PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 1637-1645
doi: 10.1098/rstb.2000.0726

THE ROYAL SOCIETY

doi 10.1098/rstb.2000.0726

Scramble in behaviour and ecology

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Nicholson's distinction between 'scramble' and 'contest' modes of competition has received widespread attention in ecology and in behaviour, though the emphasis has been different between the two disciplines. In ecology the focus has been on the effects on population; in behavioural ecology the focus has been on the consequences at the individual level. This paper reviews and develops a theory of scramble competition at the individual level, deriving a general evolutionarily stable strategy (ESS) for individual scramble expenditure in a patchy habitat in which individuals compete in local groups for available resources, and examines two population consequences. The critical parameter determining the relationship between individual scramble expenditure and the number of competitors in a patch is the expected resource per capita. If resource input, R, to a patch is constant and independent of the number of competitors, n, then as the number of competitors increases, the per-capita resources declines as R/n, and the ESS scramble level declines (in proportion to $(n-1)/n^2$). However, if the resource input to a patch is positively related to the number of competitors in the patch, scramble expenditure may increase with the number of competitors. In the case where the per-capita resource input stays constant (i.e. $R(n) = Rn$), the scramble level increases with competitor number (in proportion to $(n-1)/n$). There are plausible ecological reasons why either of these extreme limits may be approached in nature, making it important to ascertain the relationship between R and n before predicting individual scramble expenditure. For example, resource input may be constant when groups of competitors are constrained to remain together in given patches, and constant per-capita resources may be approached when ideal-free foraging rules apply. However, in the latter case, scramble expenditure must be accounted for in determining the ideal-free distribution. An analysis shows that this leads to 'undermatching', i.e. the ratio of numbers of competitors for good/bad patches becomes progressively less than the ratio of input rates for good/bad patches as the difference between the good and bad patches increases. A second population consequence of the scramble ESS relates to the fact that scrambles may dramatically affect fitness. The per-capita gain in energy can be reduced by a factor of up to $1/n$ as a result of scramble expenditure, potentially reducing realized population size to as little as the square root of the maximum potential carrying capacity, though reasons are given why such large reductions are unlikely.

Keywords: scramble competition; ideal-free distribution; evolutionarily stable strategies

1. INTRODUCTION

> 'It is necessary to distinguish between two kinds of competition, as they produce different effects upon the patterns of population growth and maintenance. *Scramble* is the kind of competition exhibited by a crowd of boys striving to secure broadcast sweets . . . . Its characteristic is that success is commonly incomplete, so that some and at times all, of the requisite secured by the competing animals takes no part in sustaining the population, being dissipated by individuals which obtain insufficient for survival. With *contest*, on the other hand, the individuals may be said to compete for prizes (such as a host individual, or an amount of favourable space an individual can arrogate to itself) which provides as much of the requisite as an individual needs to enable it to reach maturity, or provides fully for the development of one or more offspring. Thus individuals are either fully successful, or unsuccessful; and the whole amount of the requisite obtained collectively by the animals is used effectively and without wastage in maintaining the population.'
>
> A. J. Nicholson (1954, pp. 619–620)

Nicholson's seminal concept of the two forms of competitive interaction relates more to their ecological outcomes than to the underlying behaviour involved. Gains to competitors in contests are all or nothing (individuals are either 'winners' or 'losers'), whereas in scrambles, all individuals achieve some gains, if sometimes less than enough to survive and/or reproduce. The main thrust in ecology has been the analysis of the population implications of this difference. Contest and scramble are at either ends of a continuum along which all actual competitive interactions lie—in 'pure' contest there are a defined number of winners, each getting as much in a competitive situation as they would get in the absence of competition, and the number of losers (who get nothing) is given by [number competing] − [winners]; in 'pure' scramble all competitors get a share of resource, and where this is 'not enough' they die or fail to breed.

These concepts have been subject to different emphasis in behavioural ecology, where the focus has been on how animals compete behaviourally, and on the implications, at the individual level, of how the resource is divided among competitors. For contests, the aim has been to deduce what forms of behaviour (e.g. what conventional rules for settlement) may be evolutionarily stable under the game rule that resources are indivisible. For scrambles, the aim has been to deduce evolutionarily stable levels of scramble and their behavioural implications under the game rule that the resource can be shared among the competitors.

Though they retain more or less the original implications in behaviour as in ecology, the emphasis has been on understanding how the ecological rule (shareable or unshareable resources) affects the evolution of behaviour rather than on understanding how its outcome affects populations. There has been much focus on contests in behavioural ecology, starting in the mid-1970s (e.g. Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Maynard Smith 1982) and major advances were still continuing a decade later (e.g. Enquist & Leimar 1983, 1987). This literature contributed considerably to the early development of evolutionarily stable strategy (ESS) theory (for a review, see Maynard Smith 1982). In the behavioural ecology sense, in scrambles there are no clear winners or losers—individuals compete by increasing their effort in harvesting the resource. There have also been extensive ESS analyses of scrambles, both generally (Parker 1985) and in a wide variety of specific contexts: territoriality (Parker & Knowlton 1980); sexual advertisement (Andersson 1982, 1994; Parker 1982); intrafamily games (reviewed in Mock & Parker 1997); sex allocation (e.g. Charnov 1983); sperm competition (reviewed in Parker 1998); and food foraging (e.g. Shaw *et al*. 1995).

In this paper, a model for the evolution of scramble behaviour is reviewed and developed, together with a summary of its behavioural consequences and an outline of two ways in which the underlying behaviour may affect populations.

