Inuit Foraging Groups: Some Simple Models Incorporating Conflicts of Interest, Relatedness, and Central-Place Sharing

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Theory and research in evolutionary ecology and sociobiology have developed rather independently of each other. The mutual relevance of these two fields for understanding the adaptive significance of social interactions is exemplified by a consideration of cooperative foraging. Several simple models of optimal foraging group size are developed to explore the effect of the following factors: (1) conflicts of interest between group members and prospective joiners; (2) genealogical relatedness and kin-directed altruism; and (3) the scope of the sharing rule governing division of the harvest. Where the alternative is low-return solitary foraging, "joiners" are shown to prefer group sizes that are often suboptimal (in per capita efficiency) for "members." Predicted group sizes are also above per-capita optima where kin-directed altruism is important and/or where groups and individuals pool their catch at a central place. The effect of kin-directed altruism is incorporated by defining "inclusive efficiency" measures based on genealogical relatedness and group membership options. Expansion of the harvest-sharing network to include all foragers based at a central place is shown to eliminate conflicts of interest between members and joiners, as well as cancel the role of relatedness in shaping optimal group size or composition. Predictions from the models are tested quantitatively with data on Inuit (Canadian Eskimo) foraging groups. Some models offer an improvement in accounting for variation in Inuit foraging group size, but others do not; empirical and theoretical gaps in our understanding are revealed that call for further research.

Key Words: Foraging theory; Inclusive fitness theory; Group size; Human ecology; Inuit; Hunter–gatherers.

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INTRODUCTION

Current neo-Darwinian research on behavioral adaptation is guided by two major bodies of theory: evolutionary genetics, and evolutionary ecology. Although some versions of sociobiology provide a place for ecological theory, in general this approach (as exemplified in the work of Hamilton, Trivers, and the many who have applied their models and insights to various cases) draws primarily on theory from evolutionary genetics. At the same time, models in behavioral ecology, such as those of optimal foraging theory, have tended to develop rather independently of recent advances in natural selection theory (such as the inclusive fitness concept).

Because of their different theoretical sources, then, behavioral ecology and sociobiology often analyze the same set of phenomena from somewhat different perspectives. Models in behavioral ecology focus on the interaction of phenotypic traits with environmental parameters, viewing individuals as strategists who attempt to maximize the material returns on their investments of time and effort. In contrast, sociobiological models focus primarily on genetic asymmetries and other genotypic factors structuring the fitness outcomes of behavioral interactions in Mendelian populations, and view individuals as the agents of gene replication who carry out the task of maximizing inclusive fitness.

In some cases, the independence of ecological and sociobiological theory and research is fully justifiable, given the different kinds of questions addressed by the two approaches. However, it should often be the case that sociobiology and behavioral ecology are of mutual rel-

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evance in analysis of particular theoretical issues of empirical phenomena. Furthermore, I suggest that although each approach can be pursued alone to a certain extent, both contain inherent limitations that favor a combined approach [Wrangham (1982) makes a similar argument]. This is certainly not an original thesis, but it is one that bears repetition given the current state of affairs. I illustrate this general thesis with analysis of an empirical case—the adaptive significance of Inuit (Canadian Eskimo) hunting groups. I first approach the analysis of foraging group size using a simple model based on standard assumptions of optimal foraging theory. I then expand the analysis to consider factors of social interaction and genetic kinship, employing the basic logic of decision theory and evolutionary genetics.

OPTIMAL FORAGING THEORY

Optimal foraging theory is that branch of evolutionary ecology concerned with subsistence behavior. It represents an attempt to construct a set of models that specify a general (strategic) set of "decision rules for predators" (Krebs 1978). Foraging theory is based on economic optimization arguments and the assumption that foragers have been designed by natural selection, learning processes, and/or enculturation (Pyke, Pulliam, and Charnov 1977) to makes those choices that yield the greatest difference between foraging costs and benefits, and hence the greatest payoff for the individual forager's survival and reproductive success (Darwinian fitness). Since the costs and benefits of foraging options are difficult or impossible to quantify in increments of fitness, proximate currencies are employed in the models and in empirical tests. Typically, it is hypothesized that foragers seek to maximize the net rate of energy capture while foraging.

Optimal foraging theory breaks the foraging process into different decision categories, with a set of models devoted to analyzing each category. The most prominent categories include diet breadth (prey choice), time allocation and patch choice, movement rules, and group formation.

To the evolutionary theorist concerned with social behavior, several prominent features of optimal foraging theory stand out, and may indeed appear as deficiencies. First, foraging models hypothesize *phenotypic* (material) optimization, analyzing foraging decisions as if net rate of energy capture were a direct measure of individual fitness. Second, foraging theory deals with the decisions of individual foragers as if they were made in isolation from the behavior of conspecifics, ignoring the potential intricacies of social interaction. Third, when analysis of social processes in foraging is attempted, as in models of optimal group formation, the simplest case (equal abilities and needs, no competition or dominance, etc.) is usually assumed. Fourth, the possible role of population structure and genetic relatedness in altering the patterns favored by natural selection is ignored—hence the link of proximate currencies to individual, not inclusive, fitness.

Clearly the assumptions of decision making in isolation and foraging efficiency maximization ignore many potentially important factors. Is this simplification valid? I argue that it *is* valid as a first-order approximation, in that simple, parsimonious models are very useful for theory building and preliminary tests in a "young" field of inquiry. On the other hand, these simplifications become true deficiencies if and when they lead to repeated failures in explaining pertinent data. The data and analysis for Inuit foraging groups presented below will, I hope, illustrate both of these claims.

SOCIOBIOLOGY AND FORAGING STRATEGIES

The inclusive-fitness concept (Hamilton 1964) of evolutionary genetics, which played such a large role in instituting the discipline of sociobiology, could in principal remedy several of the limitations of optimal foraging theory just noted. Rather than view the decisions of individuals as affecting only their own fitness budgets, sociobiology considers that they may often affect the individual fitness of others, many of whom are relatives, reciprocators, or competitors (and perhaps all three at once!). As a consequence, the artificial notion of individuals pursuing their own best interests in blissful isolation from others, akin to the "Robinson Crusoe" fiction of classical economics, can be replaced by a socially dynamic view of adaptation, wherein the best strategy to pursue depends on what other actors are doing, and on their relatedness to each other.

However, focusing on the inclusive fitness outcomes of individual decisions brings its own limitations, of which two are most important here. First, most sociobiological models pay little or no attention to how the "ultimate" cost–benefit currency of inclusive fitness should be operationalized in any empirical application. Thus, if we are concerned with conducting empirical tests, the apparently greater rigor and realism of the inclusive fitness currency often may be illusory. This is not to argue that proximate currencies cannot be found to substitute in tests of sociobiological hypotheses—in many cases they can—but rather that these substitutes are not necessarily going to be any better measures of inclusive fitness than currencies such as individual foraging efficiency.

The second major limitation of a narrowly sociobiological approach is that the theory of evolutionary genetics that is its basis is far too general, and hence empty of specific predictions, to be sufficient in itself for explaining differences between particular social systems (Smith 1979). It is not terribly useful to account for the difference between solitary foraging in one society and communal foraging in another by the demonstration that inclusive fitness is maximized in each case. We need to go on to ask how this state of affairs came to be, and thus to inquire into the selective forces acting on each of these systems (cf. Stephens and Charnov 1981, p. 260). Since the forces of natural selection are to a large degree ecological, purely genetic models of adaptation are inherently incomplete (Slatkin and Maynard Smith 1979, p. 233), and we are brought once again to the mutual relevance of sociobiology and evolutionary ecology.

THE ADAPTIVE SIGNIFICANCE OF FORAGING GROUPS

Cooperative foraging and resource distribution systems are conspicuous features of human evolutionary history. The adaptive significance of foraging groups is of concern in ecological and evolutionary theory. In general, at least three possible relations may pertain between foraging strategies and the adaptive value of group formation (Schoener 1971, p. 392): (1) individuals foraging cooperatively may enjoy increased foraging success relative to solitary foragers; (2) individuals may simply aggregate in response to resource concentrations, with no direct benefit arising from cooperative foraging per se; or (3) group formation may have a neutral or negative effect on individual foraging efficiency but bring compensating advantages (such as improved predator avoidance, resource defense, survival of dependents, maintenance of reciprocity networks, or reduction of risk or uncertainty involved in food harvest). The first case, where groups form because of mutual advantages from group foraging, may arise in several different ways (review in Smith 1981). Groups may increase per capita harvest rates by better location of prey, by division of labor in capturing prey, or by reducing the degree of foraging-area overlap. Groups may also allow foragers to reduce the *variance* in food capture rates, perhaps at a cost to individual foraging efficiency. Finally, groups foraging from a central place and exploiting unpredictable food patches may increase per capita foraging efficiency through passive or active information sharing.

This brief discussion indicates that foraging strategies can affect group formation in a variety of ways, and can shape groups at (minimally) two levels—the foraging party, and the settlement system (Smith 1981). Because cooperative foraging and settlement patterns are outcomes of individual strategies, and because they necessarily are shaped both by ecological factors (such as resource availability in space and time) and social factors (such as patterns of reciprocity and relatedness), the analysis of group formation would likely benefit from a combined ecological–sociobiological approach [see Brown (1982) and Vehrencamp (1983) for parallel arguments].

