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The Evolution of Territory Size—Some ESS Models

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We present two classes of models for the evolution of territory size. Both are frequency dependent (employing the concept of the evolutionary stable strategy or ESS), and are based on finite population sizes and continuous strategy sets. A territorial strategy is defined in the first class by the size of territory an individual defends if it is one of the individuals successful in obtaining a territory in a patch of resources when others are excluded. The ESS for territory size may be spitefully large when the potential fecundity of individuals is low, but as fecundity (or population numbers) increases, the ESS decreases towards the size which maximizes individual reproductive success. When the costs of defending a territory are a function not only of area but also of the number of competitors (excludes plus holders) against which the area is defended, then the individuals excluded from resources (excludes) are likely to lower the ESS more markedly than the individuals who have acquired territories (holders). In the second class of models, all individuals gain access to resources, but the amount an individual acquires depends on its defensive effort strategy relative to the defensive effort of other competitors. Here, in contrast, the ESS for defensive effort increases with increasing potential fecundity. When the second class of model is extended to include phenotypic variation in individual success (at a given defensive effort), variance in phenotypic ESSs diminishes as the number of competitors increases.

1. Introduction

Most models for the evolution of territorial behaviour have assumed that natural selection will favour the size X of territory which maximizes individual reproductive success $f(X)$ (see Davies, 1978 for review). If $f(X)$ is

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an additive function of gross benefits $b(X)$ and costs $c(X)$, then the optimal size will be that which maximizes $b(X) - c(X)$ [or equivalently, the optimum is where $b'(X) = c'(X)$]. Alternatively, if $f(X)$ is a multiplicative function of $b(X)$ and $c(X) = c'(X)$ being a factor between zero and one, by which gross benefits are reduced, then $f(X)$ is maximized where $f'(X) = 0$.

The most serious weakness of simple cost-benefit models is their inability to deal with frequency-dependent selection. Costs of territory-holding could sometimes be mainly frequency-independent, relating perhaps simply to area-related energetic expenditures of patrolling, marking boundaries, etc. Usually, however, there will be underlying frequency-dependent effects, and for this reason we have preferred to use models based on Maynard Smith's (1974) concept of the evolutionarily stable strategy, or ESS. An ESS is a strategy that, once fixed in a population, cannot be invaded and replaced by an alternative strategy.

One kind of frequency-dependence of particular interest to us is the effect of territory size on the number and types of competitors that a territory-holder encounters. Using models with finite population sizes, we look at differences in costs and benefits stemming from defence against other territory-holders vs. defence against "floating" individuals without territories, as well as at the relationship between territorial strategy and overall population size. Another kind of frequency-dependence that we investigate concerns the case where territorial gains are strongly affected by the defensive efforts "played" by other members of the population.

Hamilton's (1970, 1971) papers on the evolution of spite point to another flaw in the simple cost-benefit approach; the strategy of harming oneself to harm others more (by defending resources in excess of what can be used, for example) can never be that which maximizes net benefits, $f(X)$. In Hamilton's models spite directed at individuals of less than average relatedness is favoured because inclusive fitness is considered, rather than simply individual reproductive success.

Verner (1977) has also stressed that territorial individuals may benefit by excluding others from resources because this increases their relative contribution to the gene-pool of the next generation. An essential difference between the two models is that in Hamilton's the spite is *discriminate* (directed towards individuals of less than average relatedness), whereas in Verner's it is *indiscriminate*. Alleles coding for indiscriminate spite can sometimes spread, but their evolutionary stability has been questioned (Rothstein, 1979; Tullock, 1979). We showed that some degree of indiscriminate spite will always be an ESS (Knowlton & Parker, 1979), but that the spite component of territoriality will be substantial only in small populations (see also Rothstein, 1979).

Our aim is therefore to develop some preliminary ESS models for territoriality that incorporate spite, frequency-dependence, and the feedback between territory size and competitor density. This is intended as a preliminary analysis, and we deal mainly with the case where individuals that do not hold territories (i.e. resources) are unable to reproduce and where the amount of territory gained determines reproductive success. The models are based on continuous strategy sets; that is, territory size may take any value between zero and the total number of resource units in a patch (see below). Thus they differ in structure from the two-strategy sets of Rubenstein's (in press) mating strategy models. His are designed to see whether two mating strategies (for example "guarders" and "sneaks") can be maintained as a mixed ESS (Maynard Smith, 1974); ours are to examine the ESS for territory size assuming that territorial defence is essential for reproduction. We mainly assume that territoriality is expressed only in one sex. Thus biologically, one might best apply our models to something like the population genetics of alleles at a locus controlling the amount of testosterone produced.

Finally, our models describe most accurately a panmictic species with non-overlapping generations, composed of individuals that compete for a share of the finite number of resource units available. The resource units are distributed in patches, each of which has a pool of competitors for the resource units. All patches are equal in size, as are all pools, and no individual can defend resources in more than one patch. We investigate two of the possible sets of assumptions concerning the nature and outcome of competitive interactions: (1) An individual's strategy is defined by the number of resource units it will defend if it gains access to the patch. Access to the patch by members of the pool of competitors is random with respect to strategy, and once all resource units have been taken no more individuals from the pool can gain access. Thus some individuals may be entirely excluded, while others get the full number of resource units dictated by their strategies. (2) An individual's strategy is defined by the effort it expends in attempting to defend resources. No individuals are excluded from the patch, but the number of resource units any one individual acquires is a function of its defensive effort relative to the number and defensive efforts of other competitors in the patch.

2. The Exclusion Model—Some Competitors Excluded from Resources

This model is most appropriate for species where differences in arrival time at the patch, or differences in "resource holding potential" (RHP; Parker, 1974) result in some individuals being able completely to exclude

others from the patch. Note the important assumption that there is no relationship between the probability of an individual's being a "winner" and the size of the territory it defends if it wins.

(A) THE BASIC MODEL—COSTS AND BENEFITS DEPENDENT ONLY ON AREA DEFENDED

Let:

- R = the number of resource units in a single patch
- P = the number of patches
- n = the number of competitors at each patch
- X = the number of resource units actually defended by an individual
- X_p = the strategy for resource use established in a population (i.e. the number of resource units defended by all, or all but one of the non-excluded competitors playing this strategy)
- X_m = the strategy for resource use played by a single mutant in one of the P pools of competitors

$f(X)$ = the fitness of an individual defending X resource units [$0 < f(X) < 1$], expressed in terms of gross benefit [$b(X)$] and cost [$c(X)$]
 \bar{W}_x = the mean expected fitness of individuals playing strategy X
 If we set $X_p = 1$ and assume that $n \geq R \geq X_m > 1$, then:

$$\bar{W}_{X_p} = \left[\underbrace{\frac{1}{n} \sum_{i=1}^{R-X_m+1} (R-X_m)f(1)}_{\substack{\text{patch with mutant,} \\ \text{mutant gets } X_m}} + \underbrace{\frac{1}{n} \sum_{i=1}^{X_m-1} (R-i)f(1)}_{\substack{\text{patch with mutant,} \\ \text{mutant gets fraction} \\ \text{of } X_m}} + \underbrace{\left(\frac{n-R}{n}\right)Rf(1)}_{\substack{\text{patch with mutant,} \\ \text{mutant does not gain} \\ \text{access to patch}}} \right]$$

$$+ \left(\frac{P-1}{n} \right) \left[\frac{\binom{n}{n} Rf(1)}{(Pn-1)} \right] \Big/ (Pn-1)$$

$$= \frac{f(1)}{n(Pn-1)} \left[-RX_m + \frac{X_m^2}{2} - X_m + PnR \right] \tag{1}$$

$$\bar{W}_{X_m} = \left[\frac{1}{n} \sum_{i=1}^{R-X_m+1} f(X_m) + \frac{1}{n} \sum_{i=1}^{X_m-1} f(i) \right] \Big/ 1 \tag{2}$$

(terms with n are probabilities; see Fig. 1). In general, the rare strategy X_m will initially increase in frequency when $\bar{W}_{X_m} > \bar{W}_{X_p}$.
 One can make more precise statements about the potential for a strategy X_m to increase in frequency by specifying the form of the fitness function

Possible outcomes	$R=4$ $X_p=1$ $X_m=3$		Probability	Payoffs	
	X_m	X_p		X_p	X_m
1	X_m	X_p	$\frac{1}{n}$	$f(1)$	$f(3)$
2	X_p	X_m	$\frac{1}{n}$	$f(1)$	$f(3)$
3	X_p	X_m	$\frac{1}{n}$	$2f(1)$	$f(2)$
4	X_p	X_p	$\frac{1}{n}$	$3f(1)$	$f(1)$
5	X_p	X_p	$\frac{n-R}{n}$	$4f(1)$	0

FIG. 1. Possible outcomes with probabilities and fitness of X_p - and X_m -playing individuals for $R=4$, $X_p=1$, and $X_m=3$. The size of the rectangle surrounding an X_p or an X_m "individual" indicates the size of its territory (one to four units). For patches with no mutants only the fifth outcome is possible. The total weighted fitness for X_p and X_m individuals, which can be derived from this figure, must be divided by the number of individuals playing each strategy ($Pn-1$ for X_p , 1 for X_m) to calculate \bar{W}_{X_p} and \bar{W}_{X_m} .

