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COMPONENT ANALYSIS AND MODELLING OF THE MOVEMENT PROCESS: ANALYSIS OF SIMPLE TRACKS

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INTRODUCTION

A variety of approaches have been taken to the construction of general models of ecological processes (SOUTHWOOD, 1978). One of the most successful is that described by its originator, C. S. HOLLING, as "experimental components analysis" (HOLLING 1963, 1964, 1965, 1966). This set of techniques, applied most elegantly by HOLLING in his studies of the processes of predation, demands that a particular process be divided into its component parts, which in turn can be subdivided to a greater or lesser degree. Each component or sub-component and its interactions with other such units, must then be modelled and the resulting predictions tested against experimental data gathered for the purpose. The representations thus obtained for each component can be combined to produce a model of the process as a whole. Of necessity the complexities that result dictate that such syntheses are in the form of numerical simulations rather than algebraically more tractable models. Fundamental to the approach is the idea that some of the components will be common to all incidences of the process whereas others will occur with lesser frequency. The more detailed the level of study, the more finely divided the components, then the more precise but less general will the overall model become.

The experimental dimension to components analysis dictates, of course, that information be collected for particular species of animal or plant and the actual parameter values will characterise the behaviour of that species. The generality of the models produced by this approach, then, is at the structural level and in order that they can be applied to other species, the characteristic parameter values for those species must be estimated and incorporated in the general model structure. A technical corollary of this is that in the development of a model, experimental animals or plants can and, indeed, should be chosen for convenience rather than in response to any preconceived notions on subject species.

As has been mentioned, components analysis has been used, most successfully, in the study of predation. In addition, models which approximate to this approach have been made of competition (GRIFFITHS and HOLLING, 1969; COULSON et al., 1976), movement (KITCHING, 1971; JONES, 1977) and even photosynthesis (VINBERG and ANISIMOV, 1967). The present paper and its companion (ZALUCKI and KITCHING,

1982) are the first of a projected series in which will be described the construction and application of a component model of animal movement based on ideas first expressed in KITCHING (1971) but attempting to overcome many of the shortcomings and problems identified but not resolved in that work. This particular paper examines the minimum number of parameters required to represent adequately the two-dimensional track of an animal in space and time. The companion work describes the construction and validation of a model of such simple tracks. Further works are envisaged to cover representation of more complex tracks and the interactions of moving animals with objects in their environment.

THE MOVEMENT PROCESS

It is necessary to define our usage of the term 'movement'. Quite simply, we intend it to indicate any spatial displacement of the whole animal. In this sense, we adopt BAKER's (1978) view that all instances of whole animal displacement can be viewed using the same theoretical framework whatever their magnitude, prompting or purpose. We consider, however, his selection of the term 'migration' to describe this general process unfortunate as 'migration' has been and still is used with a variety of more restricted meanings. It is for similar reasons that we avoid other potentially useful terms such as dispersal, interspersal, trivial movement and nomadism.

A great variety of more or less general models of movement have been produced over the years ranging from simple statistical descriptions of the results of the process, through others based on analogues of the process of physical diffusion, to population models which incorporate explicit immigration and emigration terms. We divide any movement process up into three temporal segments, departure, transit and arrival, and components may be identified under each of these headings. BAKER (1978) presented a similar but much more extensive analysis. JONES (1977), RICHARDSON and JOHNSON (1975) and PYKE (1978) all examined what may be regarded as selected components of the movement process in their studies of particular species.

This paper restricts itself to examination of the transit segment of the movement process and rests upon the hypothesis that there are a small number of components of movement which are sufficient to describe and simulate an animal's track. Specifically, we examined speed, continuity and directionality and this first account examines methods of analysis of tracks.

RATIONALE

An animal moving in a plane will describe a track on that plane which, in certain instances, can be recorded by the observer using filming or mapping techniques or by tracing some product left behind by the animal as it moves. Such products include

the 'slime' of slugs and snails and the disturbances left in soft ground by animals as varied as large mammals and inter-tidal polychaetes. To construct a general model of such tracks, once recorded, demands that the continuous record be broken down into a number of straight line segments as illustrated in Fig. 1. The analytical problems so raised are two-fold; how best to divide up the track and how to find a minimum number of statistics to represent the track and the behaviour it represents.

