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

Patton, J. Q. 1996. Thoughtful warriors: Status, warriorship, and alliance in the Ecuadorian Amazon. Ph.D. Dissertation, University of California at Santa Barbara.

Ross, E. B. 1976. The Achuara Jivaro: Cultural adaptation in the upper Amazon. Ph.D. Dissertation, Columbia University.

Ross, J. B. 1984. Effects of Contact on Revenge Hostilities Among the Achuara Jivaro. In *Warfare, Culture, and Environment.* R. B. Ferguson, ed. Pp. 83–109. New York: Academic Press.

Ross, J. B. 1988. A balance of deaths: Revenge feuding among the Achuara Jivaro of the northwest Peruvian Amazon. Ph.D. Dissertation, Columbia University.

Sahlins, M. D. 1961. The segmentary lineage: Instrument of predatory expansion. *American Anthropologist* 63:322–345.

Sahlins, M. D. 1965. On the sociology of primitive exchange. In *The Relevance of Models for Social Anthropology.* M. Banton, ed. Pp. 139–236. London: Travestock.

Taylor, A.-C. 1981. God-wealth: The Achuar and the missions. In *Cultural Transformation and Ethnicity in Modern Ecuador.* N. Whitten, ed. Pp. 647–677. Urbana: University of Illinois Press.

Trivers, R. L. 1971. The Evolution of Reciprocal Altruism. *Quarterly Review of Biology* 46:35–57.

de Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex Among Apes.* Baltimore: John Hopkins University Press.

de Waal, F. B. M., and A. H. Harcourt. 1992. Coalitions and alliances: A history of ethological research. In *Coalitions and Alliances in Humans and Other Animals.* A. H. Harcourt and F. B. M. de Waal, eds. Pp. 1–19. Oxford: Oxford University Press.

Whitten, N. E. 1976. *Sacha Runa: Ethnicity and Adaptation of Ecuadorian Jungle Quichua.* Urbana: University of Illinois Press.

Wright, R. 1994. *The Moral Animal. Why We Are the Way We Are: The New Science of Evolutionary Psychology.* New York: Vintage Books.

20

The Emergence and Stability of Cooperative Fishing on Ifaluk Atoll

RICHARD SOSIS

The evolution of cooperative hunting has been of immense interest to biologists and anthropologists. Biologists have observed cooperative hunting in numerous vertebrate and invertebrate species (see Packer and Ruttan 1988), and anthropologists have noted that human foragers often cooperate when hunting and fishing (see Hayden 1981). Cooperative hunting is frequently cited as a possible cause of sociality in humans and nonhuman species (e.g., Alexander 1974), although others have argued that cooperative hunting is a consequence rather than a cause of sociality (MacDonald 1983; Packer 1986; Packer et al. 1990). Anthropologists have suggested that cooperative hunting in hominids was a prominent factor in the evolution of human brain size and language (Washburn and Lancaster 1968), as well as the evolution of reciprocity in humans (Kurland and Beckerman 1985). Determining the ecological conditions under which selection pressures will favor cooperative food acquisition is essential for understanding the causes and consequences of cooperative foraging.

There are two components to the evolution of any cooperative behavior: emergence and stability. We can ask two questions to distinguish between the emergence and stability of cooperative hunting: When should a hunter join another hunter rather than hunt solitarily (emergence of cooperation)? and When should an individual free ride while others hunt cooperatively (stability of cooperation)? The goal of this paper is to test theoretical models of the emergence and stability of cooperative foraging using empirical data of cooperative sail-fishing activities on Ifaluk Atoll. Whereas prior models of the evolution of cooperative hunting have assumed that hunters share their returns equally among themselves or all group members (Boesch 1994; Packer 1988; Packer and Ruttan 1988), the models presented here will use empirically observed biases in the sharing patterns of fish in order to explain variance in male participation in cooperative fishing activities on Ifaluk.

EMERGENCE OF COOPERATIVE FORAGING

A number of factors are likely to influence the evolution of group foraging, such as resource defense (Crook 1972), vigilance and predator defense (Caraco and Pulliam 1984; Hamilton 1971), reproductive strategies (Wittenberger 1980), and foraging efficiency (Schoener 1971; see Pulliam and Caraco 1984; Slobodchikoff 1988; Smith 1981 for reviews of the benefits and costs of group foraging). Evolutionary ecologists have been particularly interested in determining the importance of foraging efficiency in the evolution of cooperative foraging, since natural selection is expected to produce foraging strategies that maximize the gain rate in time and energy limited organisms. Foraging return rates have been widely employed in optimal foraging models by anthropologists (see Kaplan and Hill 1992) and biologists (see Stephens and Krebs 1986) as a proximate currency that is assumed to be highly correlated with fitness. Two avenues for the evolution of cooperative foraging based in foraging efficiency have been proposed: variance reduction of average feeding rates (Caraco 1981; Clark and Mangel 1984; Real and Caraco 1986) and increase in average acquisition rates (Caraco 1987; Caraco and Wolf 1975; Pulliam and Millikan 1982). Greater attention has been given to the latter of these routes to cooperative foraging, and this paper will continue that trend.

Foragers are often expected to form foraging parties that maximize per capita net rate of energy capture. Following Smith (1981, 1983, 1985) we can algebraically define mean per capita net rate of energy capture as

$$R_n = \sum_{i=1}^{n} (E_a - E_e)/tn \qquad (1)$$

where n is the foraging group size, t is the duration of the foraging acquisition event, and E_a and E_e are the energy acquired and the energy expended by each of the n members of the foraging group during time t.

A necessary condition for cooperative foraging to emerge is

$$R_n > R_1 \qquad (2)$$

Thus, for cooperative foraging to emerge the mean per capita net return rate of n cooperative foragers must be greater than the mean per capita net solitary return rate.[1] Equation 2 assumes that individuals are free to decide whether to forage cooperatively or solitarily. Equation 2 does not need to hold for all n in order for cooperative foraging to be selected. In other words, the conditions for cooperative foraging to emerge may exist if there is a range of n (or only a single n) over which R_n is greater than R_1. For example, two fishermen on a large boat that they are not able to manage may have per capita fishing return rates much lower than if they were to fish alone on shore. However, the necessary conditions for cooperative foraging to emerge may exist if for some range, say 4–7 fishermen, the mean per capita net return rate of cooperative fishing is greater than the mean per capita solitary return rate.

Where cooperative foraging has emerged, there has been considerable interes[t] in determining the optimal number of foragers in a foraging acquisition group (fo[r] reviews see Giraldeau 1988 and Smith 1991). Natural selection is expected t[o] favor individuals who forage in groups of optimal size—in other words, group[s] that maximize mean resource acquisition rate and therefore genetic contributio[n] (Pulliam and Caraco 1984). However, many studies have noted that the expecta[-] tion to observe optimal group sizes among foragers may be unrealistic because o[f] conflicts of interest between group members and individuals who want to join the group. Individuals are expected to join groups if they can increase their net bene[-] fits, which may result in a net decrease in benefits for those who are already grou[p] members (Clark and Mangel 1984; Hill and Hawkes 1983; Sibly 1983; Smith 1981). This insight has motivated researchers to determine the conditions under which cooperation is stable among a group of foragers.

STABILITY OF COOPERATIVE FORAGING

Even when the prerequisites for the emergence of cooperation are met, it is still necessary to determine the conditions under which cooperation will be stable (Axelrod and Hamilton 1981; Maynard Smith 1983). The ability of a free-riding strategy to invade a group of cooperators will determine the stability of cooperation. Two factors determine the success of a free riding strategy: the ability of cooperators to control a free rider's share of returns (e.g., Boesch 1994) and the ability of cooperators to impose costs on free riders (e.g., Boyd and Richerson 1992; Enquist and Leimar 1993; Hirshleifer and Coll 1988). Mesterton-Gibbons and Dugatkin (1992:270) have defined a "mechanism" for cooperation as a "principal effect whose removal would select for noncooperative behavior." Thus, the existence of a mechanism enabling cooperators to control a free rider's share of returns or impose costs on free riders is a necessary condition for the stability of cooperative foraging. Cooperation will be stable so long as the net benefits of participating (cooperating) in an acquisition event are greater than the net benefits of not participating (free riding).

As biologists have studied the conditions under which individuals cooperate, they have asked related questions concerning the stable coexistence of cooperator and noncooperator strategies. Producer-scrounger models have shown that producers (cooperators) and scroungers (noncooperators) can coexist in a stable environment as long as the net benefits received by scroungers are less than those of cooperators (Barnard 1984; Barnard and Sibly 1981; Vickery et al. 1991). These models suggest that cooperation will be evolutionarily stable when the average payoffs of pursuing cooperation are equal to the average payoffs of free-riding (cf. Higashi and Yamamura 1993; Rannala and Brown 1994).

The goal of this paper is to test theoretical models of the emergence and stability of cooperative foraging using empirical data of cooperative sail-fishing activities

on Ifaluk Atoll. Following a brief ethnographic description, I will discuss the patterns and determinants of fish distribution on Ifaluk. Next I will evaluate whether cooperative fishing on Ifaluk meets the necessary conditions set in equation 2 for the emergence of cooperative foraging. Then, by assuming empirically observed biases in the fish distribution pattern, a model will be generated to predict the conditions under which an individual will join a cooperative pursuit. The model will be compared to observed fishing behavior on Ifaluk. The paper will conclude with a discussion of the results and directions for future inquiry.

ETHNOGRAPHIC BACKGROUND

Ifaluk is a small coral atoll (total land mass is 1.48 km² [Freeman 1951:237–238]) located in Yap State in the Caroline Islands of the Federated States of Micronesia.² Ifaluk consists of four atolls, two of which are inhabited: Falalop and Falachig. There are two villages on each of these atolls. Villages consist of 5–13 matrilocal compounds. The 36 compounds on Ifaluk range in size from 1 to 4 houses and 3 to 37 residents. Households are composed of either nuclear or extended families. The average number of residents on Ifaluk in 1995 was slightly more than 600.³

The residence pattern on Ifaluk is matrilocal. Although men reside at their wife's compound after marriage, they maintain a strong bond with the compound where they were raised, their natal compound. A man's bond to his natal compound is most prominently manifest in his responsibility to work for this compound. For example, as will be discussed below, men are expected to fish in cooperation with other men from their natal compound. Although men occasionally eat meals at their natal compound, they generally eat with their nuclear families at their residential compound.

METHODS

The data presented in this paper were collected from December 1994 through April 1995 on Ifaluk Atoll. During the field session I resided on Falalop atoll and collected observational data on fishing activities in Iyeur and Iyefang villages. I participated in 17 cooperative sail-fishing events, during which no quantitative data were collected. Table 20.1 presents the residential composition of compounds on Falalop.

The study population or risk set (i.e., those individuals who are at risk of participating in a cooperative sail-fishing event) consists of 60 males age 14 and older who either resided on Falalop atoll during the 1994–1995 field session or were raised on Falalop but resided on Falachig, typically as a result of marriage. The choice of excluding males younger than 14 from the risk set was not arbitrary.