$f(X)$. For example, using the linearly-decreasing cost relationship $f(X) = 1 - C(X-1)$ [i.e. fitness an additive function of $b(X) = 1$ and $c(X) = C(X-1)$], fitness is maximized by defending one resource unit and C is a measure of the cost of defending additional units. With this fitness function the condition for the spiteful mutant X_m to spread becomes:

$$C < 1/(Pn-1).$$

Similarly for the non-linear fitness function $f(X) = 1 - C(X-1)^2$ (in which the gradient of the cost function increases with increasing X), the condition for spread becomes:

$$C < (6R-3X)/(Pn-1)(6RX-4X^2-6R+5X).$$

This approach is very limited, however, because the conditions for the initial spread of a trait reveal little about its evolutionary stability. This is particularly true here because the threshold value for C depends on n ; as X_p increases, n may eventually decrease (see below), thus raising the cost threshold and making the spread of higher defence levels possible. To determine where this positive feedback loop winds down, we need to determine the ESS for resource defence, as follows.

If X_* is defined as the ESS for the number of resource units taken, then individuals playing X_* must be more fit when common than any single mutant which takes X_m resource units. Thus if we subtract the expected fitness of a rare mutant taking X_m units from the mean expected fitness of individuals taking X_* units, the result is positive except for $X_m = X_*$, where the result is zero.

$$\text{Therefore when } X_m = X_*, \frac{d}{dX_m} [\bar{W}_{X_p=X_*} - \bar{W}_{X_m}]_{X_*} = 0. \quad (3)$$

To solve (3) explicitly for X_* we need new formulations for (1) and (2) which are not tied to the assumption that $X_p = 1$. The model would also be more realistic for some biological systems if n were allowed to vary with X_p . An increase in the number of resource units taken by non-excluded competitors decreases the number of adults contributing offspring to the next generation, and may either increase or decrease the fecundity of these adults (depending on the value of X_p and the fitness function used). If one assumes that the number of competitors in generation $t + 1$ is directly related to the number of offspring produced by the adults of generation t , then we can write $n(X_p) = f(X_p) VR/X_p$, where V is a constant that converts $f(X_p)$ into the number of offspring an individual produces which survive to join a pool of competitors. This enables us to derive equations for X_* in which population size is in a steady state determined directly by the territorial strategy.

The formulations which are analogous to (1) and (2) but incorporate the above modifications, assuming that $f(0) = 0$, are

$$\begin{aligned} \bar{W}_{X_p} = & \left\{ \frac{a_p}{n(X_p)} + \frac{b_p}{n(X_p)} + \frac{[n(X_p) - \text{int}(R/X_p - 1)]c_p}{n(X_p)} \right. \\ & \left. + (P-1)c_p / [Pn(X_p) - 1] \right\} \end{aligned} \quad (4)$$

where

$\text{int}(X) =$ the truncated, integer value of X

$$\begin{aligned} a_p = & \sum_{i=1}^{\text{int}(R/X_p)} \left\{ f(X_p) \text{int} \left(\frac{R-X_m}{X_p} \right) \right. \\ & \left. + f \left[R - X_m - \text{int} \left(\frac{R-X_m}{X_p} \right) X_p \right], \quad \text{OR } f(X_p)(i-1) \text{ IF} \right. \\ & \left. X_p(i-1) > X_p \text{int} \left(\frac{R-X_m}{X_p} \right) + R - X_m - \text{int} \left(\frac{R-X_m}{X_p} \right) X_p \right\} \end{aligned}$$

$$\begin{aligned} b_p = & f(X_p) \text{int} \left(\frac{R}{X_p} \right), \quad \text{OR } f(X_p) \text{int} \left(\frac{R}{X_p} \right) \\ & + f \left[R - X_m - \text{int} \left(\frac{R}{X_p} \right) X_p \right] \quad \text{IF } R - X_m - \text{int} \left(\frac{R}{X_p} \right) X_p > 0 \\ c_p = & f(X_p) \text{int} \left(\frac{R}{X_p} \right) + f \left[R - \text{int} \left(\frac{R}{X_p} \right) X_p \right] \end{aligned}$$

and

$$\bar{W}_{X_m} = \frac{a_m}{n} + \frac{b_m}{n} \quad (5)$$

where

$$\begin{aligned} a_m = & \sum_{i=1}^{\text{int}(R/X_p)} \{ [R - X_p(i-1)], \quad \text{OR } f(X_m) \quad \text{IF } X_m < R - X_p(i-1) \} \\ b_m = & f \left[R - \text{int} \left(\frac{R}{X_p} \right) X_p \right], \quad \text{OR } f(X_m) \quad \text{IF } X_m < R - \text{int} \left(\frac{R}{X_p} \right) X_p \end{aligned}$$

(see Fig. 2).

Because formulations (4) and (5) cannot yield an analytic solution, we earlier (Knowlton & Parker, 1979) used the following approximations:

$$\begin{aligned} \bar{W}_{X_p} = & \left\{ \left[\frac{R/X_p}{n(X_p)} \right] \left(\frac{R-X_m}{X_p} \right) f(X_p) + \left[\frac{n(X_p) - R/X_p}{n(X_p)} \right] \left(\frac{R}{X_p} \right) f(X_p) \right. \\ & \left. + (P-1) \left(\frac{R}{X_p} \right) f(X_p) \right\} / [Pn(X_p) - 1] \\ \bar{W}_{X_m} = & \left[\frac{R/X_p}{n(X_p)} \right] f(X_m). \end{aligned} \quad (7)$$

It was assumed that (a) any rare mutant which secures a place in a patch always takes the full number of resource units dictated by the strategy it is playing (i.e. it is never forced to take less, as in the third and fourth outcomes of Fig. 1), and (b) the last X_p -playing individual to enter a patch, if forced to take some fraction α of X_p has a fitness of $\alpha f(X_p)$ [a value which may be higher or lower than the true fitness $f(\alpha X_p)$].

Substituting (6) and (7) into (3), differentiating with respect to X_m while holding X_* constant, and then substituting $X_m = X_*$ eventually resolved to

$$X_* = \frac{-f(X_*)}{f'(X_*) [Pn(X_*) - 1]} \quad \text{or } f(X_*) [PV + 1 / f'(X_*)] \quad (8)$$

Possible Outcomes	$R=4$ $X_p=2$ $X_m=3$		Probability	Payoffs	
	X_m	X_p		X_p	X_m
X_p	X_m	X_p	$\frac{1}{n(X_p)}$	$f(1)$	$f(3)$
X_p	X_m	X_p	$\frac{1}{n(X_p)}$	$f(2)$	$f(2)$
X_p	X_p	X_p	$\frac{n(X_p)-R}{n(X_p)}$	$2f(2)$	0

Possible Outcomes	$R=5$ $X_p=3$ $X_m=1$		Probability	Payoffs	
	X_p	X_p		X_p	X_m
X_m	X_p	X_p	$\frac{1}{n(X_p)}$	$f(3) + f(1)$	$f(1)$
X_p	X_p	X_p	$\frac{1}{n(X_p)}$	$f(3) + f(1)$	$f(1)$
X_p	X_p	X_p	$\frac{n(X_p)-R}{n(X_p)}$	$f(3) + f(2)$	0

Fig. 2. Possible outcomes, probabilities and fitnesses (as in Fig. 1) for two cases which require equations (4) and (5) to specify W_{X_p} and W_{X_m} precisely. These examples illustrate the need for the if/or clauses and other complexities of (4) and (5) should the reader desire to work through them. Note that the patch is divided into four resource units in the first case and five in the second; territory sizes are proportional to areas under "possible outcomes".

[assuming $n(X_*) = f(X_*)VR/X_*$]. This general result indicates that evolution may favour individuals that behave spitefully (i.e. defend more resource units than the number which maximizes their reproductive success, X_{opt}). As population size increases, however, X_* converges to the X_{opt} value where $f'(X) = 0$.

The relationship between X_* and potential population size (VR) is shown in Fig. 3, in which X_* was iterated from (8) using the explicit function:

$$f(X) = b(X) \cdot c(X) = [1 - \exp(-X)] [\exp(-CX)].$$

This form gives a skewed distribution of $f(X)$ that rises steeply from $f(X=0) = 0$ to its peak at X_{opt} , with a long tail for $X > X_{opt}$. Increasing constant C increases the relative cost of resource defence and makes $f(X)$ more sharply peaked (see Knowlton & Parker, 1979).

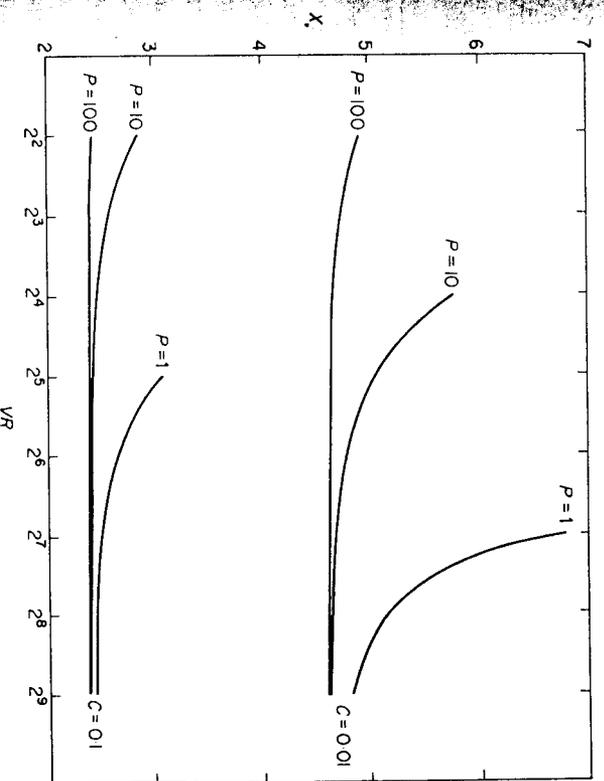


Fig. 3. The ESS for territory size (some competitors excluded) as a function of the number of patches (P), potential population size per patch (VR), and the cost of resource defence (C); see text. For any C , PVR defines a unique value for X_* . The left hand endpoint of a line which does not extend to $VR = 4$ indicates the value of VR below which the ESS is to take the entire patch (R units). For a given C and increasing PVR , X_* converges towards the value of X which maximizes $f(X)$ [i.e. where $f'(X) = 0$]. $f(X) = b(X)C(X) = [1 - \exp(-X)] \exp(-CX)$.