Although may anthropologists and biologists have speculated on the selective factors structuring hunter–gatherer group formation, relatively few formal ecological or evolutionary models have been presented, and even less often have empirical tests of such models been attempted (Heffley 1981; Smith 1980, 1981; Beckerman 1983; Hill and Hawkes 1983). In this article I focus on the adaptive significance of foraging group formation, forgoing attention to the more complex case of settlement patterns (not to mention the strategic interactions between these two levels of group formation). First we consider a very simple optimal foraging model of group size. This model is then modified or reformulated in several ways, in order to incorporate factors ignored in the initial formulation—factors such as kinship and conflicts be-

tween individuals. In each case I test hypotheses derived from the model with data on Inuit (Canadian Eskimo) foragers, in an attempt to specify the importance of different factors in structuring foraging group formation in this society (see Appendix A for methods of data collection).

THE SIMPLE OPTIMAL GROUP SIZE MODEL

Given the basic assumptions of optimal foraging theory described above, we might expect foraging groups to form whenever cooperative foraging yields higher benefits *per forager* than does solitary foraging. More precisely, foragers should seek to form groups that maximize the per capita rate of net energy capture. For any particular foraging period, this per capita rate can be defined as

$$\bar{R} = \frac{\sum^{n} (E_a - E_e)}{t \cdot n}, \qquad (1)$$

where n is the foraging group size, t is the duration of the foraging period, and E_a and E_e label food energy acquired and metabolic energy expended, respectively, by each of the n members of the foraging group during period t. We thus predict that foragers will adjust group size (n) to changing ecological conditions, since the optimal size of n under one set of prey abundances or prey types will differ from that under another state of these (and other) variables. Note that I am assuming here—and in most models in this article—that there is an equal division of the harvest among members of a foraging group (this assumption is indeed met in most cases of Inuit foraging I have observed).

Elsewhere I have shown how one can derive a variety of hypotheses concerning foraging group size from the simple per capita maximization model (Smith 1980, 1981). In testing predictions from this model with data on Inuit hunting groups, I have constructed a classification of observed foraging trips into what I call "hunt types," defined by prey species, habitat characteristics, and foraging techniques (other than group size). I argued that for any particular hunt type, there will be at least one optimal group size (i.e., for any hunt of type j, the optimal group size $\hat{n}$ is the size for which the mean per capita net return rate $\bar{R}_j$ is at maximum). One direct test of this prediction is to determine whether the modal group size for any hunt type is the one associated with the highest per capita net capture rate (maximizes $\bar{R}_j$ varying n). A test of this prediction indicates that the modal group size is indeed the most efficient in four cases but is suboptimal in the four other hunt types, with two cases yielding indeterminate results (Table 1 and Figs. 1–10).

Clearly these results offer somewhat equivocal support for the simple model of per capita maximization. A statistical test of the rank order correlation between group size frequencies and per capita return rates yields the same ratios of supported, refuted, and indeterminate results (Smith 1981). Factors that might contribute to these mixed results without calling the basic logic of the model into question include small

Table 1. Inuit Foraging Groups: Data on Group Size and Foraging Efficiency for Ten Hunt Types

Hunt type	Sample size (No. of Hunts)	Foraging Group Size			Maximum Per Capita Return Rates	
		Mode	Mean	Range	Group size	kcal/hr[a]
Lead/floe edge	54	1	2.7	1–10	2	2520
Breathing hole	19	4	3.9	1–8	3	4120
Beluga[b]	6	—	10.3	5–15	5–6	4760
Winter caribou[b]	10	3,5	4.0	1–7	6–7	12,710
Canoe seal	36	2	2.9	1–8	1	3980
Spring goose	55	1	2.4	1–7	1,3	3400, 3410
Jig/goose	25	1	2.6	1–6	1	3290
Ptarmigan	27	1	1.5	1–6	1	1370
Lake jigging	60	1	2.8	1–10	1	1770
Ocean netting	69	1	1.6	1–5	1	21,350

[a] Net kilocalories per hunter per foraging hour, calculated as described in eq. (1) and accompanying text (see also Appendix A).
[b] No modal group size occurs in this sample of beluga hunts, while group size frequencies peak bimodally for winter caribou hunts. Maximum return rates averaged over two group sizes for both of these hunt types, in order to meet a sample criterion of ≥2 hunts.

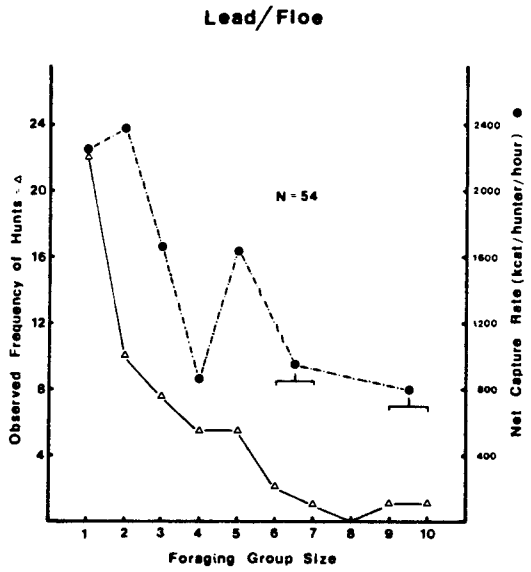

Figure 1. Return rates and observed frequencies, by group size, for Inujjuarmiut lead/floe edge hunts. Per capita net capture rates are averaged for each group size [see text, eq. (1)]; group sizes represented by a single case have been combined with data on an adjacent group size to calculate mean capture rates.

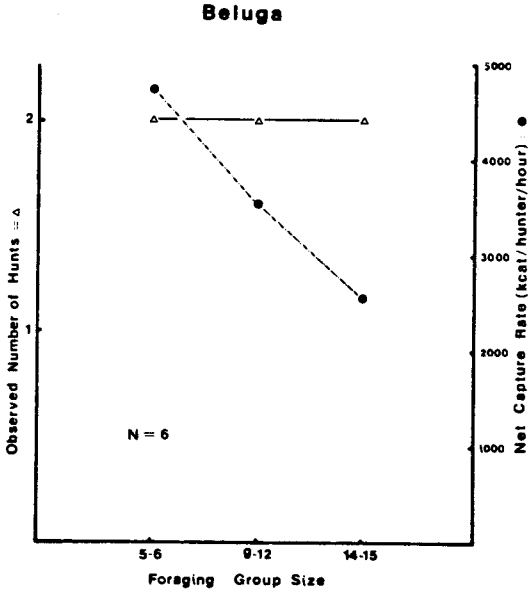

Figure 3. Beluga hunts (same format as Fig. 1).

sample sizes in several of the negative cases (breathing hole, winter caribou, beluga), minor differences in return rates of modal versus optimal group sizes (spring goose, lead/floe edge), and the possibility that imperfect knowledge constrains Inuit to form groups that are of op-

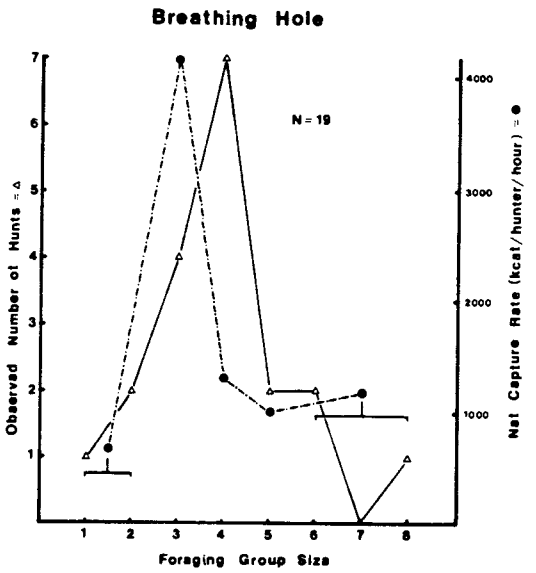

Figure 2. Breathing hole hunts (same format as Fig. 1).

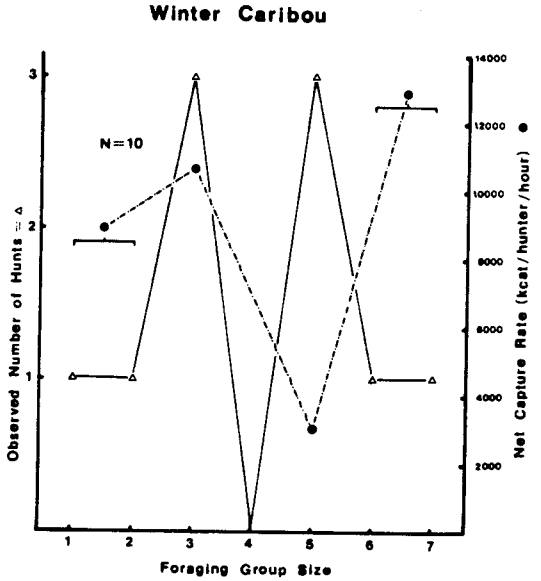

Figure 4. Winter caribou hunts (same format as Fig. 1).

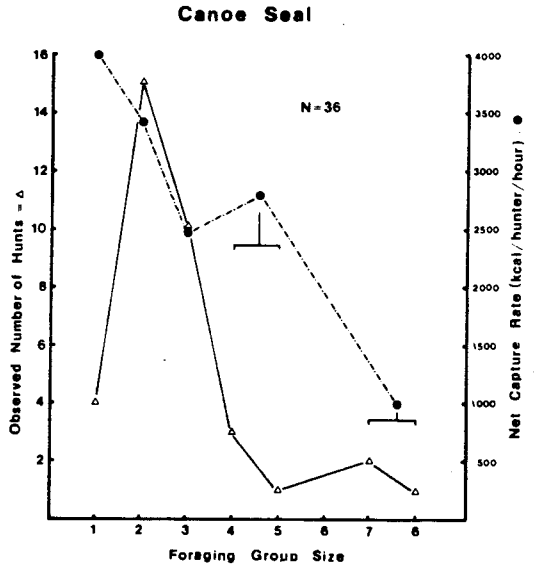

Figure 5. Canoe seal hunts (same format as Fig. 1).

