Foraging group size:
models and a test with jaegers kleptoparasitizing terns

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ABSTRACT

Foraging group size: models and a test with jaegers kleptoparasitizing terns

Marc Bélisle

In this thesis, I argue that the formation of foraging groups is likely to result from individual decisions constrained by the spatial distribution of food resources within a hierarchy of relative spatial scales. I argue further that foraging groups may form via different mechanisms, depending on the absolute levels of at least two relative spatial scales. Accordingly, I present four foraging group size models for which predictions rely on an environment that contains two nested relative patch scales. Second-order patches are assumed to contain discrete, non-overlapping first-order patches that correspond to food patches. Furthermore, individuals in a given second-order patch are assumed to be able to monitor their conspecifics' behavior. The number of individuals attending a first-order patch defines group size. Two of the models assume that foragers have perfect knowledge of the spatial distribution of the resources and distribute among available first-order patches in conformity to an ideal free distribution. The other two models assume that foragers are unaware of the location of first-order patches and form groups as some foragers join and exploit the food discoveries of others. Using four alternative fitness currencies, I then test the models' predictions with parasitic jaegers, Stercorarius parasiticus, kleptoparasitizing common terns, Sterna hirundo, at a migratory stopover. In this context, the tern fishing grounds and the flying terns that carried fish in their bill or crop were considered to be the jaegers' second- and first-order patches, respectively. None of the models could account for the observed jaeger group sizes, either because some predictions were not met or some assumptions violated. I discuss the violation of the models' assumptions and suggest how future group size models could benefit by incorporating more realistic assumptions.

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INTRODUCTION

Foraging group size models have dealt with the spatial distribution of foragers in simplistic environments without boundaries and where the food resources are contained within discrete patches at only one spatial scale (e.g. Caraco 1980; Clark and Mangel 1984; Giraldeau 1988; Milinski and Parker 1991; Tregenza 1995). Landscape ecology recognizes that spatial variance produces an uneven and non-random spatial distribution of objects that results in mosaics formed of patches, more or less connected with each other via corridors, within a background matrix (Forman 1995). Nevertheless, these mosaics occur at different absolute spatial scales depending on the species and are likely to be part of a hierarchy of relative patch scales (e.g. Kolasa 1989; Kotliar and Wiens 1990; Milne et al. 1992). For a given animal, the lower limit of the range of relative patch scales within which it is assumed to respond is the smallest patch structure it can perceive or that is relevant to its behavior. On the other hand, the upper limit corresponds to the animal's lifetime home range (Kotliar and Wiens 1990). The factors that may affect the response of an animal to a hierarchy of patch scales include the contrast between patches and the background, the level of patch aggregation, the number of scale levels and the absolute difference in scale among adjacent scale levels (Kotliar and Wiens 1990). As foragers respond to the spatial distribution of their food, which is embedded in these hierarchical scales of patchiness, we can expect their own spatial distribution to be hierarchically clumped in space. Accordingly, foraging groups and both their functional and proximal formation mechanisms need to be defined with respect to the relative spatial scales at which they occur.

Foraging group formation is often the result of individual decisions constrained by the spatial distribution of resources. It follows that the spatial distribution of foragers among food patches is thought to be mainly driven by the costs and benefits of interacting with conspecifics (Fretwell and Lucas 1970; Clark and Mangel 1984, 1986; Pulliam and Caraco 1984; Giraldeau 1988; Packer and Ruttan 1988; Milinski and Parker 1991; Tregenza 1995). Besides metapopulation and population models which have started to recognize and deal with the influence of hierarchical relative patch scales (e.g. chapter 11 in Forman 1995), the two types of cost-benefit models that address the formation and size of foraging groups at smaller absolute spatial and temporal scales, have so far ignored this issue. First, Ideal Free Distribution (IFD) models, which predict the group size (patch attendance) of foragers dispersing among food patches when the group members' fitness decreases with group size, are often assumed to be applicable without modifications at any spatial scale, and thus appropriate to explain the distribution of foragers at the "prey item", "patch" and "habitat" levels (Milinski and Parker 1991; Tregenza 1995; but see Morris 1992; Beauchamp et al. subm.). Second, Stable Group Size models, which predict the group size of foragers when the fitness of group members increases at small group sizes before decreasing below the fitness experienced by a solitary, are also scale free and do not even consider the spatial distribution of food resources (Sibly 1983; Clark and Mangel 1984, 1986; Giraldeau 1988; Giraldeau and Caraco 1993; Higashi and Yamamura 1993; but see Fretwell and Lucas 1970; Pulliam and Caraco 1984).

Yet, foraging groups that form at a given spatial scale via a functional mechanism accounted for by either an IFD or a Stable Group Size model can prompt the formation of foraging groups at a finer scale via other functional mechanisms. One of the possible mechanisms is conspecific attraction, a phenomenon characterized by searching foragers being attracted to the area, prey or host that other foragers are exploiting. Here, I focus on this mechanism as it is a widespread phenomenon among social foraging species, including invertebrates (e.g. Erlandsson 1988; Brown and Alexander 1994), fish (e.g. Pitcher and House 1987; Ryer and Olla 1995), birds (e.g. Pöysä 1992) and mammals (e.g. Packer and Ruttan 1988). The prevalence of conspecific attraction may result from the fact that animal aggregations often provide proper conditions for the establishment of a stable mixture of producer (individuals that search for their own food) and scrounger (individuals that exploit the producers' food discoveries) tactics or strategies among foragers (Barnard and Sibly 1981; Clark and Mangel 1984, 1986; Packer and Ruttan 1988; Caraco and Giraldeau 1991;

Vickery et al. 1991; Beauchamp and Giraldeau 1996). Therefore, by being attracted to producers, scroungers induce group formation. Although perceived as a consequence of animal aggregation (Caraco and Giraldeau 1991; Vickery et al. 1991), Producer-Scrounger (PS) (and Information-Sharing, see below) systems can thus be the cause of foraging group formation, yet at a smaller scale than the aggregation within which the PS system established itself.

Being aware of the alternative mechanisms by which foraging groups may form is a prerequisite to the investigation of the ecological determinants of foraging group size in a given species. Nevertheless, most studies of the ecological determinants of foraging group size do not consider alternative group formation mechanisms (e.g. Caraco and Wolf 1975; Nudds 1978; Rodman 1981; Mills 1985; Clark 1987; Giraldeau 1988; Giraldeau and Gillis 1988; Milinski and Parker 1991; Creel and Creel 1995; Tregenza 1995). I distinguish the ecological determinants and the mechanisms of group formation as the components of the fitness currency on which the individuals base their group membership decisions and the processes that lead to the formation of a group, respectively. Conversely, the few studies that try to discriminate among some alternative group formation mechanisms do not consider more than one fitness currency that the foragers may have tried to maximize, or do not control for confounding variables such as the precise shape of the relationship between fitness and group size, the resource spatial distribution or the number of recruits available to form groups (e.g. Hatch 1975; Packer and Ruttan 1988; Freeman and Grossman 1992; Brown and Alexander 1994). In this thesis, I first consider four general foraging group size models and their respective set of predictions relative to group size within an environment composed of two nested relative patch scales. The models (Aggregation, Dispersion, Rate-Maximizing PS, and Information-Sharing) cover group formation mechanisms accounted for by IFD, Stable Group Size, PS and Information-Sharing models, and take into account the resource spatial distribution and the number of recruits available to form groups. Using different fitness currencies, I then test the predictions of these models with fall migrating parasitic jaegers, *Stercorarius parasiticus*, kleptoparasitizing common terns, *Sterna hirundo*, at a migratory stopover located on the north shore of the St. Lawrence River, in Québec.

Foraging group size models

For simplicity, all four group size models presented assume that discrete non-overlapping first-order patches corresponding to food patches are nested within discrete non-overlapping second-order patches. They also assume that second-order patches are small enough so that the individuals present within their boundaries can monitor the behavior of conspecifics. Individuals cannot respond to the behavior of individuals occupying other second-order patches. Further common assumptions are that the relationship between the fitness of group members and group size is the same across first-order patches, and that all individuals are not related genetically by descent, have equal competitive ability, and behave so as to maximize their fitness. A group is defined as a monospecific aggregation of foragers within a first-order patch. The models thereby address group formation at the first-order patch scale and are not concerned by the group formation mechanisms that led to the aggregations in second-order patches. Nonetheless, it is essential for the models to incorporate second-order patches in order to constrain the foragers' knowledge of the environment and group joining behavior to a realistic spatial scale. Since the decision of an individual to join or leave a group, or to remain solitary, affects the fitness of all other individuals, group membership decision rules are modeled as n-person games (Pulliam and Caraco 1984).

Dispersion model. - This model is based on the simplest IFD game (Fretwell and Lucas 1970). It first assumes that the costs of joining an individual always exceed the benefits so that the fitness of group members W consequently decreases monotonically with group size γ $[dW(\gamma)/d\gamma < 0]$. The model also assumes that, within a second-order patch, all foragers have perfect knowledge of the spatial distribution of resources, that they are free to enter a first-order patch and join a group at no cost, and that the travel costs between first-order patches are negligible. As foragers benefit from dispersing among first-order patches, it follows that when in a given second-order patch the number of foragers N is greater than the number of first-order patches π, $(N > \pi)$, all first-order patches will be exploited and group size will, on average, increase linearly with N $[\partial\gamma(N,\pi)/\partial N = 1/\pi]$ and decrease at a monotonically decreasing rate with π $[\partial\gamma(N,\pi)/\partial\pi = -N/\pi^2]$, $\gamma(N,\pi) = N/\pi$. When $N \leq \pi$, however, all foragers will exploit first-order patches solitarily, $\gamma(N,\pi) = 1$. Consequently, N first-order patches will be exploited, and no variation in N or π will affect group size. Since all foragers are seeking a first-order patche that maximizes their own fitness, a stable distribution of foragers among first-order patches is only attained when all foragers do equally well and cannot improve their fitness by changing patches or groups $[W(\gamma_i) = W(\gamma_j)\ \forall\ \gamma]$. This condition, coupled with the fact that all first-order patches are of the same quality, implies that all groups will, on average, be of the same size. This distribution corresponds to a Nash equilibrium as no alternative course of action can increase an individual's fitness (Pulliam and Caraco 1984). Although simplistic, this model captures the essence of the more sophisticated IFD models for cases where foragers have to distribute themselves between patches of similar quality (Milinski and Parker 1991; Tregenza 1995).

