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A SIMULATION MODEL OF LOCUST MIGRATORY BEHAVIOUR

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SUMMARY

(1) A computer simulation model was developed for a migration of *Schistocerca gregaria*: the locusts were reported to have reached the United Kingdom in 1954 and were described by Rainey (1963) who concluded from meteorological evidence and current locust reports that they originated in N.W. Africa.

(2) The model follows the same basic assumptions that, whilst migratory motion in locusts is maintained behaviourally, displacement is attributed almost entirely to transport in wind systems (Rainey 1951).

(3) Laboratory estimates of flight performance from the literature were found to be inadequate to define the distribution of performance in the field.

(4) A dummy variable, equivalent to ground speed, was used to compare the effects of different distributions of flight performance.

(5) Response surfaces were defined for combinations of parameters and were found to vary qualitatively and quantitatively with different distributions of flight performance.

(6) The effect of down-wind orientation was investigated and found to affect the flight performance but in no simple way.

INTRODUCTION

In October 1954, the first locusts since 1869 were recorded in the British Isles. While they were of no economic significance, the phenomenon was regarded as being important to the interpretation of insect migration. The locusts appeared to be the remnants of a large number of migrating *Schistocerca gregaria* Förskal, which originated in N.W. Africa and had flown over 2500 km in an estimated 60 h providing one of the relatively few pieces of field evidence of such long-distance flights with a prospect of reconstructing the likely processes.

The trajectory of the air mass in which the locusts were likely to have arrived was calculated at the Meteorological Office, Dunstable by Mr G. A. Corby (Rainey 1963). This trajectory, estimated by backtracking the geostrophic winds at 100 m, passed within 130 km of a position at which flying locusts had been seen at sea. It led back to the vicinity of the Canary Islands on the night of 14–15 October, at the time of a major invasion of the islands. Swarms of sexually immature *S. gregaria* had been reported all along the coast from Mauritania north to Morocco at the beginning of the month and enormous numbers were lost at sea.

In this paper, Rainey's (1963) data are used as the basis for a stochastic computer model of this migration. Being a failure, the migration is somewhat atypical, but its track over the sea enables it to be used as a primary source of data. The ideas proposed, however, may be more generally applicable. It will be seen that the model proposed is

only broadly compatible with the available locust data and may suggest that some further physiological research in flight capacity is necessary.

The ability of numerical probability models to solve complex biological systems is limited, but it is often the essentially conservative nature of such models which makes their results so useful. Monte Carlo methods are extensively used in ecological work for this reason and have already been applied to migration studies. Saila & Shappy (1962, 1963) proposed a model with a biased random movement for the migration of Pacific salmonids. This model differs from Saila & Shappy's in that no intrinsic orientation need be assumed; direction of travel is determined entirely by atmospheric conditions (Rainey 1973, 1976).

SIMULATION MODEL

Objectives of the model

It is apparent from Rainey's (1963) discussion of the long-distance migrations of locusts that there is a significant discrepancy between the observations of powered flight performance of locusts in the laboratory and the lengths of non-stop flights in the field. This discrepancy must be explained if possible, especially since the locust is a serious pest over a considerable proportion of the Earth. An understanding of the physiological ecology is essential if the locust problem is to be solved.

Extrapolation of laboratory evidence of physiological limits to flight does not account for the field observations, but the flight behaviour of locusts may help to account for the difference, if it conserves fuel by gliding flight for example. The experimental conditions, in a wind tunnel, say, may obscure any relevant conservative behaviour. Furthermore the statistical treatment of laboratory data may not have been adequate to provide an accurate picture of the capabilities of flying locusts.

It is the purpose of this model to try to discover the relevant physiological, behavioural and ecological parameters which control locust migration, and in particular, to account for the migration of *Schistocerca gregaria* of October 1954.

Basic assumptions

The model is built around five basic assumptions which do not appear to be very restrictive. The assumptions are listed below and are followed by a discussion of the possible sources of error in them.