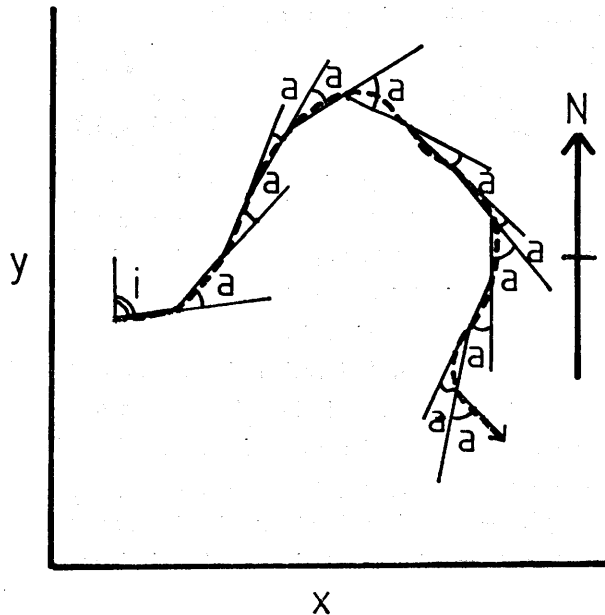


Fig. 1. The division of an animal track into chords. The original track is indicated by the dotted line, the chords by solid lines. The extensions to the lines identify the initial heading (angle i) and subsequent angular deviations (angles a).

The first problem may be approached by identifying the two basic methods by which the continuous track may be segmented; that is, on either a time or distance base. On a time basis, points along a continuous track equidistant in time are identified and joined up to define the straightline segments representative of the track. The advantage of this method is that it allows simultaneous measurement of both directionality (the distribution of angles between segments) and velocity (the distribution of the lengths of the segments). Periods of inactivity can be identified by recording number and frequency of superimposed points. The disadvantage of such a time based approach is that it is more difficult to obtain, requiring constant observations and recording in order to estimate the position of the subject at regular time intervals. Under certain circumstances, using photography or telemetry (e.g. SINIFF and JESSEN, 1969), this may be the only form of record possible, but in others, the presence of the observer may influence the animal's behaviour in an unacceptable

way. In these cases the analysis of tracks left by the animal is, arguably, the best approach and segmentation of the track using a constant segment length is appropriate. This will generate directionality statistics but not information on velocity and continuity which must be measured separately.

Whichever of these methods of analysis is used, the problem of scale must be addressed. If the step-size is too large then necessary detail is lost and the directionality distribution may be changed in shape. Alternatively if the step-size is too small then step to step changes become trivial and computational effort disproportionately large. For any particular track there will be a hypothetical level of resolution which is the largest step-size that, nevertheless, retains those features of the animal's behaviour that an investigator is interested in. Such a step-size will differ from species to species. We investigate ways of identifying such a step-size in a particular example later in this paper.

The second problem, that of identifying statistics which will describe a track once it is divided into segments has been addressed in part by KITCHING (1971). This work showed that directionality can be simulated knowing the starting bearing (the angle marked 'i' in Fig. 1) and the mean and variance of the angles between successive segments of the schematised track (the angles marked "a" in Fig. 1). This assumes normality or, at least, near-normality and symmetry about 0°—the straight-ahead direction. In addition a mean and variance for velocity is required and a measure of the proportion of time spent moving in any period of time. These six parameters are proposed as necessary, although not necessarily sufficient, statistics for characterising an animal's pattern of movement. Lack of independence between successive track segments may also occur but, we expect, these can be removed or at least minimised by careful choice of the scale of measurement (see below).

It must be mentioned, also, that the approach we and others have taken assumes that an animal has a movement pattern characterised by a few parameters. This, of course, implies that the movement is occurring in an homogeneous environment. The corollary of this assumption is that objects of interest in the environment of the animal, food or other resources, predators and other inimical agencies, may be viewed as modifying these basic characteristics of movement. Whether or not the homogeneous environment, in which the animal is not subjected to any specific directional stimuli, actually exists for species in complex, structured habitats is arguable. However, insofar as instances do exist where the assumptions seem to be upheld, the adoption of such a set of hypotheses as a canonical representation of the movement process seems justified.