It is interesting that even a large discrepancy between X_* and X_{opt} does not result in a large fitness drop; the lowest $f(X_*) : f(X_{opt})$ ratio associated with the lines of Fig. 3 was 0.980 (for $P = 1$, $VR = 32$, $C = 0.1$). Only when the strategy of taking the entire patch is established would one expect to find measurable losses in individual reproductive success as a consequence of the evolution of spiteful resource defence.

Finally we wish to compare the approximate solutions obtained in (8) to those of computer iterations that used the precise formulations (4) and (5) to search for strategies stable against invasions by mutants. The purpose of this comparison is to demonstrate the accuracy of the approximations before turning to more complex models for which similar simplifying assumptions are made to those leading to (8).

Table 1 shows that the approximate solutions are generally within one or two percentage points of the precise formulations (and that, as expected, the latter are stable against invasion by the former). In a few cases neither of these methods gave values which were stable against the strategy "take the

TABLE 1.

Comparison of "approximate" [equation (8)] and "precise" [equations (4) and (5)] solutions for X_* using the fitness function $f(X) = b(X) \cdot c(X) = [1 - \exp(-X)] \exp(-cX)$ in which C is a measure of the cost of defending resource units

C	P	VR	X_{opt}	"Approximate" X_*	"Precise" X_*	R
0.01	1	128	4.615120	6.791550	4.742386	8*
0.01	1	128	4.615120	6.791550	5.333333 ¹¹	16 ¹
0.01	1	128	4.615120	6.791550	4.637505	32*
0.01	1	128	4.615120	6.791550	4.923077	64*
0.01	1	1024	4.615120	4.723688	4.627173*	8
0.01	1	1024	4.615120	4.723688	4.684552*	16
0.01	1	1024	4.615120	4.723688	4.616912*	32
0.01	1	1024	4.615120	4.723688	4.619756*	64
0.01	1	1024	4.615120	4.723688	4.740741*	128
0.01	10	128	4.615120	4.700901	4.624702*	8
0.01	10	128	4.615120	4.700901	4.666832*	16
0.01	10	128	4.615120	4.700901	4.616540*	32
0.01	10	128	4.615120	4.700901	4.618720*	64
0.01	10	128	4.615120	4.700901	3.076333	81
0.1	1	32	2.397895	2.397895	2.666667 ¹¹	4
0.1	1	512	2.397895	2.423267	2.406805*	4
0.1	1	512	2.397895	2.423267	2.434182*	8
0.1	1	512	2.397895	2.423267	2.407472*	16
0.1	10	512	2.397895	2.400383	2.398760*	4
0.1	10	512	2.397895	2.400383	2.400947*	8
0.1	10	512	2.397895	2.400383	2.398750*	8
1	1	128	0.693147	0.709524	0.695261*	2

See text for definitions of P , R , V , X_{opt} is the value of X at the peak of $f(X)$; i.e. $f'(X) = 0$. "Precise" solutions were found by searching from X_{opt} upwards for a value of X_p such that $W_{X_p} > W_{X_m}$ for X_m values just larger than X_p ; "approximate" solutions were obtained by an iterative routine on equation (8). The stability of the two solutions, and $X = R$, to invasion by a range of X_m between X_{opt} and R was tested. Values are asterisked if they are stable against invasion, and able to invade populations playing either of the other two strategies (out of "approximate" ESS, "precise" ESS, "take R "). Roman numerals indicate that both strategies were locally stable, but that I was "more stable" than II ($W_{X_m} = II/W_{X_p} = I < W_{X_m} = I/W_{X_p} = II$).

entire patch" (i.e. defend R resource units). These exceptional situations, in which there was only local and not global stability, were however encountered only when population sizes were extremely small. Thus for most realistic population sizes, the approximate method yields a reasonably accurate analytic solution, and always yields at least local stability.

(B) A MODEL WITH COSTS DEPENDENT ON COMPETITORS

We shall now examine a similar model to the approximate model of the last section, in which there is again despotic exclusion from resources

However, we now wish to incorporate some costs in territorial guarding that are related to "competitor pressure". Even where disputes are generally settled "conventionally" by some asymmetry such as prior ownership, there must be a display of some cost to signify that the resource is occupied, and that occupancy is being contested. Where relative differences in resource holding potential (RHP) are used to settle contests, considerable energetic expenditure may be required before information concerning relative RHP is sufficient enough to allow settlement.

As before, competitor-independent costs of holding X resource units are summarized by $f(X) = b(X) \cdot c(X)$. To include costs arising from competitor pressure, we used a second multiplicative reduction factor, $c_n(X)$ so that overall relative fitness now becomes $f(X) \cdot c_n(X)$. This function $c_n(X)$ is assumed [like the $c(X)$ function] to be monotonically decreasing with increasing X , and also has $0 < c_n(X) < 1$. Thus if a territory holder shows a relatively high X value, it achieves greater gross benefits but suffers conditionally a greater reduction in those benefits because of increased costs.

We assume that pressure costs from other competitors will be identical for all individuals in all patches when the individuals all play the same strategy. But where there is a mutant territory holder in a patch, the costs $c_n(X)$ for all individuals in the patch are altered (for instance the numbers of holders and excluded are changed). Let:

$c_n(X_p)$ = the cost (reduction factor) for individuals in a patch where all play the strategy X_p

$c_n(X_p)$ = the cost for an X_p -playing individual in a patch in which there exists a single mutant playing $X_m \neq X_p$

$c_n(X_m)$ = the cost for a mutant playing X_m in a patch where all other individuals play X_p .

Following equations (6) and (7), we can write expected fitnesses as:

$$W_{X_p} = \left\{ \left[\frac{R/X_p}{n(X_p)} \right] \left[\frac{R - X_m}{X_p} \right] f(X_p) c_n(X_p) \right\} + \left[\frac{n(X_p) - R/X_p}{n(X_p)} \right] \times \left(\frac{R}{X_p} \right) f(X_p) c_n(X_p) + (P-1) \left(\frac{R}{X_p} \right) f(X_p) c_n(X_p) \left\} / [Pn(X_p) - 1] \quad (9)$$

$$W_{X_m} = \left[\frac{R/X_p}{n(X_p)} \right] f(X_m) c_n(X_m). \quad (10)$$

Substituting (9) and (10) into (3), differentiating with respect to X_m holding

X_* constant, and then substituting $X_m = X_*$ yields:

$$X_* = \frac{f(X_*)[Rc'_{nX_m}(X_*) - c_{nX_m}(X_*)]}{[f'(X_*)c_{nX_m}(X_m) + f(X_*)c'_{nX_m}(X_m)]Pn(X_*) - 1} + f(X_*)c'_{nX_m}(X_*) \quad (11)$$

Note that in (11) neither $c'_{nX_m}(X_*)$ nor $c'_{nX_m}(X_m)$ is equivalent to $c'_n(X_*)$. The relationship between the two gradients can be defined only when a more explicit form of $c_n(X)$ is supplied.

We present here a particular model which assumes that competitor dependent costs rise linearly with competitor density, and that a territory holder accrues such costs in proportion to the relative size (area) of its territory. For some species a modification of these assumptions would be more appropriate. If, for example, costs arising from competitors increase in proportion to the territorial perimeter (proportional to $\sqrt{\text{area}}$), rather than to area, while benefits continue to increase in relation to area, then ESSs will be correspondingly higher than those suggested by the present model.

Costs are separated into two components: one arising from the activities of the n_1 other neighbours holding territories (included), and one from the n_2 excluded individuals ($n_2 + n_1 = n$). If each of the n_2 excluded individuals delivers a constant pressure to the resource patch, then α is defined as the constant which converts this pressure into a cost to territory holders. Similarly, we assume that each territory holder directs a constant pressure, of cost β , within the patch. Thus the total effective pressure experienced by territory holders is:

$$\alpha n_2 + \beta n_1 = \alpha [n(X_*) - R/X_*] + \beta (R/X_*) \quad (12)$$

for patches with no mutants, and

$$\alpha n_2 + \beta n_1 = \alpha [n(X_*) - 1 - (R - X_m)/X_*] + \beta [1 + (R - X_m)/X_*] \quad (13)$$

for patches with a mutant playing X_m .

It seems probable that in many territorial systems these pressures will not be distributed evenly over the area of the patch. Holders on the periphery of the resource patch might sustain the main burden of pressure from excludeds, while centrally placed territory holders might experience most of the pressure from other holders. This will only alter our conclusions, however, if the size of territory taken by the mutant holder affects its probability of occupying a peripheral position in the patch. We assume any such distortions to be insignificant.

It is convenient to express the difference between the pressure costs as $\gamma = \alpha - \beta$. If $\gamma = 0$, then holders and excludeds exert equal pressures; where

only excludeds are important $\gamma = \alpha$; where only neighbours are important, $\gamma = -\beta$.

