes spiders revealed by field experiments. *Population Ecology* 43:97–103.

Mowrer, O. H. 1956. Two-factor learning theory reconsidered, with special reference to secondary reinforcement and the concept of habit. *Psychological Reviews* 63:114–128.

Mulder, R. A. and Langmore, N. E. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour* 45:830–833.

Nilsson, A. 2000. How cannibalism and thefts influence a freshwater lake: the behaviour and choice of prey in the northern pike. *Fauna Och Flora* 95:97–103.

Nowak, M. A. and Sigmund, K. 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* 364:56–58.

Rapoport, A. and Chammah, A. N. 1965. Prisoner's Dilemma: A Study in Conflict and Cooperation. University of Michigan Press, Ann Arbor.

Reeve, H. K. 1992. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* 358:147–149.

Reeve, H. K. and Gamboa, G. J. 1987. Queen regulation of worker foraging in paper wasps: a social feedback control system, *Polistes fuscatus* (Hymenoptera: Vespidae). *Behaviour* 102:147–167.

Sigmund, K., Hauert, C., and Nowak, M. A. 2001. Reward and punishment. *Proceedings of the National Academy of Sciences (USA)* 98:10757–10762.

Skinner, B. F. 1938. The Behavior of Organisms: An Experimental Analysis. Prentice Hall, Englewood Cliffs, NJ.

Smuts, B. B. and Smuts, R. W. 1993. Male aggression and sexual coercion of females in non-human primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior* 22:1–63.

Stephens, D. W. and Clements, K. C. 1998. Game theory and learning. *In* L. A. Dugatkin and H. K. Reeve (eds.), Game Theory and Animal Behavior. Oxford University Press, Oxford. pp. 239–260.

Thorndike, E. L. 1911. Animal Intelligence. Macmillan, New York.

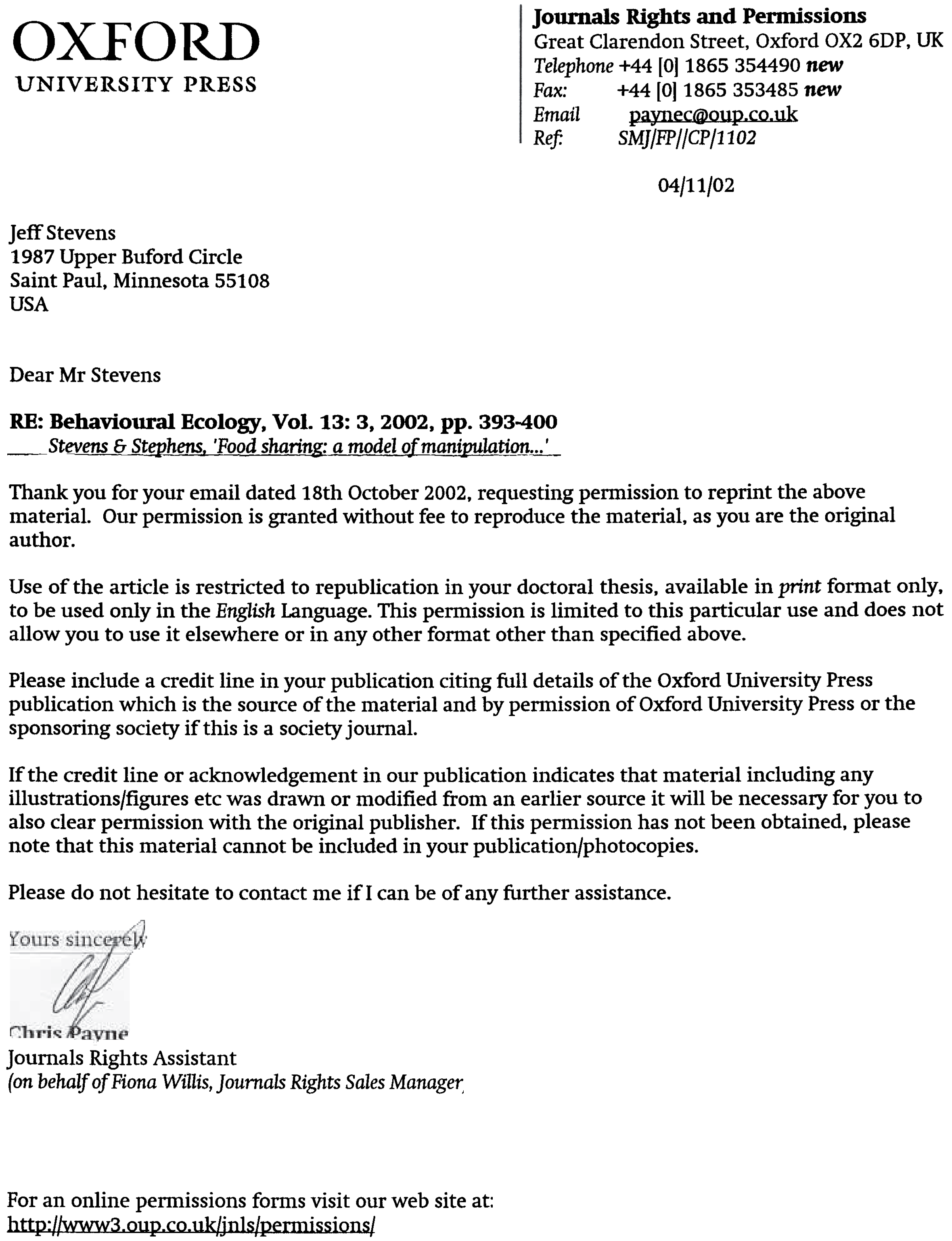
Wedekind, C. and Milinski, M. 1996. Human cooperation in the simultaneous and the alternating prisoner's dilemma: Pavlov versus generous tit-for-tat. *Proceedings of the National Academy of Sciences (USA)* 93:2686–2689.