Table 20.1. Residential composition and canoe ownership of Falalop compounds

village	compound	number of males (≥14 yr.)	number of females (≥14 yr.)	number of children (<14 yr.)	own canoe
Iyeur	Ilug	5	3	8	Y
	Harowchang	10	15	12	N
	Falichel	3	8	9	N
	Failiglow	1	7	3	N
	Hawong	4	6	5	Y
	village total:	23	39	37	N
Iyefang	Intaifou	3	4	2	N
	Woluwar	10	12	15	Y
	Falul	4	3	3	N
	Mataligob	2	5	6	Y
	Hapelmar	3	2	4	N
	Bwabwa	2	3	0	N
	Niwegitob	2	2	3	N
	village total:	26	31	33	N
	atoll total:	49	70	70	N

Although males younger than 14 often participate and contribute to cooperative fishing events, they are considered to be learning and not fully adult. They are never given any portion of the catch regardless of the distribution, and they are excluded from any men's feast.⁴ There is a cultural precept that males are expected to fish on the canoe associated with the compound where they were raised (see below). Therefore, men who were raised in compounds on Falalop were included in the risk set since they are expected to fish on canoes owned by Falalop compounds, even if they currently reside on Falachig. Males that reside on Falalop who were raised on Falachig were also included in the risk set since they often fished on canoes from Falalop.

Observational data on solitary and cooperative sail-fishing were collected daily on Falalop from December 19 to April 5 with the exception of one week in March (n = 98 observation days). Every morning at 4:00 A.M. during this period I walked to the main canoe house on Falalop and waited for the men to commence cooperative fishing. I recorded which of the four canoes set sail, names of the fishermen on each canoe, and time of departure for each canoe. I was also at the canoe house when each canoe returned. I recorded the time of return for each canoe and the weight and species of each fish caught by canoe. Following the distribution of fish from the canoe house I reweighed all the fish and recorded where each fish was distributed. If inconsistencies were found between the first and second weighing, the fish were weighed a third time and the data were corrected accordingly. Sharon Feldstein monitored eight village-level (felang) and 24 compound-level (shuliwa)

women's redistribution events. During her observations she recorded the names of the distributors, the weight and species of each share redistributed, and the name of the compound that received the share.

Solitary fishing activities occurred in the lagoon and were thus easily monitored because of their high visibility. Observation days were spent at one or several of the Falalop canoe houses that line the shore of the lagoon. All solitary fishing activities commenced from one of these canoe houses. Data collection activities that required me to leave the shoreline (e.g., spot observations) never caused me to lose sight of the lagoon for more than one half hour. Of 57 total solitary fishing events, data were missed during only 3 events. For each solitary fishing event I recorded the name of the solitary fisherman, the time of departure and return, and the weight and species of all fish caught. Data on the sharing patterns of solitarily acquired fish were recorded for 35 fishing events. I recorded the name of the recipient and the weight and type of species received.

The energetic costs of cooperative and solitary fishing were measured using the Energy Expenditure Prediction Program (EEPP) developed by the Center for Ergonomics at the University of Michigan. EEPP is a software program that predicts the energy expenditure of an individual engaged in an activity by calculating the metabolic energy expenditure of the sum of simple task elements of the activity (see Sosis 1997 for a more detailed description of EEPP and its use in this study). All statistical analyses were conducted using SAS.

RESULTS

Subsistence

The people of Ifaluk maintain a subsistence economy. The diet largely consists of pelagic and reef fish, taro, breadfruit, and coconut. Pigs, chickens, and dogs are also raised for consumption, but they are usually prepared only for bimonthly feasts. White rice is the most frequently purchased food product, although not all residents can afford it. There is no refrigeration on Ifaluk. Fish are occasionally smoked, but competition with the dogs, cats, and rats makes long-term storage difficult. For a more detailed description of subsistence on Ifaluk see Sosis 1997.

Fish is the primary source of protein and fats for the people of Ifaluk. Only males participate in fishing activities. Fishing on Ifaluk can be considered in two categories: solitary fishing and cooperative fishing. All solitary fishing methods exploit reef fish in Ifaluk's lagoon. During the observation period (n = 98 days), solitary fishing resulted in the capture of 62 different species of reef fish. The main type of solitary fishing during the trade wind season is line fishing with bait.[5] Octopus and land crabs are most frequently used as bait. Almost all males over 15 years of age own the solitary outrigger canoes used for line fishing. Spear and trap fishing were also observed during the trade wind season (see Burows and Spiro 1957 for a description). During the observation period, only 15 of 45 males who

stored their outrigger canoes on Falalop engaged in any form of solitary fishing, and their returns account for only 2.2% of the fish caught during this period.[6]

Cooperative sail-fishing accounts for 87.7% of all fish caught in the period of observation (Sosis 1997). Most mornings during the trade wind season from October through May, males congregate at the central canoe hut on Falalop in preparation for the daily cooperative sail-fishing. After the canoes are prepared, all the males who are present help to push each canoe that will be sailing that morning into the lagoon. The canoes are then sailed outside the reef where the men fish for large pelagic fish such as yellow fin tuna, mahi mahi, and barracuda. Upon their return, the men throw their catch into a pile that is distributed by a divider after all the canoes have returned (see below).

There are four large sailing canoes on Falalop and eleven on Falachig. Each canoe is owned and maintained by a specific matriline, and hence compound. Each compound is historically associated with a particular canoe, and males are expected to fish on the canoe that is associated with the compound in which they were raised. Indeed, 86.4% (n = 815) of the observed time that males fished they sailed on the canoe that was associated with their natal compound. Although residence patterns are matrilocal, married men fished on the canoe associated with their wife's compound only 5.6% (n = 177) of the times they fished. Despite the consistency with which males adhere to cultural expectations, these rules appear flexible, especially when there are not enough males to man a particular canoe.

Distribution of solitarily acquired fish

Fish acquired by solitary means are the property of the fisherman. Some of the reef fish that men catch are taboo for women to eat. Often when these species are caught the fisherman will build a fire and cook the fish on the shore and invite any male over 14 years of age to join him in a small feast. During 54 observed solitary fishing events, 11 of the 62 species caught were taboo for women to eat, constituting 17.0% of the total weight of all solitarily acquired fish. An average of 76.8% (s.d. = 31.0%; n = 35) of fish caught by solitary means was consumed by the fisherman and his residential compound. During 19 of 35 observed sharing events, there was no sharing outside of the fisherman's residential compound.

Distribution of cooperatively acquired fish

There are a variety of distribution patterns for fish caught during cooperative fishing events. Betzig (1988) has previously described the fish distribution patterns on Ifaluk following cooperative net fishing, which occurs approximately once every two weeks during the summer. Here I will describe the fish distribution patterns following cooperative sail-fishing, which occurs exclusively in the trade wind season. Upon return from a morning's cooperative sail-fishing event, fishermen from each canoe throw their catch into a communal pile that is distributed after all the canoes return. On Falalop atoll, two men have the inherited responsibility of the canoes return.

dividing the fish. The dividers determine the type of distribution and the amount of fish that is allocated to each recipient. During the 1994–1995 field session I observed five patterns of fish distribution following cooperative sail-fishing events on Falalop atoll. Multiple distribution types were often observed at the same distribution event. The five types are:

1. Canoe owner distribution (*shadiwa*): During a canoe owner distribution, compounds that own canoes receive the catch of their canoe. Table 20.1 shows which compounds own a canoe on Falalop atoll. A canoe-owning compound that receives fish subsequently redistributes the fish to other compounds, unless the catch is particularly small. Canoe-owning compounds retained an average of 59.7% (s.d. = 25.0%; n = 24) of the fish they produced. Redistributed fish are generally directed toward compounds where kin and men who fished on the canoe reside. Indeed, multiple regression analysis (Table 20.2) indicates that the number of males from a compound who fished on the canoe of the redistributing compound is a significant predictor of the amount of fish a compound receives from a canoe owner redistribution. Whether any resident of a compound is closely related to the matriarch or patriarch of the redistributing compound is a nearly significant predictor of the amount of fish received.

2. Village-level *ilet* distribution (*felang*): Villages on Ifaluk are composed of plots of land that are owned by the matriline of particular compounds. Plots of land each have an *ilet* value, which affects the flow of food resources contributed and received by the owners of the land. Plots are valued at 1 *ilet*, with the exception of two plots that are valued at 2 *ilet*. Ownership of land within a village is not restricted to compounds located in the village.

Table 20.2. Multiple regression analysis of the amount of fish (kg) received from canoe owner redistributions by compound

independent variable	parameter estimate	standard error	p value
number of fishermen from compound who fished on canoe of redistributing compound	1.2206	0.0643	<.0001
compound related*	0.0988	0.0585	0.0914
amount of fish (kg) initially distributed to canoe owning redistributing compound	0.001	0.0016	<.0001

Full model F = 165.078, df = 3, p < .0001

$r^2 = .37$

n = 840 events

*variable was input as 1 if anyone in the compound shared a coefficient of relatedness of 0.5 with the matriarch or patriarch of the redistributing compound, and 0 if nobody in the compound shared a coefficient of relatedness of 0.5 with matriarch or patriarch of the redistributing compound

Indeed, several compounds on Falachig atoll own land (and hence maintain *ilet*) within villages on Falalop atoll. On Falalop, compounds possess between one and three plots of land, and the total *ilet* maintained by compounds is also between one and three. Table 20.3 presents the number of *ilet* within Iyeur and Iyefang villages by compound and location of compound. There are 19 *ilet* in Iyeur (representing 184 residents) and 11 *ilet* in Iyefang (representing 135 residents). On Falalop, the number of *ilet* owned by a compound is positively correlated with the number of residents in the compound ($r = .72, p = .008$).

During a village-level *ilet* distribution fish are divided into two piles, one for Iyeur village and one for Iyefang village. From these piles each compound receives an amount of fish proportional to the number of *ilet* it possesses. The pile of fish for Iyeur village was typically slightly larger, but not proportional to the greater number of *ilet* or the greater number of residents represented by the *ilet* of Iyeur (n = 17 events, Iyeur mean = 69 kg, Iyefang mean = 63 kg).[7] One or two women from each compound that owns *ilet* within the village convene at their respective piles to cook and redistribute the fish. The eldest women present are in charge of the redistribution. The amount of fish that each compound receives is ideally determined by dis-

Table 20.3. Number of *ilet* and compound location of compounds which possess *ilet* on Falalop Atoll

compound id number	compound name	number of ilet in Iyeur	number of ilet in Iyefang	village of compound
1	Imtaifou	1	1	Iyefang
2	Ilug	2	0	Iyeur
3	Harowchang	3	0	Iyeur
4	Falichel	2	0	Iyeur
5	Faligilow	2	0	Iyeur
6	Hawong	3	0	Iyeur
7	Woluwar	0	3	Iyeur
8	Falul	0	3	Iyefang
9	Mataligob	0	1	Iyefang
10	Hapelmat	0	1	Iyefang
11	Bwabwa	0	1	Iyefang
12	Niwegitob	2	0	Iyefang
13	Falfeliuw	1	0	Iyefang
14	Welpiye	1	0	Rawaii
15	Halingelou	1	0	Rawaii
16	Maiyefang	1	0	Mukulong
17	Hagotag	0	1	Rawaii
18	Hatibugot	0	1	Rawaii
19	Somat	0	1	Rawaii
total:		19	11	

mined by the number of *ilet* that a compound possesses. Compounds that have 1 *ilet* expect to receive half as much fish from a redistribution as compounds that have 2 *ilet*, and one-third as much fish as compounds that have 3 *ilet*. For example, if a compound owns 2 *ilet* in Iyeur village, the compound expects to receive 2/19 of the total amount of fish received by Iyeur village.