We can now estimate the pressure cost sustained by an individual holding a territory of size X , assuming that of the total pressure sustained by the patch, it collects an amount proportional to the area it occupies within the patch, i.e. $(X/R)[\alpha n_2 + (\alpha - \gamma)n_1]$. The reduction factor, $c_n(X)$ thus becomes $1 - (X/R)[\alpha n_2 + (\alpha - \gamma)n_1]$. More explicitly, using (12) and (13):

$$c_n(X_*) = 1 - [\alpha X_* n(X_*)/R] + \gamma;$$

$$c_{nX_m}(X_*) = 1 - [\alpha X_* n(X_*)/R] + (\gamma X_m/R) - (\gamma X_m/R) + \gamma;$$

$$= c_n(X_*) \text{ if } X_m = X_*;$$

$$c'_{nX_m}(X_*) = -\gamma/R;$$

$$c_{nX_m}(X_m) = 1 - [\alpha X_m n(X_*)/R] + (\gamma X_m/R) - (\gamma X_m^2/RX_*) + (\gamma X_m/X_*);$$

$$= c_n(X_*) \text{ if } X_m = X_*;$$

$$c'_{nX_m}(X_m) = -[\alpha n(X_*)/R] + (\gamma/R) - (2\gamma X_m/RX_*) + (\gamma/X_*);$$

$$= -[\alpha n(X_*)/R] - (\gamma/R) + (\gamma/X_*) \text{ if } X_m = X_*.$$

These equations can be substituted into general equation (11), or alternatively into (9) and (10), to yield the following equation for the ESS X_* :

$$X_*^2 \left\{ f'(X_*) \frac{\alpha n(X_*)}{R} [Pn(X_*) - 1] + X_* \left\{ f(X_*) \frac{[\alpha n(X_*) + \gamma]}{R} Pn(X_*) - f'(X_*)(1 + \gamma) [Pn(X_*) - 1] \right\} - f(X_*) - f(X_*)\gamma [Pn(X_*) + 1] \right\} = 0. \quad (14)$$

Equation (14) is complex because it allows for a spite component in the ESS territory size. If we assume that population size $Pn(X_*)$ is large so that spite is insignificant, then (14) becomes much more tractable, since we can assume that $[Pn(X_*) - 1] \approx Pn(X_*) \approx (Pn(X_*) + 1]$, and that the term $-f(X_*) = 0$ [because it is the only term in equation (14) not multiplied by population size]. The two sets of equations in Table 2 are based on this simplification. Each set consists of a general form plus the cases where $\gamma = 0$ (each excluded exerts the same pressure as each holder), $\alpha = 0$ (excludeds exert insignificant pressure), and $\beta = 0$ (holders exert insignificant pressure).

The two sets differ in their treatment of the number of competitors per patch in a way parallel to the two forms of equation (8). As before, the left hand set is in terms of $n(X_*)$, which can be viewed either as a constant, or as a

TABLE 2

ESS solutions for territory size in which the number of competitors arriving at a patch is a variable $n(X_*)$ or in "steady-state" controlled directly by territorial behaviour itself [i.e. $n(X_*)$ defined as in equation (15)]. It is assumed that population size is large, so that the spite component of territoriality is insignificant

	" $n(X_*)$ -variable" model	"Steady-state" model
General equations	$X_*^2 f'(X_*) \frac{\alpha n(X_*)}{R} + X_* \left\{ f(X_*) \frac{\alpha n(X_*) + \gamma}{R} - f'(X_*) (1 + \gamma) \right\} - f(X_*) \gamma = 0 \quad (16a)$	$X_* = \frac{f(X_*) [\alpha V f(X_*) - \gamma]}{f'(X_*) (1 + \gamma) - f(X_*) \gamma [1 + \alpha V f(X_*)] / R} \quad (16b)$
Excludes unimportant $\alpha = 0; \gamma = -\beta$	$X_* = \frac{f(X_*) \beta}{f'(X_*) (1 - \beta) + f(X_*) \beta / R} \quad (17a)$	$X_* = \frac{f(X_*) \beta}{f'(X_*) (1 - \beta) + f(X_*) \beta / R} \quad (17b)$
Both pressures equal $\gamma = 0; \alpha = \beta$	$X_* = \frac{f'(X_*) - f(X_*) \frac{\alpha n(X_*)}{R}}{f'(X_*) \frac{\alpha n(X_*)}{R}} \quad (18a)$	$X_* = \frac{f(X_*)^2 \alpha V}{f'(X_*)} \quad (18b)$
Neighbours unimportant $\beta = 0; \gamma = \alpha$	$X_*^2 f'(X_*) \frac{\alpha n(X_*)}{R} + X_* \left\{ f(X_*) \frac{\alpha [n(X_*) + 1]}{R} - f'(X_*) (1 + \alpha) - f(X_*) \alpha \right\} = 0 \quad (19a)$	$X_* = \frac{f(X_*) \alpha (V f(X_*) - 1)}{f'(X_*) (1 + \alpha) - f(X_*) \alpha [1 + \alpha V f(X_*)] / R} \quad (19b)$

variable which may or may not be some function of X_* . The right hand sets for the explicit assumption that $n(X_*)$ is determined by the relative fitness of members of the previous generation, the constant which converts this relative fitness into the number of surviving offspring, and the number of breeding adults (territory holders), i.e.

$$n(X_*) = f(X_*) \cdot c_n X_* \cdot VR / X_* = \frac{f(X_*) (1 + \gamma) VR}{X_* [1 + \alpha V f(X_*)]} \quad (15)$$

Simple examination of the equations in Table 2 allows one to conclude that when excludeds are unimportant ($\alpha = 0$), the ESS (assuming that spite is unimportant) is independent of the number of competitors [shown by the equivalence of (17a) and (17b), both of which lack any terms n or V]. This is applicable in terms of the assumption that each holder exerts a constant pressure β , regardless of how many holders occupy the patch. Because the number of neighbours of a given holder stays roughly constant over a large range of n , this assumption seems plausible biologically. It is less likely to apply when n_i is low. When excludeds are important, the ESS decreases as the number of competitors (n or V) or the competitor-dependent costs (α and/or β) increase.

To get a more detailed picture of how these equations work, we iterated solutions for equations (17b), (18b) and (19b) in relation to increasing V , giving patches a value of $R = 10$ resource units, for three sets of conditions: (9) competitor-independent costs low and competitor-dependent costs high [Fig. 4; in function $f(X)$, $c(X) = \exp(-0.01X)$; $\alpha, \beta = 0.1$], (6) both types of costs high (Fig. 5; $c(X) = \exp(-X)$; $\alpha, \beta = 0.1$), and (c) competitor-independent costs high and competitor-dependent costs low [Fig. 6; $c(X) = \exp(-X)$; $\alpha, \beta = 0.01$]. The optimum territory size for the case where there are no competitor-dependent costs (i.e. $\alpha = \beta = 0$) given by $f'(X) = 0$, is included in Figs 4(a) 5(a) and 6(a) for comparison with the other three ESS's from Table 2 (only neighbours important, $\alpha = 0$; only excludeds important, $\beta = 0$; both equally important, $\gamma = 0$). The lower graph in each figure shows the proportion of excluded individuals (n_e/n) for each ESS.

Conclusions from these figures are as follows:

- As noted above, the $\alpha = 0$ ESS is independent of the number of competitors and parallels the $\alpha = \beta = 0$ ESS. As expected, the former approaches the latter when competitor-independent costs are relatively more important [i.e. C high, $f(X)$ sharply peaked] and/or when β is low.
- At low competitor densities, the $\beta = 0$ and $\gamma = 0$ ESS's are close to the $\alpha = \beta = 0$ ESS, especially when α , or α and β , are small and competitor-independent costs are high. The $\beta = 0$ and $\gamma = 0$ ESS's fall with increasing

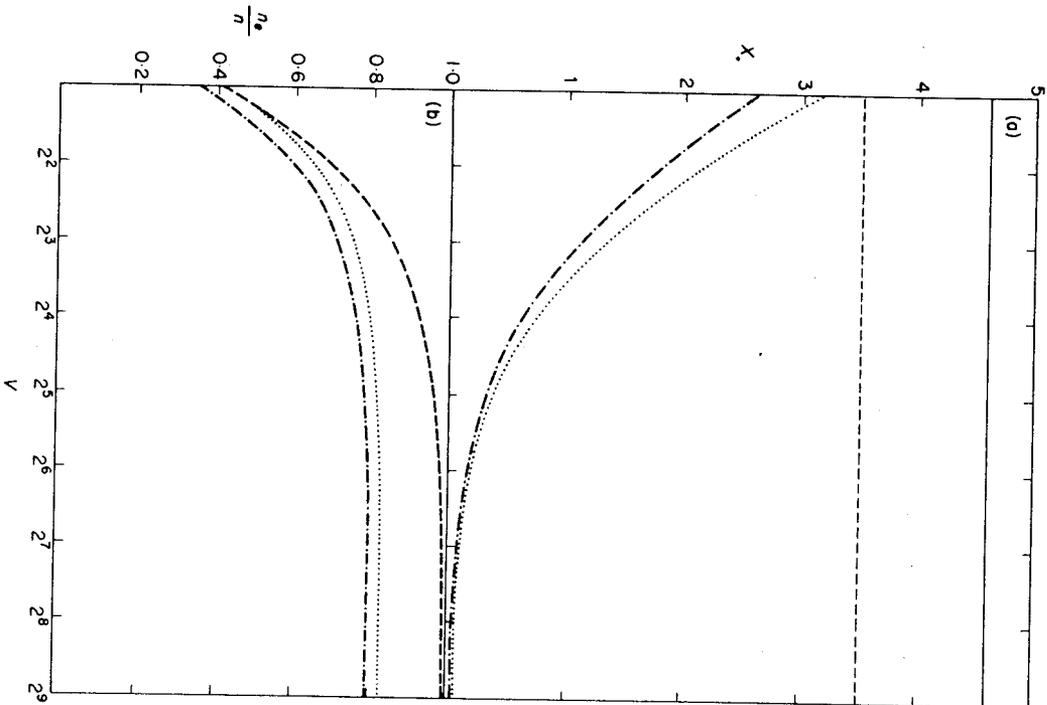


FIG. 4. The ESS for territory size (a) and proportion of competitors excluded (b) as a function of potential population size per resource unit (V), for the case where competitor-dependent costs are high (α and/or $\beta = 0.1$) and competitor-independent costs are low ($C = 0.01$). R was set = 10. For details of model, see text. —, X_{opt} ; - - -, $\gamma = 0$; ·····, $\alpha = 0$; ·····, $\beta = 0$; $f(X) = b(X)$. $c(X) = [1 - \exp(-X)] \cdot \exp(-CX)$.