METHODS

(a) Choice of experimental animal

The intertidal gastropod, *Polinices incei* PHILIPPI (Naticidae) is widespread on

sandy shores in eastern Australia. It is a predatory species foraging for small bivalves a few millimetres below the surface of waterlogged sand. For our present purposes, it was an ideal experimental animal for two principle reasons. Firstly, large segments of its environment are homogeneous, at least to the human eye. They are flat and smooth, regularly washed by the incoming waves and comprised of sand of uniform grain size. Areas of ridged, sloping or dry sand can be avoided easily in choosing experimental animals. Secondly, as the snail forages below the surface of the sand it leaves behind a furrow on the surface, effectively drawing the path of its movements in the sand. Such tracks can be timed and traced with ease. Prey detection by the snails seems to be by mechanoreception and occurs at about 15 cm distance (KITCHING and PEARSON, 1981).

(b) Recording animal tracks

Individual snails on the move in homogeneous areas of sand were chosen and their subsequent movement patterns timed over a 3-4 min period using two stop-watches. One of these was used to time periods of movement only and the second to provide the time-base for the whole experiment. Comparison of the two times provides a measure of continuity of movement. Following each observation the track was traced onto plastic with the aid of a perspex-bottomed frame which could be placed over the area of sand concerned. A compass bearing for magnetic North was added to the tracing. Forty-two such tracks were collected over the experimental period. Any tracks which involved pursuit and/or capture of prey items were abandoned for our present purposes. The shell diameter of each snail was noted also and a sample of sand from the immediate vicinity collected and used later to determine water-content gravimetrically.

Observations were made during the period approximately one hour on each side of low tide and climatic conditions were more or less uniform throughout the periods of observation although no detailed records were kept.

RESULTS

Figure 2 is a representation of the forty-two snail tracks collected, brought to a common origin and orientated appropriately with respect to North. All results and analyses presented relate to these tracks which are numbered in order of collection for individual reference.

Directionality

The tendency for an animal to travel in a straight line can be represented by the frequency distributions of angles turned through once the track has been divided into segments. The distribution can be summarised by its mean and standard deviation if it is symmetrical and akurtotic. Such a summary can then be used to generate random variates from a given distribution having the same mean and variance as the measured one (for an introduction to appropriate methods, see