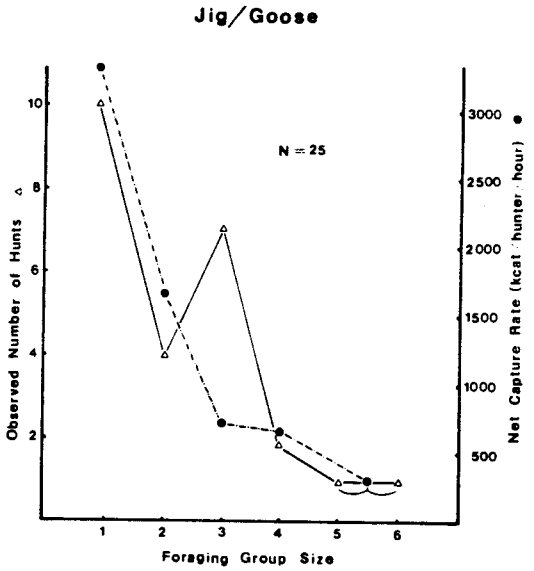

Figure 7. Jig/goose hunts (same format as Fig. 1).

timal size in the long term but may be suboptimal for a particular season. To leave it at that, however, is not very satisfactory. I prefer to view the simple per capita maximization model as a reasonable starting point, consistent with a fair share of the data, with the inconsistent results serving to suggest where further research and hypotheses are needed. For this reason, simple optimal foraging models are useful even when they fail to account for a substantial amount of the data used to test them, by virtue of the role of precise predictions and clear refutations in stimulating further research.

In the present case, I think it instructive to note that all four of the hunt types where the hypothesis of per capita maximization is confirmed have an optimal (and modal) group size

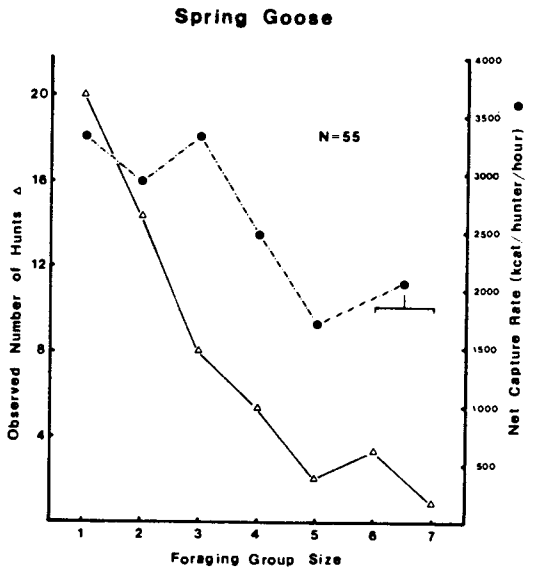

Figure 6. Spring goose hunts (same format as Fig. 1).

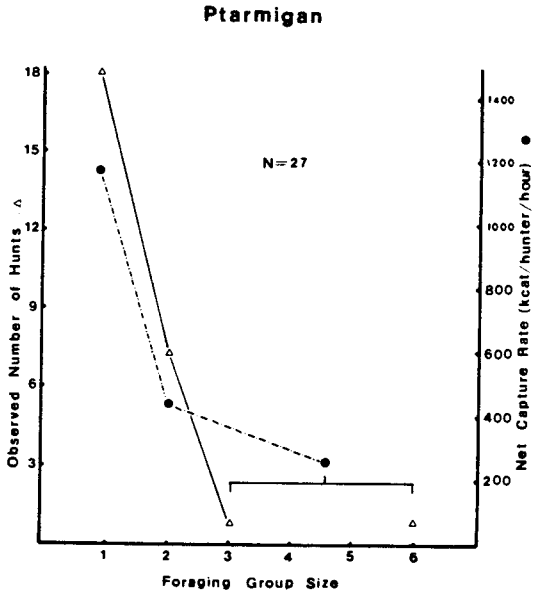

Figure 8. Ptarmigan hunts (same format as Fig. 1).

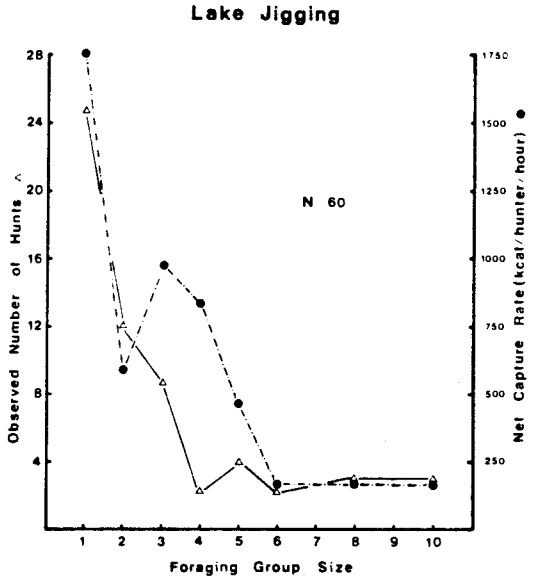

Figure 9. Lake jigging (same format as Fig. 1).

of 1, while only one of the negative or indeterminate cases has the optimum at $n = 1$. This suggests that while Inuit foragers are often quite capable of assessing the expected per capita return rate for different group sizes under various foraging conditions, they are more likely to behave so as to maximize this rate when the most efficient option is to forage alone, *unconstrained by social interactions*. It follows that we need to consider factors that might alter either the (proximate) currency individuals are attempting to maximize, or their ability to actually maximize this currency, when we are dealing with foraging processes that involve social interactions. The following three sections present models that attempt, in various ways, to do just that.

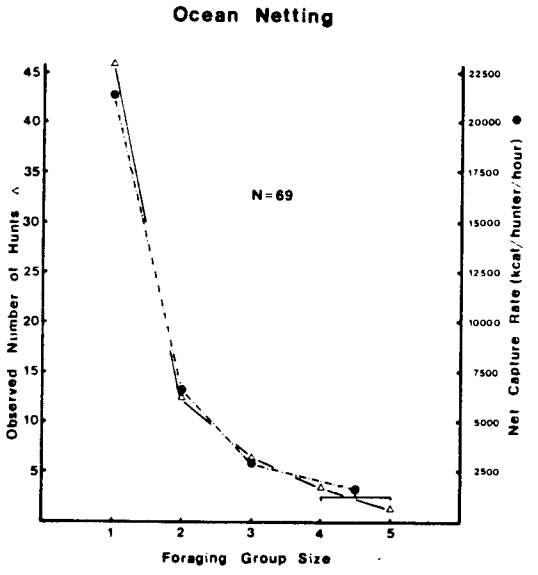

Figure 10. Ocean netting (same format as Fig. 1).

CONFLICTS OF INTEREST BETWEEN MEMBERS AND JOINERS

In the best of all possible worlds, an individual would not only know what the optimal group size was under each foraging condition but would also be under no constraints in finding a place in such a group. Obviously, in the real world there are many such constraints on the exercise of individual preferences. To maintain the analytical clarity provided by simple models, let us consider the effect just one such constraint might have on our basic per capita maximization model. Specifically, what happens if a forager cannot always find precisely $\hat{n} - 1$ other foragers to team up with (where $\hat{n}$ is the optimal group size as defined above)? In that case, while he or she may not be able to forage in a group of *optimal* size, the optimal forager should still try to join the group that yields the highest per capita return among the options available.

For simplicity, consider the case where there are only two options: to join a group of $n - 1$ foragers (and thus become the nth member), or to forage alone. In this case, the forager's preference is to join the group as long as

$$\overline{R}_n > \overline{R}_1 , \qquad (2)$$

where $\overline{R}_n$ is the per capita return rate for a group of size n and the actual share for each member if equal sharing occurs. At the point where this inequality reverses, it will be preferable to forage alone. We can call this the "joiner's rule."

Once one is a member of a group, however, one's options are different, and hence one's preferences undergo a significant shift. In particular, the options are between maintaining the group size at $n - 1$ members or allowing another forager to join. With the same goal of per capita return rate maximization, a group member should favor the addition of an nth forager as long

$$\overline{R}_n > \overline{R}_{n-1}. \qquad (3)$$

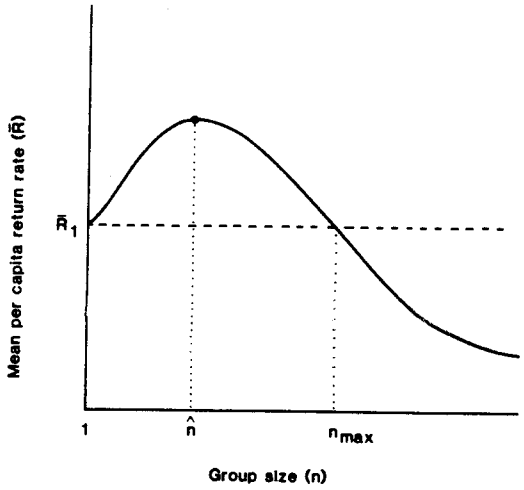

Figure 11. A graphical representation of the conflict between the "joiner's rule" and the "member's rule" [see text, eqs. (2)–(4)]. Per capita return rates peak at $\hat{n}$, the size at which members will obtain the maximum share, but foragers faced with option of solitary foraging will improve their return rate by joinging groups as large as n_{max} (the size where the per capita return rate $\bar{R}_n$ is equal to the solitary return rate $\bar{R}_1$). This model can be generalized by substituting $\bar{R}_a$—the expected return rate from *all* available alternatives open to a prospective joiner—for the solitary return rate ($\bar{R}_1$); where the relevant data are available, this is the more robust hypothesis.