Aggregation model. - This model is based on the ESS model of habitat selection of Pulliam and Caraco (1984), which in turn was inspired by Fretwell and Lucas' (1970) Allee-type IFD model. The model first assumes that the fitness of group members increases with group size $[dW(\gamma)/d\gamma > 0]$, peaks at a single optimal group size $\gamma^* \geq 2$ $[dW(\gamma)/d\gamma = 0$ and $d^2W(\gamma)/d\gamma^2 < 0]$, and decreases at larger group sizes as the costs of sociality (e.g. competition) bring the net benefits lower than what a solitary experiences $[dW(\gamma)/d\gamma < 0]$. The model also assumes that, within a second-order patch, all foragers have perfect knowledge of the spatial distribution of resources, that they are free to enter a first-order patch and join a group at no cost, and that the travel costs between first-order patches are negligible.

General predictions about group size under these constraints are difficult to make as they depend on the exact shape of the fitness function. In order to illustrate how the game is played, I present four possible scenarios (Fig. 1). All four depict the expected typical group sizes (sensu Jarman 1974) within a second-order patch occupied by $\underline{N}$ foragers as π increases. Scenarios A and B have the same fitness function but differ in $\underline{N}$, while scenarios C and D have the same $\underline{N}$ but differ in their fitness function. When $\underline{N}$ is large relative to π and γ^*, the group formation mechanism is analogous to the one in the Dispersion model as the fitness function decreases beyond γ^*. Accordingly, when $\pi = 1$, $\gamma = \underline{N}$, and as π increases, foragers will disperse among first-order patches in order to reduce the detrimental overcrowding effects. In contrast to the Dispersion model, group size will not always decrease down to one with π, and not all first-order patches will necessarily be occupied. For instance, in scenario A, when π increases from four to five, groups will stay put if foragers are allowed to move only one at a time; four groups of three would then be the only stable distribution (i.e. Nash equilibrium). A forager would leave a group solitarily if and only if this would improve its fitness (Sibly 1983; Clark and Mangel 1984; Pulliam and Caraco 1984). On the other hand, if foragers can move in concert or some groups break because of external causes (Clark and Mangel 1984; Kramer 1985; Giraldeau 1988), foragers could adopt a stable combination of group sizes where all foragers experience, on average, higher fitness. One might thus expect group sizes to vary between these two extremes. Still in scenario A, when π reaches six, all foragers will be in groups of optimal size, and no increase in π will further affect group size as no forager would gain by moving. This situation in which $\underline{N}/\pi \leq \gamma^*$ and $\underline{N}/\gamma^*$ is a positive integer, illustrates the special case where $\gamma = \gamma^*$ and N/γ^* first-order patches are exploited. In scenario B, however, not all foragers can be in groups of optimal size as $\underline{N}/\gamma^*$ is not a positive integer. Even though four groups of optimal size could be formed, the remaining forager would join one of them as it would experience a higher fitness than by exploiting a first-order patch solitarily. Although groups of one may be found under certain conditions [e.g. $\underline{N} =$

3, $\pi = 2$, $\gamma^* = 2$ and $\underline{W}(\gamma^* + 1) < \underline{W}(1)$], the average individual of a second-order patch occupied by more than one forager would never be found in a group of one, even when $\pi > \underline{N}$ as opposed to the Dispersion model. Scenarios C and D differ in that the fitness experienced in groups of two is higher than in groups of four in scenario C, and conversely in scenario D. In scenario C, when $\pi \geq 5$, groups are expected to vary between two extremes for the same reasons as in scenario B. In scenario D, however, no group size alteration can lead to a stable combination of group sizes when $\pi \geq 5$; the two additional groups of optimal size that could be formed as in scenario C would fusion back into a group of four since being in groups of two yields a lower fitness than being in groups of four.

Rate-Maximizing PS model. - This conspecific attraction model is based on the rate-maximizing PS game of Vickery et al. (1991) which was developed to predict the stable level of conspecific attraction in a given population. In contrast to the two previous models, foragers are assumed to be unaware of the spatial distribution of resources, i.e. they do not know where first-order patches are located within a second-order patch. Foragers must therefore either search for (produce) their food or search for opportunities to exploit (scrounge) the food of others. It is assumed that in a given round of the game, a forager can only play one tactic or strategy, i.e. either be a producer or a scrounger as the tactics are assumed to be incompatible. Still, a forager can change tactics between consecutive rounds. It follows that during a given round of the game, the proportion of foragers playing producer $\underline{p}$ and of foragers playing scrounger $\underline{q}$ in a second-order patch must sum to one ($\underline{p} + \underline{q} = 1$). Each first order-patch is assumed to contain $\underline{F}$ food items or a single item divisible into $\underline{F}$ portions. Although first-order patches deplete, π is assumed to be constant. Once a producer finds a first-order patch, it starts to exploit it. The portion of the patch that the producer is able to monopolize before the scroungers arrive to share equally what remains $\underline{A}$, is called the producer's advantage $\underline{a}$ ($\underline{F} = \underline{a} + \underline{A}$). $\underline{a}$ is assumed to be independent of the number of scroungers $\underline{qN}$ joining a producer. Since food is shared and foragers are assumed to maximize their gross rate of food intake, the group members' fitness, on average, decreases strictly monotonically at a decreasing rate with group size [$W(\gamma, F) = F/\gamma$ and $\partial W(\gamma, F)/\partial\gamma = -F/\gamma^2$]. It is assumed that the travel time to a produced first-order patch is negligible compared to the time required to exploit it. Likewise, the time needed to exploit a patch is assumed to be negligible compared to the time required by producers to find a first-order patch. Crucial to the model is that the payoffs of the scrounger tactic are assumed to be strongly, negatively frequency-dependent [$d\Omega_S(q)/dq < 0$ where Ω_S is the fitness of each scrounger within a given second-order patch] and that when rare, producers fare better than scroungers. When scroungers are rare, they are expected to do better than producers since many producers will be available to exploit. Conversely, when producers are rare, they are expected to do better than scroungers as the latter will be faced with less scrounging opportunities and less food to share once a first-order patch is produced.

In a second-order patch, a stable mixture of producers and scroungers corresponding to a Nash equilibrium will thus occur when the payoffs to each tactic are equal [$\Omega_P(q) = \Omega_S(q)$]. This is only possible when the producer is not able to monopolize enough food so that $A/F \leq 1/N$, otherwise only producers should be found within a second-order patch and groups will form by chance when producers end up simultaneously in the same first-order patch (see Beauchamp et al. subm.). Note that an increase in the energetic costs of producing is analogous to a decrease in a (Giraldeau et al. 1994). When $A/F > 1/N$, the stable proportion of scroungers in a second-order patch q^* is expected to vary according to $A/F - 1/N$, and will thus increase linearly with A up to $(N-1)/N$ when $a = 0$ [$\partial q^*(A,F,N)/\partial A = 1/F$], and increase at a monotonically decreasing rate with N toward an asymptote defined by A/F [$\partial q^*(A,F,N)/\partial N = 1/N^2$]. As group size is determined by q^* [$\gamma(q^*,N) = 1 + q^*N$], group size will therefore increase linearly with A, reaching N when $a = 0$ [$\partial\gamma(A,F,N)/\partial A = N/F$], and increase linearly with N [$\partial\gamma(A,F,N)/\partial N = A/F$]. Note that the rate at which producers find food patches is assumed to be directly proportional to their abundance pN. However, if producers interfere with each other while searching or if their individual search areas overlap, the rate at which producers find first-order patches will be reduced and so will the scrounging opportunities and possibly group size (Giraldeau et al. 1994). π is assumed to have no effect on q^* although there is some evidence that as π increases, q^* and consequently group size, will show a slight decrease because of simultaneous food discoveries by producers (Beauchamp and Giraldeau 1996).

Information-Sharing model. - This other conspecific attraction model is based on a tradition of models that address foraging group formation at the second-order patch scale (Caraco 1981, 1987; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987; Mangel 1990; Ranta et al. 1993; Ruxton et al. 1995; but see Packer and Ruttan 1988). In contrast to PS models, Information-Sharing models usually assume that all foragers search for food patches independently while simultaneously monitoring their conspecifics' behavior such that when one forager finds a patch, all the remaining individuals join the finder to share the food in an equal manner. Accordingly, $(N-1)/N$ of the N foragers are expected to play scrounger once a first-order patch is found and $\gamma(N) = N$. The food sharing implies that the group members' fitness decreases strictly monotonically at a decreasing rate with group size [$W(\gamma,F) = F/\gamma$ and $\partial W(\gamma,F)/\partial\gamma = -F/\gamma^2$]. Note that these predictions are also made by the Rate-Maximizing PS model when $a = 0$. In that particular case, determining whether groups are formed under the Information-Sharing or Rate-Maximizing PS model will require a detailed analysis of the animals' searching behavior (Vickery et al. 1991). The joining behavior of the foragers is assumed to be independent of π, although it is possible as in the PS model, that as π increases, the joining frequency, and consequently group size, will show a slight decrease because of simultaneous food discoveries.

Testing the models' predictions

Earlier work on the ecological determinants of foraging group size simply searched for a match between the optimal group size predicted under a given fitness currency and the actual mean or modal group size observed in nature (e.g. Caraco and Wolf 1975; Nudds 1978; Mills 1985; Clark 1987; Boesch 1994; Creel and Creel 1995); IFD studies have historically not been used to investigate the ecological determinants of group size. A match between expected and observed group sizes suggested that the animals based their group membership decisions on the fitness currency that correctly predicted the actual mean or modal group size. This rationale was also used with Stable Group Size models, but this time with Sibly's (1983) "stable" group size instead of the optimal group size (Giraldeau 1988; Giraldeau and Gillis 1988; Packer et al. 1990). The four models I presented above show, however, that the actual group size observed in nature will vary with the number of individuals available to form groups and the number of first-order patches. Moreover, the way in which group size varies will depend on the shape of the fitness function and whether there is some conspecific attraction or not. All of these factors must therefore be considered concurrently in order to discriminate among the potential formation mechanisms and ecological determinants of foraging group size. Furthermore, previous studies often used the mean group size as a measure of the group size containing the average or typical individual of a population (e.g. Caraco and Wolf 1975; Clark 1987; Giraldeau and Gillis 1988; Creel and Creel 1995). Such a measure of central tendency is inappropriate as it depicts the behavior of an average group and not that of an average individual (Giraldeau 1988). The "typical group size" measure developed by Jarman (1974; see methods) was found to be more appropriate (Giraldeau 1988). In addition, most studies have been conducted on animals living in complex social systems where groups are likely to be maintained to perform many functions in addition to foraging. These systems include lions (*Panthera leo*; Caraco and Wolf 1975; Rodman 1981; Clark 1987; Giraldeau and Gillis 1988; Packer et al. 1990), hyaenas (*Crocuta crocuta*; Mills 1985), wild dogs (*Lycaon pictus*; Creel and Creel 1995), wolves (*Canis lupus*; Nudds 1978; Rodman 1981), chimpanzees (*Pan troglodytes*; Boesch 1994), and humans (*Homo sapiens*; Smith 1985).