2. A SIMPLE MODEL FOR SCRAMBLE BEHAVIOUR

The original version of the scramble model developed here is due originally to Parker (1985; see also Parker & Knowlton 1980), and a more recent treatment was given in Shaw *et al.* (1995). A rather similar model that examines the effect of kin selection on scramble behaviour was analysed by Godfray & Parker (1992). The explicit assumption is that individuals compete by scramble competition to obtain fitness-related resources from a patch within a habitat. An individual can increase its share of the resources by increasing its foraging activity or 'scramble level'.

The population is structured into local patches containing (say) food resources. Each patch contains a number of competing foragers, and each competitor adopts a scramble strategy that is related to the number of competitors in the patch and the quality of that patch. An ESS scramble level is sought in relation to the two variables: number of foragers and the patch quality. For present purposes it is assumed that the resources in a patch are shared equally among the foragers, i.e. competitive abilities are equal. (The model could be extended to include unequal competitive abilities, e.g. by following the approach of Sutherland & Parker 1985; Parker & Sutherland 1986.) Let

n = the number of competing foragers in a patch;

$R(n)$ = the rate of input of resources to a patch (patch quality), which may relate to the number of foragers;

S = a competitor's strategy for its scramble level, where S^* is the ESS scramble level;

$E(S)$ = a competitor's rate of energy expenditure through scrambling at level S (E is assumed to increase as S increases);

$G(S)$ = the rate of net gain in energy through scrambling at level S (equal to uptake rate minus expenditure rate).

A competitor can increase its share of the gains by increasing its scramble level, S. Explicitly, it is assumed that it gains a proportion of R that matches its contribution as a proportion of the total scramble, i.e. its share of the resource is equal to its own scramble level divided by the total of the scramble levels of all the competitors in the same patch. Though a variety of relations are possible, such an assumption would be approximated under a wide range of biological conditions, the most obvious occurring where scramble level is foraging speed and foragers search randomly in the patch for prey items. Thus if an individual scrambles to level S in a patch where all other competitors scramble at the ESS level S^*, its net gains will be

$$G(S) = c_1\left[\frac{R(n)S}{S + (n-1)S^*}\right] - E(S), \tag{1a}$$

where constant c_1 converts the food items gained per unit time into the same energy units as are spent through scrambling at level S. Obviously, if the model is to be used for some other form of scramble (e.g. mate searching), $E(S)$ would be in some other units, and c_1 would scale the resources gained appropriately. If all competitors play the ESS, S^*,

$$G^* = \frac{c_1 R(n)}{n} - E(S^*). \tag{1b}$$

It is unlikely that net energy gain converts linearly into fitness. Suppose that the fitness gain due to a net energy uptake of $G(S)$ units is $W(G(S))$, where W is some monotonic increasing function of G. To find the ESS, we require that

$$\frac{\mathrm{d}W(G(S))}{\mathrm{d}S} = 0, \text{ at } S = S^*, \tag{2}$$

subject to the second derivative $\mathrm{d}^2W/\mathrm{d}S^2 < 0$, at $S = S^*$, for a maximum (see Maynard Smith 1982).

Substituting (1) into (2) and differentiating gives the result that

$$\frac{\mathrm{d}W}{\mathrm{d}G}\left[c_1\left(\frac{R(n)}{n}\right)\left(\frac{n-1}{nS^*}\right) - \frac{\mathrm{d}E(S)}{\mathrm{d}S}\right] = 0,$$

and thus we can see that the explicit way that energy converts into fitness, $W(G)$, is unimportant—all that is required is that W is some increasing function of G so that the derivative $\mathrm{d}W/\mathrm{d}G$ is positive in order to produce the ESS solution

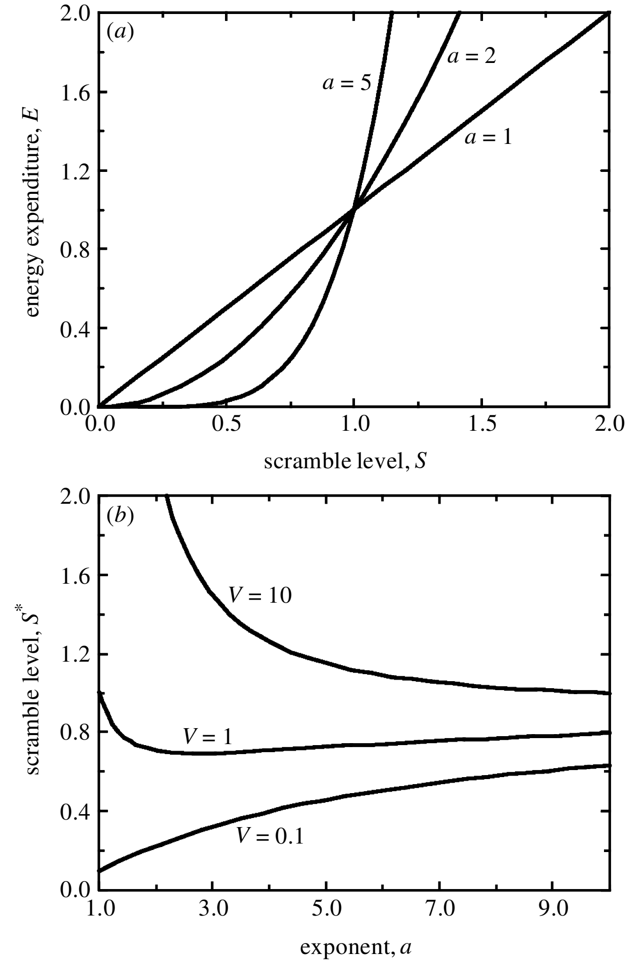

Figure 1. (*a*) Energy expenditure, E, in relation to scramble level, S, from equation (4), with $a = 1$, 2 and 5 ($c_2 = 1.0$). (*b*) ESS scramble level, S^*, in relation to the exponent, a, from equation (5), with $V = 0.1$, 1 and 10 (see § 2).

$$S^* = c_1 \left(\frac{R(n)}{n}\right)\left(\frac{n-1}{n}\right)\left[\left(\frac{\mathrm{d}E(S)}{\mathrm{d}S}\right)^{-1}\right], \tag{3}$$

(see also Shaw *et al.* 1995). The reason for bracketing the terms in (3) will become apparent later.