As Figure 20.1 shows, the amount of fish that compounds actually received from observed village-level *ilet* distributions closely matches the amount of fish that compounds are predicted to receive. In other words, compounds with 2 *ilet* received roughly twice as much fish as compounds with 1 *ilet*, and compounds with 3 *ilet* received roughly three times as much fish as compounds with 1 *ilet*. In addition, only compounds that possess *ilet* within a village received fish from the redistribution. Compounds 1–12 are located on Falalop atoll and compounds 13–36 are located on Falachig atoll. These graphs show that compounds located on Falachig atoll tend to receive slightly less than predicted by a village-level *ilet* distribution and compounds located on Falalop atoll tend to receive slightly more than predicted by a village-level *ilet* distribution.

3. Atoll-level *ilet* distribution (*metalilet*): Similar to a village-level *ilet* distribution, in an atoll-level *ilet* distribution fish are distributed according to *ilet*. However, during an atoll-level *ilet* distribution fish are distributed directly from the canoe house to the compounds. Therefore, if as above a compound owns 2 *ilet* in Iyeur, the compound will receive 2/(19+11) or 1/15 of the total catch distributed via an atoll-level *ilet* distribution. Since Iyeur does not receive fish during a village-level *ilet* distribution proportional to the number of *ilet* in Iyeur (Iyeur on average receives 52.3% of the fish [n = 17] but maintains 63.3% of the *ilet*), compounds that have *ilet* located in Iyeur receive a greater proportion of the total catch during an atoll-level *ilet* distribution than during a village-level *ilet* distribution, whereas the converse is true of compounds that possess *ilet* in Iyefang village.

4. Fishermen distribution (*gagolagol*): Fish are distributed directly to males who fished on the canoe that caught the fish. Fish are subsequently cooked and consumed by the residential compound of the fisherman. Fishermen distributions apparently take two forms. In the first type fish are divided equally amongst all of the crew members (egalitarian distribution). In the second type fish are distributed separately to any residents of Falachig that participated in the fishing event (Falachig resident distribution).

5. Men's feast (*yafileo/giubal*): Fish are cooked at the men's house and eaten by any male over 14 years old who desires to eat.

These distribution patterns can be classified as primary and secondary distribution types. The primary distribution types (canoe owner, village-level *ilet*, and atoll-
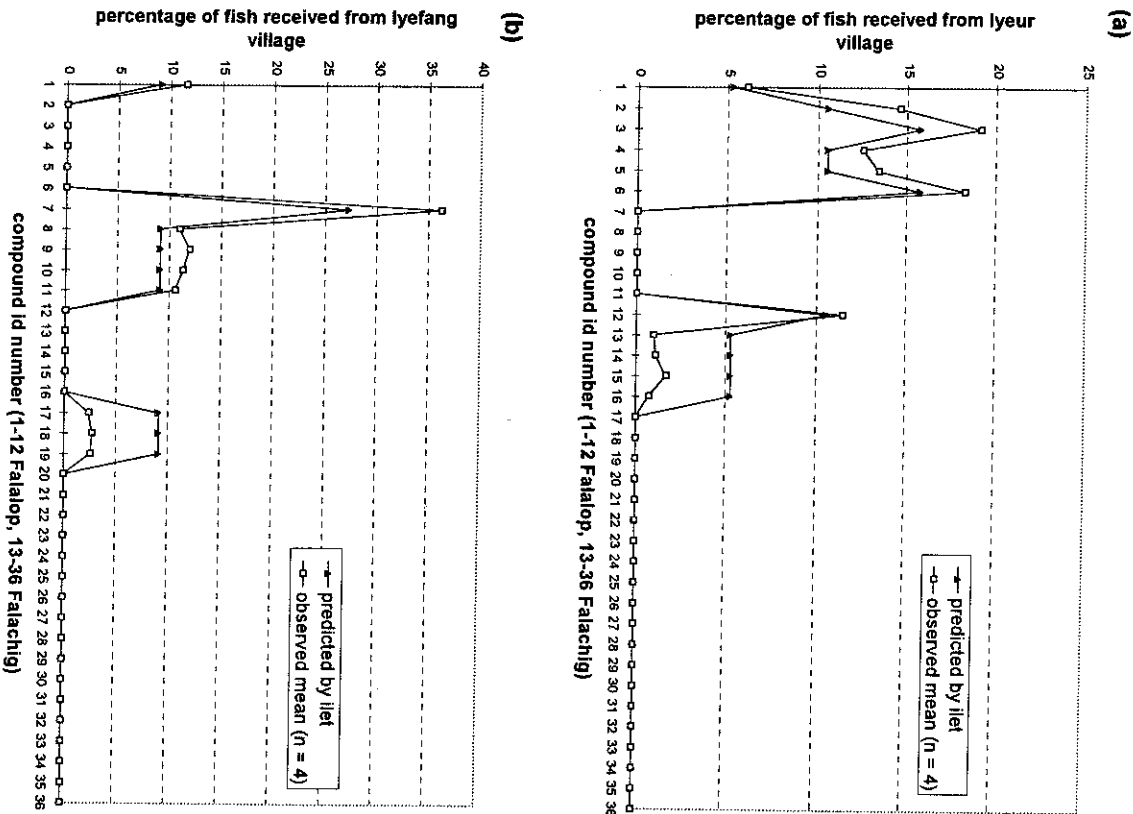
(a)

percentage of fish received from Iyeur village

compound id number (1-12 Falalop, 13-36 Falachig)

predicted by ilet
observed mean (n = 4)

(b)

percentage of fish received from Iyefang village

compound id number (1-12 Falalop, 13-36 Falachig)

predicted by ilet
observed mean (n = 4)

Figure 20.1. Predicted and observed percentage of fish received from village-level *ilet* redistribution to compounds from (a) Iyeur village and (b) Iyefang village.

level *ilet*) never co-occur, and nearly all distributions include one of these distribution types. The secondary distribution types (men's feast and fishermen distribution) generally occur in conjunction with one of the primary distribution types or with the other secondary distribution type. Table 20.4 presents the frequency that each distribution type was observed. The most frequently observed distribution type was the canoe-owner distribution, which occurred during 63.1% of all distribution events. Table 20.5 presents the percentage of fish that was distributed via each distribution type during the observation period. The primary distribution types account for more than 90% of the total fish distributed. Canoe-owner and village-level *ilet* distributions were clearly the most important distribution types observed. Together these distributions account for 80.9% of the total fish distributed and occur during 89.2% of all fish distributions.

Determinants of distribution of cooperatively acquired fish

Following a cooperative sail-fishing event, how do the dividers determine the distribution that will be used to disburse the catch? The most important determinant of distribution type appears to be the size of the catch. Figure 20.2 presents each distribution type by the total weight of fish caught.

Table 20.4. Frequency of fish distribution types observed on Falalop atoll following cooperative sail-fishing events

	observed frequency
cooperative sail fishing events	79
cooperative sail-fishing events with no catch	14
fish distribution events following cooperative sail-fishing	65

number of observation days = 98

Distribution Types	observed frequency	% of total distribution events
canoe owner	23	35.4
canoe owner, men's feast	16	24.6
canoe owner, men's feast, Falachig resident	1	1.5
canoe owner, men's feast, egalitarian	1	1.5
village-level *ilet*	6	9.2
village-level *ilet*, men's feast	6	9.2
village-level *ilet*, men's feast, Falachig resident	4	6.2
village-level *ilet*, Falachig resident	1	1.5
men's feast	3	4.6
men's feast, egalitarian	1	1.5
atoll-level *ilet*, men's feast, Falachig resident	3	4.6

Table 20.5. Total amount of fish distributed following cooperative sail-fishing events by distribution type (*n* = 65 distribution events)

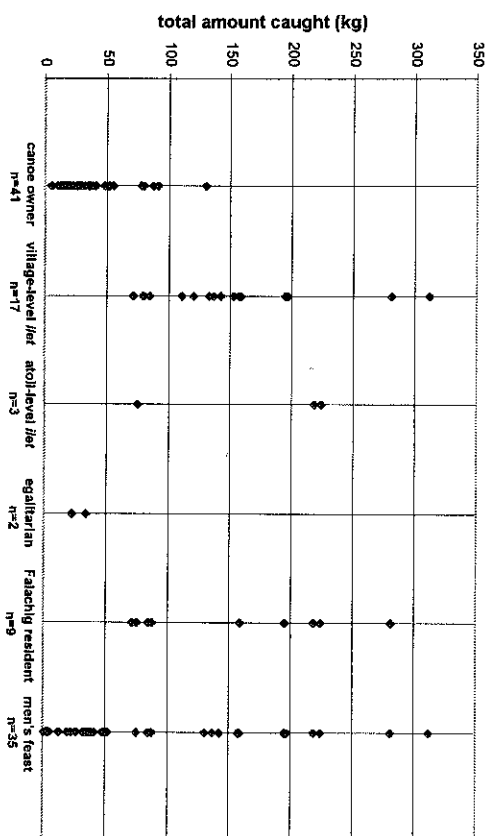| distribution type	total amount distributed (kg)	percentage of total amount distributed
canoe owner	1271.5	27.9
village-level *ilet*	2411.3	53.0
atoll-level *ilet*	445.4	9.8
Falachig resident	82.7	1.8
egalitarian	23.5	0.5
men's feast	316.8	7.0
total:	4551.2	100.00

Figure 20.2. Total amount caught by distribution type (n = 65 distribution events).

Primary distribution types Figure 20.2 shows that when the catch is small, fish are distributed via canoe owner distributions, and when the catch is large, fish are distributed via *ilet* distributions. Table 20.6 presents the results of a logistic regression procedure where primary distribution type (canoe owner or *ilet*) is the response variable, and the total weight of the catch, number of fishermen, number of canoes that fished, and number of fish caught are predictor variables. The results show that the total weight of the catch is a significant predictor of whether a distribution is either a canoe-owner or an *ilet* distribution. The number of fishermen, number of canoes, and the number of fish caught do not have independent significant effects on the distribution type. Figure 20.3 indicates that the total amount caught is a function of the number of males who fish.

Table 20.6.　Logistic regression analysis of the probability of a distribution type occurring

dependent variable: distribution type

independent variable	parameter estimate	standard error	p value
canoe owner distribution = 0			
ilet distribution (village-level or atoll-level) = 1			
−2 log likelihood for model covariates = 56.2; $p < .0001$			
df = 4			
$n = 60*$			
total amount caught (kg)	0.0625	0.0238	**0.0085**
total number of fish caught	0.0858	0.0529	0.1051
number of canoes	0.6137	1.4381	0.6696
number of fishermen	−0.1434	0.3817	0.7071

*data on number of fishermen is missing for 1 event

$$y = 0.1181x^2 + 3.5177x + 1.5841$$
$$R^2 = 0.199$$
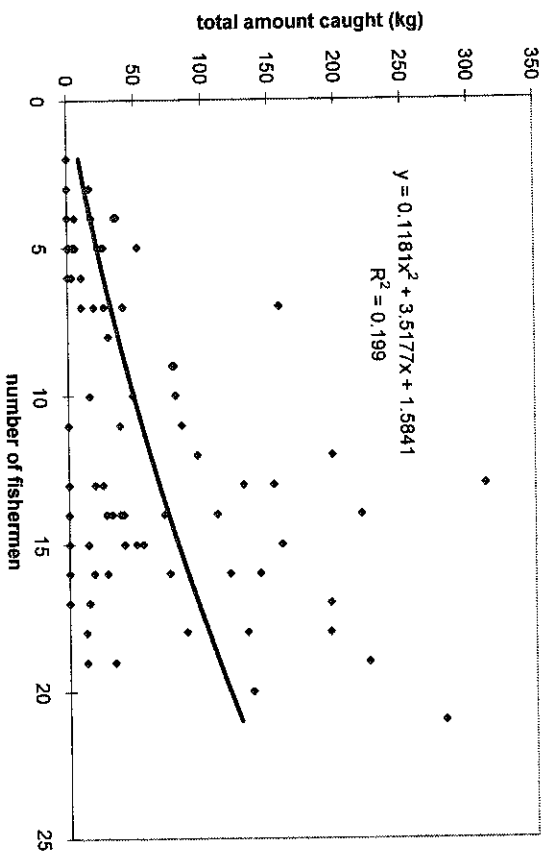
Figure 20.3.　Total amount caught for 78 cooperative sail-fishing events by number of fishermen ($F = 9.34$, $p < .001$, df = 2).