Migrating parasitic jaegers, on the other hand, offer an excellent system to investigate the formation mechanisms and ecological determinants of foraging group size. This is because jaegers congregate at terns' migratory stopovers where, in groups of varying sizes, they chase potential tern hosts. Tern fishing grounds at these migratory stopovers are often small enough to be second-order patches for jaegers (Bélisle pers. obs.; see Wuorinen 1992). Terns carrying fish in their bill or crop within these fishing grounds correspond to first-order patches for jaegers. Therefore, the number of jaegers chasing a given tern defines group size. The jaegers' chasing behavior is intensive and groups form a distinctive compact line of individuals pursuing a given tern. Hence, the group sizes of jaegers are clearly distinguishable from the jaegers' abundance on the tern fishing grounds. As both the jaegers and terns vary in abundance on the tern fishing grounds, predictions about the relationships between jaeger group size and the number of individuals that can form groups and the number of first-order patches, are testable. Moreover, jaeger groups are ephemeral and only form for foraging purposes. Migrating jaegers also experience an extremely low predation risk, have free access to groups, do not establish dominance hierarchies, cannot defend the resources obtained in chases, and are not related genetically by descent (Bélisle pers. obs.; Furness 1987a).

Models of optimal foraging theory have commonly used one of three fitness currencies: gross intake rate, net intake rate or efficiency (Ydenberg et al. 1994; Houston 1995). The maximization of a given currency by an animal is thought to be principally related to the energetic and time constraints it faces (Ydenberg et al. 1994; Houston 1995). Having no a priori indications of which currency jaegers maximize in their group membership decision rules, I hypothesized four alternative currencies that either represent gross intake rate, net intake rate, or efficiency.

METHODS

Study area and observation periods

Field work was conducted on a 4 km sandbar at the mouth of the Portneuf River (48° 38' N, 69° 06' W), a tributary of the St. Lawrence River in Québec. Observations were made from 9 August to 5 September 1994 and from 30 July to 21 September 1995. In early fall, the sandbar serves as a migratory stopover for parasitic jaegers, common terns, black-legged kittiwakes (Rissa tridactyla), and many shorebird species. There, jaegers feed by kleptoparasitizing larids, mainly common terns, and by preying upon shorebirds (Bélisle and Giroux 1995). Observations were made at the tip of the sandbar where terns congregate and where most kleptoparasitic attempts occur while predation events are rare. Daily observations lasted approximately 10 h for a total of 707 h over the two years and took place between 07:00 and 19:00 (EST). Observations were spread over the entire tidal cycle. Tides were mixed and semidiurnal with two daily complete oscillations unequal in height and duration. Data were collected by two observers equipped with binoculars (8 X), telescopes (25 X), stopwatches and portable audio tape recorders. Three research assistants participated equally in the data collection.

Estimation of the abundance of jaegers and terns

Days were divided into 15 min observation blocks (four blocks/h). At the start of each block, I counted the abundance (number) of parasitic jaegers and of common terns (flying and not flying) within a given observation perimeter (second-order-patch). The boundaries of the observation perimeter were defined by a field of 270° centered on the observer and a radius of ≈ 0.75 km as determined by landmarks. The observation perimeter was small enough to allow jaegers present within its boundaries to be potential recruits of any chase that occurred in the perimeter. The perimeter was also big enough to cover the area where jaegers chased terns, hence limiting the potential impact of jaegers that may have been outside the perimeter and joined chases. Moreover, jaegers and terns were usually concentrated in an area much smaller than the observation perimeter and the main alternative fishing grounds for terns were more than 3 km away from the tip of the sandbar. The outcome of all kleptoparasitic interactions that occurred within the perimeter could be determined clearly and independently of the weather conditions. Jaegers could be recognized individually by referring to age and individual plumage characteristics (e.g. color morph, width of breast band, relative length of central tail-feathers). The duration of observation blocks was short enough so that the counts provided reliable estimates of the abundance of the birds within a given block, but was long enough to allow consecutive counts to be considered independent of one another (determined by autocorrelation analyses, unpubl. data). The number of flying terns per jaeger present within the observation perimeter (henceforth referred to as tern availability) was used as an index of tern host (first-order patch) availability for the jaegers.

Description of chases

A chase occurred when one or several jaegers accelerated toward an obvious target tern that was then pursued as it tried to escape the jaegers. Jaeger group size was defined as the number of jaegers that took part in a chase. A chase ended successfully either when the tern dropped a fish it was carrying across its bill or regurgitated an already swallowed fish. It ended unsuccessfully when the tern did not provide any food. For each chase, the following details were recorded on an audio tape recorder by the observer that followed the chase: date, time of day, jaeger group size, occurrence of physical contacts, presence of a dangling fish in the bill of the tern, and whether the tern dropped a fish. We also noted whether the fish was secured by the jaegers, and whether the individual that secured the fish was the initiator of the chase and its position in the line of pursuit in terms of proximity to the tern when the fish was dropped. The proportion of chases in which a tern dropped a fish determined the chasing success rate. Securing rate was defined as the proportion of dropped fish that were secured by the jaegers. I refer to group feeding yield as the proportion of chases in which a jaeger obtained a fish. It is calculated for a given group size as the total number of fish secured divided by the total number of chases. The cause of unsuccessful chases was either attributed to interference from other birds such as gulls and terns or to the tern's escape when the jaegers suddenly abandoned the chase for no apparent reason.

Using a stopwatch, we measured to the nearest second the duration of chases from their onset to the time that a fish was secured by a jaeger or that jaegers gave up the pursuit. Jaegers were considered patrolling when they were either alert on the ground or water with head up, or flying within the observation perimeter. We measured patrol time to the nearest second on an opportunistic basis with a stopwatch. Patrol time was defined as the time separating two consecutive chases by the same jaeger. If it happened that the focal jaeger engaged itself in other activities such as bathing, the patrol time was discarded. The level of participation of individual jaegers during an observation block was defined as the number of times an average individual participated in a chase during the block. It was computed by summing the group sizes of all the chases that occurred during a block and dividing the latter by the abundance of jaegers during that block.

Estimation of the typical group size

All the chases occurring within the observation perimeter during an observation block were recorded along with the jaeger group sizes. An estimate of the jaeger typical group size was calculated for each observation block from the block frequency distribution of jaeger group sizes. Typical group size was computed as:

$$\sum_{i=1}^{n} \gamma_i^2 \Big/ \sum_{i=1}^{n} \gamma_i$$

where γ_i is the jaeger group size of the ith chase and n the total number of chases that occurred in an observation block (Jarman 1974).

Assessment of the fitness functions

Currency definitions. - The first currency is the per capita probability of obtaining a fish in a group of size γ, $PE(\gamma)$, expressed in fish per chase. It is calculated as the total number of fish secured divided by the total number of chases divided by γ. The second currency is the gross rate of energy intake achieved during a chase, $\underline{GREI}(\gamma)$, expressed in kJ/s and given by:

$$\underline{GREI}(\gamma) = \underline{PF}(\gamma) \cdot \underline{E}/\underline{t}(\gamma)$$

where $\underline{E}$ is the mean energetic value of a dropped fish in kJ and $\underline{t}(\gamma)$, the mean duration of a chase involving γ jaegers in s. Since the common terns of the Portneuf sandbar fed exclusively on sandlance (_Ammodytes americanus_), I estimated $\underline{E}$ via Harris and Hislop's (1978) allometric relationships for sandlance that convert total length to mass and then predict energetic value as a function of mass. Length of sandlance was obtained by measuring 25 sandlance carried by terns each day in terms of tern bill lengths to the nearest 0.33 bill (1.2 cm). The length measurements were made throughout the first three quarters of the study period. The length of the fish was subsequently transformed in cm using the average length of common terns' exposed culmen (3.6 cm; Olsen and Larsson 1995).

The third currency is the net rate of energy intake achieved during a chase, $\underline{NREI}(\gamma)$, expressed in kJ/s and takes the form:

$$\underline{NREI}(\gamma) = \frac{\underline{PF}(\gamma) \cdot \underline{E} - \underline{C}[\underline{t}(\gamma)]}{\underline{t}(\gamma)}$$

where $\underline{C}[\underline{t}(\gamma)]$ is the energetic cost of a chase for an individual in a group of γ jaegers in kJ. For simplicity, I assumed that acceleration, speed and chasing effort were independent of group size. The chasing costs could then be treated as a linear function of $\underline{t}(\gamma)$. I estimated $\underline{C}[\underline{t}(\gamma)]$ from Castro and Myers' (1988) multiple linear regression using body mass, wing length and flight duration as independent variables. Average body mass (450.7 g, $\underline{n} = 233$ males and 217 females, sexes weighted equally) and average wing length (32.4 cm, $\underline{n} =$ 143 males and 131 females, sexes weighted equally) of jaegers were taken from Furness (1987a).

The last currency is the energetic efficiency of a chase, $\underline{EFF}(\gamma)$:

$$\underline{EFF}(\gamma) = \frac{\underline{PF}(\gamma) \cdot \underline{E} - \underline{C}[\underline{t}(\gamma)]}{\underline{C}[\underline{t}(\gamma)]}$$

with no units since it is a ratio of two values having the same units (i.e. kJ/s).