The "member's rule" clearly differs fromt the "joiner's rule." It follows from the existence of two different rules or preference criteria that the rules, and hence the individuals holding those preferences, will sometimes be in conflict. Specifically, a conflict of interest between members and joiners will occur whenever

$$\bar{R}_{n-1} > \bar{R}_n > \bar{R}_1, \qquad (4)$$

that is, whenever the nth addition to a group could obtain a higher share from group foraging than from solitary foraging but by doing so would depress the total group harvest (and hence the shares the members would obtain without this additional member). A graphical version of this model (Fig. 11) makes this "zone of conflict" clear.

Under the assumptions of this model, conflicts of interest should be a quite common occurence, especially when the expected returns from solitary foraging ($\bar{R}_1$) are low relative to the per capita returns from group foraging. As long as the expected share from group foraging is higher than that from solitary foraging, an individual will prefer to join the group—even if the resulting group size is not globally optimal. Once group size reaches the optimum, however, members should prefer to exclude additional foragers from joining.

Clearly, the predictions just derived depend on a number of assumptions that are less than exhaustive of the possibilities. In particular, the reduction of the decision problem to two choices—forage alone or join a group of size n—limits the realism, and complexity, considerably. A more realistic model would specify in some detail the initial frequency distribution of "seed groups" and potential joiners, the processes of group formation, the costs of and limits to obtaining information on these, and other aspects of the process of group formation. Furthermore, there are circumstances in which conflicts of interest between members and joiners will be avoided—whenever the highest returns come from solitary foraging, for example. Nevertheless, the present model clearly shows that the simple per capita maximization model is rather limited, since even when individuals share the same optimality criterion different opportunities may lead to different preferences. The occurrence of conflicts of interest considerably complicates the task of predicting the group sizes optimal foragers will form. For while the member/joiner model does clearly specify the preference rules for different circumstances, and pinpoints the conditions under which conflicts of interest will arise, it does not address the question of how such a conflict will be resolved. To predict this, we would need to build an evolutionary or game theoretic model specifying the equilibrium outcome(s) (for important work along this line, but treating residential rather than foraging groups, see Vehrencamp 1983 and Pulliam and Caraco, in press).

Lacking a clear prediction of expected outcome, we can at least inquire what balance seems to have been achieved between member's and joiner's rules among Inuit foragers. Does the member/joiner model provide an improvement in accounting for variation in Inuit foraging group size? The relevant data are summarized in Table 2 (see also Figs. 1–10). Of the ten hunt types considered earlier, five can be ignored because the optimal size is $n = 1$, and we have already noted that in this case foragers will always maximize their own return rates by for-

Table 2. Test of the Joiner's Rule and the Members' Rule for the Preferred Size of Inuit Foraging Groups

Hunt type	Modal Group Size	Group Size Associated with[a]		
		$\bar{R}_{max}$	$\bar{R}_n > \bar{R}_1$	$\bar{R}_n > \bar{R}_{n-1}$
Lead/floe edge	1	2	2	2
Breathing hole	4	3	8	3
Beluga	—	6	9	6
Winter caribou	3,5	6	7	6
Spring goose	1	3,1	3	3

[a] For each hunt type, the foraging group size that is associated with the highest mean per capita return rate, $\bar{R}_{max}$ [see eq. (1)], the largest group an individual should join if the alternative is solitary foraging [see eq. (2)], and the largest size that members should wish to see their group grow to [see eq. (3)]. All calculations derived from data presented in Smith (1980, Appendix H).

aging alone. The remaining five hunt types do not fall into any neat pattern. In two or three cases (lead/floe edge, spring goose, and probably winter caribou), member's and joiner's rules lead to the same preferences, which do not differ much from that predicted by the simple per capita maximization model. Two suggestive cases remain. For the breathing hole hunt type, members should prefer to limit group size to that which maximizes per capita rates ($\bar{R}_{max}$), which is $n = 3$, while the relatively low expected returns from solitary foraging mean that joiners will increase their expected returns by joining any group of up to eight members—which is in fact the maximum observed for this hunt type (see Fig. 2). It is conceivable that the reason modal group size exceeds the per capita optimum for this hunt type is that the observed range of group sizes reflect various "compromises" between the interests of joiners and members. Testing this idea would require further information on the dynamics of group formation for breathing hole hunts. These hunts are organized a day or two in advance, and are highly structured and cooperative affairs, but I lack data on precisely how the size and composition of these hunting parties are determined.

The case of beluga hunting is less ambiguous. These hunts are relatively infrequent, since they are limited to the relatively short period when the whales are concentrated in the Nastapoka estuary, and require a long (ca. 210 km) journey from the village. I have quantitative time and energy data on six hunts, covering group sizes from 5 to 15 hunters and over 4100 hunter-hours of foraging. As can be seen from Figure 3, the per capita returns show a steady decline as group size increases. According to eq. (3), then, members should try to limit group size to six foragers. A joiner's preference depends on the expected returns from solitary foraging, and in this case we have no data on what these would be for beluga hunting. Informants' statements indicate that several canoes are usually required for successful beluga hunting, and my observations plus the absence of any solo kills supports the assumption that the expected return for solo beluga hunters in the study locale is very low. Furthermore, since productive beluga hunting is limited to a particular time and place, it would rarely be possible for individuals to hunt beluga there on their own. However, individuals still have the option of solitary foraging involving other hunt types, and I have assumed that the mean return from all non-beluga hunting during July (the period when organized beluga hunts occur), which consists primarily of solo hunts, is the relevant value for $\bar{R}_1$ that joiners following the rule formalized in eq. (3) would employ. Using this measure, the data indicate that joiners should prefer to join any group of beluga hunters to $n = 9$; interpolating missing values for $n = 10$ and $n = 11$ would suggest that even these group sizes yield per capita returns greater than $\bar{R}_1$. This means that a conflict of interest between members and joiners exists between $n = 6$ and $n = 9$ or 11. Since beluga hunts are announced in advance, but foragers who wish to participate travel separately in small groups (two to three hunters per canoe), and all who show up participate and share equally in the catch, we can predict that the joiner's rule will prevail over the member's rule. This would account for group sizes above the per capita maximum of $n = 5$, but not for groups above $n = 11$. I would suggest that lack of information about the number of foragers that will show up at the site (perhaps coupled with uncertainty concerning the density of whales) explains why some extremely large parties do form. In any case, the member/joiner model does seem to offer a better, if less than perfect, explanation for beluga hunting than does the simple per capita maximization model.

SOCIAL FORAGING AND INCLUSIVE FITNESS

In the preceding section, we modified the simple per capita maximization model by incorporating

some constraints and options affecting individual decision makers but maintained the same currency of individual foraging efficiency. In seeking to understand foraging decisions in a social context, another possibility we might consider is that the currency that individuals seek to maximize should itself be modified. In sociobiology, the concept of inclusive fitness (Hamilton 1964) has fundamentally altered the way in which behavioral costs and benefits are assessed in evolutionary studies. The basic idea is that when actors are genetically related to each other, natural selection will favor those who take each other's interests into account and do *not* act purely in terms of "self-interest" (i.e., personal survival and reproduction). More precisely, inclusive fitness theory predicts that actors will weigh the costs and benefits absorbed by themselves and by other individuals *as a result of the actor's behavior* according to the closeness of genealogical relationship in each case—unity for costs and benefits absorbed by oneself, half that much for those of full siblings, etc.—and act so as to effect the maximum net benefits calculated in this way.

But what are the implications of this theory for analyses of optimal group size? There have been surprisingly few attempts to analyze this issue—a result no doubt of the lack of integration between behavioral ecology and sociobiology discussed in the introduction to this paper. Recently, however, several authors (Rodman 1981; Emlen 1982; Wrangham 1982; Vehrencamp 1983) have presented models treating the effects of relatedness on group formation. Rodman's model considers the relation between group size and foraging efficiency, and hence is the most relevant to this article. He concludes that ". . . if individual fitness reaches a maximum at some group size, then inclusive fitness (of which individual fitness is a component; Hamilton 1964) will always peak at a larger group size (at which individual fitness is no longer maximized)" (Rodman 1981, p. 275). Rodman's model predicts this to be the case whenever there is some relatedness among group members, while there are large benefits to belonging in a group. That is, the model predicts that if group members have much higher individual fitness than those who are excluded from the group, then members should allow relatives to join or remain even if this lowers the members' own individual fitness, as long as the gain in relatives' fitness, devalued by the coefficient of relatedness, exceeds the loss in members' individual fitness.

Rodman uses this model to comment on data showing that groups of lions (Caraco and Wolf 1975) and wolves (Nudds 1978) often occur above the sizes that would be optimal for individual foraging efficiency, and he suggests that the model has very wide applicability. There are certain assumptions and simplifications in the model, however, that lead me to suggest that its predictions may not apply so broadly. First, Rodman does not distinguish between temporary groups, such as foraging parties, and more long-lasting social formations, such as residential groups (e.g., lion prides, wolf packs, hunter–gatherer bands). The selective factors affecting foraging groups should often be rather different than those affecting residential units (cf. Smith 1981). Second, Rodman's model assumes that the fitness of solitary individuals is zero, an assumption that—and this relates to the point just raised—might be plausible in the case of exclusion from the coresidential unit but is unlikely to be true in the case of exclusion from a temporary hunting party.