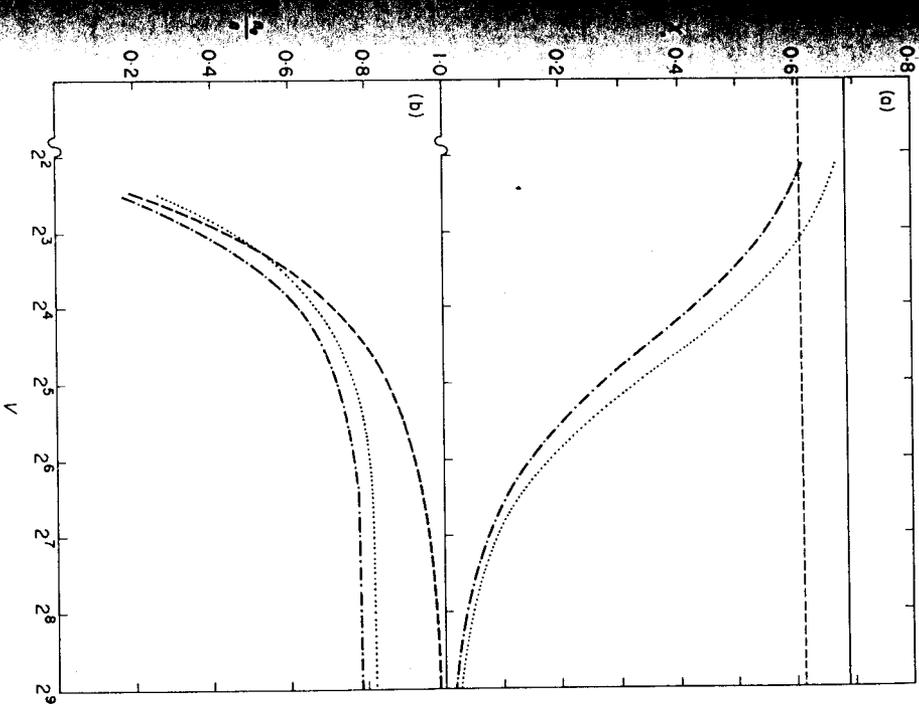


FIG. 5. As in Fig. 4, but for the case where both competitor-dependent costs are high ($\alpha = 0.1$) and competitor-independent costs are high ($C = 1.0$); see text. —, X_{opt} ; - - -, $\gamma = 0$; ·····, $\alpha = 0$; ·····, $\beta = 0$.

number of competitors, however, and do so more rapidly when competitor-dependent costs are relatively large.

(ii) The similarity between the $\beta = 0$ and $\gamma = 0$ ESS's suggests that if pressure from other holders is to exert much effect on the ESS, then each holder must exert a rather high pressure compared to each excluded ($\beta \gg \alpha$), especially where the number of competitors is high.

(iii) Where competitor-independent costs are high, the proportion of individuals included is more sensitive to changes in V . The proportion of individuals

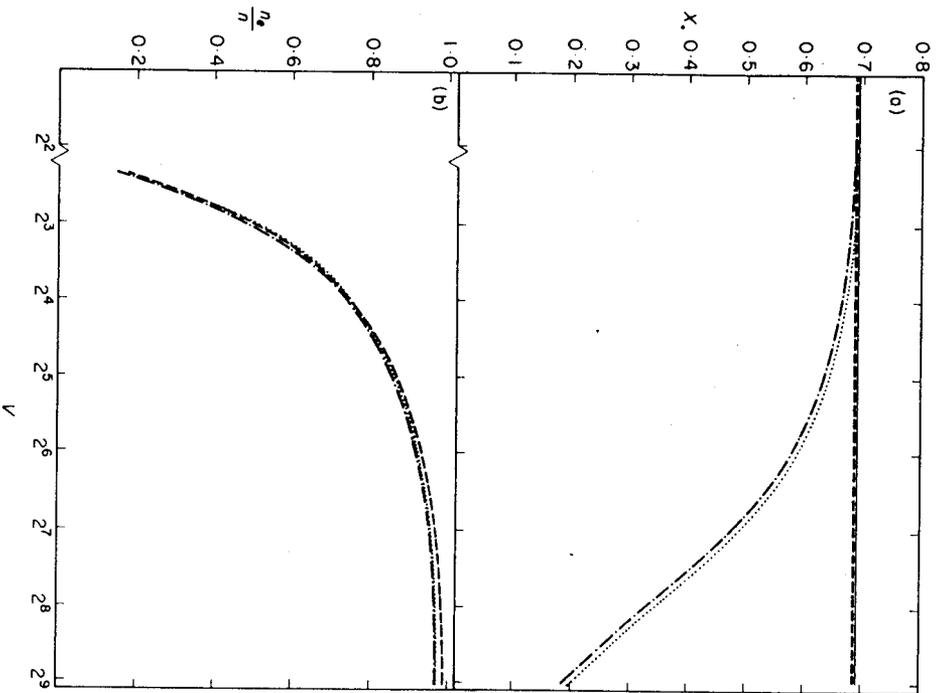


FIG. 6. As in Fig. 4, but for the case where competitor-dependent costs are low ($\alpha = 0.1$ and $\beta = 0.01$) and competitor-dependent costs are high ($C = 1.0$); see text. —, X_{opt} ; - - -, $\alpha = 0$; ·····, $\beta = 0$.

excluded can rise towards 1.0 if $\alpha = 0$ because of the lack of dependence this ESS on the number of competitors. But where β or $\gamma = 0$, the proportion n_e/n asymptotes, eventually becoming independent of V . The higher the competitor-dependent costs, the lower the asymptotic value for and range n_e/n .

How important is patch size R ? Table 3 shows some ESS and n_e/n values under various conditions of V and α or β , for three values of R (3, 10, 50). The $\gamma = 0$ ($\alpha = \beta$) ESS is unaffected by R [see equation (18(b))]. The effect

TABLE 3

effect of R on the ESS's X_* (17b), (18b), (19b) for territory size n_e/n is included in brackets. Throughout, $f(X) = [1 - \exp(-X)] \exp(-X)$

Condition	$R = 3$	$R = 10$	$R = 50$	
$V = 8$	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6301(0.4421)	0.6183(0.4411)	0.6143(0.4407)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.5533(0.3885)	0.5533(0.3885)	0.5533(0.3885)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6128(0.4513)	0.6236(0.4522)	0.6274(0.4524)
$V = 64$	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6875(0.4949)	0.6864(0.4949)	0.6860(0.4949)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6787(0.4899)	0.6787(0.4899)	0.6787(0.4899)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6843(0.4950)	0.6855(0.4950)	0.6859(0.4950)
$V = 1024$	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6301(0.9303)	0.6183(0.9301)	0.6143(0.9301)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.1518(0.7708)	0.1518(0.7708)	0.1518(0.7708)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.1827(0.8076)	0.1842(0.8076)	0.1848(0.8078)
$V = 8$	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.6875(0.9369)	0.6864(0.9369)	0.6860(0.9369)
	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.5801(0.9266)	0.5801(0.9266)	0.5801(0.9266)
	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.5865(0.9274)	0.5876(0.9274)	0.5880(0.9274)
$V = 64$	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.6301(0.9956)	0.6183(0.9956)	0.6143(0.9956)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.0098(0.7985)	0.0098(0.7985)	0.0098(0.7985)
	$\alpha = 0.1$; $\beta = 0.1$; $\gamma = 0$	0.0117(0.8320)	0.0117(0.8321)	0.0117(0.8321)
$V = 1024$	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.6875(0.9961)	0.6864(0.9961)	0.6860(0.9961)
	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.0966(0.9783)	0.0966(0.9783)	0.0966(0.9783)
	$\alpha = 0.1$; $\beta = 0.01$; $\gamma = 0$	0.0986(0.9787)	0.0986(0.9787)	0.0986(0.9787)

is very weak indeed, but greatest at low R ; such effects are of debatable importance in view of the approximation used to calculate the ESS's (see section 4).