We cannot proceed further unless the function $E(S)$ is defined. The most plausible relationship biologically is that energy expenditure increases with increasing gradient as an individual's scramble level increases. Such increasing costs are well established for the physiology of movement: for example, in fishes the energetic costs of movement increase in proportion to the cube of the speed (e.g. Wardle & Videler 1980). A simple but flexible explicit form for $E(S)$, and one often used in physiological studies, is

$$E(S) = c_2 S^a, \tag{4}$$

where c_2 is a constant of proportionality. At a given c_2, increasing the exponent constant a above 1.0 causes an increasingly bowed relationship between scramble level, S, and energy costs, E (see figure 1), making scramble levels below 1.0 cheaper and levels above 1.0 more expensive. An exponent $a < 1.0$ implies that costs rise progressively less steeply with scramble level, something generally not found and biologically implausible. Hence a minimum limit for a can be regarded as 1.0.

Substituting equation (3) into equation (4) gives the ESS scramble level

$$S^* = \left[\left(\frac{c_1}{ac_2}\right)\left(\frac{R(n)}{n}\right)\left(\frac{n-1}{n}\right)\right]^{1/a}. \tag{5}$$

Before analysing the behavioural and population implications of competition, the effect of the exponent a on the ESS scramble level, S^*, requires clarification. If equation (5) is simplified as $S^* = (V/a)^{1/a}$, where $V = (c_1/c_2)(R/n)[(n-1)/n]$, we can see how S^* varies with a when all the other terms are held constant. Figure 1*b* shows the relationship between S^* and a at different values of V. Though the ESS scramble level S^* converges to 1.0 as $a \rightarrow \infty$, the approach to this asymptote can be from above (high V) or from below (low V), and at intermediate V, S^* drops to a minimum and then converges to the asymptote from below.

However, two points must be noted. First, at a given a, the ESS scramble level is always increased by increasing V: it is in a sense the biology of V that is the subject of the present paper. Second, although the relationship between the ESS scramble level, S^*, and exponent a is rather complex, the relationship between the energetic costs of S^* and a are simple: energetic costs of S^* are inversely proportional to a (see § 3). Thus increasing costs of scramble can be modelled by decreasing a from some hypothetical maximum towards infinity (generating zero costs) to its plausible minimum of 1.0 (generating highest scramble costs). In real systems, a will be determined by obtaining the best fit for parameters a and c_2 from physiological or other data.

3. BEHAVIOURAL CONSEQUENCES OF THE MODEL

Note that the right-hand side of the ESS equation (5) contains three parts within the square brackets:

(i) a constant term, c_1/ac_2;
(ii) a 'resource share' term, $R(n)/n$, which is the number of resource items input per competitor;
(iii) a term $(n-1)/n$, which is dependent only on the number of competitors.

Two plausible ecological applications of the second term will be considered in detail. The simplest and most obvious interpretation of the model is that input of resources to a patch is entirely independent of the number of competitors exploiting it, so that $R(n)$ is constant $= R$. The second term becomes $R(n)/n = R/n$. For this case, n becomes a component of both the second and third terms, generating the term $(n-1)/n^2$, which decreases with n (approximating to $1/n$ at high n).

However, in some instances the resource input is likely to correlate positively with the number of foragers in a patch. For instance, if foragers distribute themselves in an ideal-free fashion within a habitat, the number of competitors in a patch will tend to match the input rate of resource (Parker 1978), so that $R(n) \approx Rn$. Then the term $R(n)/n$ will tend to be held constant $\approx R$—except that we must, of course, take account of the scramble costs themselves in calculating the ideal-free distribution (analysed in § 4(a)). Since it forms an interesting upper bound under ideal-free considerations, the case where $R(n)/n$ is held

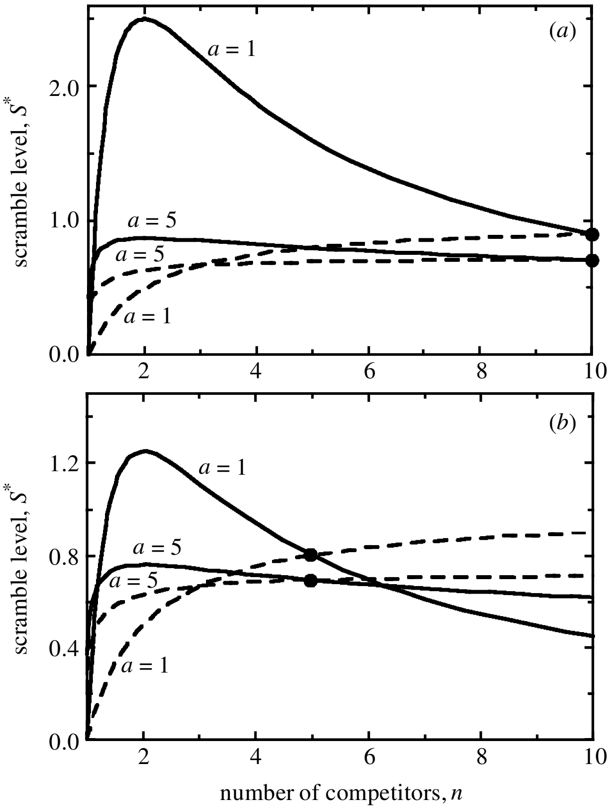

Figure 2. ESS scramble level, S^*, in relation to the number, n, of competitors present in the patch, from equation (5). Continuous lines, scramble level when resource input, R, is held constant; broken lines, scramble level when resource input per capita, R/n, is held constant. Two values of a are plotted for each condition, and $c_1/c_2 = 1.0$. (*a*) R or $R/n = 10$. (*b*) R or $R/n = 5$. The black dots at the intersection of the continuous and broken lines occur where the resource per capita is equal ($n = 10$ in (*a*), $n = 5$ in (*b*)), and where the ESS is the same.