Fitting of the fitness functions . - As the computation of the currencies under the form presented above could lead to only one value per group size, a method that calculates a variance around these values is mandatory to compare the values of a given currency among group sizes. I have relied on nonparametric bootstrapping procedures (Efron and Tibshirani 1993) to calculate estimates on which to base the fitness function for each of the four currencies. Bootstrap estimates and their confidence intervals were computed from 2000 bootstrap replicates following the recommendations of Efron and Tibshirani (1993). The mean of the bootstrap replicates was used as the estimate of a currency magnitude. Each bootstrap replicate was derived from bootstrap samples obtained by resampling randomly with replacement from the original data sets. The resampling algorithm operated as follows: for a group of size γ, draw an observation from the $\underline{PF}(\gamma)$ data set, if the observation is a chase where a fish was secured, then draw a chase duration from the pool of chase durations where a fish was secured, if not, then draw a chase duration from the pool of chase durations where no fish was secured. This procedure was iterated as many times as there were observations in the $\underline{PF}(\gamma)$ data set. The resulting bootstrap samples contained values from which $\underline{PF}(\gamma)$ and $\underline{t}(\gamma)$ could be calculated and then used to compute a bootstrap replicate of any of the four currencies for a given group size. The bootstrap replicates for each currency were based on the same bootstrap samples so that variation among currencies are not due to resampling biases. Confidence intervals (CI = 95%) for the bootstrap estimates were based on bootstrap percentiles of the frequency distribution of bootstrap replicates (Efron and Tibshirani 1993). The lower and upper boundaries of a 95% CI are given by the 2.5th and 97.5th percentiles, respectively.

Differences among group sizes of one to three in the mean value of a given currency were tested with a bootstrap unplanned multicomparison procedure. The procedure consists in deriving confidence intervals based on bootstrap percentiles of the frequency distribution of the bootstrap replicates estimating the difference in values between each combination of group size (Efron and Tibshirani 1993). The $\underline{P}$-value under which the null hypothesis of no difference between two groups can be rejected is based on the number of replicates outside the smallest symmetrical confidence interval around the difference bootstrap estimate within which zero can be found, divided by the total number of bootstrap replicates ($B = 2000$) (Efron and Tibshirani 1993). To keep the experiment-wise type I error rate at 0.05, a Bonferroni correction was applied by dividing the significance level by the number of comparisons being performed (Day and Quinn 1989). The bootstrap replicates used in these analyses came from the same bootstrap samples that were used to obtain the fitness functions.

Other statistical analyses

Data were pooled between years. Backward elimination stepwise logistic regression analyses (SLR) were performed using SPSS/PC+ v. 3.1 (SPSS, Inc. 1989). Factorial analyses of variance (ANOVA) were performed using SuperANOVA v. 1.11 (Abacus Concepts, Inc. 1991). All tests were two-tailed and the significance level was set at 0.05. Values are presented as the mean ± 1 SD. The median is depicted as θ.

RESULTS

Abundance of jaegers and terns

I completed 2015 observation blocks of which 1247 included parasitic jaegers. Within blocks where jaegers were observed, their mean abundance was 2.5 ± 1.4 ($\theta = 2.0$, range: 1 - 9). Jaegers were either adults or third winter immatures. Based on plumage characteristics, at least 80 different individuals were recorded within the observation perimeter. The mean total abundance of common terns in the presence of jaegers was 95.9 ± 58.7 ($\theta = 85.0$, range: 0 - 492) and the mean abundance of flying terns, 27.7 ± 29.1 ($\theta = 19.0$, range: 0 - 310). The abundance of jaegers during a block was more closely related to the abundance of flying terns (Spearman rank-order correlation, $r_s = 0.218$, $P < 0.0001$, $n = 2015$; Siegel and Castellan 1988) than to the total abundance of terns ($r_s = 0.102$, $P <$

0.0001, $n = 2015$). Tern availability was strongly correlated with the abundance of flying terns ($r_s = 0.778$, $P < 0.0001$, $n = 1247$).

Kleptoparasitism of terns by jaegers

All kleptoparasitic interactions ($n = 2896$) were directed towards larids, most of which were common terns (92.3%). Other host species included black-legged kittiwakes (5.0%), ring-billed gulls (*Larus delawarensis*; 1.8%), herring gulls (*L. argentatus*; 0.5%) and Bonaparte's gulls (*L. philadelphia*; 0.5%).

Chasing behavior. - Chases were always directed against flying terns and never involved physical contact. Chases were common, occurring in 822 blocks for a mean of 3.3 ± 2.9 chases/block ($\theta = 2.0$, range: 1 - 21). Jaegers initiated their chases either while flying (85%), standing (9%), or swimming (6%). Jaegers that joined in a chase did so shortly after it started, lining up behind the initiator. Frequent abrupt changes in the tern's flight path made it difficult for one jaeger to maintain the lead so positions in the line were frequently exchanged. Chase initiators had shorter patrol times (191 ± 35[illegible], $\theta = 48$ s, $n = 151$) than joiners (281 ± 368 s, $\theta = 146$ s, $n = 26$; Wilcoxon-Mann-Whitney test, $U' = 2535.000$, $P = 0.018$; Siegel and Castellan 1988). The participation level of individual jaegers increased with tern availability (Kendall partial rank-order correlation controlling for jaeger abundance, $\tau = 0.086$, $P < 0.0001$, $n = 1247$; Siegel and Castellan 1988). Most (73%) of the terns that were chased had a fish in their bill. This proportion did not vary across jaeger group sizes (G-test with William's correction, $G = 1.435$, df = 2, $P = 0.488$, $n = 673$, excluding groups of four; Sokal and Rohlf 1981).

Correlates of group size. - The number of jaegers chasing a tern ranged from one to five. Typical group size increased with jaeger abundance (Kruskal-Wallis test, $H = 26.545$, df = 5, $P < 0.0001$, $n = 668$, excluding abundances of 8 and 9 jaegers; Siegel and Castellan 1988), but plateaued at 1.6 ± 0.6 ($\theta = 1.5$, data pooled for abundances of 3 to 7 jaegers) when the jaeger abundance reached three (determined via a Joint-Rank Ryan test; Day and Quinn 1989; Fig. 2). The typical group size distributions were positively skewed, rarely extending beyond three. The 75th percentile of all typical group size distributions, except for an abundance of seven jaegers, was less than two (Fig. 2).

Typical group size was not significantly influenced by tern availability except when three jaegers were present (Table 1). At this jaeger abundance, typical group size decreased with tern availability but leveled off at ≈ 1.5 as tern availability exceeded 10 flying terns/jaeger (Fig. 3). Yet, typical group size ranged between one and three jaegers until the number of flying terns/jaeger reached 19. Tern availability ($\underline{\bar{x}}$ ± SD and θ) was comparable for the different abundances of jaegers at which the relationship between typical group size and tern availability was investigated (Table 1).

Chasing success. - Jaeger group size and whether the terns carried a fish in their bill were the only two factors found to influence the chasing success rate (SLR, $\chi^2 = 103.523$, df = 2, $\underline{P} < 0.0001$, $\underline{n} = 1027$; Norusis 1994). These two variables were present in the fully factorial model which also contained tern availability as an independent variable. Success rate increased with group size, reaching a plateau for groups of three before it declined back to the level of a solitary's for groups of four ($\chi^2 = 50.345$, df = 1, $\underline{P} < 0.0001$; Table 2). Chasing a tern carrying a fish in its bill increased the success rate by 21.5% ($\chi^2 = 53.554$, df = 1, $\underline{P} < 0.0001$). The SLR model correctly classified 67.5% of the observations and was better at classifying unsuccessful chases (93.0%) than successful ones (24.7%; Goodness of Fit $\chi^2 = 1028.613$, df = 1024, $\underline{P} = 0.454$).

Jaegers were efficient at securing the fish dropped by terns at all group sizes ($\underline{G} = 2.851$, df = 2, $\underline{P} = 0.240$, $\underline{n} = 1038$; data pooled for groups of 3 and 4), securing the fish usually while still in midair (Table 2). Consequently, the SLR analyses for group feeding yield selected the same model as for the probability that a tern dropped its fish except for some slight variations in the coefficients' value ($\chi^2 = 104.954$, df = 2, $\underline{P} < 0.0001$, $\underline{n} = 1027$; Goodness of Fit $\chi^2 = 1028.632$, df = 1024, $\underline{P} = 0.454$; Table 2). Securing rate was influenced by a jaeger's proximity to the tern in groups of two as the closest jaeger obtained most of the fish (Goodness of Fit $\underline{G}$-test with William's correction, $\underline{G} = 16.809$, df = 1, $\underline{P}$

< 0.0001, $n = 246$; Sokal and Rohlf 1981; Table 3). In groups of three, however, securing rate remained relatively constant across positions (Goodness of Fit $G = 4.173$, df = 2, $P = 0.124$, $n = 30$). Since individual feeding yield directly depends on securing rate, individual feeding yield followed the same trend as securing rate (Table 3). An individual's securing rate was independent of whether it initiated the chase, both in groups of two (initiators: 54.5%; Goodness of Fit $G = 1.983$, df = 1, $P = 0.159$, $n = 244$) and three (initiators: 41.9%; Goodness of Fit $G = 0.980$, df = 1, $P = 0.322$, $n = 31$).

Chase duration. - Mean and median chase durations followed the same pattern (Table 4). Mean chase duration depended on both group size and whether the chase was successful or not (two-way ANOVA with type III sums of squares on log-transformed data, group size (1-3): $F = 11.076$, df = 2, 1263, $P < 0.0001$, outcome: $F = 2.843$, df = 1, 1263, $P = 0.092$, group size × outcome: $F = 13.791$, df = 2, 1263, $P < 0.0001$; Sokal and Rohlf 1981). Successful chases were longer than unsuccessful ones for solitary jaegers, but the opposite was true for groups of two and three jaegers. Furthermore, the mean chase duration for solitary jaegers was the lowest of all group sizes for unsuccessful chases but the highest of all for successful ones.

Unsuccessful chases. - Jaegers gave up their chases without obtaining a fish because terns outmaneuvered them (95.6%) or more rarely because other birds joined in the chase and interfered (4.4%). This interference mostly involved terns mobbing the jaegers (84.8%), but also included herring and ring-billed gulls joining the chase (6.1%) or territorial jaegers attacking the chasers while defending a nearby bay (9.1%). The cause of unsuccessful chases did not vary across group sizes ($G = 3.771$, df = 2, $P = 0.152$, $n = 1509$; data pooled for groups of 3 and 4).

Fitness functions

The length of the sandlance carried by terns averaged 8.7 ± 1.7 cm ($n = 887$) which corresponds to a mass of 1.9 g and an energetic value of 12.9 kJ. As the length varied little among days, the energetic value of a fish E was treated as a constant. The sample sizes of the original data sets that were used to obtain the bootstrap samples for $\underline{PE}(\gamma)$ and $\underline{r}(\gamma)$ are found in Table 2 and 4, respectively.

All four currencies show a decline with group size (Fig. 4). However, the $\underline{PE}(\gamma)$ function has a plateau at group sizes of one and two after which a decline is significant (Fig. 4A). An increase in variance with group size is also observed for all currencies.