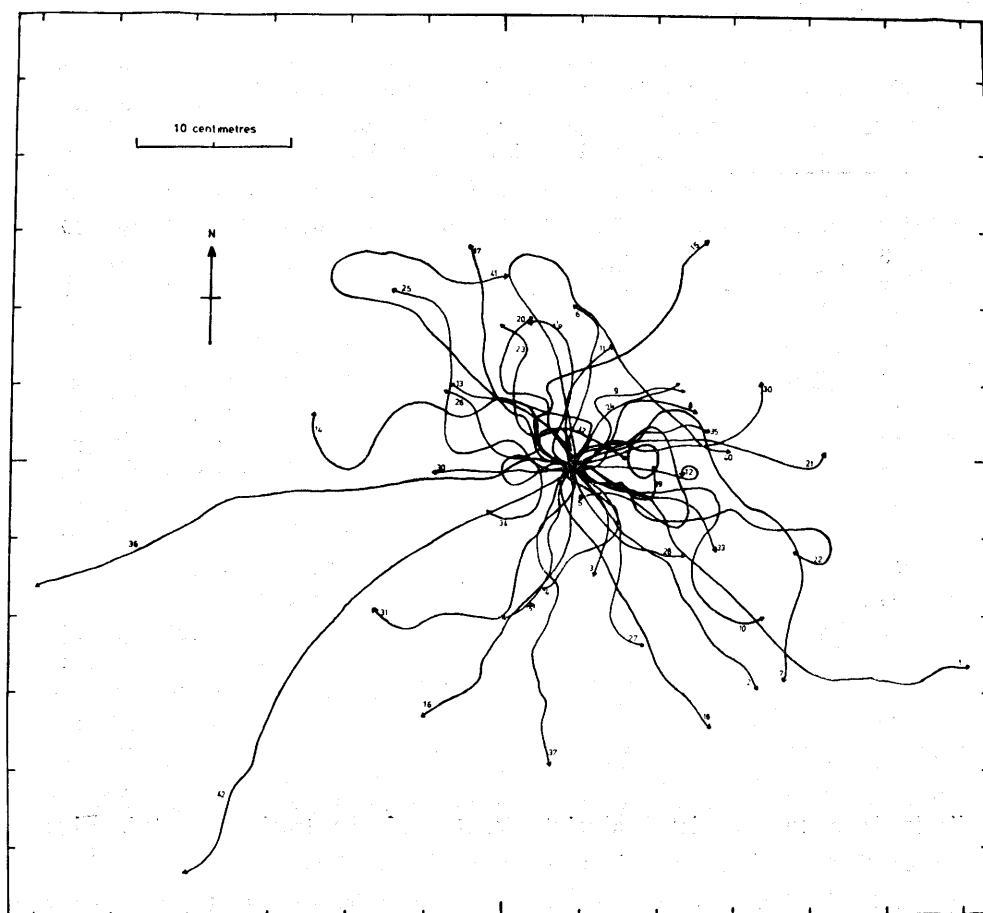


Fig. 2. Tracings of the tracks of the intertidal snail, *Polinices incei*, used in all subsequent analyses.

GORDON 1969). Such variates may then be used in the simulation of the original patterns of movement and their consequences. The actual distribution, of course, is a circular normal one and the use of statistics based on the ordinary distribution is strictly inappropriate. As a first approximation, however, it serves very well and, indeed, the use of trigonometrical techniques in simulation for the calculation of successive coordinates obviates the problem due to the periodic nature of sines and cosines.

As already mentioned the key problem in analysis is the choice of an optimal step-size for efficient summary of a particular track. For the snail tracks, division into chords of length one centimetre produced the most detailed representation of the tracks we collected. The statistics of directionality could then be calculated using a step-size of 1 (the 1 cm chords), 2 (by 'joining' the ends of two adjacent chords), 3 and so on up to 7. Seven was the size above which insufficient data points were

Table 1. Means, standard deviations, 95% confidence limits and sample sizes for angles turned between adjacent 1 cm chords representing tracks of *Polinices inaei*. Track numbers correspond with those in Fig. 1. Only those tracks of a length of 20 or more such chords (18 angles) are included in the analysis.

Track Number	Mean	Standard Deviation	95% confidence limits		n
			Lower	Upper	
1	2.91	22.135	-3.74	+9.56	30
2	-3.21	16.556	-9.46	+3.04	19
5	-21.15	29.662	-30.91	-11.39	25
7	-3.43	17.846	-9.08	+2.22	27
10	1.25	22.828	-7.15	+9.65	20
11	1.99	22.533	-6.30	+10.28	20
14	3.24	31.424	-6.90	+13.38	26
15	1.55	30.944	-7.90	+11.00	29
16	-7.45	21.166	-15.24	+0.34	20
18	-2.72	32.384	-14.63	+9.19	20
22	-9.61	31.389	-20.88	+1.66	21
25	-9.29	43.787	-25.40	+6.82	20
31	-11.61	37.539	-25.78	+2.56	19
36	-3.19	27.859	-10.94	+4.56	35
37	-3.58	28.628	-14.11	+6.95	20
40	-0.33	20.827	-6.21	+5.55	34
41	0.54	22.102	-5.70	+6.78	34
42	-3.40	22.486	-9.65	+2.85	35

available from the restricted absolute lengths of the tracks collected. Figure 3 illustrates the effects of step-sizes of 1, 2, 4 and 7 on the representation of a particular track (No. 14 in Fig. 2) by way of example. As a first step the mean and standard deviation of the angles turned between adjacent 1 cm chords were calculated for all tracks of sufficient length (that is: all those which generated sufficient data points for the calculation—arbitrarily chosen at 18, the number of angles involved in a twenty-chord track). Turns to the left were designated negative and those to the right positive, giving a range of permissible turns from -180° to $+180^\circ$. Table 2 contains the results of these calculations. Of the 18 tracks so examined 17 showed very substantial overlap on the basis of the calculated 95% confidence limits. This coincidence is sufficient, in our opinion, to justify combining the data from all tracks.