Not all of the conclusions listed above are intuitively obvious. Perhaps the most interesting conclusion is that neighbours have relatively little effect on the pressure they exert considerably exceeds that exerted by excluded individuals, particularly when competitor densities are high. Even when there are relatively few excluded, the ESS's for $\beta = 0$ and $\gamma = 0$ are not very similar because of the bunching towards the competitor-independent optimum [where $f'(X) = 0$]. The weakest part of the model is undoubtedly the assumption that each individual exerts constant "pressure". It seems much more likely that excluded will show an increase in attention to the patch as the number of competitors increases, because higher proportions of excluded may mean that eventual prospects for holding a territory are increased. This should not weaken the conclusion about the relative influence of neighbours vs. excluded; rather it reinforces it.

3. No Competitors Excluded: The Defensive Effort Model

In contrast to the models presented above, we assume here that individuals in a group acquire some of the resource units in the patch. If number an individual acquires, however, varies with the number of resource units in the patch, the number of competitors in the pool, and the defensive effort that the individual makes relative to the defensive efforts of other individuals in the group. Biologically, this could correspond to situations which territory size is determined not so much by convention as by relative levels of aggression.

P , R , V , and n are defined as before, but let:

D = the effort an individual invests in defending resources

D_p = the population strategy for defensive effort

D_m = the strategy played by a single mutant in one of the P pools competitors

$f(D)$ = the fitness of an individual making a defensive effort of D

\bar{W}_D = the mean expected fitness of individuals playing strategy D .

(A) THE BASIC MODEL—EFFECTIVENESS OF A GIVEN D DOES NOT VARY BETWEEN INDIVIDUALS

Again we assume that $f(D)$ is a multiplicative function of cost and benefit. As in the first basic model, cost is a simple function, this time of the defensive effort expended by the individual [$0 < c(D) < 1$]. Benefit, however, is a complex function of patch quality R , and an individual's defensive effort relative to the defensive efforts of the other $n-1$ individuals in the patch.

If all individuals play the same defensive effort D_p , we assume that each will gain R/n resource units and that net benefits become $b(R/n) \cdot c(D_p)$ for individual. We also assume that where individuals do not all play the same strategy, each gains territorial space in proportion to its own defensive effort relative to the sum of all n defensive efforts. Thus a mutant playing D_m in a patch where all other competitors play D_p will gain a net fitness of:

$$b \left[\frac{D_m \cdot R}{(n-1)D_p + D_m} \right] \cdot c(D_m).$$

Thus

$$\bar{W}_{D_p} = \underbrace{\left\{ 1(n-1)b \left[\frac{D_p R}{(n-1)D_p + D_m} \right] c(D_p) \right\}}_{\text{Patch with mutant}} + \underbrace{\left\{ (P-1)nb \left(\frac{R}{n} \right) c(D_p) \right\}}_{\text{Patches with no mutant}} / (Pn-1)$$

$$\bar{W}_{D_m} = \left\{ 1 \cdot 1 \cdot b \left[\frac{D_m R}{(n-1)D_p + D_m} \right] c(D_m) \right\} / 1. \quad (21)$$

We again solve for D_* by substituting (20) and (21) into (3); this initially resolves to

$$D_* = \frac{-P(n-1)b'(R/n)c(D_*)R}{(Pn-1)b(R/n)c'(D_*)n}. \quad (22)$$

If n is very large ($Pn-1 = Pn$), then the spite component can be lost and (22) reduces to

$$D_* = \frac{-(n-1)b'(R/n)c(D_*)R}{nb(R/n)c'(D_*)n}. \quad (23)$$

When $b(R/n)$ is a linear function [$b(R/n) = BR/n$, B a positive constant], $n b'(R/n) = B$ and (22) simplifies to

$$D_* = \frac{-P(n-1)c(D_*)}{Pn-1} c'(D_*). \quad (24)$$

Result resembling that obtained by Macnair & Parker (1979) and Parker & Macnair (1979) in their formally similar analysis of parent-offspring conflict.

For a population at steady-state fixed by defensive effort strategy, the interpretation of n in this model becomes more complex than in previous models, because it is not explicitly defined by R , V , and D_* . But because D_* is a function of n , it must be true that $n_{t+1} = n_t$. (If this were not true then D_* could not be stable.) Thus the equation

$$Vf(D_*) = V(BR/n)c(D_*) = 1$$

can be used to provide an explicit expression for n to be substituted into (24).

If $b(R/n)$ is non-linear so that, say, $b(R/n) = 1 - \exp(-BR/n)$, then (22) becomes

$$D_* = \frac{-P(n-1)[B \exp(-BR/n)]c(D_*)R}{(Pn-1)[1 - \exp(-BR/n)]c'(D_*)n}. \quad (25)$$

this case as value for n must be iterated using the equation

$$V[1 - \exp(-BR/n)]c(D_*) = 1$$

Figure 7 plots D_* solutions based on the non-linear cost function $c(D_*) = \exp(-CD_*)$, and the linear and non-linear benefit functions discussed above, for several values of P , C , and V with $B = 1$ and $R = 1$. (All solutions were also checked by iterative techniques which directly searched for

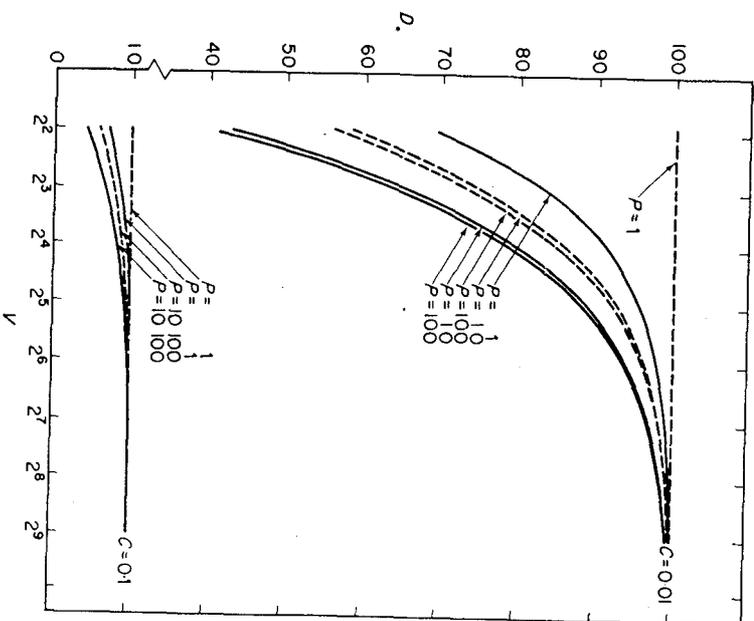


FIG. 7. The ESS for defensive effort (no competitors excluded) as a function of the number of patches (P), potential population size per resource unit (V), and the cost of defensive effort (C), see text. For any C , the value PVR does not define a unique D_* . For a given C and increasing V , D_* converges towards $1/C$. R was set equal to 1 for these iterations. When benefits $b(X)$ yield diminishing returns (continuous curves), the ESS is higher at any V than when benefits rise linearly with the amount of resource acquired. —, $f(D) = [1 \exp(-R/n)] \exp(-CD)$; - - -, $f(D) = R/N \exp(-CD)$.

strategies stable against invasion by mutants; no discrepancies between the two sets of results were found.) The most interesting feature of the solutions for D_* is that defensive effort increases with increasing V , in contrast to the opposite pattern found for territory size X_* in earlier models (Fig. 3).

(1) *Effects of phenotype on the ESS—effectiveness of a given D varies between individuals*

Our models have so far ignored phenotypic differences between individuals. Features such as environmentally-determined size and other RHP differences could modify the effectiveness of a given defensive effort. We

now attempt a prospective ESS analysis of how an individual's strategy is expected to vary with its phenotype.

For simplicity, we assume that in each patch there exists the same distribution of phenotypes amongst the n competitors; we also ignore the finite component of the model by assuming a very large number of patches, n . Notation is as before, but K_i is defined as a factor that modifies the effectiveness of individual i that has a defensive effort D_i ; i.e. the impact on a patch from individual i is equal to $D_i K_i$, so that it obtains:

$$D_i K_i / (D_a K_a + D_b K_b \dots + D_i K_i \dots + D_n K_n)$$

of the available resource, R .

Let the total impact on the patch, all strategies at their ESS, be:

$$I = D_{*a} K_a + D_{*b} K_b \dots + D_{*i} K_i \dots + D_{*n} K_n.$$

For D_{*i} to be an ESS, by the usual technique:

$$\frac{d}{dD_{*i}} \left[b \left(\frac{RD_{*i} K_i}{I + D_{*i} K_i - D_{*i} K_i} \right) \cdot c(D_{*i}) - b \left(\frac{RD_{*i} K_i}{I} \right) \cdot c(D_{*i}) \right] \Big|_{D_{*i}} = 0, \text{ for } D_{*i} = D_{*i}.$$

Note that the above equation postulates that D_{*i} must do better than any mutant competitor D_{mi} within the sub-population of phenotype i . It gives:

$$b \left(\frac{RD_{*i} K_i}{I} \right) \left[\frac{RK_i(I - D_{*i} K_i)}{I^2} \right] c(D_{*i}) + b \left(\frac{RD_{*i} K_i}{I} \right) c'(D_{*i}) = 0. \quad (26)$$

For the case of linear benefits, $b(RD_{*i} K_i/I) = BRD_{*i} K_i/I$, and exponential costs, $c(D_{*i}) = \exp(-CD_{*i})$, in which B and C are constants, (26) reduces to:

$$D_{*i} = \frac{I}{(K_i + IC)}. \quad (27)$$

Ideally, we would want to compare the ESS D_{*i} in (27) with that of an individual having a mean phenotypic RHP \bar{K} . This is not possible unless we establish the distribution of K_i and even then becomes a complex problem. However, we can make some deductions about D_{*i} by comparing it with the ESS for an individual g that has an exactly average impact on the patch (and gains R/n resource units).