DISCUSSION

Prior to analyzing the performance of the foraging group size models in explaining the group formation mechanism of jaegers, and thus in predicting observed jaeger group size, I shall address some of the factors that may have influenced the success of kleptoparasitic interactions of jaegers against terns. The results obtained in this study are comparable to the ones I obtained when investigating the feeding behavior of migrating parasitic jaegers at the same site in 1991 and 1992 (Bélisle and Giroux 1995) and are also consistent with general patterns found in studies of other (mono and interspecific) seabird systems that make use of aggressive kleptoparasitism (Furness 1987a, b).

Kleptoparasitism of terns by jaegers

Chasing success rate increased with jaeger group size but plateaued rapidly as group size reached two and declined for groups of four. This rapid increase in chasing success rate at small group sizes and the leveling at larger ones are both common trends in kleptoparasitic interactions involving parasitic jaegers and common puffins (*Fratercula arctica*; Arnason and Grant 1978), parasitic jaegers and terns (*Sterna hirundo*, *S. paradisaea* and *S. sandvicensis*; Taylor 1979; Bélisle and Giroux 1995), and other larid dyads (e.g. Hatch 1970, 1975; Hulsman 1976; Verbeek 1977; Oro and Martinez-Vilalta 1994). The increase in chasing success rate with group size could result from groups putting more stress on the host, being better at constraining the tern's escape, and being more perseverant as the duration of successful chases decreased and the duration of unsuccessful chases increased with group size. However, both Hatch (1975) and Taylor (1979) observed an increase in chase duration with group size independently of chase outcome. Nevertheless, they report that successful chases were shorter than unsuccessful ones at all group sizes. This was also the case in this study except for solitaries for which successful chases were longer. One would expect kleptoparasites to have a giving up time beyond which it would not be worth continuing a chase, and thus to experience unsuccessful chases longer than successful ones. It could still be argued that many of the chases categorized as unsuccessful include chases during which kleptoparasites assess the profitability of their host, an action that would result in a shorter duration of unsuccessful chases (Furness 1987a, b; Osorno et al. 1992). The leveling of the chasing success rate at large group sizes is likely to be due to interference among kleptoparasites and to the actual proportion of chased hosts that can drop food (Furness 1987b; Bélisle and Giroux 1995).

Chasing success rate increased substantially when the jaegers chased terns carrying a fish in their bill. This was also reported by Bélisle and Giroux (1995). They explain this by the host being more inclined to drop a fish not already swallowed. They do not, however, exclude the possibility that a visible prey induces jaegers to chase more energetically and that it reduces the time to assess host suitability which thereby increases the jaegers' surprise effect (Furness 1978; Taylor 1979). Carrying a fish in the bill could simply hinder the host in its escape movements. Chasing success rate has also been found to vary with the type and size of the fish carried by hosts (e.g. Dunn 1973; Hulsman 1976; Fuchs 1977), but these factors are likely to have played a minor role as terns carried only one fish species that showed little variation in size. Tern availability did not affect the chasing success rate of jaegers. Nevertheless, Dunn (1973) observed that the chasing success rate of roseate terns, Sterna dougallii, increased with the abundance of its tern hosts, Sterna spp.. He attributes this relationship to the fact that at high host abundance, roseate terns benefited from the confusion prevailing above the tern colony which increased its surprise effect and made the hosts' escape more difficult. The overall density of birds in this study was much lower than what Dunn reported and could therefore explain the absence of a relationship between chasing success rate and tern availability. The low percentage of correct classification of the SLR for chasing success rate indicates that many other factors affecting the latter were not taken into account. For instance, neither the jaegers' surprise effect, the physiological state of either jaegers or terns, nor the prey value for either jaegers or terns were considered; all of which are known or hypothesized to affect chasing success rate (see Furness 1987a, b).

As for the chasing success rate, many factors are known to affect the efficiency of kleptoparasites at securing dropped fish. These include among others, the suitability of the prey, the height at which the chase ends, the chasing group size, the position of the kleptoparasite in the line of pursuit, and the presence of interspecific competitors (e.g. Arnason and Grant 1978; Furness 1983; Furness 1987a, b; Bélisle and Giroux 1995). The high securing rate of jaegers is likely to have resulted from the fact that terns dropped whole fish instead of a bolus, that terns often escaped by gaining altitude, and from the absence of interspecific competitors in successful chases as they caused chases to abort when present. Neither the group size nor the jaeger's position in the line of pursuit had an impact on securing rate except for groups of two, where the jaeger closer to the tern was more successful. Given that there are no constraints on joining groups and no dominance hierarchy within groups, and that jaegers change position stochastically during the course of a chase and terns have to be chased constantly to drop their fish, jaegers might not be able to position themselves in an optimal position to secure dropped fish (Arnason and Grant 1978; Bélisle and Giroux 1995).

Performance of the foraging group size models

Previous foraging group size models addressed the spatial distribution of foragers within simplistic environments of only one spatial scale. I presented four simple foraging group size models for which predictions rely on an environment that contains two nested relative patch scales. Second-order patches were assumed to contain discrete, non-overlapping first-order patches corresponding to food patches. Furthermore, individuals in a given second-order patch were assumed to be able to monitor their conspecifics' behavior, and the number of individuals attending a first-order patch defined group size. As the predictions of the four models depend on these basic assumptions, it is essential to assess their validity before proceeding further in the performance analysis of the models. The tern fishing grounds and the flying terns that carried fish in their bill or crop were considered to be the jaegers' second- and first-order patches, respectively. The tern fishing grounds located at the tip of the sandbar are likely to meet the criteria of second-order patches as they were small enough to allow jaegers to participate in any chase and were separated by at least 3 km from the nearest main alternative tern fishing grounds, thereby preventing jaegers from alternative tern fishing grounds to join chases occurring at the tip of the sandbar.

Since some terns carried fish within their crop, it was impossible to evaluate host availability directly. However, terns can fish only when in flight, and jaegers only chase flying terns. Hence, the number of flying terns per jaeger (tern availability) on the tern fishing grounds is likely to be a reliable index of host availability. That jaegers adjusted their own abundance in response to the total abundance of terns on the tern fishing grounds on a 15 min basis and that jaeger abundance paralleled even more closely the abundance of flying terns, both point toward the validity of the availability index. Moreover, the participation level of jaegers increased with tern availability, indicating that patrol time is likely to have decreased with an increase in tern availability and thus that host availability might have been limited. Nevertheless, the strong, positive correlation between tern availability and the abundance of flying terns means that the abundance of jaegers increased at a decreasing rate with flying tern abundance. This suggests that host availability was not linearly related to tern availability. The fact that jaegers chased other host species on the tern fishing grounds could have affected the linearity of this relationship. Still, more than 92% of all chases were directed toward terns, and jaegers strongly select terns over other larid species as their main host at the Portneuf sandbar (Bélisle and Giroux 1995). The nonlinearity between host and tern availability could also have resulted from a limited abundance of jaegers at larger spatial scales, an imperfect ability to assess the quality of second-order patches by jaegers which thereby have to rely on sampling to learn the quality of the environment, and the presence of travel costs when moving between second-order patches (Bernstein et al. 1988, 1991; Beauchamp et al. subm.). That the jaegers' chasing behavior is incompatible with other activities and that a jaeger can only chase one tern at a time, are both consistent with the assumptions that terns are discrete, non-overlapping first-order patches and that the number of jaegers chasing a given tern qualifies as a group. It is reasonable, therefore, to consider the tern fishing grounds and the flying terns that carried fish in their bill or crop as jaegers' second- and first-order patches, respectively.

Of the four fitness functions studied, only the PF(γ) function does not strictly decrease with group size for $\gamma > 1$ (Fig. 4). Indeed, the PF(γ) function presents a plateau for group sizes of one and two jaegers before it decreases at larger group sizes. Therefore, on the basis of the PF(γ) currency, there were no advantages or disadvantages to chase terns solitarily or in groups of two. On an energetic basis though, whether in terms of GREI(γ), NREI(γ) or EFF(γ), it was disadvantageous to join other jaegers. Moreover, jaegers in groups of four may have found themselves in a negative energetic balance as shown by the CIs of the NREI(γ) and EFF(γ) functions. Still, the increase with group size in the variance of the currency magnitudes results mainly from the bootstrapping of decreasing sample sizes. Consequently, the CIs for groups of four should be interpreted carefully. The decreasing fitness functions can be explained by t(γ) remaining relatively constant, although showing a slight increase at $\gamma = 2$ and thereby breaking the plateau found with PF(γ), and by C[t(γ)] being a linear function of t(γ). On the ground of the hypothesized currencies, the possibility that jaegers form groups in conformity to the Aggregation model can be ruled out as no peaked fitness function was found.

Jaegers that initiated and joined chases had equal chances of obtaining the fish dropped by a tern. Assuming that initiating and joining a chase correspond to a producing and a scrounging event, respectively, then initiators did not benefit from any producer's advantage, i.e. $a = 0$. Initiators might even have suffered some additional energetic costs compared to joiners as they chased terns for about one to three more seconds. When producers gain no extra share of a food patch ($a = 0$), both the Rate-Maximizing PS model and the Information-Sharing model predict that group size is the same as the number of foragers occupying a second-order patch ($\gamma = N$), independently of the number of first-order patches π. However, the jaeger typical group size plateaued around 1.5 when the jaeger abundance reached three (Fig. 2), so both the Rate-Maximizing PS model and the Information-Sharing model can be discarded as potential formation mechanisms of the jaegers' foraging groups. Note that the models' predictions are sensitive to the size of second-order patches. For instance, imagine that the observation perimeter had been smaller than the jaegers' actual second-order patch. If jaegers had formed groups according to either the Rate-Maximizing PS model when $a = 0$ or the Information-Sharing model, then jaeger group size would have overmatched jaeger abundance in the observation perimeter [$\gamma >$ "N" and $d\gamma$("N")/d"N" > 1, where "N" is the number of individuals in the observation perimeter] (Clark and Mangel 1984). Conversely, if the observation perimeter had been greater than the jaegers' actual second-order patch, then jaeger group size would have undermatched jaeger abundance in the observation perimeter [$\gamma <$ "N" and $d\gamma$("N")/d"N" < 1].