constant $= R$ is also examined. Then, the only term relating behaviour to competition level is the third term, $(n-1)/n$, which increases with n up to an asymptote of 1.0 for large n. In addition to ideal-free foraging, there are other biological circumstances where R/n may remain roughly constant. One example might be nestling feeding when parent(s) supply resources in proportion to the number of offspring in the brood. If one egret chick dies, the parents reduce their total input to keep the input per chick roughly the same (Mock & Lamey 1991). Similar effects are found in siblicidal brown pelicans (Ploger 1997). Another example may be sexual advertisement scrambles of displaying males (Parker 1982), in which the total number of females attracted to a lek increases approximately in proportion to the number of lekking males (e.g. Sutherland 1996).

To differentiate between the two cases, call

(i) 'resources constant' (or R constant) the case where $R(n) = R$; i.e. resources are independent of the number of competitors;
(ii) 'per-capita resources constant' (or R/n constant) the case where $R(n) = Rn$; i.e. resources increase in direct proportion to the number of competitors.

(a) *Scramble level*

Figure 2 shows the ESS scramble level for the two cases, calculated from equation (5) using two values of a (1 and 5). In figure 2*a*, $R = 10$, and in figure 2*b*, $R = 5$. There will be one value of n at which the ESS scramble level must be equal under both interpretations: this is where the resource per capita is equal ($n = 10$ in figure 2*a*, $n = 5$ in figure 2*b*). The following conclusions emerge.

(i) If resources are constant (continuous curves), the scramble level declines gradually towards an asymptotic minimum of zero (for vast n) as the number of competitors increases above $n = 2$. At $n = 1$ (no competition), the scramble level is zero; at $n = 2$, the scramble level is maximum.
(ii) If per-capita resources are constant (broken curves) there is a monotonic increase in scramble level from zero as n increases from zero towards an asymptotic maximum set by the constants R/n, a, c_1/c_2.
(iii) If the costs of scramble level are sharply accelerating ($a = 5$, see figure 1), the two cases give rather similar ESS scramble levels, and there is very weak dependence on n. This occurs because the gradient of $E(S)$ changes very rapidly as S changes, confining the ESS to a relatively narrow range of S (see equation (4)) across a wide range of n. If the costs of scramble level simply increase linearly ($a = 1$, see figure 1), the gradient of $E(S)$ is constant, the two cases can give very different scramble levels and there is strong dependence on n across a wider range of n. The dependence is positive for the resources constant case, and negative for per-capita resources constant.
(iv) Increasing the available resource (R) increases scramble level in both cases (compare figure 2*a*,*b* at given values of a and n).

Thus there are important ecological influences on the expected behaviour: above $n = 2$, the ecological assumption about the resource–competitor relationship changes the sign of the predicted relationship between competitor density and scramble level.

(b) *Energy expended per unit of energy gained*

A measure with both behavioural and ecological implications will be the amount of energy loss by each individual in the scramble. Substituting equation (5) into (4), note that the exponents cancel, giving the ESS scramble energy expended as a function of both R and n:

$$E(S^*(R,n)) = \left(\frac{c_1}{a}\right)\left(\frac{R(n)}{n}\right)\left(\frac{n-1}{n}\right). \tag{6a}$$

Substituting into equation (1*b*), we see that the net energy gain at the ESS is

$$G(S^*) = \left(\frac{c_1 R(n)}{n}\right)\left(\frac{(a-1)n+1}{an}\right). \tag{6b}$$

In figure 2, at a given set of constant values, the two cases (R constant, R/n constant) only experience one point at which the per-capita uptake of resources is equal (shown by the black dots in figure 2*a*,*b*). The energy expended per unit of resource gained for the two cases can be calculated to generate a more direct comparison of scramble expenditure that relates simply to competitor

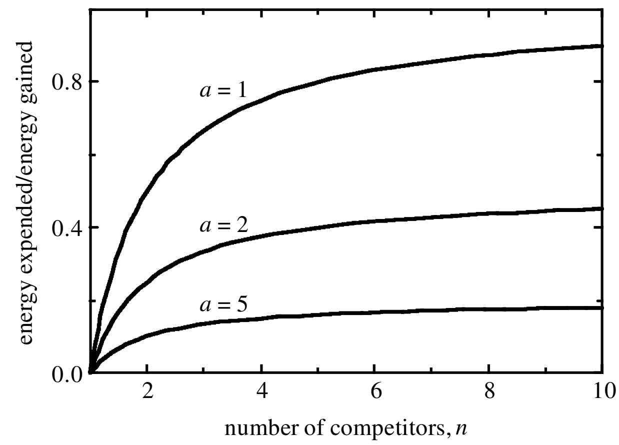

Figure 3. Energy expended for each unit of energy gained at the ESS, in relation to the number, n, of competitors present in the patch, from equation (7) with $a = 1$, 2 and 5.

density. At the ESS, each competitor gets a rate of energy uptake of $c_1R(n)/n$ for a rate of energy expenditure of E^*. The ratio (energy expended : energy unit gained) at the ESS is therefore independent of the ecological assumption, and is

$$\frac{E(S^*(R,n))}{c_1R(n)/n} = \left(\frac{1}{a}\right)\left(\frac{n-1}{n}\right). \qquad (7)$$

Thus at the ESS, the scramble level is geared to keep the ratio of energy loss to energy gain directly proportional to $(n-1)/n$. As n increases, scramble level maintains a constant cost/benefit balance of energy with an asymptotic ratio of a^{-1} (see figure 3), following equation (7). The higher the a value, the more favourable the cost/benefit ratio at the ESS (figure 3). If $a = 1$, the asymptotic ratio is 1; scramble causes all the energy gains to be offset by energetic costs if the number of competitors is high.