Although the current data set does not show a significant difference in the size of the catch when village-level or atoll-level *ilet* distributions occur, I expect that with an increased sample size the data would show that the largest catches are distributed via atoll-level *ilet* distributions. However, the main distinguishing feature between village-level and atoll-level *ilet* distributions is the divisibility of the catch, i.e., the number of fish caught. The range of the number of fish caught when fish were distributed via village-level *ilet* distributions was 9–39 with a mean of 18.1 ($n = 17$ events), whereas the range of the number of fish caught when fish were distributed via an atoll-level *ilet* distribution was 52–267 with a mean of 126.3 ($n = 3$ events). If there are enough fish to distribute via an *ilet* distribution without any processing, fish are distributed by the men via atoll-level *ilet* distributions. If not, fish are cut, cooked, and distributed by the women via village-level *ilet* distributions.

Secondary distribution types　Egalitarian distributions occur when the total weight of the fish caught is small, but the number of fish caught is large (i.e., prey size is small). The total weight of the catch for the two observed egalitarian distributions was 33.8 kg and 22.4 kg. If we consider all distributions where the total catch weighed 20–35 kg, it is clear that there is a significant difference between the number of fish caught when fish are distributed via egalitarian versus other distributions. The total number of fish caught during each of the egalitarian distributions was 48, whereas the total catch from the nine other distributions (20–35 kg each) ranged from 3 to 5 fish, with a mean of 3.7.

Falachig resident distributions occurred only when a male from Falachig fished and a large quantity of fish was caught. Eight of the nine Falachig distributions occurred in conjunction with an *ilet* type of distribution. In other words, Falachig resident distributions compensated Falachig fishermen for their fishing effort under conditions where they would otherwise not receive fish, since Falachig residents are unlikely to reside in compounds that possess *ilet* on Falalop.

Although Figure 20.2 shows that men's feasts occur for all catch sizes, they are more likely to occur when the total amount caught is large. Men's feasts occurred during 11 of 12 events (92%) where the total catch was >125 kg, and only 24 of 53 events (45%) where the total catch was ≤125 kg. When men's feasts occur, they account for only 10.0% ($n = 35$) of the fish distributed.

To summarize the primary distribution pattern, if few fish are caught, compounds that own canoes receive the catch of their canoe. These compounds typically retain most of the catch. Fish that are redistributed are primarily directed towards compounds where related kin and males who fished on the canoe of the redistributing compound reside. If the size of the catch is large, fish will be distributed throughout the atoll either via village-level or atoll-level *ilet* distributions. Regardless of whether or not an individual cooperatively fished, he (or more specifically, his residential compound) will receive a fixed percentage of the fish

distributed. Secondary distribution patterns account for less than 10% of all fish distributed and appear to be aimed at rewarding those who fished (egalitarian and Falachig resident) as well as assuring that all men can eat a meal of fish regardless of their effort or fishing success (men's feast).

The fish distribution patterns following cooperative sail-fishing events are a mix of investment-based distribution types (canoe-owner, egalitarian, and Falachig resident), which reward men who fish, and population-wide distributions (*ilet*), which ensure that all residents, or at least all male residents (in the case of men's feasts), receive fish regardless of their participation in production. If fish are caught, men who fished ordinarily receive some of the catch. Free riders can only expect to receive fish for their families infrequently; population-wide distributions (village-level or atoll-level *ilet*) occurred in only 30.8% of all observed distributions. Thus, although there is potential for free riding when fish are distributed to all residents on the atoll, the investment-based distribution types limit the success of a free riding strategy.

EMERGENCE OF COOPERATIVE FISHING ON IFALUK

Sail-fishing on Ifaluk meets the necessary conditions set in equation 2 for the emergence of cooperative foraging. The mean per capita cooperative sail-fishing production rate is 1.57 kg/hr (36 individuals, 980 events) and the mean per capita solitary fishing (all types of solitary fishing) production rate is 0.86 kg/hr (12 individuals,[8] 54 events). The energetic costs of cooperative and solitary fishing were measured using the EEP and calculated as 4.7 kcal/min and 4.9 kcal/min, respectively. There are 1,080 calories in 1 kilogram of raw yellow fin tuna (Genesis R&D Nutrition and Labeling Software), which was the primary species of fish caught cooperatively (89% of the total kilograms of fish caught cooperatively was yellow fin tuna [n = 79 events]). For solitary fishing, since there are 62 different species in my sample, an average of the caloric values of 5 species of reef fish (1,074 kcal) was used as an estimate of the caloric value of reef fish. Thus, the mean per capita net production rate of cooperative sail-fishing is 1,408.8 kcal/hr and the mean per capita net production rate of solitary fishing is 630.0 kcal/hr. This difference is significant (t = 7.11, df = 156.6, p < .0001). The mean per capita net cooperative sail-fishing production rate of the 12 solitary fishermen is 1,467.6 kcal/hr (355 events), which is also significantly higher than the mean per capita net solitary production rate of those men (t = 5.79, df = 300.5, p <.0001).

However, as a result of the biases in the distribution patterns described above, cooperation may not emerge if men who fish cooperatively have lower consumption rates than men who fish alone. By assuming the empirically observed distribution patterns, the consumption rates for cooperative and solitary fishing were calculated as the amount of fish received by ego's residential compound divided by the amount of time ego fished. Based on my personal observations, I am assum-

ing that the within-compound sharing patterns are the same for fish caught cooperatively or solitarily. The mean per capita net consumption rate for cooperative fishing is –139.8 kcal/hr (36 individuals, 950 events) and the mean per capita solitary fishing production rate is –254.6 kcal/hr (8 individuals, 35 events). This difference is significant (t = 11.57, df = 94.5, p < .0001). The mean per capita net cooperative sail-fishing consumption rate of the 12 solitary fishermen is –130.7 kcal/hr (397 events), which is also significantly higher than the mean per capita solitary production rate (t = 9.94, df = 193.3, p < .0001).[9]

STABILITY OF COOPERATIVE FISHING ON IFALUK

Cooperative fishing on Ifaluk will be stable as long as the net benefits of cooperation outweigh the net benefits of not cooperating. Given the bias in the sharing patterns on Ifaluk, these conditions will vary considerably between individuals. When a man decides whether or not to fish it is assumed that he makes this decision based on an evaluation of his expected payoff—in other words, the fitness gains that he can expect given the way that fish he produces will be distributed. In many cases this will be a monotonically increasing function of the net kilograms of fish that he and his close kin will consume as a result of his fishing effort. This assumption is adopted in the model below. Here I assume the sharing pattern and its determinants rather than try to explain it.

Fishing is a probabilistic activity with high variance in returns even for the most skilled fishermen. Environmental cues such as rainfall, wind patterns, strength of the tide, and the amount that was caught on the previous day can indicate better or worse fishing conditions; however, a fisherman does not know beforehand what his actual returns will be. Under the cooperative conditions of fishing on Ifaluk, environmental cues must also be coupled with knowledge of how others will respond to these cues for a fisherman to assess what his actual return rate will be.

For each male at risk to participate in a cooperative fishing event, there is an amount of fish that he expects to receive given the amount of fish that are caught, the distribution type, and whether or not he participated in the event. For each number of fishermen there is some probability that a specific distribution type will occur. Knowledge of these parameters will enable us to calculate a male's expected payoff in nutritional gains if the fishes or does not fish for each number of fishermen. We anticipate that when a male's expected payoff for cooperative sail-fishing is greater than his expected payoff for not cooperating he will fish cooperatively. Thus, we expect individual k to join a group of n fishermen if

$$Y_{ck}(n + 1) > Y_{dk}(n) \tag{3}$$

where Y_{ck} = individual k's net caloric gain from participating in a cooperative fishing event and Y_{dk} = individual k's net caloric gain from not participating in a cooperative sail-fishing event. This model assumes that:

1. Individuals are free to decide whether or not to participate in any cooperative sail-fishing event.
2. Individual decisions to join or leave a group of fishermen are independent (i.e., the model is static).
3. Individual decisions to join or leave a group of fishermen are only based on an evaluation of individual caloric intake. The additional caloric benefits accrued by kin are not included in the model.
4. Individuals possess accurate knowledge of how their caloric payoffs vary with the number of participants in a cooperative fishing event.

This model additionally assumes that individuals know the number of members in the group they are deciding whether or not to join. Under the conditions of cooperative fishing on Ifaluk, this assumption appears to be violated; individuals do not know exactly how many men will be fishing until they arrive at the canoe house in the morning. However, it seems likely that the same ecological cues that indicate the quality of the fishing conditions are also used to determine how many others will fish on a given morning. Therefore, it is reasonable to assume that men can assess with some accuracy how many males will fish on a given day. For example, the total amount that was caught on the previous day appears to be an important determinant of individual fishing decisions. Table 20.7 presents the results of a logistic regression analysis where the dependent variable is whether or not an individual fished and the independent variable is the total amount of fish caught on the previous day. The results indicate that, controlling for participation on the previous day, the total amount caught on the previous day is a significant positive predictor of cooperative sail-fishing participation. In other words, if the catch on the previous day was large, it is probably a reliable indication that fishing returns will be favorable today. It is also probably one of many cues used to assess the number of men that will fish on a given day.[10]

Table 20.7. Logistic regression analysis of the probability of cooperative sail-fishing

independent variable	parameter estimate	standard error	p value
total amount of fish caught (kg) on previous day	0.0042	0.0006	<.0001
fishing status on previous day	2.6224	0.0963	<.0001

–2 log likelihood for model covariates = 871.3, p < .0001
df = 2
n = 4999

participated in cooperative fishing event = 1
did not participate in cooperative fishing event = 0

The currency of this model is the net gain rate per day. The return rate per hour is often the currency of choice among evolutionary ecologists; however, if free riding is an available strategy (resources can be acquired without time investment), return rate per hour is not an interpretable currency. Therefore, the difference between output (caloric gains) and input (caloric expenditure) was used as a currency to measure individual fitness gains, which is simply the return rate per day.