Using this combined data, track statistics were computed for tracks of increasing step-size and Table 2 presents these results. There is a distinct trend apparent in the data with the mean angle of displacement increasing in absolute magnitude with step-size and a similar increase in standard deviation. This increase is not linear and, although monotonic, it shows decreasing slope with step-size.

To approach the question of what is an appropriate step-size to adopt as adequate we have found it necessary to go beyond these analyses which, in this regard, tell us only that there is increasing loss of information and accuracy as step-size increases.

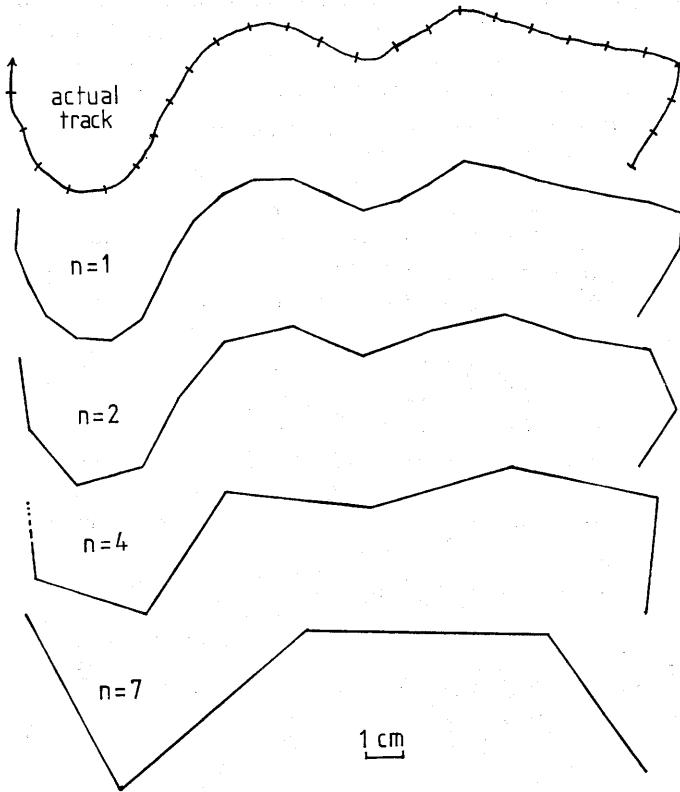


Fig. 3. The effects of increasing step size on the representation of a snail track. Step sizes of 1, 2, 4 and 7 based on an original division of the track into 1 cm chords are shown.

Table 2. Means, standard deviations, 95% confidence limits and sample sizes for the distributions of angles turned through between chords of increasing size representing 42 tracks of *Polinices inaei* (see text for further explanation).

Step Size	Mean	Standard Deviation	95% confidence limits		n
			Lower	Upper	
1	-1.53	33.12	-3.54	+0.48	732
2	-3.15	47.10	-7.26	+0.96	356
3	-5.97	57.03	-12.04	+0.10	228
4	-5.83	63.47	-13.83	+2.20	169
5	0.20	69.02	-9.64	+10.04	133
6	-0.15	73.72	-12.10	+11.80	103
7	2.53	78.62	-11.67	+16.73	83

A simple examination of the correlations between signs of pairs of angles along the segmented tracks does, however, provide assistance in this regard. If, for increasing step-sizes, we record sign-sequences between pairs of angles ($++$, $+-$, $-+$, $--$) and sum these, we obtain 2×2 contingency tables which can be compared with

Table 3. Observed and expected sign sequences in tracks of *Polinices inaei* following division of the tracks into 1 cm chords and using steps of increasing length. Signs to the left of tables are of the first angle, those above each table of the second angle, of each pair, (see text for further explanation).