(c) *Scramble level per unit of energy gained*

The scramble level per unit of energy gained is

$$\frac{S^*(R,n)}{c_1R/n} = \frac{\left[\left(\frac{c_1}{ac_2}\right)\left(\frac{R(n)}{n}\right)\left(\frac{n-1}{n}\right)\right]^{1/a}}{c_1R(n)/n}, \qquad (8)$$

which will again be different in the two conditions (R constant, R/n constant), except if $a = 1$ (when the right-hand side denominator then cancels with the middle term of the numerator), and/or at the value of n where the same per-capita energy uptake occurs, as shown previously in figure 2. S^* is plotted against n in figure 4 for $a = 1$ and 5. With $a = 5$, the R constant case rises almost linearly across the range $n = 1$–10, but the R/n constant case very quickly asymptotes and becomes virtually independent of competitor density for $n \geqslant 2$.

(d) *An experimental example*

An experimental study has provided some evidence for the above predictions. Shaw *et al.* (1995) investigated feeding scrambles directly in the cichlid fish *Aequidens portalegrensis* by taking swimming speed (number of squares crossed per 120 s in a grid on the side of the tank) as the measure of scramble level. From $n = 1$–10 fishes in an aquarium were fed from above with standard-sized flaked food and movement rates during each feeding trial were recorded with a video camera. Two rates of feeding were used, one item every 5 s, whatever the number of fishes (resources constant), and one item every 50 s for each fish (per-capita resources constant), with $n = 10$ fishes having the same per-capita gain in both experiments. The relationship between energy expenditure E and swimming speed S was taken from a biophysical expectation (see Wardle & Videler 1980), which predicts E to increase as the cube of swimming speed ($a = 3$), multiplied by constants relating to water density, surface area of the fish and the coefficient of friction between the fish and the water. These constants would enter into equation (5) within the general constant $c_1/3c_2$. Shaw *et al.* (1996) obtained a best estimate of this general constant from all their data, then used it to predict the relationship between foraging speed and number of competitors in each feeding regime. The two regimes showed significantly different responses to increasing fish density. As expected, the R constant case showed a decrease in foraging speed with competitor density, but the R/n case showed little effect of density (a weak positive relationship was expected). The observed average movement rate per fish against fish density showed a good fit to the predicted relationship in each feeding regime (qualitatively resembling the $a = 5$ curves in figure 4). Overall, the fit between observation and prediction was encouraging, though the behaviour of solitary or paired foragers ($n = 1$, $n = 2$) was not predicted by the model in the R/n constant case, being much higher than expected.

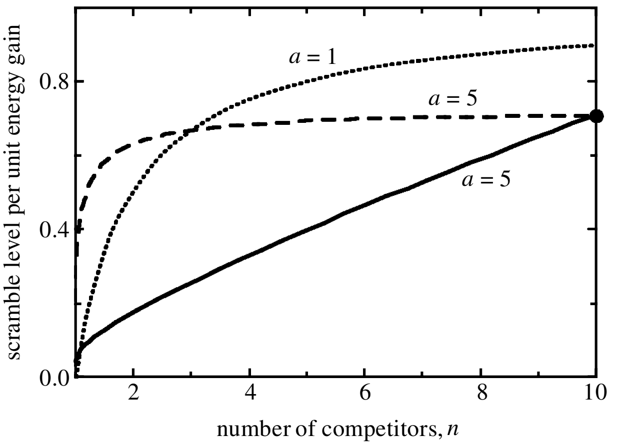

Figure 4. Scramble level per unit energy gained at the ESS, in relation to the number, n, of competitors present in the patch, from equation (8) with $a = 1$ and 5; $c_1 = c_2 = 1.0$. Continuous lines, scramble level when resource input, R, is held constant is 10; broken lines, scramble level when resource input per capita, R/n, is held constant is 10. When $a = 1$ (dotted line) the scramble level is the same for the two cases, since $R(n)/n$ then cancels from the right-hand side of equation (8).

4. POPULATION CONSEQUENCES OF THE MODEL

Two population consequences of the scramble model are considered. The first concerns the way in which scramble may affect ESS distributions of competitors within a habitat, and the other concerns its effects on net gains, fitness and ESS population size.

(a) *Ideal-free distributions under scramble competition*

Under the ideal-free distribution theory (Fretwell 1972), equal competitors are distributed in habitat patches such that each individual cannot do better by moving to an alternative patch. At the ideal-free ESS, individuals all achieve equal fitness whatever patch they are in (e.g. Parker 1970). For our purposes, equal fitness is achieved by equal gains per individual across all patch types i, j, k, etc. For fitnesses to be equal, net per-capita gains must be equal, so that

$$G_i(S_i^*) = G_j(S_j^*) = G_k(S_k^*) = \ldots \qquad \text{constant } G^* \text{ for all patches,}$$

where G^* is the expected gain, all scramble levels optimized at S_i, S_j, S_k, etc., from the entire habitat. Thus where the numbers in each patch i, j, are n_i, n_j, ... etc., we can write

$$G_i(S_i^*) = c_1 R_i(n_i)/n_i - E(S_i^*) = G^* \text{ for all } i, j, \ldots . \tag{9a}$$

The difficulty immediately arises (as in most analyses of ideal-free foraging) that biology requires solutions to have integer values for n, though this will seldom apply from the mathematics. I will follow tradition and ignore this problem.