Now that the Aggregation, Rate-Maximizing PS and Information-Sharing models have been ruled out as potential explanations of the jaegers' group formation mechanism, only the Dispersion model remains. Consistent with the latter is the leveling of jaeger typical group size with jaeger abundance when N/π = a constant $\forall\ N$ (Fig. 2). Indeed, tern availability remained relatively constant across the different jaeger abundances (Table 1). As the $GREI(\gamma)$, $NREI(\gamma)$ and $EFF(\gamma)$ fitness functions have the same shape, the Dispersion model would make the same predictions about group size with any of these fitness currencies. I will thus deal with these three currencies first. When $N > \pi$, the

Dispersion model predicts that $\gamma > 1$, which is in agreement with the observed group size. Nevertheless, the Dispersion model also predicts that group size should decrease with an increase in π when holding $\underline{N}$ constant. This was not the case as jaeger typical group size was not correlated with tern availability when jaeger abundance was controlled for (Table 1), therefore ruling out the possibility that jaegers form groups according to the Dispersion model with either $\underline{GREI}(\gamma)$, $\underline{NREI}(\gamma)$ or $\underline{EFF}(\gamma)$ as fitness currency when $\underline{N} > \pi$. On the other hand, when $\underline{N} \leq \pi$, the Dispersion model predicts that $\gamma = 1$, independently of π. As the typical group size of jaegers leveled off at 1.5 when the jaeger abundance reached three, the possibility that jaegers formed groups according to the Dispersion model with either $\underline{GREI}(\gamma)$, $\underline{NREI}(\gamma)$ or $\underline{EFF}(\gamma)$ as fitness currency when $\underline{N} \leq \pi$ must also be rejected.

In the case of the $\underline{PF}(\gamma)$ currency, however, it makes no difference for jaegers to chase terns alone or in groups of two. Using this fitness currency, the Dispersion model predicts that group size should vary between one and two, independently of π, when $\underline{N} \leq 2\pi$, and decrease with π once $\underline{N} > 2\pi$. Jaeger typical group size was not correlated with tern availability when jaeger abundance was controlled for and rapidly leveled off at 1.5 with jaeger abundance, therefore supporting the hypothesis that jaegers form groups according to the Dispersion model with the $\underline{PF}(\gamma)$ currency when $\underline{N} \leq 2\pi$. The significant correlation between the jaeger typical group size and tern availability at an abundance of three jaegers nevertheless indicates that the number of tern hosts might have been limited in that particular case.

The conclusion that jaeger group formation mechanism conforms to the Dispersion model with the $\underline{PF}(\gamma)$ currency when $\underline{N} \leq 2\pi$ is appealing but requires further discussion relative to the other assumptions underlying the model. The Dispersion model assumes that first-order patches are available concurrently. Chases of terns by jaegers often happened sequentially, although simultaneous chases also occurred. Since the exact host abundance was unknown, it is impossible to determine with absolute certainty whether sequential chases occurred because there was only one tern host to chase at any one time. However, because many terns with fish dangling from their bill were frequently observed flying concurrently with sequential chases, it seems unlikely that all sequential chases can be attributed to sequential host availability. Moreover, sequential chases often did not involve all of the jaegers observed on the tern fishing grounds, suggesting that jaegers often refrained from joining an ongoing chase. This, along with the possibility that jaegers might have encountered hosts stochastically, challenges the "ideal" assumption of the Dispersion model, i.e. that individuals have perfect knowledge of the resource spatial distribution.

The decision to join a group already exploiting a food patch or to wait and continue to search for an unattended food patch or another group is likely to depend on the forager's energetic state and the time constraints it faces. Risk-sensitive behavior arguments have been applied to groups forming at the second-order patch scale in a wide variety of models (Caraco 1981, 1987; Pulliam and Millikan 1982; Clark and Mangel 1984, 1986; Ekman and Rosander 1987; Mangel 1990; Beauchamp and Giraldeau 1996). These models usually predict that individuals trying to maximize their fitness through survival should join groups when their metabolic requirements are met or likely to be met by the end of the foraging period considering the expected intake rate [net energy gained/(searching + handling time)] within a group. In this context, joining is expected to reduce a forager's variance in food intake rate by increasing its encounter rate with food patches, and thus to minimize its risk of starvation. On the other hand, individuals expecting some difficulty in meeting their metabolic requirements by the end of the foraging period should forage solitarily. By doing so, they avoid the costs of sharing food with conspecifics and increase their chance of finding enough food for themselves, providing that the expected intake rate within a group is lower than or equal to a solitary's. It follows that individuals should tend to form groups when food is abundant. The concept of risk-sensitive behavior was analogously applied at the first-order patch scale in a risk-sensitive PS model (Caraco and Giraldeau 1991; Koops and Giraldeau 1996; but see Mangel 1990). The model usually predicts that the relative use of the scrounger tactic in a given population, and thus the propensity to join a group as well as group size, should increase when foragers try to reduce their variance in food intake. Still, at either scale, the above predictions will depend on how the resources are shared between foragers (Caraco 1981, 1987; Caraco and Giraldeau 1991; Koops and Giraldeau 1996). Future foraging group size models would benefit by including risk-sensitivity arguments, especially when dealing with non-breeding animals such as migrating jaegers. Furthermore, "un-ideal" foragers have, if possible, to learn the quality of the environment through sampling in order to decide which food patch to attend. IFD studies suggest that foragers fail to learn the quality of the environment adequately if the existence of food patches is short relative to the foragers' learning rate, if there are significant travel costs between food patches, and if the level of interference between competitors within a food patch is high (Bernstein 1988, 1991; Beauchamp et al. subm.).

The Dispersion model further assumes that foragers are free to enter a first-order patch and join a group at no cost, and that travel costs between first-order patches are negligible. Since jaegers have to pursue and harass terns constantly during chases in order to be successful, it is quite possible that they cannot keep conspecifics from joining them. When engaged in one chase, jaegers never abandoned it in order to join another, even if it involved a smaller group size and hence presented some advantage to join. Fidelity to a chasing group is probably related to the short but variable duration of chases such that jaegers that change groups run the chance of not being involved in any chase at all. In this context, traveling between such ephemeral food patches implies some opportunity costs. Moreover, changing groups in order to benefit from a smaller group size is not a sure option as other jaegers are likely to make the same decision. Jaegers are thus free to join a group but not to change groups, thereby violating the "free" assumption of the Dispersion model.

Group members are expected to impose restrictions on group membership only when the group is equal to or greater than the optimal size and the costs of repelling an individual are less than those of accepting its presence (Giraldeau and Caraco 1993). These constraints are expected to reduce group size and disperse individuals in space (e.g. Fretwell and Lucas 1970; Pulliam and Caraco 1984; Giraldeau 1988; Milinski and Parker 1991; Tregenza 1995). In a conspecific attraction context, constraints on joining groups can occur through resource monopolization and defence which both increase the producer's advantage and hence reduce the payoffs and the relative use of the scrounger tactic (Vickery et al. 1991). The imposition of these constraints will not only depend on the competitive ability of the individuals but also on the characteristics of the resources. For instance, resources that are spatially clumped and temporally dispersed, as well as predictable in space or time will favor resource monopolization and defence (e.g. Pulliam and Caraco 1984; Grant 1993; Ryer and Olla 1995).

The Dispersion model also assumes that all first-order patches are identical. That terns carried fish of similar length throughout the study period is in conformity with this assumption. However, that jaegers chased both terns that carried fish in their bill and within their crop, and experienced a significant increase in success with the former, violates the assumption that first-order patches are identical. Differences in the ability to escape jaegers and in the value of the fish for the tern could also violate this assumption. Variations across patches of a given scale in the relationship between the fitness of group members and group size are likely to be the rule in many systems. These variations can arise from patches differing in resource quality and availability, and in the intensity with which foragers compete with each other (Milinski and Parker 1991; Tregenza 1995).

In addition, the Dispersion model assumes that foragers are of equal competitive ability. Unfortunately, it was impossible to measure a solitary jaeger's ability to kleptoparasitize terns. Still, jaegers that initiated chases had shorter patrol times than jaegers that joined chases, suggesting that joiners might be poorer searchers. Note, however, that many jaegers were observed initiating as well as joining chases. A violation of the "equal competitive ability" assumption in this context can lead to many different predictions relative to group size and phenotypic composition. These predictions depend on the aspect(s) in which foragers differ (e.g. searching or handling efficiency, resource holding potential) and on the characteristics of the patches (e.g. type and distribution of food resources). As a result, many fitness functions can be defined for a given patch according to the phenotypic composition of the group attending that patch, and in addition, these functions are likely to differ across patches. Because of this, a stable spatial distribution of foragers might be difficult or impossible to attain, especially at small forager abundances and when there are negligible costs to changing patches or groups (Pulliam and Caraco 1984; Caraco et al. 1989; Milinski and Parker 1991; Ranta 1993; Ranta et al. 1993; Tregenza 1995). Such an unstable spatial distribution of foragers can arise when a dominant individual can benefit from the presence of subordinates by evicting the latter from their food discoveries, while preventing subordinates from scrounging its own food discoveries. In this case, dominants will seek the presence of subordinates while the latter will try to avoid the dominants' presence (e.g. Caraco 1981, 1987; Pulliam and Caraco 1984; Caraco et al. 1989). Still, this asymmetric tag game between subordinates constrained to act as producers and dominants that can use either tactic is likely to stop if the resources are patchily distributed, constraining subordinates to remain within groups (Vickery et al. 1991; see also Rohwer and Ewald 1981). Nevertheless, stable spatial distributions of foragers where groups of only one phenotype are formed are also possible (Milinski and Parker 1991; Ranta 1993; Ranta et al. 1993; Tregenza 1995).

Given that many of the assumptions pertaining to the Dispersion model (as well as to some of the other three models) were violated, the hypothesis that jaegers form groups according the Dispersion model with the $\underline{PF}(\gamma)$ currency, and this when $\underline{N} \leq 2\tau$, must also be rejected. Although it remains the most likely hypothesis, why jaegers form groups to kleptoparasitize terns has yet to be determined. Future work should pay closer attention to how jaegers select their hosts in order to develop a better estimate of host availability. Establishing time and energy budgets of jaegers relative to their daily foraging time and their maximum daily sustainable energy expenditure would also provide insight on the type of currency that jaegers are actually maximizing and the extent of jaegers' risk-sensitivity (Ydenberg et al. 1994; Houston 1995). Measuring the jaegers' ability at kleptoparasitizing hosts as solitaries and relating this to their propensity to initiate and join chases would also shed some light on the group formation mechanism of jaegers.