A third and more general problem is in deciding how individual preferences will interact. Since each individual is likely to have a different set of genealogical ties to other foragers, the costs and benefits of admitting or excluding different individuals will also vary from one member to another. In addition, each potential joiner will also have a unique cost–benefit calculation dependent on particular coefficients of relatedness to group members. Thus, although one might suppose that a group composed of related individuals would be more likely to "altruistically" admit another related individual even though this decreased the net return per member, it also follows that the potential joiner should carefully weigh the benefits it receives from joining against the costs of decreasing the foraging profits of relatives. Again, since foraging alone should often have much less deleterious consequences than living alone, this tradeoff may often favor solitary foraging rather than depressing the foraging efficiency of the group. Furthermore, Rodman's specific predictions seem to depend on the assumption that a single dominant individual can exclude or include group members at will [Vehrencamp (1983) makes the same assumption, while Sibly (1983) makes the opposite assumption that no member can exclude joiners]. This problem of differential

power of individuals to affect group size is one that we return to below.

Finally, among human foragers (as well as some social carnivores) the harvest from any hunt is generally shared widely beyond the confines of the foraging party itself. This sharing is reported to be kin-preferential in many hunter–gatherer societies (though often including affinal as well as consanguineal relatives). This means that foragers who are able to join foraging groups of sizes that maximize per capita harvest rates will make greater contributions to the time/energy budgets (and hence presumably fitness) of dependent kin.

In sum, the conclusion reached by Rodman that if there is any positive relatedness ($\bar{r} > 0$) kin selection will always favor groups above the individual selection optimum should apply generally. However, the *magnitude* of this effect may vary considerably. Only when costs and benefits to members versus (related) joiners are highly asymmetrical should we expect to find a marked effect of kin selection on group size. Although such asymmetry may be fairly common when considering membership in residential units, it should be less evident for membership in temporary foraging groups. (It may arise in the latter case, however—for example, when allowing young and inexperienced relatives to accompany a foraging party will provide them with valuable experience, even at the cost of some depression in the per capita harvest.) Furthermore, as shown above, individual selection alone can favor group sizes above the average per capita optimum (see also Sibly 1983; Pulliam and Caraco, in press). Hence, observations of "above-optimal" group sizes are not clear evidence in favor of kin-selection effects.

A MODEL OF THE EFFECTS OF RELATEDNESS ON FORAGING GROUP SIZE

In order to empirically test the possible effect of relatedness on the size of Inuit foraging groups, we need a model that predicts individual preferences for this variable, considering the effect of this preference on the individual's own benefits as well as on benefits that accrue to other (related) members of the foraging group.

By assuming that the inclusive fitness effect of different foraging group sizes can be directly calibrated in terms of energy capture rates, we can modify our previous inequalities for joiner's and member's rules, adding terms to express these effects. An individual deciding whether or not to become the nth member of a foraging group, at least some of whose members are close kin, should prefer to join if the sum of his share plus the share of the $n - 1$ members (devalued by $\bar{r}$, the mean coefficient of relatedness between the joiner and the members—see Appendix B) would exceed the sum of his harvest from solitary foraging plus the harvest the same group of foragers would obtain without him (again devalued by ($\bar{r}$) over the same period of time. That is, a joiner's preference rule should be to become the nth member of a group whenever

$$\bar{R}_n + [\bar{r}\bar{R}_n(n - 1)] > \bar{R}_1 + [\bar{r}\bar{R}_{n-1}(n - 1)]. \quad (5)$$

(Again, I assume here that the harvest is equally divided among group members.) The second term on each side of this inequality express what we might call the "inclusive efficiency effect" of adding an nth forager to the group, *from this joiner's point of reference*.

It is clear from eq. (5) that the closer the degree of genealogical relationship between the joiner and the group members (the larger the value of $\bar{r}$), the greater the role we can expect the inclusive efficiency effect to play in determining a joiner's preferences. Specifically, the larger $\bar{r}$ becomes (all else being equal), the more important the effect on members' shares of joining becomes to the joiner, and hence the less likely a joiner is to act selfishly in joining a group and depressing the per capita return rates simply because the joiner's share will be higher that way.[1] Note also that if there is no kinship rec-

[1] A worked example might make this clearer. Suppose there is a group of four members that would be increased to five if a prospective joiner were to be admitted ($n = 5$). Suppose further that the expected per capita return rate would decline from 1200 kcal/hr (R_{n-1}) to 1000 kcal/hr (R_n) if the fifth individual were to join, whereas the expected return from solitary foraging is 800 kcal/hr. Finally, suppose that all the individuals in question (members and joiner) are full siblings ($\bar{r} = 0.5$). Using eq. (5), we find that the inclusive efficiency of joining is 3000 kcal/hr, whereas that of solitary foraging (counting the effect on other members devalued by the coefficient of relatedness) is 3200 kcal/hr; hence, we predict that this joiner should prefer to forage alone, even though his or her personal return rate will be 200 kcal/hr *lower*. If the mean coefficient of relatedness between the joiner and the members were lowered to 0.1 (slightly less than that of first cousins), the joiner's inclusive efficiency would now be greater in the group (1400 kcal/hr) than alone (1280 kcal/hr), and the joiner's predicted preference would reverse. [At this point the predicted preferences of members and joiner would be in conflict, as calculated from eq. (6), below, whereas at the higher $\bar{r}$ of 0.5 they were not.]

ognized between the joiner and group members ($\bar{r} = 0$), the inclusive efficiency terms go to zero, and this preference rule thus reduces to that given in eq. (2)—the special case for joiner's preference with no relatedness.

The cost–benefit criterion from a group member's point of view is of course different, and considerably more complex. In this case, the inclusive efficiency measure must take into account the effects of adding a new member on the shares of (1) the decision maker, (2) the joiner, and (3) other members, as well as the effect on (4) the members' shares if the prospective joiner is excluded and (5) the joiner's expected return from solitary foraging—all devalued by the appropriate coefficients of relatedness between the decision maker and the other affected parties. To construct appropriate preference rules, one must know which member one is considering as decision maker, since each member may have a unique set of geneaological ties to the joiner and to other members. In the empirical cases I consider below, it is not known which, if any, individual is the prime decision maker, nor which individual should be considered the "joiner" (the last to join the observed foraging group). Hence, I have employed a simplified version of the decision rules for members and joiners (see Appendix B for a detailed discussion of the various forms the rules can take). Specifically, I have assumed that all members of a foraging group have equal say in size limits, and that the mean coefficient of relatedness between all individuals, both "members" and "joiners" ($\bar{r}_n$), is the appropriate weighting device. Under these assumptions, the preference rule for members is to add additional foragers to the group as long as

$$\bar{R}_n + [\bar{r}_n\bar{R}_n(n-1)] > \bar{R}_{n-1} + \bar{r}_n\bar{R}_1 + [\bar{r}_n\bar{R}_{n-1}(n-2)]. \quad (6)$$

This rule expresses the idea that each member will evaluate the effect of adding an additional member by assessing the changes in his or her own share ($\bar{R}_n$ vs. $\bar{R}_{n-1}$) as well as the effects on the other $n-1$ members if the nth individual joins, or the effects on the excluded forager plus the $n-2$ other members, devalued by the coefficient of relatedness. Since we are concerned with the average preference of all individuals, any one of whom could be the joiner, this coefficient is simply the mean relatedness between all the n individuals involved ($\bar{r}_n$).

As we might expect, eq. (6) predicts that the higher the coefficient of relatedness, the more likely members will be to prefer to admit another member (and the more likely members are to *agree* on this preference), even if this reduces all members' shares somewhat but markedly increases the share of the joiner. This result is clearly consistent with Rodman's (1981) model, discussed above. Note that, as was the case with the joiner's preference rule [eq. (5)], where relatedness is zero or unrecognized, all terms in eq. (6) except the first term on each side of the inequality go to zero, and eq. (6) thus reduces to the preference rule for members deduced prior to the consideration of inclusive efficiency [eq. (3)].[2]

Before considering the degree of fit between the inclusive efficiency predictions and the observed variation in Inuit group size, it is worth noting the gross patterns evident in the structuring of genealogical relationships within Inuit hunting groups. The population I studied spent much of the year concentrated in a single settlement (Inujjuaq) of over 600 residents, with approximately one fifth this number being individuals (primarily adult males) who engaged in at least a moderate amount of foraging during the study year. Thus, individual foragers could in theory choose from a large pool of potential hunting partners—a number without real historical precedent for this population, which until very recently lived in camps of 20–60 people.

Historically, Inuit camps were loosely amalgamated into regional groupings by extensive intermarriage and residential movement between camps, although boundaries of exogamy or territory were not clearly defined in the eastern Arctic. Hence, present residents of Inujjuaq (termed Inujjuarmiut) are linked by a web of kinship ties encompassing all but a few of the village residents. Nevertheless, individuals classify their relatives by genealogical closeness, and association into foraging groups does not approach

[2] All the expressions in this section (and in Appendix B) assume that selection favors increased inclusive fitness, and hence increased inclusive efficiency. However, recent theory demonstrates that selection does not maximize inclusive fitness under certain conditions of frequency dependence or strong selection (see Michod 1982 for a review). Nevertheless, given the rather hypothetical link between fitness and efficiency, a more rigorous derivation of predictions would be of little relevance here—hence, the simplifying assumption that selection favors traits that maximize inclusive fitness will be maintained.

randomness with respect to kinship for any but the largest beluga hunts. Since I have not completed a genealogical analysis of the entire village population, I cannot quantitatively demonstrate the degree to which positive assortment (by kinship) structures hunting groups in comparison to a random assortment model. However, I have analyzed the genealogical linkages between individuals in a sample of hunting groups, and can thus calculate the coefficient of relatedness specified in eqs. (5) and (6) (see Appendix B regarding methodology).