Appendix

Letter of permission to publish

Attached is a letter from the Oxford University Press permitting the reproduction of previously published material in this thesis. Chapter 3 consists of the following copyrighted material:

Stevens, J.R. and D.W. Stephens. 2002. Food sharing: a model of manipulation by harassment. *Behavioral Ecology* 13(3):393-400. ©Oxford University Press



OXFORD
UNIVERSITY PRESS

Journals Rights and Permissions
Great Clarendon Street, Oxford OX2 6DP, UK
Telephone +44 [0] 1865 354490 ***new***
Fax: +44 [0] 1865 353485 ***new***
Email paynec@oup.co.uk
Ref: *SMJ/FP//CP/1102*

04/11/02

Jeff Stevens
1987 Upper Buford Circle
Saint Paul, Minnesota 55108
USA

Dear Mr Stevens

RE: Behavioural Ecology, Vol. 13: 3, 2002, pp. 393-400
Stevens & Stephens, 'Food sharing: a model of manipulation...'

Thank you for your email dated 18th October 2002, requesting permission to reprint the above material. Our permission is granted without fee to reproduce the material, as you are the original author.

Use of the article is restricted to republication in your doctoral thesis, available in *print* format only, to be used only in the *English* Language. This permission is limited to this particular use and does not allow you to use it elsewhere or in any other format other than specified above.

Please include a credit line in your publication citing full details of the Oxford University Press publication which is the source of the material and by permission of Oxford University Press or the sponsoring society if this is a society journal.

If the credit line or acknowledgement in our publication indicates that material including any illustrations/figures etc was drawn or modified from an earlier source it will be necessary for you to also clear permission with the original publisher. If this permission has not been obtained, please note that this material cannot be included in your publication/photocopies.

Please do not hesitate to contact me if I can be of any further assistance.

Yours sincerely

Chris Payne
Journals Rights Assistant
(on behalf of Fiona Willis, Journals Rights Sales Manager

For an online permissions forms visit our web site at:
http://www3.oup.co.uk/jnls/permissions/