CONCLUSIONS

None of the four foraging group size models could account for the observed group size of jaegers kleptoparasitizing terns. Even though the system used to test the models appears simple, many of the models' assumptions were challenged. Future foraging group size models would benefit by incorporating more realistic assumptions about the animals' behavior relative to their state, and especially concerning the "ideal", "free", and "equal competitive ability" constraints. Assumptions relative to the influence of the contrast between patches and the background, the level of patch aggregation, the absolute difference in scale among adjacent scale levels (see Kotliar and Wiens 1990), as well as the depletion and renewal of food patches and environmental stochasticity on the animals' behavior, are also needed. Nonetheless, future work should focus on identifying the relative spatial scales at which animals respond and on measuring how different fitness currencies are influenced by forager density at these relative spatial scales. This should allow further testing of the existing group size models, and thereby generate information that will permit to define more realistic assumptions.

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Table 1. Sample size (n), Spearman rank-order correlation (r_s) and corresponding P-value for the relationship between parasitic jaeger typical group size and common tern availability (flying terns/jaeger) for different jaeger abundances, at the Portneuf sandbar, 1994 and 1995.

Jaeger				Tern availability		
abundance	n	r_s	P-value	Mean	SD	Median
1	150	-	-	28.1	26.3	19.0
2	284	-0.093	0.117	13.2	15.6	9.0
3	184	-0.199	0.007	9.4	10.2	6.7
4	92	0.004	0.967	9.3	8.4	8.0
5	61	0.054	0.673	8.8	5.1	8.0
6	30	0.069	0.710	5.9	4.3	4.6
7	17	0.117	0.641	9.4	7.2	8.0
8	2	-	-	14.3	3.6	14.3
9	2	-	-	6.8	0.9	6.8

Table 2. Success rate, securing rate and feeding yield of kleptoparasitic interactions aimed at common terns by parasitic jaegers as a function of jaeger group size, at the Portneuf sandbar, 1994 and 1995. The success rate, securing rate and feeding yield are expressed in terms of % fish dropped/chase, % fish secured/fish dropped and % fish secured/chase, respectively.

				Feeding yield	
Group size	No of chases	Success rate	Securing rate	Group	Individual
1	1836	33.7	96.6	32.6	32.6
2	592	59.5	98.3	58.4	29.2
3	109	58.7	98.4	57.8	19.3
4	10	30.0	100.0	30.0	7.5
5	1	0.0	-	0.0	0.0

Table 3. Feeding yield and, in parentheses, securing rate of parasitic jaegers chasing common terns as a function of jaeger group size and jaeger position in the chasing line, at the Portneuf sandbar, 1994 and 1995. The feeding yield, securing rate and position in the chasing line are expressed in terms of % fish secured/chase, % fish secured/fish dropped and proximity to the tern when the fish was dropped, respectively.

		Position in the chasing line			
Group size	No of chases	1th	2nd	3rd	4th
1	598	32.6 (100.0)	-	-	-
2	246	36.8 (63.0)	21.6 (37.0)	-	-
3	30	23.1 (40.0)	25.0 (43.3)	9.6 (16.7)	-
4	1	0.0 (0.0)	0.0 (0.0)	30.0 (100.0)	0.0 (0.0)

Table 4. Duration of chases aimed at common terns by parasitic jaegers as a function of jaeger group size and whether the chase was successful (S) or unsuccessful (U), at the Portneuf sandbar, 1994 and 1995.

Group size	Chase outcome	No of chases[a]	Chase duration (s)		
			Mean	SD	Median
1	S	298	20.7	14.0	17
1	U	626	17.1	12.7	14
2	S	169	19.8	11.5	17
2	U	116	23.8	12.5	22
3	S	32	15.3	6.0	15
3	U	28	24.5	15.4	21
4	S	1	26.0	-	26
4	U	5	20.6	11.2	18

[a] The number of chases that were used to calculate $\underline{t}(\gamma)$ in the bootstrap replicates are 1S: 289, 1U: 635, 2S: 168, 2U: 117, 3S: 31, 3U: 29, 4S: 1, 4U: 5; numbers refer to group sizes, S, to a chase where a fish was secured, and U, to a chase where no fish was secured. The difference in sample sizes results from the fact that not all the fish dropped by terns were secured.

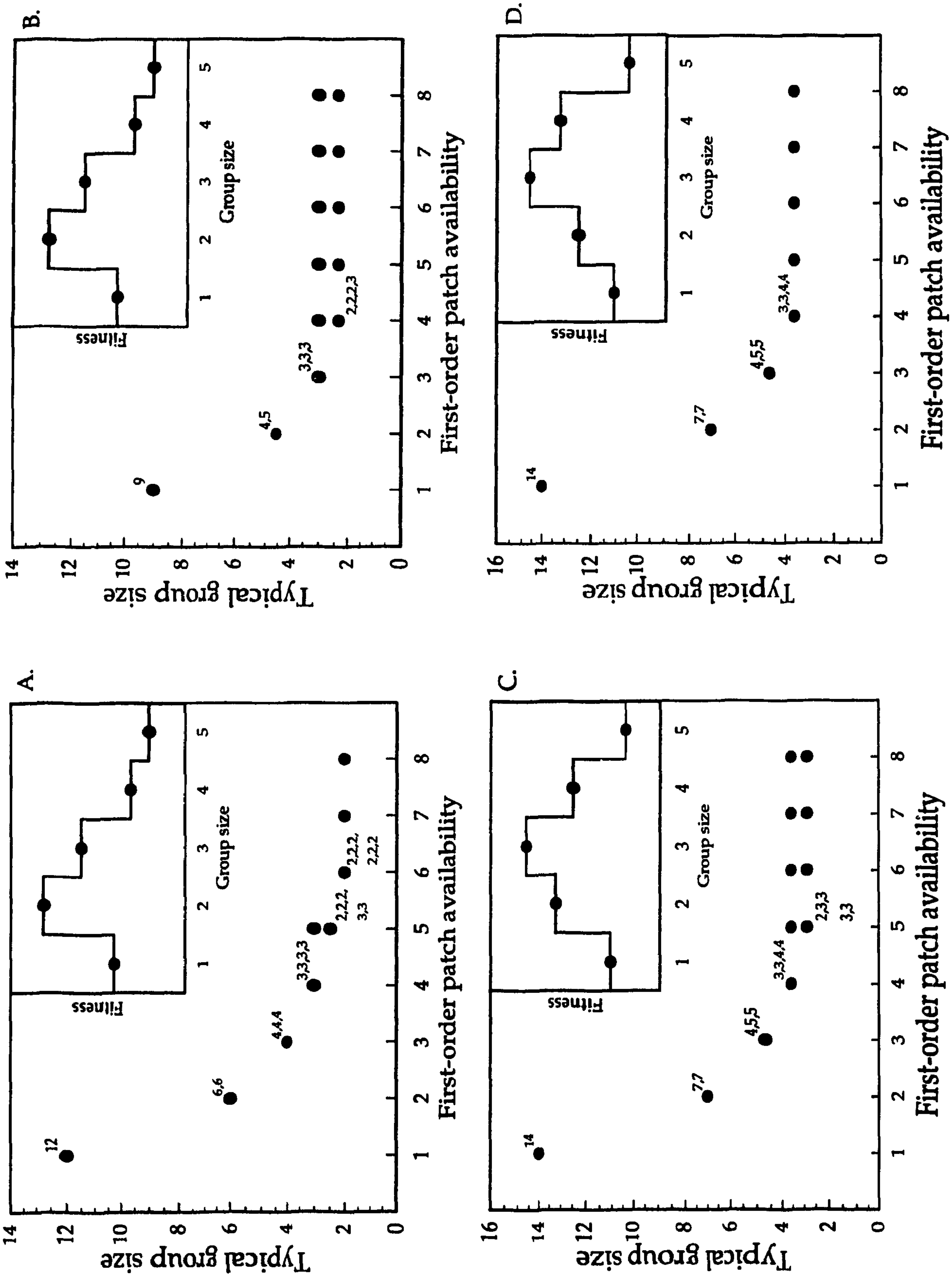
FIGURE LEGENDS

Fig. 1. Four scenarios illustrating how groups form under the Aggregation model. All scenarios depict the expected typical group sizes within a second-order patch occupied by $\underline{N}$ foragers as the number of first-order patches π increases. Scenarios A and B have the same fitness function (inset) but differ in $\underline{N}$ (A: $\underline{N} = 12$ and B: $\underline{N} = 9$), while scenarios C and D have the same $\underline{N}$ (= 14) but differ in their fitness function (inset). The points refer to the typical group size, i.e. the group size in which an average or typical individual of the population of $\underline{N}$ individuals is found. It is computed as $\sum_{\underline{i}=1}^{\underline{n}} \gamma_{\underline{i}}^2 \Big/ \sum_{\underline{i}=1}^{\underline{n}} \gamma_{\underline{i}}$, where γ_i is the $\underline{i}$th group size and $\underline{n}$ the total number of groups. The numbers beside the points refer to the combination of group sizes in a given condition; e.g. in scenario A, when $\pi = 2$, 6,6 refers to two groups of six individuals. The points were obtained by numerically working out a simple hypothetical example (see text).

Fig. 2. Frequency distributions of the typical group size of parasitic jaegers chasing common terns at different jaeger abundances at the Portneuf sandbar, 1994 and 1995. The bottom, middle, and upper lines of the box plots correspond to the 25th, 50th, and 75th percentiles, respectively. The dot indicates the mean. The whiskers extend to the last point occurring between either the 25th or 75th percentile and their respective inner fence, i.e. 1.5 times the distance between the 25th and 75th percentile. The asterisk indicates a data point occurring between 1.5 and 3 times the distance between the 25th and 75th percentile. See Table 1 for the sample size of the distributions.

Fig. 3. Typical group size of parasitic jaegers as a function of common tern availability at an abundance of three jaegers at the Portneuf sandbar, 1994 and 1995. The curve was fitted via a locally weighted regression scatterplot smoothing procedure (LOWESS, $\underline{f} = 0.40$, $\underline{n} = 184$; Trexler and Travis 1993). Each data point refers to the jaeger typical group size within a given 15 min observation block. Note that a single data point located at (103.33 flying terns/jaeger, 1.00 jaeger) is not shown, although it was used to fit the curve.