Given knowledge of the distribution patterns as well as the frequency of distribution types across number of fishermen,[11] we can more accurately define equation 3 as

$$\sum_{s=c,v,a,rm} [P_s(n+1) \times I_{sfk}(n+1)] \times T_k - E_k > \sum_{s=c,v,a,rm} [P_s(n) \times I_{sdk}(n)] \times T_k \quad (4)$$

where:

P_s = probability of a distribution type occurring

I_{sfk} = caloric gains individual k's residential compound expects to receive from a distribution type if k fishes

I_{sdk} = caloric gains individual k's residential compound expects to receive from a distribution type if k does not fish

c = canoe owner distribution

v = village-level *ilet* distribution

a = atoll-level *ilet* distribution

r = Falachig resident distribution

m = men's feast

E_k = individual k's cooperative sail-fishing expected energy expenditure

T_k = consumer ratio, proportion of fish received by individual k's residential compound that individual k consumes

We can consider equation 4 in two parts. The left-hand side of the equation is individual k's expected payoff if he fishes and the right-hand side is k's expected payoff if he does not fish. The expected caloric gains if individual k fishes (LHS) is the probability of a distribution type occurring as a function of the number of fishermen if k fishes, multiplied by the expected caloric payoff of individual k for the distribution type, as a function of the number of fishermen if individual k fishes. Since fish are given to compounds and not directly to individuals (with the exception of the men's feast)[12] distribution types must be multiplied by the proportion of fish received by individual k's residential compound that k will consume, the proportion of fish received by individual k's residential compound that k will consume, T_k, which is called the consumer ratio. It is assumed that food is shared equitably within a compound but that an individual will consume an amount of fish in relation to his or her age, sex, and weight.[13] The five distribution-type payoff probabilities are

summed and the expected caloric expenditure of individual k is subtracted from this value. Individual k's expected payoff if he does not fish (RHS) is calculated as the probability of a distribution type occurring as a function of the number of fisher-men if he does not fish, multiplied by the expected caloric payoff of individual k for men if he does not fish. As a function of the number of fishermen if individual k does not fish. As on the LHS of equation 4, the distribution payoff probabilities must be multiplied by k's consumer ratio and all five distribution-type payoff probabilities are summed.

Distribution type as a function of number of fisherman

In order to test the model presented for the stability of cooperation empirically it is necessary to calculate the hazard of a distribution type as a function of the num-ber of fishermen. The hazard is simply the probability that an event will occur given that it is possible for the event to occur. Hazard functions were calculated for each distribution type using data from 78 observed cooperative sail-fishing events. [1] Fig-ures 20.4a–e present the probability of a distribution type occurring by the number of men that participate in a cooperative sail-fishing event. Functions were calcu-lated as the least squares fit for the data using a set of linear and second-order poly-nomial functions. Figure 20.4a shows that the probability of a canoe-owner distribution occurring decreases linearly as the number of fishermen increases. The function that depicts this trend, $y = -.0165x + .6977$, was put into equation 4 as $P_c(x)$, where x is the number of men who participate in a cooperative fishing event. Similarly, the function $y = .0263x-.0768$, which characterizes the probability of a village-level *ilet* distribution occurring by number of fishermen (see Figure 20.4b, was put into equation 4 as $P_v(x)$. Figures 20.4c–e present the functions that char-acterize the probability of atoll-level *ilet*, men's feast, and Falachig resident distri-butions occurring by number of fishermen, respectively. These functions were entered into equation 4 as $P_a(x)$, $P_r(x)$, and $P_m(x)$, respectively.

Mean share of returns by distribution type

Individuals from different compounds expect to receive a different share of the catch for a given distribution type. Using quantitative data on the amount distrib-uted to each compound following cooperative sail-fishing events, a function was calculated for each residential compound of the 60 men in the risk set for each dis-tribution type.

Canoe owner distribution Figure 20.5a presents the average amount of fish received by compound 4 from a canoe-owner distribution by number of fishermen. It was shown above (Table 20.2) that participation affects the amount of fish that an individual can expect to receive via a canoe-owner distribution. Therefore the data in Figure 20.5a are separated by whether or not any resident of the compound par-ticipated in the fishing event. The functions that describe the data shown in Figure

---

Erratum

This figure replaces Figure 20.4a–e on page 457. The publisher regrets the error.
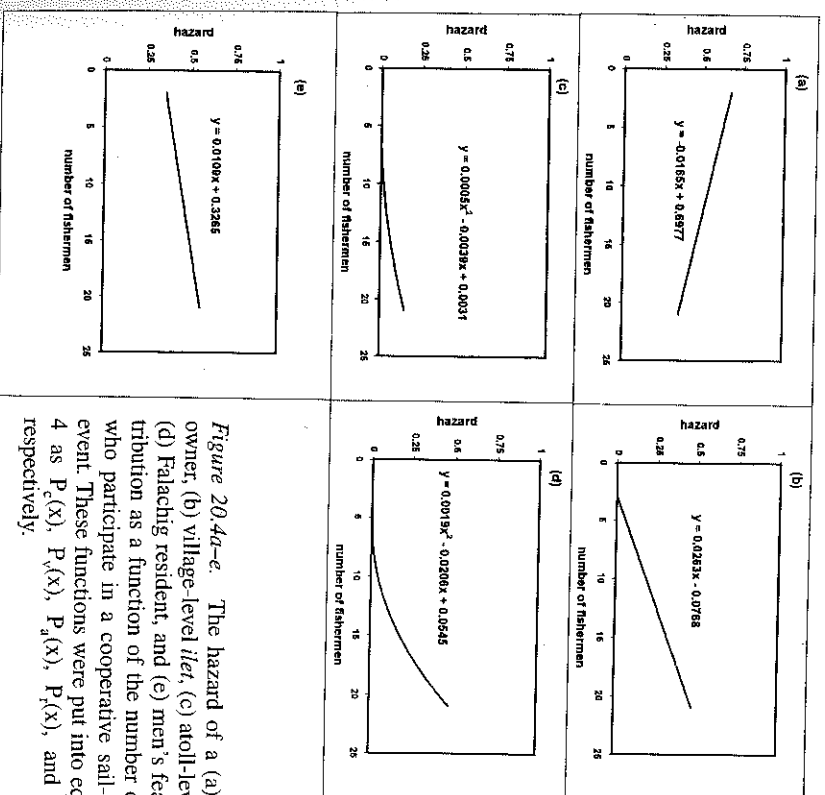

Figure 20.4a–e. The hazard of a (a) canoe owner, (b) village-level *ilet*, (c) atoll-level *ilet*, (d) Falachig resident, and (e) men's feast dis-tribution as a function of the number of men who participate in a cooperative sail-fishing event. These functions were put into equation 4 as $P_c(x)$, $P_v(x)$, $P_a(x)$, $P_r(x)$, and $P_m(x)$, respectively.

20.5a are curvilinear with a peak between ten and eleven fishermen. As more men participate in a cooperative fishing event, fish are not likely to be distributed via a distribution unless the catch is particularly small. The polynomial functions that characterize the data in Figure 20.5a (as well as the functions calculated for each compound, which are not presented here) were put into equation 4 as $I_{cf4}(x)$ and $I_{ub}(x)$, respectively. Although the absolute amount of fish received from canoe-owner distributions by each compound varies, the shape of the functions that char-acterize the data (i.e., curvilinear with a peak around 10 fishermen) is similar for all compounds.

Because of a lack of data on fishing activity by residents of several compounds, canoe owner distribution data had to be averaged across a set of variables that
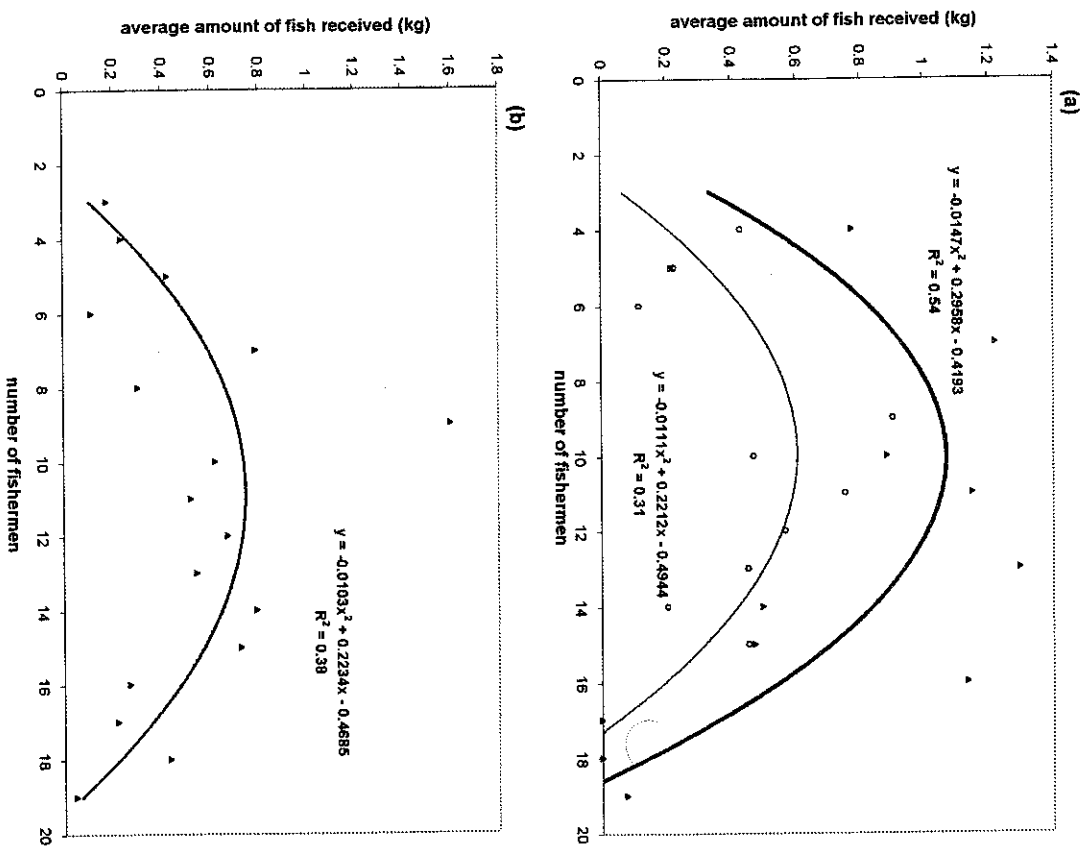
(a)

y = -0.0147x² + 0.2956x - 0.4193
R² = 0.54

average amount of fish received (kg)

(b)

y = -0.0111x³ + 0.2212x - 0.4944
R² = 0.31

y = -0.0103x² + 0.2234x - 0.4685
R² = 0.38

average amount of fish received (kg)

number of fishermen

Figure 20.5. (a) Average amount of fish received by compound 4 from canoe owner *redistribution* by total number of fishermen. Data are separated by events when 1 or more men from compound 4 fished (solid triangles and thick line), and events when no men from compound 4 fished (open circles and thin line). (b) Average amount of fish received by non-canoe-owning compounds on Falalop from canoe owner *redistribution* if 1 or more males from compound fishes, by total number of fishermen.

characterize the compound. For example, no male residents of compound 8 ever cooperatively sail-fished. Therefore we do not know what function describes the relationship between expected returns of compound 8 and the number of fishermen when someone from compound 8 fishes. In this and similar circumstances data were combined across two variables: whether or not the compound owned a canoe, and location of compound, either Falalop or Falachig atoll. Compound 8 is a non-canoe-owning compound located on Falalop. Figure 20.5b presents the average amount of fish received by all non-canoe-owning compounds located on Falalop atoll when one resident from the compound participated in a cooperative sail-fishing event. The function $y = -.0103x^2 + .2234x - .4685$, which describes the combined data, was put into equation 4 for compound 8 as $I_{cfk}(x)$. This appears to be the most parsimonious solution to the problem of nonparticipation in estimating expected payoffs; individuals that never cooperatively fish can only know what their payoffs would be through knowledge of what others are receiving when they fish.