Note that for individual g ,

$$D_{*g} K_g = \bar{D} \bar{K}; \quad nD_{*g} K_g = I$$

and where there is a mutant g in the patch, the total of all impacts can be written as $[(n-1)D_{*g}K_g + D_{mg}K_g]$. Hence for D_{*g} to be an ESS,

$$\frac{d}{dD_{mg}} \left\{ b \left[\frac{RD_{mg}K_g}{(n-1)D_{*g}K_g + D_{mg}K_g} \right] c(D_{mg}) - b \left(\frac{R}{n} \right) c(D_{*g}) \right\} \Big|_{D_{*g}} = 0,$$

when $D_{mg} = D_{*g}$

which gives, for linear benefits and exponential costs:

$$nD_{*g}K_g = \frac{K_g(n-1)}{C} = I. \tag{28}$$

Substituting (28) into (27) yields:

$$D_{*i} = \frac{K_g(n-1)}{C[K_i + K_g(n-1)]}. \tag{29}$$

It is evident from (29) that as n increases, the strategy of all individuals converges towards $D_{*i} = 1/C$. This is also the strategy that an individual of very low RHP ($K_i \ll K_g$) is expected to play. As K_i approaches K_g , the ESS decreases somewhat towards $D_{*i} = (n-1)/nC$, the strategy played by g ; as K_i increases beyond K_g , then D_{*i} decreases still further. The relationship

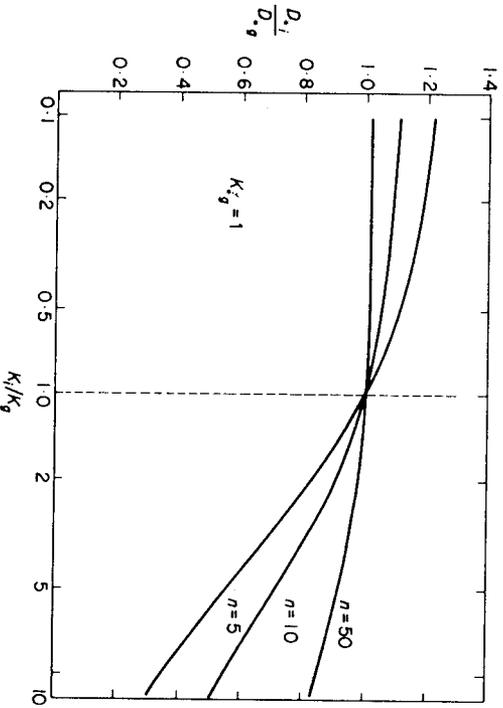


FIG. 8. The ESS for defensive effort of the i th phenotype relative to phenotype g , that has an exactly average amount of territorial resource, as a function of K_i/K_g (the relative RHP of i compared to g ; $K_g = 1$) for various numbers of competitors (n). Benefits $b(X)$ are linear and costs $c(X)$ exponential; P is very large (see text). K_i/K_g is plotted on an \log_e scale. Variance in ESS D_{*i}/D_{*g} decreases markedly with increasing n .

between D_{*i}/D_{*g} , K_i/K_g and n is plotted in Fig. 8, which shows that the variance in strategies is rather small compared to the variance in K .

It is clear why an individual of high RHP should play a relatively low defensive effort; such an individual is assured of a large share of the resource even with rather low D , and increasing D therefore gives only small returns relative to costs.

We can also estimate how fitness varies with RHP. The ratio of fitness, $F_{i/g}$, of an individual with RHP = K_i to that with RHP = K_g is

$$F_{i/g} = \frac{b \left(\frac{RD_{*i}K_i}{nD_{*g}K_g} \right) \cdot c(D_{*i})}{b \left(\frac{R}{n} \right) \cdot c(D_{*g})}$$

with linear benefits and exponential costs,

$$F_{i/g} = \frac{D_{*i}K_i \exp(-CD_{*i})}{D_{*g}K_g \exp(-CD_{*g})}$$

and substituting D_{*i} , D_{*g} from (26) and (27) eventually gives:

$$F_{i/g} = \frac{nK_i}{[K_i + K_g(n-1)]} \exp \left\{ \frac{(n-1)(K_i - K_g)}{n[K_i + K_g(n-1)]} \right\}. \tag{30}$$

As expected, $F_{i/g} > 1$ if $K_i > K_g$; $F_{i/g} < 1$ if $K_i < K_g$. Further, it can be deduced from (30) that as n becomes very large, $F_{i/g}$ approximates to K_i/K_g ; i.e. the fitness ratio approximates to the RHP ratio. At lower n , individuals with $K_i < K_g$ have a fitness ratio marginally greater than K_i/K_g ; as $K_i \gg K_g$ then $F_{i/g}$ becomes markedly lower than K_i/K_g (see Table 4).

TABLE 4.

Fitness ratios $F_{i/g}$ calculated from equation (30). $F_{i/g}$ = fitness of individual i (has RHP = K_i) over the fitness of individual g (has RHP = K_g and experiences mean gains from the patch). K_g is standardized to 1

K_i/K_g	Fitness ratio $F_{i/g}$		
	$n = 5$	$n = 10$	$n = 50$
0.1	0.102	0.101	0.100
0.5	0.508	0.502	0.500
1.0	1.000	1.000	1.000
2	1.904	1.989	1.999
5	3.964	4.619	4.978
10	5.973	8.061	9.841

4. Discussion

The models discussed above represent two ends of a spectrum range from situations in which some individuals are completely excluded from reproduction through the territorial activities of others, to situations in which all individuals pack into the available resources. In the former variance in individual reproductive success alters with population size, while in the latter there is no variance in reproductive success if all individuals pursue the same effective strategy. In this respect the "no exclusion" model resembles those fitting Fretwell's (1972) "ideal free" distribution, in which the fitness of crowded individuals in high quality habitats equals that of individuals occupying poorer habitats but at lower densities.

Most species clearly fall between the extremes represented by these two sets of assumptions. Red grouse are perhaps the best well-studied example of the territorial exclusion model; individuals unable to acquire breeding territories during the autumn often die during the winter months (Watson 1967). In contrast, the data of Kluyver & Tinbergen (1953) on tinninids shows little difference in reproductive success between adults in various habitats during one year (see Davies, 1978). Krebs' (1971) classic study of great tits, however, gave a result that appears to be intermediate: pairs in low quality habitats breed, but with reduced success. When territorial males of good territories were experimentally removed, they were quickly replaced by owners of poorer territories or by floaters.

Our models have been framed around a hypothetical species in which an individual has only one opportunity to acquire the resources necessary for reproduction. Extending our models to situations involving multiple breeding attempts is reasonably straightforward, however. Using the basic exclusion model with the additional assumption of several breeding seasons does not change the balance between \bar{W}_{x_p} and $\bar{W}_{x_{\infty}}$ when success (i.e. being a holder) in one season correlates *exactly* with success in the next season (e.g. developmentally-induced RHP differences determine success). Nonetheless, the balance affected where success is entirely *random* from season to season (e.g. prior ownership determines success). This robustness to assumptions of multiple breeding attempts is important, for one would not expect natural selection to favour animals giving up an opportunity to breed (i.e. being excluded) unless there were likely to be opportunities later, or unless large differences in RHP prior to (or as a consequence of) the fight made withdrawal the best solution.

In the defensive effort models, multiple breeding attempts can be incorporated by weighting the total defensive effort made by an individual over several seasons against the total efforts made by other members of the

population. These models may also be useful in considering species in which individuals "exclude themselves" from breeding in one or several seasons. For example, in many species young, sexually mature individuals postpone attempting to breed until size and/or experience makes success likely (see Williams, 1966). Thus in terms of our model, the number of competitors in a given season would simply be the number that have "decided" to breed. Although the models predict the ESS level of investment, they do not indicate when the decision to breed should be made, or in general how total effort should be distributed through time.

Our models treat the number of competitors, n , in one of two ways; as a direct function of the reproductive output in the previous generation, (see all ESS equations that include term V_t), or as a constant determined by factors intrinsic to the territorial behaviour of adults (see all ESS equations that include term n), such as a physical refuge required by pre-reproductives. In order to make biological sense, this constant must be below the number of individuals of the previous generation could produce. In either case population size could be assumed to be at a steady-state, an assumption appropriate for species which fluctuate significantly in number (through the action of weather, for example). If we allow that individuals will be selected to monitor competitor density, however, then the ESS equations expressed in terms of n define the ESS strategies conditional upon the assessment of n .

It is interesting that the exclusion and defensive effort models appear to generate rather different conclusions about responses to V . In biological terms, V may be equated with habitat quality, in that it translates the number of resource units acquired (devalued by the cost of acquisition) into a number of offspring that survive to compete. When exclusion of competitors is possible and costs are a simple function of the area defended, increasing the pool of competitors by increasing V reduces the benefits of behaving spitefully (i.e. reduces the relative increase in the spiteful individual's contribution to the gene pool) without changing the costs. When excluded individuals in themselves represent an additional cost, increasing the number of excludeds by increasing V reduces X_* still further. However, in the defensive effort models (no exclusion of competitors) increasing V increases increased defensive effort costs at the ESS that maintains a stable population size. For both types of models, however, strong dependence of V on n through V is usually found only for relatively small values of V (the case where excludeds create significant additional costs being an exception). It is also important to remember that defensive effort is not in any sense equivalent to territory size, although it is true that as D_* increases, candidacy decreases, n decreases and thus territory size increases.