Step size	Observed frequencies		Expected frequencies		χ^2 and p	
1	+	224	+	182	38.6633	$p < 0.05$
	-	140	-	182	183	
2	+	94	+	83.6	4.88524	NS
	-	79	-	89.4	94.6	
3	+	56	+	55	0.0696	NS
	-	55	-	56	58	
4	+	27	+	35.01	5.6048	NS
	-	49	-	40.99	49.08	

NS—not significant

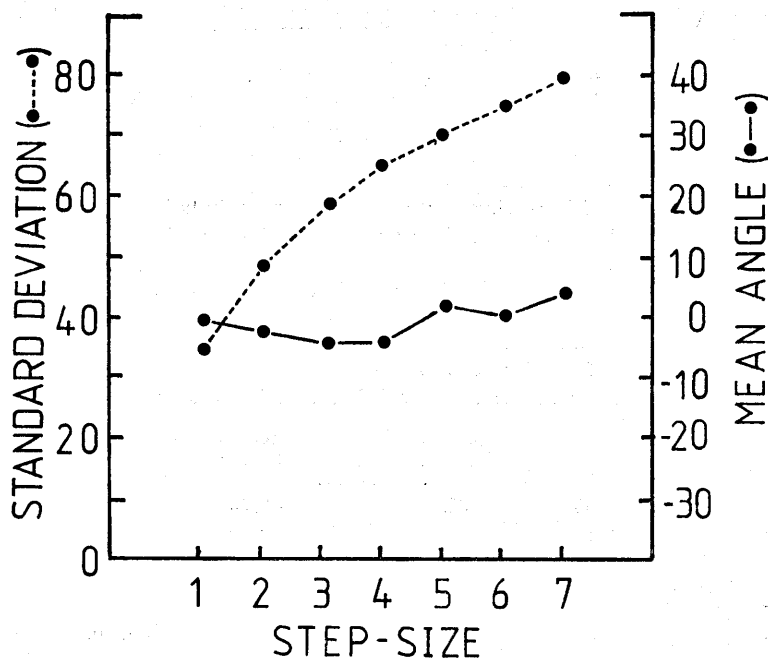


Fig. 4. The effects of increasing step size on the mean and standard deviation of the angular deviations.

expected values obtained by assuming an equal probability of positive and negative angles of deviation following any particular previous angle. Table 3 shows these observed and expected contingency tables for step-sizes 1 to 4 with associated χ^2 values. There is a substantial deviation from the expected model for step-size of 1 and a

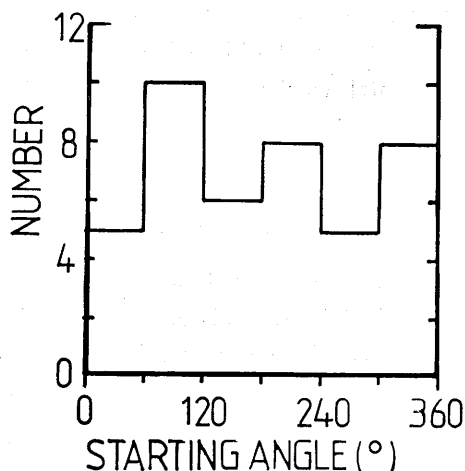


Fig. 5. The distribution of initial headings from 42 tracks of *Polinices inaei*. The distribution does not differ significantly from uniform.

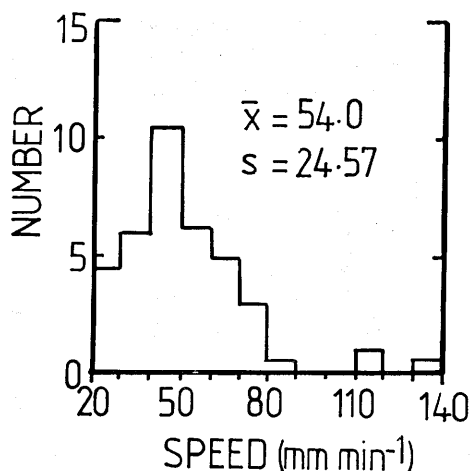


Fig. 6. The distribution of speeds measured in 41 tracks of *Polinices inaei*.

highly significant χ^2 value. This significance is removed at step-size 2 and all higher values. This result suggests that a step-size of 2 may be an appropriate choice for this species avoiding the overdetailed representation of using single steps yet retaining all necessary major features of the track. This decision is confirmed, informally, by examination of Figs. 2 and 4.