Village-level ilet *distribution*   Figure 20.6a presents the average amount of fish received from a village-level *ilet* distribution by number of fishermen for compound 7. The data are characterized by the function $y = -0.004x^2 + 1.708 - 1.1$. For compound 7, this function was put into equation 4 as $I_{vfk}(x)$ and $I_{vdk}(x)$. The shape of the function that characterizes the data in Figure 20.6a is similar for all compounds, although each compound will have a distinct function for village-level *ilet* distribution. Participation has no effect on the amount of fish that a compound will receive for village-level *ilet*, whether or not anyone from compound 7 cooperatively fished. Participation has no effect on the amount of fish that a compound will receive for village-level *ilet*, atoll-level *ilet*, or men's feast distributions (although the addition of one fisherman will increase the expected amount caught, and hence the amount distributed).

Atoll-level ilet *distribution*   Atoll-level *ilet* distributions were only observed three times during the observation period. Therefore, the data are insufficient to determine what function characterizes the relationship between the amount received during an atoll-level *ilet* distribution and the number of fishermen. For each compound the mean percentage received of the total amount distributed via atoll-level *ilet* distributions was calculated and entered into equation 4 as $I_{afk}(x)$ and $I_{adk}(x)$.

Falachig resident distribution   Males at risk of receiving fish from a Falachig resident distribution are assumed to receive equal amounts of fish as a function of the number of fishermen. In other words, in contrast to other distribution types, it was assumed that there is no variation in the amount received by residential compounds of Falachig fishermen via Falachig resident distributions. This assumption is necessary because of the small number of Falachig resident distributions (n =
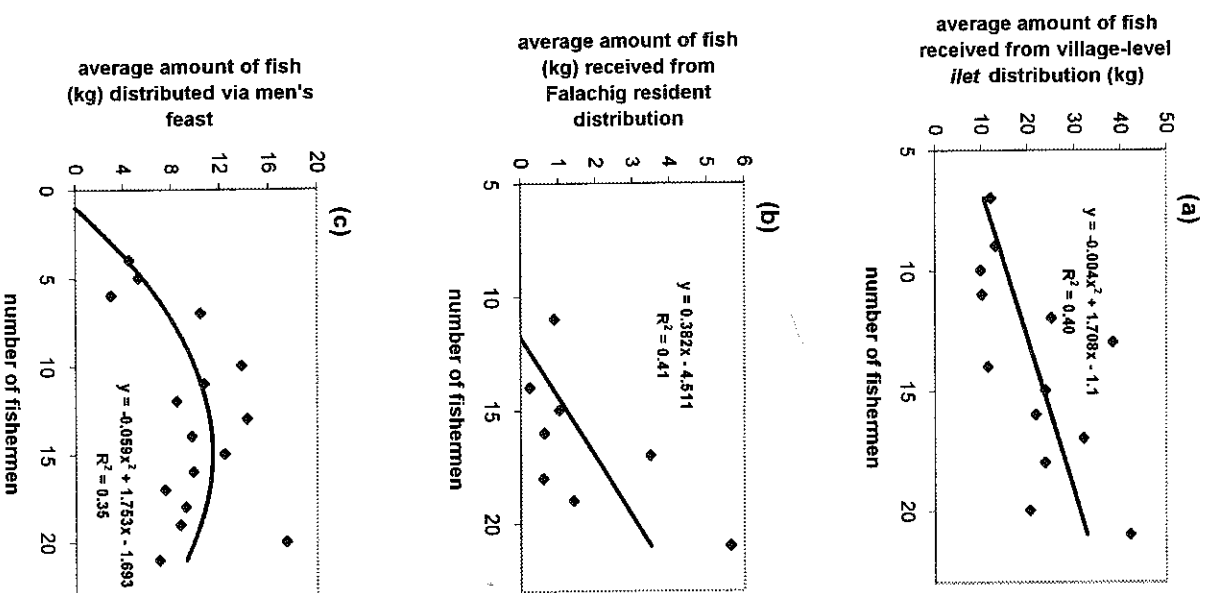
(a)

average amount of fish received from village-level *ilet* distribution (kg)

$y = -0.004x^2 + 1.708x - 1.1$
$R^2 = 0.40$

number of fishermen

(b)

average amount of fish (kg) received from Falachig resident distribution

$y = 0.382x - 4.511$
$R^2 = 0.41$

number of fishermen

(c)

average amount of fish (kg) distributed via men's feast

$y = -0.059x^2 + 1.753x - 1.693$
$R^2 = 0.35$

number of fishermen

Figure 20.6. (a) Average amount of fish received from village-level *ilet* distribution by number of fishermen for compound 7 ($n = 17$ events). (b) Average amount of fish received from Falachig resident distribution by number of fishermen ($n = 9$ events). (c) Average amount of fish distributed via men's feast by number of fishermen ($n = 35$ events).

9), however, since there was no expectation of a systematic bias in the amount received by Falachig residents at the observed distributions (e.g., if two Falachig residents fished, their residential compounds would receive an equal quantity of fish), it is unlikely that an increased sample size of Falachig resident distribution events would affect this assumption. Figure 20.6b shows the average amount of fish received by a Falachig compound from a Falachig resident distribution by number of fishermen. The function, that characterizes this data, $y = 0.382x - 4.511$, was entered into equation 4 as $I_{fjk}(x)$ for those individuals at risk of receiving fish via a Falachig resident distribution. $I_{fjk}(x)$ is always zero since a Falachig resident must fish in order to receive fish via a Falachig resident distribution.

Men's feast. Figure 20.6c presents the relationship between the amount distributed via men's feasts and the number of participants in the fishing event. This function, $y = -0.059x^2 + 1.753 \times -1.693$, multiplied by the ratio $\frac{1}{N}$, where N is the total number of men at risk of partaking in a men's feast, was entered into equation 4 as $I_{mfk}(x)$ and $I_{mik}(x)$ (see note 12). It was assumed that there is an equal probability of any male who is at risk of cooperative sail-fishing of partaking in a men's feast, regardless of whether or not they actually fished.[15]

Energetic Expenditure

As stated above, males on average expend 4.7 cal/min during cooperative sail-fishing. Males on average cooperatively sail-fished 179.7 minutes per event, thus expending 844.6 calories per event. In most traditional societies, protein is valued more than alternative caloric sources such as carbohydrates because of its scarcity or expense of acquisition. On Ifaluk we are able to determine precisely how much more protein is valued than carbohydrates because both can be assigned a monetary value. Parents of children enrolled at the Head Start program on Ifaluk can sell food for cash to Head Start (the option of providing food is rotated between parents). Food is sold raw and subsequently cooked by Head Start employees. The primary starch of the winter season is taro. Parents are paid $0.65 /lb. of taro (485.3 kcal) and $1.20 /lb. of fish (489.9 kcal)). Thus, parents can receive one dollar for 408.2 kcal of fish or 746.6 kcal of taro. Therefore we assume that a unit of carbohydrate holds .547 the value of a unit of protein. Although males on average expend 844.6 kcal during a cooperative sail-fishing event, this must be multiplied by .547 when subtracted from gains in the currency of fish calories, owing to the higher value of fish relative to carbohydrate calories on Ifaluk.[16]

Results of the Model

Expected payoff curves were generated from equation 4 for each of the 60 males at risk of cooperative sail-fishing. Males from the same compound have

similar expected payoff curves since fish are distributed to compounds and not directly to individuals, with the exception of men's feasts. However, the variance in expected payoffs of males from different compounds is high. Each individual at risk has two payoff curves: one if the fishes and one if he does not fish. Figure 20.7 shows a range of expected payoffs that males face. Notice that each set of payoff curves generates a different prediction concerning when a male will and will not fish. From Figure 20.7a we predict that male 209 from compound 7 will always fish since his payoff curve for fishing is always greater than his payoff curve for not fishing. Male 273 from compound 10 is predicted not to fish if fewer than 16 other males fish, but he should always fish if he expects that 16 or more males will fish (Figure 20.7b). Male 157 from compound 18 is never expected to fish (Figure 20.7c) and male 316 from compound 33 is predicted to fish only if he expects 17 or more others to fish (Figure 20.7d). We can also predict in Figures 20.7a–d that as the distance between the payoff curves increases a male's payoffs for alternative decisions will become less ambiguous, and hence motivation will increase to either fish, if the difference is positive, or not fish, if the difference is negative.

All payoff curves for the 60 males at risk of cooperative sail-fishing are monotonically increasing. This is important because it implies that over the observed range of fishermen (2–21) there is no conflict between joiners and members. A member will always expect to receive higher payoffs if another male wants to join the fishing party. This is consistent with my observations that no male was ever turned away from a fishing event, and once at the canoe house no male ever decided not to fish, as long as men took out a canoe.[17]

The model predictions can be compared with observed fishing behavior. Logistic regression analyses were conducted to test whether the model was a significant predictor of cooperative foraging decisions. The risk set for the analyses consists of the number of males at risk of participating in a cooperative sail-fishing event multiplied by the number of cooperative sail-fishing days. Over the 79 cooperative sail-fishing days, the number of males at risk (see "Methods") changed 11 times and ranged between 50 and 60 men as a result of individuals arriving and departing from Ifaluk. Thus, the total risk set consists of 4,083 person days. The dependent variable of the model is whether or not an individual fished. The independent variable was generated from the model as the difference in an individual's expected payoff curves between fishing and not fishing. As the difference between the payoff curves increases, males should have greater motivation either to fish, if the difference is positive, or to not fish, if the difference is negative. Results of the logistic procedure presented in Table 20.8 indicate that the model is a highly significant positive predictor of male cooperative fishing decisions. The effect on cooperative fishing participation of the expected difference between an individual's payoff curves is substantial. For example, if the difference in payoff curves is –250 kcal, the hazard of cooperative fishing is 0.06, whereas if the difference in payoff curves is 250 kcal the hazard is 0.39.
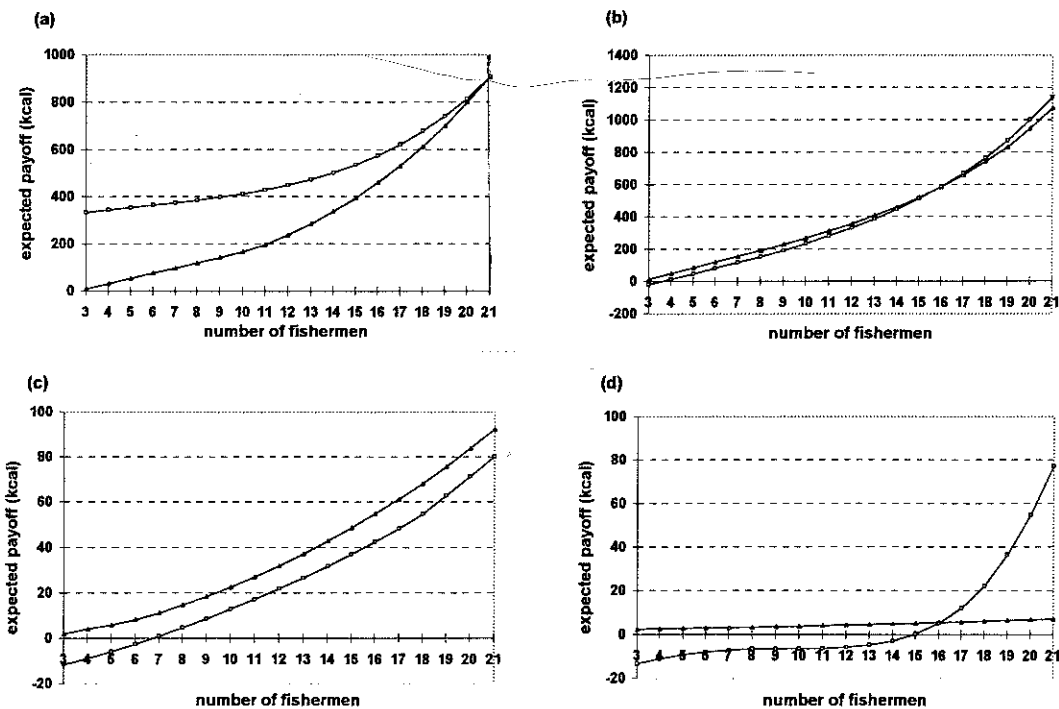
Figure 20.7.   Expected caloric payoff by number of fishermen for (a) male id #209 of compound 7, (b) male id #273 of compound 10, (c) male id #157 of compound 18, and (d) male id #316 of compound 33. Expected caloric payoffs when only 2 men fish are not shown since they are identical for all males (no fish were ever caught when only 2 men fished). Solid triangles denote the payoffs for not fishing and open squares denote the payoffs for fishing. The scale of the y-axes are not the same in each graph.