In the present analysis, assume that resource input to patches is constant, so that R is independent of n (i.e. $R(n) = R$). Then if energy costs follow equation (4),

$$G_i(S_i^*) = c_1 R_i(n_i)/n_i - c_2 S_i^{*a} = G^*, \tag{9b}$$

where the expected gain at optimization is

$$G^* = \sum p_i\left(\frac{c_1 R_i}{n_i^*} - c_2 S_i^{*a}\right), \tag{9c}$$

in which p_i is the frequency of patch types i, j, etc. across the entire habitat.

Assume that the competitors distribute themselves in an ideal-free fashion by some rule that takes into consideration that in each patch i, the n_i competitors will then play their ESS scramble level $S^*(n_i)$. We can then substitute S^* from equation (5), with $R(n) = R$, into equation (9b), giving the result that

$$\left(\frac{c_1 R_i}{n_i^*}\right)\left(\frac{(a-1)n_i^* + 1}{a n_i^*}\right) = G^*, \qquad \text{for all patches } i, j, k, \ldots \text{etc.} \tag{10a}$$

(cf. equation (6b)). This gives a quadratic solution for the number of competitors in a given patch i

$$n_i^* = \left(\frac{(a-1) + \sqrt{(a-1)^2 + 4\alpha_i}}{2\alpha_i}\right), \text{ where } \alpha_i = \left(\frac{aG^*}{c_1 R_i}\right). \tag{10b}$$

If we look at the ESS ratio of numbers of competitors in patch i to the number in patch j, we see that this ratio is

$$\frac{n_i^*}{n_j^*} = \left(\frac{R_i}{R_j}\right)\left(\frac{(a-1) + \sqrt{(a-1)^2 + 4\alpha_i}}{(a-1) + \sqrt{(a-1)^2 + 4\alpha_j}}\right),$$
$$\text{where } \alpha_i = \left(\frac{aG^*}{c_1 R_i}\right), \ \alpha_j = \left(\frac{aG^*}{c_1 R_j}\right). \tag{10c}$$

I first compare this result with the typical result for continuous input studies but without the effect of scramble. For such studies, the net energy gain per competitor in patch i is simply $G_i(S_i^*) = c_1 R_i / n_i^*$ because there are no scramble costs. Applying a parallel analysis, we get the familiar input matching rule (Parker 1978):

$$n_i^* = \left(\frac{c_1 R_i}{G^*}\right), \tag{11a}$$

i.e. the number of competitors in a patch i should simply match the input rate to the patch scaled by a constant term. Calling the ratio of patch inputs or qualities $\rho_{ij} = R_i/R_j$, the ratio of competitors in patch i to competitors in j becomes

$$\frac{n_i^*}{n_j^*} = \frac{R_i}{R_j} = \rho_{ij}. \tag{11b}$$

This can be compared with equation (10c), in which the competitor ratio is also related to ρ_{ij}. With input matching equation (11b), increasing the total population of competitors in a habitat will not alter the proportions exploiting the different patches (see Tregenza 1995; Tregenza *et al.* 1996). However, the right-hand side of equation (10c) contains the term G^* within the constants α_i, α_j, which is a function of n_i, n_j, ... etc. (see equation (9c)). Therefore under scramble, changing the total competitor density in the habitat may change the ratios of competitors in the patches.

Two extreme limits for a can readily be examined in equation (10b). The extreme, where $a = 1$ (resulting in highest scramble level), gives

$$n_i^* = \sqrt{\frac{c_1 R_i}{G^*}}, \tag{12a}$$

i.e. the number of competitors in a patch should equal the square root of the resource-input rate times a constant. The competitor ratio from equation (10c) is simply

$$\frac{n_i^*}{n_j^*} = \sqrt{\frac{R_i}{R_j}} = \sqrt{\rho_{ij}}, \tag{12b}$$

i.e. it equals the square root of the input ratio, rather than the input ratio direct, as in the non-scramble version of ideal-free under continuous input. The other extreme has a approaching infinity (resulting in zero scramble expenditure at the ESS in all patches, see equation (6)). Here we obtain results equal to equations (11a) and (11b) for ideal-free without scramble.

Figure 5 shows how the competitor ratio in equation (9b) changes with a at different input ratios of resources to the patches, $\rho_{ij} = R_i/R_j$, between these two extremes. The broken line is for input matching (limit where $a \to \infty$). As a decreases towards 1, the deviation from input matching becomes marked: there is pronounced 'undermatching', i.e. fewer competitors occur in the

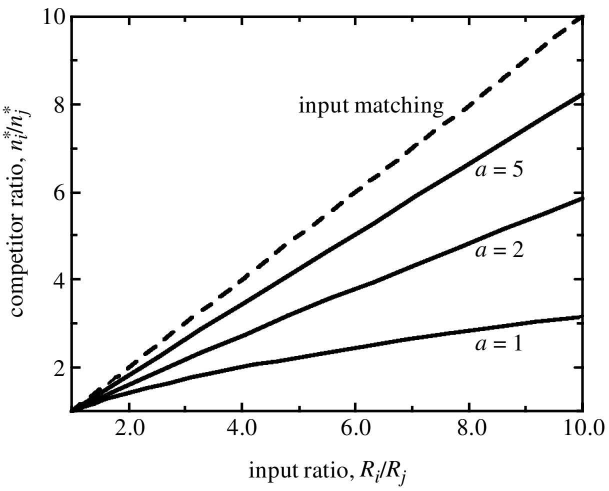

Figure 5. ESS ratio of competitors in patch i to those in patch j, n_i^*/n_j^*, in relation to the ratio of resource inputs to the two patches, R_i/R_j, with $a = 1$, 2 and 5; $c_1 = G^* = 1.0$. The expected relation for input matching is shown as a broken line.

better patch than suggested by the patch ratios. Undermatching is a common feature of continuous input studies (for a review, see Tregenza 1995).