Starting Angles

Figure 5 represents the distribution of starting directions, relative to magnetic North, observed in the experimental tracks. It does not differ significantly from uniformity ($\chi^2_5 = 2.857$, $0.50 < p < 0.75$). Parenthetically a similar uniformity is found in the final headings of the experimental animals. This result suggests that in simulation of an animal's track the initial bearing can be selected using a uniform

random number generator scaled to produce any angle between 0° and 360°

Velocity

For each of the experimental tracks, speed was calculated by measuring the length of the traced track and dividing this by the recorded time taken by the animal to traverse this distance. Only periods of actual movement were included in this analysis. The resulting mean, standard deviation and distribution of recorded speeds are shown in Fig. 6. The distribution of speeds is skewed about the mean, firstly, because of truncation at the lower speeds and, secondly, as a result of 3 outlying values representing very 'fast' individuals. The distribution differs significantly from normal ($\chi^2_5=58.45$, $p<0.005$) but this significance is removed wholly if the 3 outlying values are excluded from the analysis ($\chi^2_4=5.689$, $0.25>p>0.10$). The approximation of velocity using normal random variates for these tracks is discussed below.

Continuity

The proportion of time spent in movement by the experimental animals is shown as a frequency distribution in Fig. 7. The results are highly skewed towards 1.00 with a mean of 0.89.

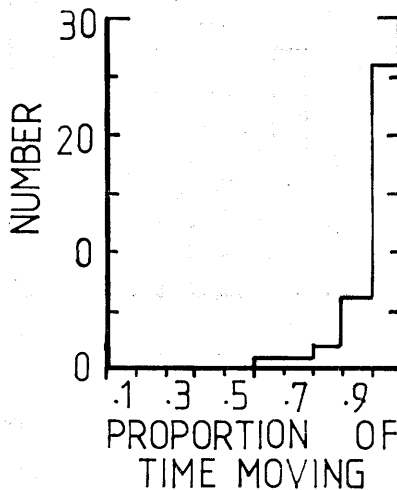


Fig. 7. The distribution of the proportion of time spent moving in 41 tracks of *Polinices inaei*.

DISCUSSION

As mentioned earlier, we propose that the basic movement pattern of *Polinices inaei* can be represented adequately using the parameters of its tracks that we have measured. Precisely how this is done and what we mean by "adequately" are described and discussed at length in a companion paper (ZALUCKI and KITCHING, 1982a). Some shortcomings are apparent in the procedures of measurement and analysis we have described here and these are discussed below.

Firstly, measurements of directionality of movement, both of means and variances, are sensitive to the selection of step-size once the actual tracks have been divided into simplifying chords. The rule-of-thumb we have proposed for selection of an appropriate step-size based on lack of correlation between the signs of subsequent angular displacements is somewhat arbitrary. Our decision in the case of the tracks of *P. incei* was based on the retention of the major changes in direction evident in the track while using the largest possible step-length. This coincided, perhaps not unexpectedly, with the loss of correlation between signs of turns just mentioned. For other purposes a cruder representation of the track may be adequate and a larger step-size feasible. The use of a large step-size will shorten substantially the length of a track due to the 'corner cutting' effect involved, and in analysis and simulation this must be borne in mind as it will interact significantly with any incorporation of parameters for movement velocity.

The measurement of speed produced a skewed distribution which can be generated by simulation using non-statistical programming devices (such as FORTRAN data-statements for the relative frequencies actually measured) rather than by techniques based on standard statistical distributions. However, there are circumstances which suggest that representation using a normal approximation may be warranted. These are twofold. Firstly, very slow-moving individuals: the missing left-hand tail of the distribution may have been omitted unwittingly—movement at speeds of less than 20 mm min^{-1} being very hard to detect by eye. Secondly, as pointed out with the results, normality is a tenable hypothesis once three outlying points are removed and the significance of the deviation from normality is even substantially reduced by removal of the single extremum. We have no a priori reasons for making these removals of course, but more detailed investigation of the velocity component (see below) may throw light on the occurrence of these occasional very 'fast' animals.

Lastly, on the shortcomings of measurement, we consider the continuity parameter. The use of the mean derived from our experiments, although probably useful as a first-pass measure, has two associated problems. Firstly, the associated variance term has little meaning because of the non-normality of the distribution. This can be circumvented in simulation by using the actual frequency distribution as measured. Secondly, this is only a measure of the continuity of movement of a group of experimental animals which were selected because they were already on the move at the start of observation. As a probability of movement it is, therefore, conditional upon this restrictive starting state.