Table 20.8. Logistic regression analysis of the probability of cooperative sail-fishing

independent variable	parameter estimate	standard error	p value
difference between cooperative fishing and not fishing expected payoff (kcal)	0.0045	0.0004	<.0001

-2 log likelihood for model covariates = 167.06, p < .0001

df = 1

$n = 4083$

DISCUSSION

Emergence of Cooperative Fishing on Ifaluk

The simple model (equation 2) presented above as a necessary condition for the emergence of cooperative foraging is consistent with our observations of fishing on Ifaluk. The per capita net production and consumption rates of cooperative sail-fishing are significantly greater than the per capita net production and consumption rates of solitary fishing. Given the twofold difference between solitary and cooperative production rates, why does solitary fishing occur at all? First, the cooperative production activities are mutually exclusive. Cooperative sail-fishing requires strong winds and tide, whereas solitary fishing can only occur when the winds and tide are calm. Thus, when the winds and tide are calm we expect the mean solitary fishing return rate to be much higher than the mean cooperative sail-fishing return rate. Second, only five males fished alone three or more times. Most males that attempted to solitary fish may have simply been trying their luck. Because schools of fish constantly move in and out of the lagoon where solitary fishing occurs, it may be worthwhile to occasionally assess the profitability of solitary fishing.

It is often argued that Western influences such as individualism and capitalism have negative effects on the cooperative social structure of traditional societies (e.g., Bethlehem 1975; Meeker 1970). In many cases this may be true. Within Yap State, Ifaluk is the only atoll where men still regularly fish cooperatively. The most obvious explanation for the breakdown of cooperative fishing on the other atolls is the introduction of motor boats and freezers, both of which the chiefs have prohibited on Ifaluk. Motor boats can be operated solitarily with very high return rates, and large catches can be stored in a freezer for long-term consumption. My results suggest, however, that westernization may actually have a positive effect on the prevalence of cooperative fishing on Ifaluk. Time constraints imposed by institutionalized schooling, a product of American colonialism in Micronesia, has probably resulted in a generation of males who are less skilled fishermen than their

ancestors. Less time to invest in acquiring fishing skills is likely to have a greater impact on solitary fishing success than on cooperative fishing success, since solitary fishing is a skill-intensive activity. Certain roles in cooperative sail-fishing are also highly skilled, such as locating patches of fish and directing the canoe, but only one or two members of the crew need to perform these tasks. The remainder of the tasks involved in cooperative fishing require almost no skill. Indeed, the author, who had never fished a day in his life prior to visiting Ifaluk, proved to be a productive crew member simply by holding a fishing line. Although some boys skip school occasionally to fish, most males fish only on the weekends and holidays. In addition, most males leave the atoll after the eighth grade to continue school on Woleai and then Ulithi, where the traditional fishing practiced on Ifaluk does not occur. Thus, with the introduction of Western schooling, males may not be acquiring the necessary fishing skills that would make solitary fishing a profitable winter activity. It is interesting to note that the individual who fished alone most frequently and maintained the highest mean solitary return rate had dropped out of school by second grade.

Technology also plays an important role in the emergence of cooperation on Ifaluk. The resource patch that is being exploited on Ifaluk consists of distinct, large packages typically weighing 5–20 kg. The most important technology utilized to exploit this patch is the sailing canoe, which requires cooperative participation. Operating a sailing canoe not only requires multiple individuals, it also necessitates a coordinated division of labor. Improvements in technology can also encourage cooperation by lowering the costs of acquisition. The recent transition from using heavy sails woven of palm fibers to lightweight American-made sails (purchased on Yap) has certainly lowered the energetic costs of cooperative sail-fishing on Ifaluk.

Stability of Cooperative Fishing on Ifaluk

Although the necessary conditions for cooperative foraging seem to hold on Ifaluk, these conditions are not sufficient for cooperation to be stable. Stability of cooperative foraging requires a mechanism that either controls a free rider's share of returns or imposes costs on free riders. The model presented here has specifically considered the first of these mechanisms. Concerning the latter mechanism, it may be that cooperative behavior is promoted through social controls such as the negative effect of gossip on reputation, although the costs in terms of reproductive fitness of a negative reputation are difficult to measure.

Unlike previous models of the evolution and stability of cooperation, which assume equal sharing among foragers or group members, the model presented here used empirically observed biases in the fish-sharing patterns on Ifaluk. The model has shown that the observed sharing patterns help us to predict the conditions under which an individual will join a cooperative pursuit. The sharing patterns appear to be the mechanism by which a free rider's share of returns is limited.

Although the model is a significant predictor of cooperative fishing participation, inclusion of at least two variables would improve the model's ability to approximate the conditions of production on Ifaluk. These elements will provide the basis for future research on the evolution of cooperative fishing on Ifaluk.

Opportunity costs   One of the most notable shortcomings of the model is that the opportunity costs of cooperative sail-fishing have been ignored, primarily because of the difficulty in determining activities that were foregone. The most obvious consideration would be solitary fishing. However, the mutually exclusive weather conditions necessary for the success of these fishing activities makes this prospect unlikely. Another possibility is that the opportunity costs could be measured as a tradeoff between paternal care and cooperative fishing. However, the fitness benefits for men of, say, an hour of childcare may be much lower than the fitness benefits of an hour spent fishing, given an abundance of related female caregivers. Indeed, Sosis et al. (1998) found that the number of coresidential offspring was positively correlated with cooperative fishing participation. The most prominent type of male childcare observed consisted of boys joining their fathers or kin on a sailing canoe. If we consider what males who are not fishing are doing while others are out fishing, it is not obvious how the opportunity costs could be measured. Males who are not fishing in the morning are typically sleeping. Generally, males return from cooperative sail-fishing between 7:00 and 8:00 A.M., which is when males who do not fish usually begin their day. This may suggest that the opportunity costs to cooperative fishing could be measured as a tradeoff with somatic investment.

Relatedness   The model would also be greatly improved if it accounted for the effect of a male's relatedness to the recipients of the catch on his fishing decisions. Preliminary analyses of a model that incorporates the amount of fish that a man expects his kin to receive into his payoff curves has yielded significant results (Sosis 1998). There are conditions under which the predictions of an inclusive fitness model differ from the predictions of a direct fitness model, such as the one presented above. For example, if the increase in foraging efficiency of joining a group is outweighed by the costs of lowering an individual's inclusive fitness by reducing the foraging efficiency of related group members, the individual is not expected to join the group (Rodman 1981; Smith 1985). However, this is not likely to be relevant to cooperative fishing on Ifaluk since the monotonically increasing payoff curves (see Figure 20.7a–d) suggest a lack of conflicts between joiners and members. One interesting consequence of including kin in the model is that the energetic costs of fishing become inconsequential. In other words, the addition of inclusive fitness benefits to the model would vastly increase an individual's benefits whereas energetic costs would remain the same as in the model presented above.

The importance of a man's relatedness to the recipients of his production is evident in the pattern of canoe use—namely, that men fish on the canoe of their natal compound rather than the canoe of their residential compound. If fish are distributed via a canoe-owner distribution, married men are largely acquiring fish for their sister's families rather than their own. When married men were asked why they do not fish on the canoes of their residential compound more often, they invariably communicate a sense of duty, claiming that they must "fish on the canoe that fed me when I was young." Whether the inclusive fitness benefits for a married man of fishing on the canoe of his natal compound are greater than the inclusive fitness benefits of fishing on the canoe of his residential compound needs to be further explored.

SUMMARY

1. This paper tests theoretical models of the emergence and stability of cooperative foraging using empirical data on cooperative sail-fishing activities on Ifaluk Atoll.

2. Consistent with a necessary condition for the emergence of cooperative foraging, it was found that the mean per capita net production and consumption rates of cooperative fishing are significantly greater than the mean per capita net production and consumption rates of solitary fishing.

3. Once cooperative foraging has emerged, a necessary condition for its stability is that the benefits of cooperation must outweigh the benefits of free riding. Two factors determine the success of a free riding strategy: the ability of cooperators to control a free rider's share of returns, and the ability of cooperators to impose costs on free riders.

4. The fish distribution patterns following cooperative sail-fishing events are a mix of investment-based distribution types, which reward men who fish, and population-wide distributions, which ensure that all residents, or all male residents, receive fish regardless of their participation in production. Although there is potential for free riding when fish are distributed to all residents on the atoll, the investment-based distribution types limit the success of a free riding strategy. The distribution patterns are a likely mechanism that enables the stability of cooperative fishing on Ifaluk.

5. By using empirically observed biases in the fish distribution pattern, a model was generated that predicts the conditions under which an individual will join a cooperative pursuit. Predictions from the model were compared with observed fishing behavior on Ifaluk. The results indicate that the difference in expected caloric payoff curves if an individual fishes or does not fish is a significant predictor of men's participation in cooperative sail-fishing.

ACKNOWLEDGMENTS

NOTES

1. Equation 2 is not a decision variable, such as the choice of whether to join a cooperative group or forage solitarily. Models of optimal group size, such as Smith's (1981) joiner's rule, assume that cooperation exists. The joiner's rule assumes that the decision variable that a forager faces is a choice between foraging solitarily or joining a *group of foragers*. Equation 2 does not assume that group foraging already exists, rather, it is an attempt to establish the conditions that must exist for cooperative foraging to emerge.

2. For a more detailed ethnographic description of Ifaluk see Burrows and Spiro (1957), Bates and Abbot (1958), Turke (1985), Lutz (1988), and Sosis (1997).

3. During the 1994–1995 field session the movement of residents on and off the atoll were monitored for Falalop but not for Falachig atoll. Census data on Falachig were collected over a two-month period in which there were several opportunities for residents to return to and leave the atoll. No data were collected on the number of residents for all of Ifaluk at any specific point in time; thus the estimate of slightly more than 600 residents, rather than an exact figure.

4. Males under 14 years of age may of course receive fish within their own compound.

5. Informants claimed that solitary line fishing with bait was the main type of fishing (solitary or cooperative) during the season of calm winds (*lecheg*) from May to October.

6. These data refer to daytime solitary fishing. I did not collect systematic data on nighttime solitary fishing activities. However, casual discussions about solitary fishing indicate that nighttime solitary fishing occurred less frequently than daytime solitary fishing, and no individual exclusively fished at night.

7. On average Iyeur received 9.5% more fish than Iyefang during village-level *ilet* distributions, but it maintains 72.7% more *ilet* than Iyefang and the *ilet* represent 36.3% more residents ($n = 17$).