In summary, scramble competition could result in a marked deviation from ideal-free distribution, with fewer competitors in the best patches than would be expected by input matching. The effect causes a more even spread of competitors among patches than would otherwise be expected from the variation in resource input rates among patches.

(b) *Fitness reduction and ESS population size*

Parker (1985) noted that there could be a dramatic fitness reduction arising from a simple version of this scramble model. The net energy gain under the scramble ESS in a patch i containing n_i competitors is given in equation (10*a*). Note that the first term in brackets in this equation is the per-capita gross gain and the second bracketed term is a reduction factor, which represents a proportionate loss of this gross gain due to the scramble expenditure. Thus when there is zero scramble level (equivalent to very large a), this second term becomes 1.0, and the gross gain per competitor is retained by all individuals. When scramble expenditure is maximal and $a = 1$, the second term becomes $1/n_i$, and the gross per-capita gain is reduced by a factor $1/n_i$ because of the scramble expenditure. This could obviously exert major effects on populations.

If scramble expenditure alone controls populations, we can make some estimate of the maximum reduction in population size that it could cause. For simplicity, imagine that all patches in a habitat are of equal size and quality. We seek an ESS number, n^*, of foragers per patch, maintained by the effect of scramble, which when multiplied by the number of patches in the entire habitat gives a measure of the ESS population size.

To do this, we need to know the relationship between fitness and net gains, i.e. $W(G^*)$. For simplicity, assume that net gain converts linearly into fitness, so that $W(G^*) = bG^*$, where b is a positive constant. (In reality, fitness is unlikely to be linearly related to per-capita gain and more likely to show diminishing returns with G.) Then at stable state, the number of foragers returning to each patch at the next generation occurs where number of competing foragers $n^* = bG^*n^*$, i.e. where $W(G^*) = 1$. Defining $K = n_{\max}$ as the maximum carrying capacity per patch, achieved when there is no scramble expenditure, we see that if there is no scramble expenditure, $G_{\max} = c_1R/n_{\max}$, so that $K = bG_{\max}n_{\max} = bc_1R$; i.e. K is proportional to the total resource input to the patch. Substituting G^* from equation (12) gives

$$n^* = K\left(\frac{(a-1)n^* + 1}{an^*}\right); \qquad (13a)$$

so that

$$n^* = \frac{K(a-1) + \sqrt{K^2(a-1)^2 + 4aK}}{2a}. \qquad (13b)$$

It is easy to see that equation (13*a*) gives the expected result that $n^* = K$ if a is very large so that there is no scramble expenditure, and (13*b*) gives $n^* = \sqrt{K}$ when there is maximum scramble expenditure ($a = 1$). Thus in principle at least, scramble competition could reduce the population to the square root of potential maximum carrying capacity. Note, however, that this is a maximum and can occur only under maximum scramble and when the number of competitors in a patch is equal to the 'effective number of competitors' (see § 5).

(c) *Effect of distribution on net gains*

Finally, it is of interest to compare the net gains under various types of distribution. To make the analysis more tractable, suppose that we categorize patches within the habitat as 'good' (A) or 'bad' (B), having respectively the input rates R_A, R_B, and let A and B types occur with equal probability (0.5). Thus the average total input per patch is $\overline{R} = (R_A + R_B)/2$.

Suppose first that the number of competitors in a patch is constrained at n in all patches—individuals are not free to move to better patches. However, assume that they can monitor the patch input rate and play their ESS scramble level S^* in relation to R and n. The expected net gains to an individual, assuming that competitor number in patches is equal, is

$$G^* = [(c_1R_A/n - c_2S_A^{*a}) + (c_1R_B/n - c_2S_B^{*a})]/2,$$

which gives

$$G^* = \left(\frac{c_1\overline{R}}{n}\right)\left(\frac{n(a-1)+1}{an}\right); \qquad (14)$$

cf. equation (10*a*).

Suppose now that we remove this constraint so that individuals adopt the ideal-free distribution. From equation (10*a*), we set the net gains equal in patch types A and B and obtain an expression in terms of ideal-free competitor numbers, n_A^*, n_B^*,

$$\frac{R_A}{R_B} = \rho_{AB} = \frac{n_A^{*2}}{n_B^{*2}}\left[\frac{n_B^*(a-1)+1}{n_A^*(a-1)+1}\right]. \qquad (15)$$

Where the mean number of competitors per patch is $n = (n_A^* + n_B^*)/2$, then equation (15) can be used to solve n_A^*, n_B^*, and hence G^* (from equation (10*a*)) at any value

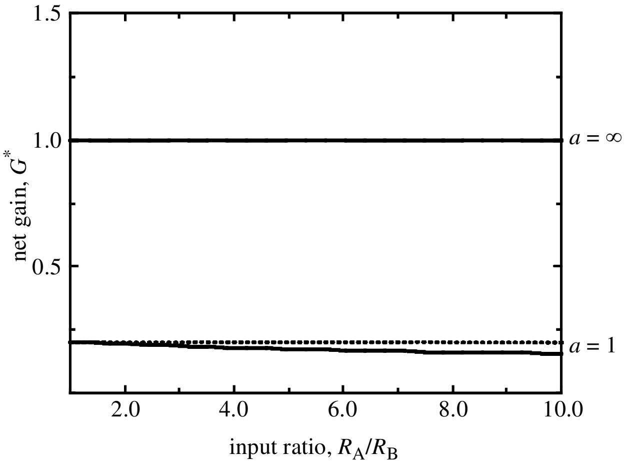

Figure 6. Net per-capita gain, G^*, in relation to the input ratio R_A/R_B, at the limits for scramble of $a = \infty$ (zero scramble expenditure) and $a = 1$ (maximum scramble expenditure) for ideal-free distribution of competitors (continuous lines) and constrained movement (dotted line). G^* for $a = \infty$ for constrained movement is the same as for ideal-free. Parameters are $\overline{R} = 5$, $n = 5$, $c_1 = 1$.