The simplifications and problems associated with measurement of the parameters of movement lead to a consideration of the next phase in the work. What is required is that the six basic parameters identified here need to be expanded in depth by incorporation of their sub-components. In addition, to make the movement model more realistic they must be added to, allowing the relaxation of some of the simpli-

fying assumptions inherent in our work to date. Table 4 suggests a scheme for these additions.

Table 4. The structure of the movement process. The sub-components may apply to any of the basic components among the biological properties.

	Basic Components	Sub-components
Biological Properties	Starting Direction	Size/age
	Angular Deviation: Mean	Hunger
	Angular Deviation: Variance	Temperature
	Velocity: Mean	Environmental "viscosity"
	Velocity: Variance	Environmental gradients
	Continuity	Directional stimuli
Environmental Properties	Density of objects of biological significance	
	Dispersion Parameters	
	Areas of influence	

Each of the basic components by which animal tracks may be represented may be qualified by one or a number of sub-components of which six of the most obvious are listed in the Table. We already have evidence of a weakly significant relationship between mean velocity and size for the snails studied ($y=5.244x+8.1568$, $r=0.33$, $f=4.785$, $p=.0348$). The snails studied are likely to be appropriate subjects for the experimental investigation of the role of at least the first five subcomponents listed and our present programme includes these endeavours.

The relaxation of the assumption of environmental homogeneity is probably best approached through the incorporation of a set of 'point' resources in the organism's environment with an associated 'area of influence' around each, within which the movement of the organism may be modified by directional stimuli. Further modifiers, such as physico-chemical environmental gradients, can then be superimposed over this pattern. The effects of the density, dispersion and nature of these point resources will bear investigation and such work is planned. *Polinices incae* does not promise well in this regard as its basic resources, small bivalves, are themselves mobile which, at this stage, leads to undesirable complications in the interactions. The study of the interaction of butterflies with their foodplants has already proved feasible and rewarding when studied from a population point of view (ZALUCKI and KITCHING, 1982 b) and may well provide the required tool for this further investigation of movement. A study of the interaction of questing ants with the pits of ant-lions (Neuroptera: Myrmeleontidae) will be undertaken also as an approach to more complex spatial situations.

SUMMARY

The construction of a general model of animal movement using the 'experimental

components' approach of C.S. HOLLING is proposed. The process of 'movement' is interpreted very generally as any displacement of the whole organism in space. The rationale for modelling such processes rests upon the idea that there is a basic "canonical" pattern of movement characteristic of a species moving in a homogeneous environment, which pattern is overlaid by the various directional stimuli present in more usual heterogeneous environments.

The 'canonical movement model' is a necessary first step in construction of more realistic representations. We suggest it can be made using six components viz. the initial heading of the animal, the mean and variance of the angular displacements made by the animal as it moves, the mean and variance of the speed of the animal, and a term for the continuity of the movement. We have measured all these components in the field for the two-dimensional movement of the inter-tidal snail, *Polinices incei* and these results are presented here. Difficulties inherent in the measurement of angular displacement in particular are discussed and means of resolving them proposed.

The shortcomings involved in the measurements and techniques for their more detailed representation and the next steps in the proposed modelling sequence are discussed.

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動物の動きのプロセスの要素分析とモデル化

——単純な動きの軌跡の解析——

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動物の動きの一般モデルをホリングの experimental component analysis によるアプローチを用いて作製した。「動き」にみられる過程はその動物全体の空間における転置としてごく一般的に解釈した。このような過程をモデル化する根拠は、均質な環境での動きには種特有の“基本的”なパターンがあり、より異質な環境ではその基本パターンが様々な指向刺激によって変型されるという考えに基いている。

この“基本的な動きのモデル”は、より現実的なものを作製するうえでの最初のステップであり、それには次の6つの要素を考慮する必要があると考えた。つまり、動物の最初の定位、動きの角度の変化の平均値と分散、動きの速度の平均値と分散、および動きの連続性を示す要素を考えた。これらの要素について野外条件で潮間帯にすむ巻貝の一種 *Polinices incei* の2次元での動きから測定した。角度の変化の測定にともなう困難性については特に考慮し、それを解決する方法を提示した。