Data analyzed thus far covers 65 hunting groups representing 6 different hunt types, with groups ranging in size from 2 to 16 individuals (Table 3). These data indicate that average relatedness, even for small groups, is not terribly high. specifically, $\bar{r}_n$ rarely averages more than 0.2, and usually falls below 0.1 (for comparison, a dyad consisting of full sibs has $r = 0.5$, while one of first cousins = 0.125). Given the large family size typical of Inujjuarmiut, it would certainly be feasible to assemble foraging groups of siblings, cousins, and other close relatives on a more consistent basis than is revealed in the present data. Thus, although genealogical kinship certainly plays some role in structuring Inujjuarmiut foraging groups, it does not appear to play a dominant one.

It is worth noting the contrast these data present to data on Yu'pik Eskimo whaling crews from St. Lawrence Island, Alaska reported by Morgan (1979). Whaling crews range from five to seven men, drawn from a village of 350 total population, and Morgan's sample documents an average coefficient of relatedness of 0.31 (weighted by number of hunts per crew). The reasons for this striking difference cannot be explored here, but I suspect the presence of corporate kin groups with well-defined property interests in the St. Lawrence case, and their absence in the Inuit case, may be crucial. The differences between these two related hunting societies might ultimately be ascribed to their differing ecological contexts, which presumably generate rather different selective pressures on patterns of social interaction, favoring unilineal kin groups with hereditary membership in the Yu'pik case (e.g., Hughes 1960) but an emphasis on bilateral kinship, widely extended social networks, partnerships, extensive adoption, and fictive kinship devices of several sorts that have been well documented in the Inuit case (e.g., Guemple 1976, 1979). These are differences for which the concepts of inclusive fitness and genetic relatedness are relevant but by no means analytically sufficient.

Reasons for the patterns of variation in foraging-group relatedness summarized in Table 3 cannot be analyzed in detail here, and in many ways remain obscure. A few points may be noted, however. First, variation in group relatedness *between* hunt types does not seem to follow any simple pattern. Hunt types characterized by high degrees of cooperation and division of labor exhibit both relatively high (winter caribou) and low (breathing hole, beluga) coefficients of relatedness. Second, the genealogical and social relationships underlying similar $\bar{r}$ values are often quite different: thus, caribou hunts typically consist of a group of related men in their prime, age-mates with similar hunting abilities and experience, whereas the relatively high degree of relatedness observed for groups engaged in ocean netting usually represents teacher–pupil relationships (e.g., an adult and

Table 3. Genealogical Relatedness of Inuit Foraging Groups, by Group Size and Hunt Type

Hunt type	Mean Coefficient of Relatedness[a] ($\bar{r}_n$) for All Groups of Size n										Overall
	$\bar{r}_2$	$\bar{r}_3$	$\bar{r}_4$	$\bar{r}_5$	$\bar{r}_6$	$\bar{r}_7$	$\bar{r}_9$	$\bar{r}_{10}$	$\bar{r}_{14}$	$\bar{r}_{16}$	$\bar{r}$
Lead/floe edge	∅	0.021	0.021	0.063	—	—	—	—	—	—	0.013
Breathing hole	—	0.021	0.021	0.025	—	—	—	—	—	—	0.024
Beluga	—	—	—	0.006	0.070	0.065	—	0.017	0.032	0.013	0.046
Winter caribou	0.125	∅	—	0.159	—	0.208	0.141	—	—	—	0.132
Spring goose	0.225	0.025	0.063	0.050	0.063	0.060	—	—	—	—	0.121
Ocean netting	0.203	0.167	0.165	—	—	—	—	—	—	—	0.185

[a] Relatedness coefficients are calculated as specified in Appendix B. and averaged for each group size for each hunt type. ∅ indicates no known genealogical relationship between any members of the foraging group(s). A dash indicates lack of data on relatedness, or lack of occurrence of groups of that size in the sample for that hunt type. Overall $\bar{r}$ is weighted by the number of hunts per group size.

his adolescent nephew). Finally, I would stress that variation in $\bar{r}$ is often a poor indicator of the inclusive fitness consequences of different associations. For example, while cases of brothers hunting together are fairly rare in my sample, teams of brothers-in-law are quite common (see Fig. 12 for a graphic but not atypical example). Yet the first dyad, with an $\bar{r}$ value of 0.5, may often be no better an avenue towards inclusive fitness enhancement than the latter, where $\bar{r}$ normally equals 0 in this rather exogamously inclined population.[3] Raymond Hames (1981) reports a similar case where the genetic relatedness of cooperators, such a seductively convenient measure, is a misleading index of the inclusive fitness consequences of social interaction (see also Smith 1979).

Imperfect as they are, do measures of genetic relatedness help us understand variation in the size of Inujjuarmiut foraging groups? The inequalities stated above predict the maximum or optimum group sizes that joiners [eq. (5)] and members [eq. (6)], respectively, will prefer when they are attempting to maximize their inclusive efficiency. As was the case before we considered relatedness, our main interest is in hunt types where individual efficiency is *not* maximized by solitary foraging, since otherwise the inclusion of a relatedness weighting has no effect on the optimum or preferred group size.

From Table 4, we see that joiners and members often have the same preference, which in these cases does not differ from the preferences predicted on the basis of individual foraging efficiency alone (see Table 2). In two cases, however, the inclusive efficiency rule for joiners does lead to a conflict with that for members. For breathing hole hunts, individuals should prefer to join any group in the observed range if the only alternative is solitary foraging; the low degree of relatedness found among groups for this hunt type has no effect on the conclusion reached earlier that joiners and members are potentially in conflict when group size exceeds three hunters. For beluga hunting, members continue to prefer small groups ($n = 6$), whereas joiners should be willing to join parties as large as 10—almost identical to the predictions made without consideration of relatedness (Table 2). From these somewhat limited data, I conclude that genealogical ties and inclusive efficiency play little or no role in structuring the *size* of Inuit foraging groups, although kinship does play some role in shaping their *composition*.

[3] It is possible to reformulate measures of inclusive fitness effects to take such factors into consideration (e.g., West-Eberhard 1975; Emlen 1982). Thus, the effect of foraging interactions on a brother-in-law's *offspring* (who, barring extramarital paternity, have a coefficient of relatedness to ego of 0.25) could be taken into account by knowing how much of the brother-in-law's harvest was allocated to those offspring. Given the present data, however, this modification cannot be made operational.

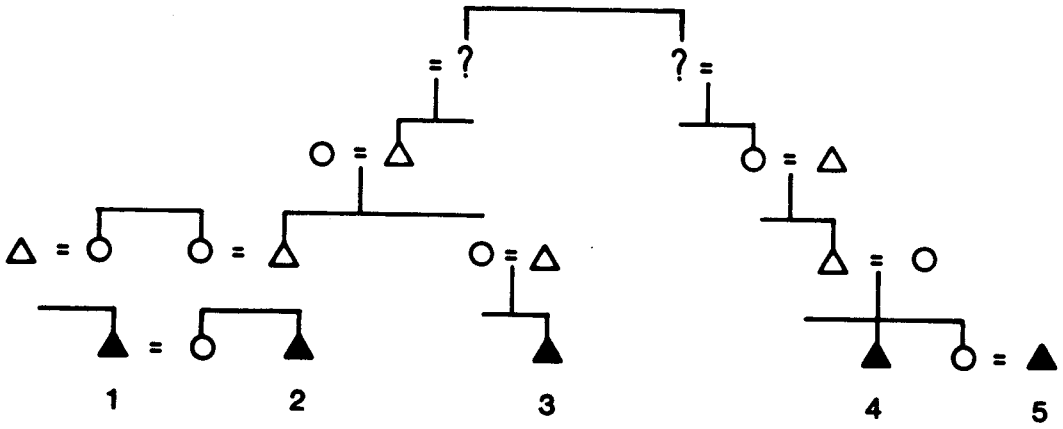

Figure 12. Genealogical composition of a single Inujjuarmiut breathing hole hunt. The five foragers, all males, are identified by darkened symbols. Note that three men (numbers 1, 2, and 5) have no known consanguineal links to each other or to any other group member, but are linked by affinal ties (in particular, the links between 1 and 2, and between 4 and 5, are those of "brothers-in-law").

Table 4. Inuit Foraging Group Size and Inclusive Efficiency Measures for Members and Joiners

Hunt Type	Modal Group Size	Group Size Satisfying Inclusive Efficiency Rule for	
		Joiners[a]	Members[b]
Lead/floe edge	1	2	2
Breathing hole	4	5	3
Beluga	—	10	6
Winter caribou	3.5	6	6
Spring goose	1	3[c]	3[c]

[a] The largest group size that a joiner seeking to maximize his or her inclusive efficiency would wish to join, if the alternative is solitary foraging [see eq. (5)].

[b] The group size that maximizes the inclusive efficiency of the average member [see eq. (6)].

[c] Because of the very small difference between $\bar{R}_1$ and $\bar{R}_3$ (see Table 1), joiners and members might be predicted to be indifferent between $n = 1$ and $n = 3$.