8. Fifteen males were observed fishing alone; however, data were not collected for three events that were the only solitary fishing events for three males.

9. It is not surprising that all consumption rates are negative given the wide distribution of fish on Ifaluk. In addition, these consumption rates do not account for the high value of fish calories, since it is the primary source of protein on Ifaluk (see below).

10. Whatever ecological cues individuals are using to assess the fishing conditions, they will never generate *exact* knowledge about the number of fishermen on a given day. Not will an individual possess precise knowledge of his payoffs for a given number of fishermen. This is a problem that all deterministic models face; strategists rarely have perfect

knowledge of all the factors relevant to the outcome of their behavioral decision. A stochastic model that took into account errors in individual estimates of the number of participants would be more realistic, although considerably more complex than the model presented here.

11. Egalitarian distributions were not included in the following model since this type of distribution was only observed twice and accounts for less than 1% of the total fish distributed.

12. The caloric gains individual k expects to receive from a men's feast was calculated as the expected caloric value of a men's feast multiplied by the ratio $\frac{1}{N}$, where N is the total number of men at risk of partaking in a men's feast. In order to simplify equation 4, men's feast was not designated by a separate variable from the other distributions. However, in generating predictions and testing the model, men's feasts were not multiplied by the consumer ratio as implied in equation 4.

13. Women's and children's weights were not measured. I have used Hillard Kaplan's calculation of consumer proportions by age, sex, and weight for the Piro (University of New Mexico, unpublished data) to estimate consumer proportions for Ifaluk residents. The Piro data were used because the physiques of the Piro and the people of Ifaluk are similar. Kaplan (1994) followed a procedure used by the World Health Organization (1985) and the National Research Council (1989a, Table 3-1; 1989b) for calculating the resting metabolic energy expenditure of individuals as a function of age, sex, and weight. The following table presents the consumer proportions that were used to determine the number of consumers in a compound on Ifaluk.

Proportion of Consumer

Age	Male	Female
0-2	0.3	0.3
3-5	0.5	0.5
6-8	0.6	0.6
9-11	0.7	0.7
12-14	0.9	0.8
15-17	1.2	0.9
18-20	1.1	0.9
21-24	1.1	0.9
25-39	1.1	1.0
40-49	1.1	0.9
50-59	1.1	0.9
>59	.8	0.7

14. Only 78 (rather than 79) cooperative sail-fishing events were used since data are missing on the number of fishermen for one fishing event.

15. Fish from a men's feast were generally left in the main canoe house for the duration of the day. Thus, any males over 14 years of age were able to consume this fish.

16. Ideally, to determine the value of a unit of protein and carbohydrate we would want to know the price that a kilogram of fish could be purchased on Ifaluk, not sold. However, these data are unavailable since individuals never purchased fish or taro from each other.

17. In contrast, Smith (1991) found that over the observed range of Inuit hunters in 16 hunt types, net return rates decreased at the largest group sizes for 15 of the hunt types analyzed, and thus there was expected to be a conflict of interest between joiners and members.

REFERENCES

Alexander, R. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.

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

Barnard, C. Editor. 1984. *Producers and Scroungers: Strategies of Exploitation and Parasitism*. London: Croom Helm.

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

Bates, M., and D. Abbott. 1958. *Coral Island: Portrait of an atoll*. New York: Charles Scribner's Sons.

Bethlehem, D. 1975. The effect of westernization on cooperative behaviour in Central Africa. *International Journal of Psychology* 10:219–224.

Betzig, L. 1988. Redistribution: equity or exploitation? In *Human Reproductive Behavior: A Darwinian Perspective*. L. Betzig, M. Borgerhoff Mulder, and P. Turke, eds. Pp. 49–63. Cambridge: Cambridge University Press.

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

Boone, J. 1992. Competition, Conflict, and the Development of Social Hierarchies. In *Evolutionary Ecology and Human Behavior*. E. Smith, and B. Winterhalder, eds. Pp. 301–337. New York: Aldine.

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

Burrows, E., and M. Spiro. 1957. *An Atoll Culture: Ethnography of Ifaluk in the Central Carolines*. Westport, Connecticut: Greenwood Press.

Caraco, T. 1981. Risk sensitivity and foraging groups. *Ecology* 62:527–531.

——. 1987. Foraging games in a random environment. In *Foraging Behavior*. A. Kamil, J. Krebs, and H. Pulliam, eds. Pp. 389–414. New York: Plenum Press.

Caraco, T., and H. Pulliam. 1984. Sociality and survivorship in animals exposed to predation. In *A New Ecology: Novel Approaches to Interactive Systems*. P. Price, C. Slobodchikoff, and W. Gaud, eds. Pp. 279–309. New York: Wiley.

Caraco, T., and L. Wolf. 1975. Ecological determinants of group sizes of foraging lions. *American Naturalist* 109:343–352.

Clark, C., and M. Mangel. 1984. Foraging and flocking strategies: Information in an uncertain environment. *American Naturalist* 123:626–641.

Crook, J. 1972. Sexual selection, dimorphism, and social organization in the primates. In *Sexual Selection and the Descent of Man, 1871–1971*. B. Campbell, ed. Pp. 231–281. Chicago: Aldine.

Enquist, M., and O. Leimar. 1993. The evolution of cooperation in mobile organisms. *Animal Behaviour* 45:747–757.

Freeman, O. Editor. 1951. *Geography of the Pacific*. New York: John Wiley and Sons.

Giraldeau, L. 1988. The stable group and the determinants of foraging group size. In *The Ecology of Social Behavior*. C. Slobodchikoff, ed. Pp. 33–53. San Diego: Academic Press.

Hamilton, W. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295–311.

Hawkes, K. 1992. Sharing and collective action. In *Evolutionary Ecology and Human Behavior*. E. Smith and B. Winterhalder, eds. Pp. 269–300. New York: Aldine.

Hayden, B. 1981. Subsistence and ecological adaptations of modern hunter-gatherers. In *Omnivorous Primates: Hunting and Gathering in Human Evolution*. G. Teleki and R. Harding, eds. Pp. 344–422. New York: Columbia University Press.

Higashi, M., and N. Yamamura. 1993. What determines animal group size? Insider-outsider conflict and its resolution. *American Naturalist* 142:553–563.

Hill, K., and K. Hawkes. 1983. Neotropical hunting among the Ache of Eastern Paraguay. In *Adaptive Responses of Native Amazonians*. R. Hames and W. Vickers, eds. Pp. 223–267. New York: Academic Press.

Hirshleifer, J., and J. M. Coll. 1988. What strategies can support the evolutionary emergence of cooperation? *Journal of Conflict Resolution* 32:367–398.

Kaplan, H. 1994. Evolutionary and wealth flows theories of fertility: Empirical tests and new models. *Population and Development Review* 20:753–791.

Kaplan, H., and K. Hill. 1992. The evolutionary ecology of food acquisition. In *Evolutionary Ecology and Human Behavior*. E. Smith and B. Winterhalder, eds. Pp. 167–201. New York: Aldine de Gruyter.

Kurland, J., and S. Beckerman. 1985. Optimal foraging and hominid evolution: labor and reciprocity. *American Anthropologist* 87:73–93.

Lutz, C. 1988. *Unnatural Emotions*. Chicago: University of Chicago Press.

MacDonald, D. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.

Maynard Smith, J. 1983. Game theory and the evolution of cooperation. In *Evolution from molecules to man*. D. Bendall, ed. Pp. 445–456. Cambridge: Cambridge University Press.

Meeker, B. 1970. An experimental study of cooperation and competition in West Africa. *International Journal of Psychology* 5:11–19.

Mesterton-Gibbons, M., and L. Dugatkin. 1992. Cooperation among unrelated individuals: evolutionary factors. *The Quarterly Review of Biology* 1992:267–281.

National Research Council. 1989a. *Diet and Health*. Washington D.C.: National Academy Press.

——. 1989b. *Recommended Daily Allowances*. Washington D.C.: National Academy Press.

Packer, C. 1986. The ecology of sociality in felids. In *Ecological Aspects of Social Evolution: Birds and Mammals*. D. Rubenstein and R. Wrangham, eds. Pp. 429–451. Princeton: Princeton University Press.

——. 1988. Constraints on the evolution of reciprocity: lessons from cooperative hunting. *Ethology and Sociobiology* 9:137–147.

Packer, C., and L. Ruttan. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.

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

Pulliam, H., and T. Caraco. 1984. Living in groups: is there an optimal group size? In *Behavioural Ecology: An Evolutionary Approach*. J. Krebs and N. Davies, eds. Pp. 122–147. Sunderland, Massachusetts: Sinauer Associates.

Pulliam, H., and G. Millikan. 1982. Social organization in the nonreproductive season. In *Avian Biology*. D. Farner and J. King, eds. Pp. XX–XX. New York: Academic Press.

Rannala, B., and C. Brown. 1994. Relatedness and conflict over optimal group size. *Trends in Ecology and Evolution* 9:17–119.

Real, L., and T. Caraco. 1986. Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics* 17:371–390.

Rodman, P. 1981. Inclusive fitness and group size with a reconsideration of group sizes in lions and wolves. *American Naturalist* 118:275–283.

Schoener, T. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.

Sibly, R. 1983. Optimal group size is unstable. *Animal Behaviour* 31:947–948.

Slobodchikoff, C. 1988. Cooperation, aggression, and the evolution of social behavior. In *The Ecology of Social Behavior*. C. Slobodchikoff, ed. Pp. 13–32. San Diego: Academic Press.

Smith, E. A. 1981. The application of optimal foraging theory to the analysis of hunter-gatherer group size. In *Hunter-Gatherer Foraging Strategies*. B. Winterhalder and E. Smith, eds. Pp. 36–65. Chicago: University of Chicago Press.

———. 1983. Anthropological applications of optimal foraging theory: A critical review. *Current Anthropology* 24:625–651.

———. 1985. Inuit foraging groups: Some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethology and Sociobiology* 6:37–57.

Sosis, R. 1991. *Inujjuamiut Foraging Strategies.* New York: Aldine de Gruyter.

———. 1997. *The Collective Action Problem of Male Cooperative Labor on Ifaluk Atoll.* Unpublished Ph.D. dissertation, Department of Anthropology, University of New Mexico.

———. 1998. *Explaining Variation in Cooperative Fishing Participation on Ifaluk Atoll.* Invited Lecture, Department of Anthropology, University of Connecticut, April 20.

Sosis, R., S. Feldstein, and K. Hill. 1998. Bargaining theory and cooperative fishing participation on Ifaluk Atoll. *Human Nature* 9:163–203.

Stephens, D., and J. Krebs. 1986. *Foraging Theory.* Princeton: Princeton University Press.

Turke, P. 1985. Fertility Determinants on Ifaluk and Yap: Tests of Economic and Darwinian Hypotheses. Unpublished Ph.D. dissertation, Department of Anthropology, Northwestern University.

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

Washburn, S., and C. Lancaster. 1968. The evolution of human hunting. In *Man the Hunter.* R. Lee and I. DeVore, eds. Pp. 293–303. Chicago: Aldine.

Wittenberger, J. 1980. Group size and polygamy in social mammals. *American Naturalist* 115:197–222.

World Health Organization. 1985. *Energy and protein requirements. Report of a joint FAO/WHO/UNU expert consultation.* Technical Report Series 724. Geneva: World Health Organization.

PART VI

CONCLUSION