of n and ρ. For present purposes, we will confine interest to the limits $a = 1$ (maximum scramble) and $a \rightarrow \infty$ (no scramble, input matching applies). This gives

$$a = 1, \quad n^*_A = 2n\sqrt{\rho_{AB}}/(1 + \sqrt{\rho_{AB}}); \qquad (16a)$$

$$a \rightarrow \infty, \quad n^*_A \rightarrow 2n\rho_{AB}/(1 + \rho_{AB}). \qquad (16b)$$

Net gains, G^*, can now be calculated from equation (16) via equation (10*a*), and from equation (15). Since $R_A = \rho_{AB}R_B = 2\overline{R}\rho/1 + \rho)$, we obtain

$$a = 1, \quad G^* = \left(\frac{c_1\overline{R}}{n}\right)\left(\frac{(1 + \sqrt{\rho_{AB}})^2}{2n(1 + \sqrt{\rho_{AB}})}\right); \qquad (17a)$$

$$a \rightarrow \infty, \quad G^* = \left(\frac{c_1\overline{R}}{n}\right); \qquad (17b)$$

see figure 6. As expected, if $a \rightarrow \infty$ there is no scramble and so the net energy gain is proportional to the mean patch quality divided by the mean competitor number (equation (17*b*)), exactly as it is if competitors movement is constrained (equation (14)). This at first appears odd; higher net gains might be expected with ideal-free since individuals are free to exploit the habitat in a way that competitively maximizes individual fitness. However, without any scramble costs, the expected gain per capita in both cases is simply the total resources divided by the total competitors. Only the variance in net gain between individuals changes between the models—under ideal-free, all individuals get equal gains, under constraint, some individuals gain more than others, depending on ρ_{AB}. Consider the extreme case where $\rho_{AB} \rightarrow \infty$: if individuals cannot move freely, half the individuals get double the gain that all would get under ideal-free and the other half get nothing. Thus the fact that expected net gains are equal does not mean that it will not pay individuals to move—if free to move, individuals in a bad patch will always gain in the constrained model by moving to a good patch. Although expected per-capita gains are equal in both models, fitnesses will only be equal if fitness increases linearly with *G*. Fitness will be higher under ideal-free if *W* shows diminishing returns with *G*.

With maximum scramble, the net gain is proportional to $\overline{R}/n^2$ when movement is constrained (equation (14)); i.e. it is $1/n$ that of the former case because of the scramble costs (equation (17*b*)), and unrelated to ρ_{AB}. However, under ideal-free assumptions, G^* becomes related to the disparity between patch types (equation (17*a*)), declining weakly with ρ_{AB} (figure 6). Rather counter-intuitively, under ideal-free, as patch variance increases and ρ_{AB} increases above 1.0, maximum scramble conditions cause net per-capita gains to be lower than when free movement is constrained (figure 6). The difference between the two is small, reducing as n increases. This occurs because, at maximum scramble, the ideal-free competitor ratio increases only as the square root of the patch input ratio (see equation (12*b*) and figure 5), so that the competitor numbers differ less from n than might at first be imagined, damping down the difference in net gains between the models. Thus the main influence on G^* is the extent of scramble costs rather than any difference in distribution due to free or constrained movement between patches.

5. DISCUSSION

This paper shows that the average per-capita resources, $R(n)/n$, and the way in which scramble costs rise with the level of scramble (defined by a), exert major effects on scramble behaviour. An experimental study designed to test this (Shaw *et al.* 1996) was in general successful. Scramble will affect the predictions of ideal-free distribution theory, and some degree of undermatching is expected. While undermatching is implicit or explicit in several of the cases reviewed by Tregenza (1995), two cases of overmatching are noted. These cannot be explained readily by the present analysis.

It is interesting that Nicholson (1954) saw scramble competition as having potentially more drastic effects on populations than contest competition. To assess the maximal effects of scramble on populations implied by the present analysis, it is important to distinguish between the number of individuals exploiting a patch, which we can call N, and the 'effective number of competitors', which we call n. We have until now assumed that $N = n$. But in a large assemblage of N competitors, it seems likely (from the point of view of a given focal individual) that only a subset of $n - 1$ others actually compete for a subset of the total R items that are being input to the entire patch. If $zn = N$, then we expect that the subset of items for which n competitors compete is R/z. Calling, as before, the maximum potential carrying capacity for the entire patch $K = bc_1R$, then applying an analysis parallel to that in equation (4*c*), we find that that under conditions for maximum scramble ($a = 1$), the ESS population size now becomes $N^* = z\sqrt{K/z}$. For $z = 1$, the prior result that $N^* = \sqrt{K}$ again applies since $n^* = N^*$. As z increases above 1, N^* becomes closer to K than the previous estimate of $\sqrt{K}$. A theoretical maximal limit of $z = K$ (i.e. effective competitor number $= 1$) implies that this effect can raise N^* to K. A second reason why populations are unlikely to be reduced to $\sqrt{K}$, even if scramble competition were to be the sole determinant of stable population size, is that the energy costs of increased scramble may be very bowed ($a >> 1$; see figure 1) resulting in rather little expenditure, so that N^* approaches K. Shaw *et al.* (1995) used published expectations from biophysics to estimate a as three in their study on fishes, on the basis that swimming speed would best fit the notion of pay-offs through S as defined in equation (1).

For the past quarter of a century, John Maynard Smith has had an influence on my research far exceeding that of any other person. This seems an appropriate place to express my warmest thanks to him, not only for this influence, but also for his friendship, stimulation and inspiration. I also thank S. J. Hutchinson for useful suggestions for improvement of this paper.

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