COMMUNAL SHARING AT THE SETTLEMENT LEVEL

The models discussed above all assume that the catch of a foraging group is divided equally among the members of that group, these shares then being utilized as each group member sees fit. This sharing rule was not chosen at random, but because it matches the pattern I usually observed among Inuit foragers. Alternative sharing rules are conceivable, and this section models the consequences of adopting a different rule. Specifically, I consider the case where all foragers coresident in a camp (often termed a "band" in the hunter–gatherer literature) pool their catch, whether obtained by solitary foragers or by groups. Such band-level sharing has been documented in detail for Aché Indians in Amazonia (Kaplan et al. 1984), and something like it occurs among Inuit in certain situations.

Let us assume that the sharing rule operates as follows: each day foragers leave camp and forage singly or in one or more groups, returning their catch to the camp, where it is pooled and then divided into equal shares for each resident. For simplicity, I will ignore differences between individuals in foraging effort and success and will consider only the case where a single foraging group forms. The decision thus concerns how large this group will be, and hence how many (if any) individuals will forage alone on any day. Note that at the end of each foraging period, every individual's share will equal

$$\frac{n\bar{R}_n + m\bar{R}_1}{N},$$

where n is the size of the foraging group, m is the number of solitary foragers, and N is the total membership of the band ($N \geq n + m$). The goal of each forager should then be to maximize this share, which is achieved by adding an nth forager to the foraging group, thus reducing the number of solitary foragers from m to $m - 1$, as long as

$$n\bar{R}_n + (m - 1)\bar{R}_1 > (n - 1)\bar{R}_{n-1} + m\bar{R}_1. \quad (7)$$

which simplifies to

$$n\bar{R}_n > (n - 1)\bar{R}_{n-1} + \bar{R}_1. \quad (8)$$

[A similar model is presented in Hill and Hawkes (1983); an earlier version of eq. (7) is given in Smith (1983).]

The interesting results of the band-sharing model concern the ways in which its predictions differ from those derived above under conditions of equal sharing within the foraging group. First, under settlement-wide sharing, eq. (8) expresses the optimal decision rule for *all* foragers in the sharing network, since every individual's share is the same regardless of whether or not they are a member of a foraging group. Second, the decision rule given in eq. (8) holds true regardless of the coefficients of relatedness characterizing the foraging group or the band; indeed, these coefficients have no effect on optimal foraging group size or composition under this sharing rule. Third, because the model predicts that each forager should attempt to maximize the per capita share of band members, and hence the total band harvest, rather than their own personal catch, conflict of interest over group size per se should not occur. This last point assumes that each forager faithfully observes the sharing rule and is never tempted to cheat [e.g., to maximize their personal catch for prestige reasons, at the expense of the band harvest—see Hill and Hawkes (1983) for discussion of this point]. Fourth, the optimal group size under the band-sharing rule will always be greater than or equal to the size that maximizes the per capita harvest of the foraging group, and less than or equal to the maximum size allowed by the joiner's preference rule.

This last point deserves emphasis. The optimal group size rule under band-wide sharing, as given in eq. (8), combines some elements of both joiner's and members' preference rules given earlier in eqs. (2) and (3), respectively. As

in eq. (2), the preference for joining a particular group size depends on whether this will give a greater return than solitary foraging: but the precise criterion is not whether the per capita harvest rate of the group ($\bar{R}_n$) is greater than the return rate for solitary foraging ($\bar{R}_1$), but rather whether the *marginal gain in the group harvest rate* will exceed the solitary rate. This can easily be seen by transposing eq. (8) to read

$$n\bar{R}_n - (n-1)\bar{R}_{n-1} > \bar{R}_1. \qquad (9)$$

The difference expressed by the left-hand side of this inequality is simply the marginal gain in the group harvest rate obtained by adding the nth member to the foraging group.

Indeed, under band-wide sharing, we can view the band as equivalent to a single production unit (a "firm") attempting to maximize overall foraging profits, and the group-size problem is thus the classical one of optimizing the input of each factor of production (in this case, labor allocation to group versus solitary foraging). The (neo)classical solution to this classical problem is, in the terminology of microeconomics, to add units of the production factor (group members) until marginal gains (in group harvest rate) equal marginal costs ($\bar{R}_1$, the harvest rate for a solitary forager that is forgone by taking one forager away from solo foraging and allocating his or her labor to group foraging).

Of course, hunter–gatherer bands (and wolf packs) do not operate like firms: there is no centralized management, or even usually much asymmetry in power (except by age and gender). My point is simply that where division of the harvest is even approximately on a settlement-wide basis, each individual forager will maximize his or her share by behaving *as if* the band is a unified production unit.[4] Evolutionary theory suggests that we then go on to ask why such a sharing rule might evolve, and how it might be maintained in the place of more individualistic strategies. This extremely interesting question cannot be explored here, but current research suggests that one answer might lie in ecological contexts favoring risk (variance) reduction via pooling of the catch among a large group of coresidents (Kaplan and Hill, 1985).

[4] Technically, then, a foraging band is not a firm, but rather a *team*—a group of individuals cooperating to maximize a shared goal (see Marschak and Radner 1971). This correction, and the reference, was provided by Rob Boyd (personal communication).

If the band-sharing rule often generates foraging group sizes above the optimum for individual foraging efficiency, then it may be an alternative explanation for the frequent occurence of such groupings in human and nonhuman foragers. That is, in contrast to Rodman's (1981) arguments, individual-fitness enhancement rather than kin selection might be responsible for the evolution of these large foraging parties, if accompanied by a consistent tendency to pool the catch with other foragers at the home base.[Of course, the joiner's rule given in eq. (2) is another possible alternative explanation for such phenomena.]

In principle, then, the band-sharing rule can generate predictions concerning variation in foraging group size that differ systematically from those obtained using individual efficiency or inclusive efficiency rules, and lacking band-wide sharing of the harvest. In practice, Hill and Hawkes (1983) have shown that a rule similar to eq. (8) predicts that Aché foragers will amalgamate into large parties for certain prey types, even though any individual's personal foraging efficiency would be maximized by solitary pursuit of the same prey. As it turns out, observed group sizes approach a random distribution, and evidence suggests that certain constraints on movement and communication prevent the band-maximizing strategy from prevailing in the Aché case.

The Inujjuarmiut data are even more ambiguous: for all ten hunt types, calculations using inequality (8) yield precisely the same predicted group sizes as are obtained using the simple per-capita maximization rule [eq. (1)], or the equivalent rule for members [eq. (3)]. It should be noted that at present most Inujjuarmiut hunts do not end wtih a village-wide or camp-wide sharing of the harvest, and even in the past when settlement was in small, economically integrated camps, sharing of the harvest was often more restrictive than is assumed under the band-sharing rule. But even for beluga and winter caribou hunt types, where actual sharing practices sometimes approximate settlement-wide sharing, eq. (8) does not predict group sizes over six, nor does it predict a different grouping pattern than if the catch were shared strictly within the foraging group.

In sum, for the Inujjuarmiut case, the band-sharing rule does not make predictions that can be distinguished from those of other rules, and

like these other rules it fails to account for a substantial portion of the observed variation in foraging group size. Nevertheless, the band-sharing rule may well have explanatory value in other foraging societies where its assumptions are more closely met—among Amerindian bison hunters, or Subarctic caribou specialists, for example.

CONCLUSIONS

A variety of simple models that illuminate aspects of the decision rules individuals might employ in structuring cooperative foraging have been presented here. Models of this sort should specify at least three elements: the currency individuals seek to maximize, the sharing rule governing the distribution of the harvest, and the relative power different individuals can exert when their preferences conflict. The models presented above have explored the implications of varying each of these elements to some degree, although many possibilities have been left uncharted, or even unstated.

Two currencies have been employed: individual (per capita) expected energy harvest rates, and inclusive (genealogically fractionated) energy harvest rates. The former is the standard currency in OFT, while the inclusive efficiency measure has been introduced here to model the nepotism (kin-directed altruism) that has become the cornerstone of sociobiological analysis. The results reported here suggest that the inclusion of a nepotistic weighting factor has very limited value in predicting variation in the size of Inujjuarmiut foraging groups, although this result should not be assumed to be general unless replicated among other foraging societies.

Two alternative sharing rules are incorporated in the present set of models: equal division of the harvest within the foraging group, and communal sharing with other groups and individuals who are members of the same settlement or band. The first sharing rule is capable of generating conflicts of interest over group size between potential "joiners" and existing "members" of foraging groups, whereas the second rule avoids this possibility. A communal sharing rule, where it prevails, may often act to increase the optimal foraging group size well above that which is optimal where sharing is restricted to foraging group members, although in the Inuit case examined above this does not occur.

The occurence of conflicting individual interests is a fascinating problem that is still relatively unexplored. Here foraging models have the most to learn from sociobiology (as well as from microeconomics and game theory). My efforts in this direction are quite modest: the models presented here stress the difference between a joiner's preference and those of a group member but do not attempt to predict how these conflicting interests will be resolved when they arise. The prediction that joiners will frequently benefit from joining groups even when this will increase the size above the individual members' optima is a result that is probably quite robust. Inclusion of nepotistic considerations in the "inclusive efficiency" model greatly complicates the analysis of conflicting interests. Because each individual will generally have different genealogical ties to other foragers, there might be not just two conflicting preferences (joiner's versus members'), but a variety of them.