Interpreting these predictions in the light of other theories and observations concerning habitat quality and population density is common. Eickworth's (1977) observations of the megachild bee, *Hoplitis antipoides*, fit well. Males patrol areas containing flowers that are visited by females. Population density increases markedly as the season progresses and simultaneously males patrol smaller and smaller areas, eventually holding strongly-defended territories around single flowers. Some authors have predicted and observed territorial breakdown at certain population densities (this is formally impossible in our models because of our assumption that no reproductive success can be achieved without guarding a resource). For instance it is sometimes predicted (for an early model, Oite & Joern, 1975) that there will be a breakdown of territoriality at population density "because of the exorbitant expenditures of time and energy required to repel a constant stream of intruders" (Alcock, 1975). This does appear to occur on occasions in nature (e.g. Evans, 1966). It is interesting that such phenomena require:

- (a) that there is some possibility of reproductive success, even in the absence of resource-guarding;
- (b) that the territorial costs at high population density must be a pure *passive* artefact of having to dispel intruders that are searching for undefended resources. (If an individual showing territoriality at high population density is at a disadvantage, "non-guarder" strategists cannot be expected to expend *direct* pressure to take its territory).

Carpenter & MacMillen (1976) predicted two thresholds in a model based more on habitat quality than population density, though the two are obviously related. Above one extreme of food availability, all requirements can be obtained in the absence of any territorial defence. Below another extreme, the food abundance in a territory may become so low that, even with the extra yield gained by defence, the territorial strategy becomes unfavourable. They obtained some evidence for their model from data on the Hawaiian honeycreeper, *Vestiaria coccinea*. Their model viewed defence costs as constants; ideally one wishes such analyses to involve frequency-dependence (see Introduction).

Another aspect of territorial behaviour that needs further study concerns the stable maintenance of several coexisting strategies. Several studies showed mixtures of territorial males and wandering breeding males ("floaters", "sneak-maters", "satellites" etc., see e.g. Davies, 1978; Alcock, 1979; Rubenstein, in press), mainly in species in which males contribute nothing to the offspring regardless of their mating strategy and thus do not depress the numbers of surviving offspring by investing energy in territory

defence. To our knowledge, only Rubenstein (in press) has demonstrated mixtures of sneaks and guarders may be the result of frequency-dependent selection; his paper deserves special note. Such systems again involve resources being "leaky" (i.e. some resources escape the attention of territorial individuals and thus allow non-territorial individuals to produce).

Our preliminary work on variability in RHP in the no exclusion models provides one possible mechanism for the maintenance of several defensive strategies (although they are pure ESSs conditional upon phenotype, not mixed ESSs). Modifications of our exclusion models may also have potential. All our exclusion equations were based on the assumption that $P < R/X_*$ (i.e. that the costs of territorial defence never reduce the number of surviving offspring to such a low level that some resources remain in the patch). Were this assumption to be violated, a mixture of territory holders and opportunistic users of unguarded resources could conceivably result (although a uniformly smaller territory size might also be evolutionarily stable). Also, after suitable modification, our models may be used for stipulating the ESS amount of defensive effort for guarders in systems with leaky resources in which there is a mixed ESS for sneaks and floaters.

Finally, the "spite" component of our models deserves some comment. If the term spite implies that an individual invests more in territorial defence than the level that maximizes individual reproductive success, then a spiteful ESS can be found only in the exclusion models. In the defensive effort models, all individuals pack in and a mutant with a lower defensive effort produces less progeny. However, there is still in a sense a spite component to the model, detectable by dependence of the ESS (22) on population size and patch number. Because a component of a mutant's defensive effort $D_m > D_*$ causes a lowering in the fitness of others as well as if then this causes D_* to be higher when P is low, especially at low n . In the exclusion models, an individual is (in evolutionary terms) trading some fitness for the benefits of preventing others from breeding at all. Even if, territory size will only be enlarged by spite to a significant degree when the costs of spite are small and when the species is broken up into small, discrete units (each distributed around one or more patches of resources) with little gene flow between them. Rothstein (1979) has given a detailed survey of the sort of conditions that will favour the evolution of spite, and so further emphasis here is unnecessary. It now seems clear that the amount of spite must be rather less than many authors have envisaged (e.g. for territoriality, Chitty, 1967; Gill, 1974; Brown, 1974; Verner, 1976; for sexual interference, Arnold, 1976).

We have retained Hamilton's (1970, 1971) use of the term "spite" [rather than Rothstein's (1979) "inhibition"] for the strategy of harming oneself to harm others more. But there is an important distinction to be made. Hamilton's models concerned what could be termed "discriminate spite", the idea being that selection may favour behaving spitefully to individuals who have less than average (for the population) relatedness to self. The spite of spite discussed in the present paper—and that relevant to all authors cited in the paragraph above—could be described as "indiscriminate spite" because no recognition of non-relatives is involved.

Rothstein (1979) and ourselves (Knowlton & Parker, 1979) independently reached similar conclusions concerning the likely magnitude of spite in natural populations (see also Tullock, 1979; Pleasants & Pleasants, 1979). Rothstein made the further point, however, that even small degrees of spite would be evolutionarily unstable against "resistors" (individuals who are not themselves spiteful but who thwart the efforts of neighbours attempting to take spitefully large territories). In our competitor exclusion models, successful individuals obtain the number of resource units specified by the strategy they are playing by virtue of some convention associated with an asymmetry independent of the resource use strategy (such as prior ownership or RHP, see Maynard Smith & Parker, 1976). A resistor mutant would suffer the considerable costs of escalation against the convention in addition to the energetic costs of resistance itself. Although Rothstein did not formally analyse resistance in his models, the strategy resembles "retaliator" in Maynard Smith's (1976) hawk-dove game (Getty, 1979). If the two are formally similar, then resistance may be an important component of models based on discrete strategy sets (spiteful vs. non-spiteful behaviour); it is not likely to affect the conclusions of ours (or other similar models) which seek an ESS from a continuous strategy set.

Recently Colgan (1979), considering the two strategy game (spiteful vs. non-spiteful), suggested that in a mixed population the non-spiteful territory holders benefit from the action of spiteful individuals with superterritories. He therefore suggests that "spitefulness has become altruism". This semantic paradox arises through considering specific individuals rather than aggregate effects on specific genes. In estimating the fitness of the non-spiteful strategists, one must include both territory holders and non-holders since they both carry genes for acting non-spitefully. When the spiteful strategy is rare, there is never likely to be more than one superterritorial individual per patch, and any extra exclusion must therefore fall upon non-spiteful strategists. So superterritoriality can spread, essentially because its effects can be non-random with respect to alternative alleles for spiteful and non-spiteful. Thus although we term superterritoriality "indis-

criminate" spite (to imply no recognition of non-relatives), it can spread only because its effects can act discriminately.

Finally, we would like to conclude with a cautionary note on the patch assumptions of our models. Throughout this and our earlier paper (Knowlton & Parker, 1979) we described P as a fixed number of patches of resources and examined the evolutionary outcome should a single mutant arise in one of the P patches. In the defensive effort model this is a reasonably accurate representation because mutant fitness is deterministically expressed. In the competitor exclusion model, however, mutant fitness is an expected, rather than exact value, because it is weighted by the set of probabilities that apply to taking up resources or being excluded. This probabilistic situation makes it desirable to model populations with a number of mutants such that on average there is a single mutant in P patches. Framed in this way, however, P becomes related both to mutation rate (which also could be under selective influence) and to the number of individuals per patch. We have not attempted to incorporate these complexities into our models, but it should be remembered that they only affect the spite component of the ESS, which may be very small.

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A Model Linking Segmentation, Compartmentalization and Regeneration in *Drosophila* Development

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Four important aspects of insect development, namely the establishment of the primary embryonic axes, the appearance of segments in the embryo, compartmentalization in imaginal discs during development, and regeneration of discs after experimental interference, have been the object of extensive investigation. To account for each phenomenon, an internally-consistent hypothesis has been formulated during the last few years. As yet, however, little attempt has been made to relate these four fields to each other. A model, based on the sequential establishment of a series of gradients whose function is to provide positional information to the cells and cause them to initiate defined developmental programmes, has been developed to account for the clonal restrictions that occur throughout development, for the way in which cells behave during regeneration, and for the action of a number of mutations.

1. Introduction

Much recent research on insect development has concentrated on four major problems: the establishment of the anterior-posterior axis, and of segments (see Sander, 1976), the subdivision of segments into compartments (García-Bellido, Ripoll & Morata, 1973, 1976), and the properties of morphic regulation of imaginal discs and cockroach limbs after surgical manipulation (Bryant, 1975*a,b*, 1979; French, Bryant & Bryant, 1976). Hypothesis have been formulated in order to explain the findings in each of these fields: a model of lateral inhibition (Gierer & Meinhardt, 1972; Meinhardt & Gierer, 1974) for the specification of the longitudinal axis (Meinhardt, 1977) and the subsequent division of this axis into segments (Meinhardt, 1978*a*); the "selector" gene hypothesis for compartment formation (García-Bellido, 1975); and the "polar co-ordinate" model for the regeneration of imaginal discs and cockroach limbs (French *et al.*, 1976).

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