Fig. 4. Four fitness functions for parasitic jaegers chasing common terns at the Portneuf sandbar, 1994 - 1995; A) per capita probability of obtaining a fish in a chase [$\underline{PF}(\gamma)$]; B) gross rate of energy intake achieved during a chase [$\underline{GREI}(\gamma)$]; C) net rate of energy intake achieved during a chase [$\underline{NREI}(\gamma)$]; D) energetic efficiency of a chase [$\underline{EFF}(\gamma)$]. Means and their 95% confidence intervals based on 2000 bootstrap replicates are shown.


A.
B.
C.
D.
Typical group size
First-order patch availability
Fitness
Group size
12
6,6
4,4,4
3,3,3,3
2,2,2,
3,3
2,2,2,
2,2,2
9
4,5
3,3,3
2,2,2,3
14
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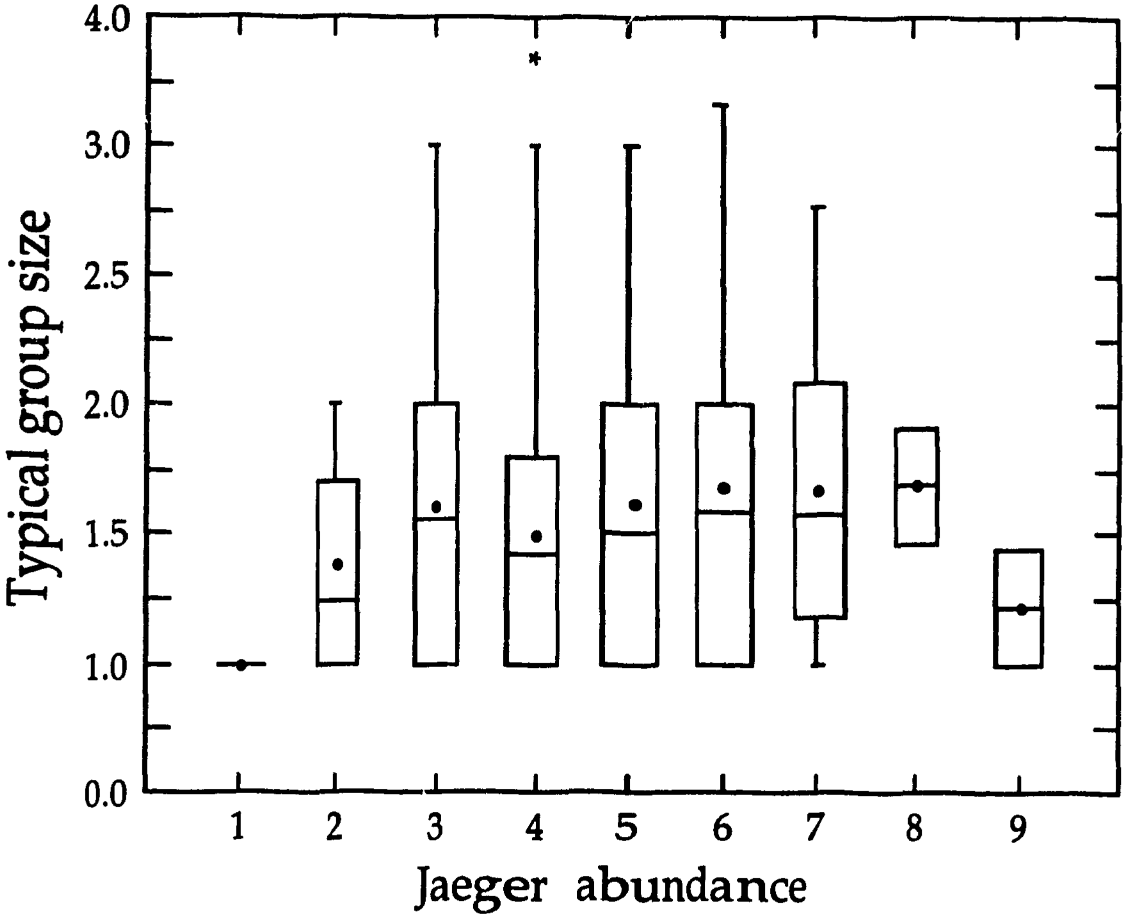
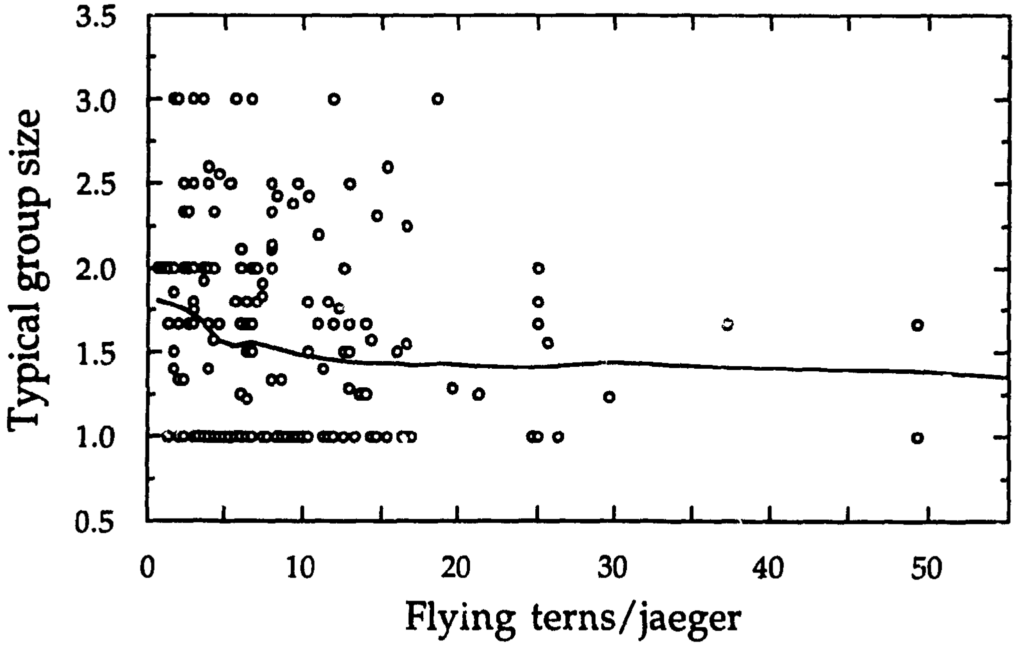
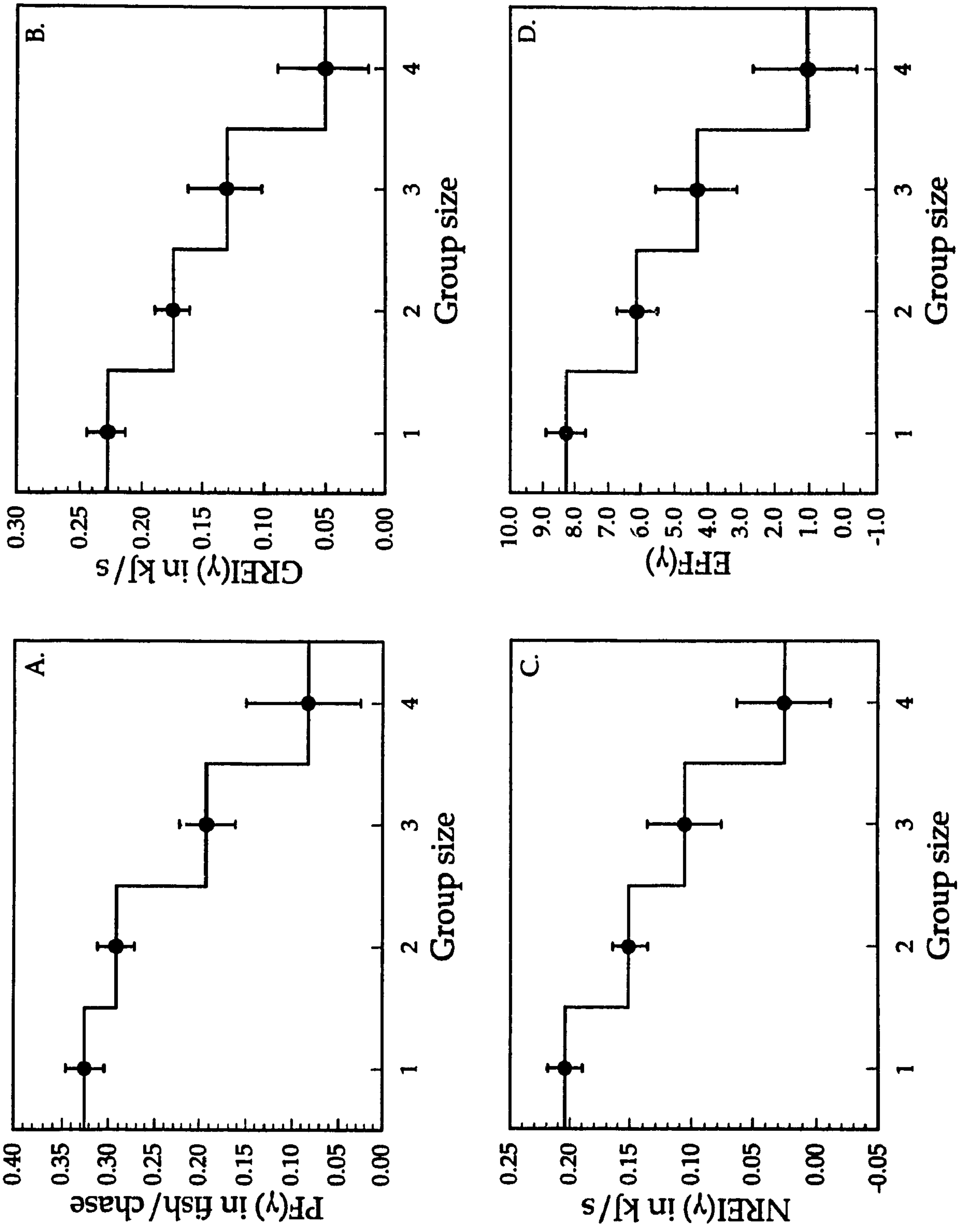
7
8


Typical group size
4.0
3.0
2.5
2.0
1.5
1.0
0.0
1
2
3
4
5
6
7
8
9
Jaeger abundance


3.5
3.0
2.5
2.0
1.5
1.0
0.5
Typical group size
0
10
20
30
40
50
Flying terns/jaeger


A.
PF(y) in fish / chase
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1
2
3
4
Group size
B.
GREI(y) in kJ / s
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1
2
3
4
Group size
C.
NREI(y) in kJ / s
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
1
2
3
4
Group size
D.
EFF(y)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
1
2
3
4
Group size