The models presented in this article are all very simple ones. The primary justification for this is that simple models are easier to test, manipulate, and understand than are more complex models. Especially in the early stages of theory building, simple models allow us to isolate particular factors and to examine (theoretically and empirically) the effects of changes in these factors, one at a time. In the present case, it seemed wise to begin with simple models in order to explore the roles and relative importance of factors that have received little attention in previous models of cooperative foraging—that is, nepotism and individual conflicts of interest. Future models and tests will have to consider the role of additional factors and explore additional issues, as well as treating the above factors and problems in greater depth via more complex models. I am confident that this future research will demonstrate the mutual relevance of theory from evolutionary ecology, sociobiology, and the social sciences for analyzing strategies of cooperative foraging, and I hope that the present article has contributed toward such a demonstration.

APPENDIX A: DATA COLLECTION AND ANALYSIS

The data discussed in this article were collected over a 13-month period (July 1977 to August 1978) in and around the village of Inujjuaq (a.k.a.

Port Harrison, Inoudjouac, etc.), on the east coast of Hudson Bay, arctic Quebec, Canada. A brief description of methods of data collection and analysis are given here; a detailed account can be found in my thesis (Smith 1980).

The 600-plus permanent residents of Inujjuaq, termed Inujjuarmiut ("people of Inujjuaq"), are all members of the Inuit (Canadian Eskimo) ethnolinguistic category. Although no Inujjuarmiut in the area have relied exclusively on foraging for their sustenance in the last two decades, comprehensive statistics collected by other researchers (NHRC 1978) demonstrate an annual harvest of approximately 180,600 kg (edible weight) of game, which amounts to an average daily harvest of 0.85 kg (1500 kcal) per capita. The foraging economy in this area is heavily marine-oriented in summer and fall, but terrestrial foraging in winter and spring accounts for the greater portion of the total annual harvest from the land. Virtually all foraging activities involve the use of mechanized transport (canoes with outboards, snowmobiles) and imported tools (rifles, fishnets, etc.). Fox trapping, commercial soapstone carving, wage labor, and government transfer payments are the main sources of cash income, allowing the purchase of fuel and equipment for foraging, as well as store foods and other goods.

Inujjuarmiut harvest a wide range of species, ranging from fish and waterfowl to caribou and fairly large marine mammals (ringed seal, bearded seal, and beluga whale). The diversity of prey species, microhabitats, and foraging conditions result in a fairly large number of hunt types, including traditional forms such as seal hunting at breathing holes. Inujjuarmiut foraging is often a solitary occupation, but cooperative foraging is also common, and extremely important in both economic and social dimensions.

Data on Inujjuarmiut foraging were collected in two principle ways: by direct observation, and via systematic interview. The first data set was generated by accompanying hunters on a total of 41 hunts covering approximately 400 hours of observation time. Interviews were conducted throughout the study period and utilized a self-recording "calendar" system to facilitate recall; interviews generated a sample of over 650 hunts and information on more than 25,500 hunter-hours of foraging effort. Neither observed nor interviewed foragers were selected at random, as this was not feasible in case where informed consent was necessary and individuals varied in their willingness to be accompanied or interviewed. Nevertheless, the set of foragers included in my sample is quite large relative to the total number, and representative of Inujjuarmiut foragers in at least several respects (Smith 1980, pp. 223ff).

Observational data focused on the collection of detailed time–motion diaries. These were used in conjunction with published tables (Durnin and Passmore 1967; Godin and Shephard 1973) to estimate energy expenditure rates for each age-sex class, by hunt type (see Smith 1980, Appendix B). Both observational and interview data include measures of time inputs, number and type of prey harvested, fuel consumption, trip itineraries, and (for a fraction of hunts) identities of all members of the foraging group. Edible weights of prey species were calculated using a combination of field measurements and published and unpublished values; these were converted to caloric estimates in accordance with standard tables (where available) or unpublished laboratory measures (details in Smith 1980, Appendix A). These measurements or estimates of time expenditure, group size, energy expenditure, and energy harvest were then averaged over various categories of foraging trips to produce measures of mean net capture rates, as specified in the text [especially eq. (1)].

Genealogical information was collected from a number of informants, primarily older women, as part of a study of Inujjuarmiut demography. The genealogical charts published in Willmott (1961) were also consulted. The genealogical depth of the data extends to ancestors born in the late 1800s, about four generations. Genealogical data on the members of foraging groups was analyzed for 65 hunts; the method used to calculate coefficients of relatedness is described in Appendix B.

APPENDIX B: GENETIC RELATEDNESS AND INCLUSIVE EFFICIENCY

The measure of kinship employed in this article is the coefficient of genetic relatedness, r, given its modern sociobiological form and role in Hamilton's (1964) theory of kin selection and inclusive fitness maximization. Although I realize that there are some ambiguities associated with defining and measuring r (see Kurland and Gaulin 1979, Michod 1982, and Pamilo and Crozier

1982). I have followed standard practice and calculated this parameter by counting the genealogical pathways between each pair of individuals, ignoring any possible inbreeding that could not be traced genealogically. Thus, for any dyad, the coefficient of relatedness is given by

$$r = (\tfrac{1}{2})^N, \qquad \text{(B1)}$$

where N is the number of genealogical links between the two individuals. (If more than one common ancestor is involved, a more complicated formula needs to be used, but this was not encountered in my sample.)

To calculate the *average* coefficient of relatedness for a group of n individuals, one simply uses eq. (B1) to calculate r for each dyad included in the group, and then averages these values. Specifically,

$$\bar{r}_n = \frac{\sum_r^d}{d}, \qquad \text{(B2)}$$

where $d = (n^2 - n)/2$, the number of dyadic pairs.

The manner in which r is used to construct cost–benefit criteria for foraging group size decision rules is discussed in the text. Here I expand on the discussion of alternative decision rules that can be generated for predicting members' preferences.

Consider first the problem of specifying the preference for a single member of a foraging group regarding whether or not to let another forager join the group. If we label the coefficient of relatedness between the ith member and the jth joiner as r_{ij}, and that between i and k other members ($k = n - 2$) as $\bar{r}_{ik}$, then member i should prefer to admit j as the nth member of the group as long as

$$\bar{R}_n + r_{ij}\bar{R}_n + [\bar{r}_{ik}\bar{R}_n(n - 2)] > \bar{R}_{n-1} + r_{ij}\bar{R}_1 + [\bar{r}_{ik}\bar{R}_{n-1}(n - 2)]. \qquad \text{(B3)}$$

Note that the three terms on each side of this inequality are parallel expressions of the inclusive efficiency of a given group size from a focal member's point of view: the first expression is the return rate for ego (not devalued, since $r_{self} = 1$), the second expression is the return rate to the joiner, either if admitted ($\bar{R}_n$) or excluded ($\bar{R}_1$) and devalued by the degree of relatedness to the focal member (r_{ij}), and the third expression is the return rate for the $n - 2$ other members, devalued by the appropriate mean coefficient of relatedness to the focal member ($\bar{r}_{ik}$).

Although eq. (B3) gives the optimal preference rule for maximization of each member's inclusive efficiency, changing the identify of i will alter the various coefficients of relatedness (except in the special case where each member is identically related to all other members and to the joiner, as in a set of full siblings). Hence, each member will usually have differing inclusive efficiency values for adding or excluding j, which may even result in different optimal group sizes for each i.

The actual decision-making process in such situations may be rather complex, but let us consider the case where all $n - 1$ members of the group have an equal voice in deciding whether to accept j as a member. Label the mean coefficient of relatedness between j and the members as $\bar{r}_{jm}$, and that between the group members themselves as $\bar{r}_m$. Then two of the three terms on each side of eq. (B3) can be collapsed, such that the "average preference" of the group members is to admit j as the nth member of the group as long as

$$\bar{R}_n + [\bar{r}_{jm}\bar{R}_n(n - 1)] > \bar{R}_{n-1} + \bar{r}_{jm}\bar{R}_1 + [\bar{r}_m\bar{R}_{n-1}(n - 1)]. \qquad \text{(B4)}$$

Note that this last expression specifies the *average* preference of group members as a function of their *average* relatedness to the joiner and to each other, and hence the outcome of following this rule might not be optimal for any one of them. That is, eq. (B4) is a compromise solution in the case of conflicting interests and assuming equal power among members (but not for the joiner) and equal sharing of the costs of excluding joiners. Although somewhat simpler than eq. (B3), it is hardly a rule of thumb that actual foragers might reasonably employ in reaching decisions about group size, but it does provide a precise and testable expectation of what the outcome of such decisions might look like.

Finally, what if the potential joiner has an equal say in the matter? Then we seek the expression that specifies the optimality criterion for all n individuals, *on average*. With equal division of the catch, each forager will attain a capture rate of $\bar{R}_n$ if the nth individual joins, or

$$\frac{(n - 1)\bar{R}_{n-1} + \bar{R}_1}{n}$$

if the group is limited to $n - 1$ members and the nth individual forages alone (note that this as-

sumes that the solitary forager shares his catch with group members, or at least that the expected solitary return rate is a weighting factor in reaching a group decision concerning admission of the nth individual). The average relatedness between any individual and the $n - 1$ other individuals is labeled $\bar{r}_n$. Hence, *on average* any individual will benefit from increasing group size to n foragers as long as

$$\bar{R}_n + [\bar{r}_n \bar{R}_n (n - 1)] > \left[\frac{(n - 1)\bar{R}_{n-1} + \bar{R}_1}{n}\right] + \bar{r}_n \bar{R}_1 + [\bar{r}_n \bar{R}_{n-1}(n - 2)]. \quad \text{(B5)}$$

This is a more exact formulation than the similar inequality given in the text [eq. (6)], where five of the six parameters are identical to those in eq. (B5). An even more general and rigorous formulation might be possible using the matrix approach developed by Hughes (1983).

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