(i) The average direction of flight (heading) taken by a locust during any one hour is independent of the direction flown in any preceding hour and independent of the direction of flight of other locusts in the swarm.

(ii) Individuals landing at any time do so independently of the rest of the swarm.

(iii) Individuals ceasing to fly are lost to the swarm.

(iv) The potential duration of continuous flight is a stochastic variable, fixed in the individual, but the parent distribution is characteristic of the species.

(v) Flight speed is a stochastic variable, varying in the individual from hour to hour, but the parent distribution is characteristic of the species.

Sources of error in the assumptions

(i) In their model Saila & Shappy (1962) postulated a preferred orientation during migration. Their computer simulation showed that the bias towards one particular direction need not be very strong to account for the observed returns of Pacific salmon

to their natal streams in Canada and in Washington state. Zero orientation, Sailer & Shappi pointed out, is equivalent to the so-called random walk and represents the limiting condition in a spectrum of orientations.

In the model presented here it is assumed that there is no preferred direction of movement, so that any displacement of the swarm is achieved by displacement of the supporting medium. This assumption seems quite reasonable in view of Sayer's (1956) evidence from double-exposure photographs, which showed that locusts within a swarm do not have any single preferred orientation, though local groups may fly together. Locusts reaching the edges of the swarm turn back towards the centre, a behavioural adaptation contributing to swarm cohesion, possibly in response to visual and auditory stimuli (Rainey 1958, 1959). Sayer's (1956) photographs showed that although there was no systematic orientation on the part of the locusts in the swarm, local groups of individuals tended to be headed in the same direction. The assumption of independence is therefore too limiting. The model could be generalized to overcome this discrepancy by regarding the fate of the single hypothetical computer locust as being representative of one of these groups. This assumption has been discussed at length by Rainey (1960) and is investigated using Sailer & Shappi's (1962) model.

(ii) The same argument applies to individuals (or local groups) alighting.

(iii) The assumption that alighting locusts do not return to the swarm is not unreasonable since, with the exception of the Canary Islands and passing ships, the insects can land only on water and are presumed to be unlikely to be able to take off again.

(iv) The power for flight is provided by the oxidation of fat, and an upper limit for the potential duration of continuous flight without feeding is set by the ratio of size of fat resources to the rate of consumption in steady flight. Weis-Fogh (1952) estimated a maximum endurance of locusts flying in a wind tunnel to be about 20 h continuous flight. He concluded (Weis-Fogh 1956) that the average air speed during steady horizontal flight in nature would probably be about 15 kph giving a cruising range in still air of only 300 km. Clearly Weis-Fogh's estimates are insufficient to account for the distances flown by the locusts reported by Rainey. In another wind tunnel study, Wootten & Sawyer (1954) recorded speeds of between 9 and 23 kph while double exposure photographs by Sayer (1956), when corrected for turbulence and vertical gradients, gave mean air speeds of 20 kph. The estimates of flight endurance require some revision: the distribution of individual flight endurances within the population is of great importance and is unknown.

(v) The flight speed data are so variable that a wide range of estimates of flight speeds seems appropriate. Therefore a normal distribution of mean 15 kph and standard deviation of 9 kph was used. This symmetrical distribution gives a range of flight speeds, of which 68% will be between 6 and 24 kph. The distribution is truncated at zero. The minimum *powered* flight recorded was 9 kph (Weis-Fogh 1976): this distribution does not distinguish between powered flight and any other behaviour which contributes to displacement.

The selection of flight endurance presents a bigger problem since the longest observed sustained powered flight in the laboratory recorded by Weis-Fogh was 20 h. A distribution which allows a small proportion of values to exceed 60 (corresponding to individuals which frequently glide on the wind) but has a mean below 20 is therefore required. The lognormal distribution is proposed for the endurance of continuous flight in nature.

Description of the model

The few 'survivors' (a survivor in the simulation model is defined as a locust which arrives at the target area defined as north of the 50th parallel and east of the 8th meridian) that were recorded in the U.K. almost certainly travelled in the strong winds associated with a deep depression in the Atlantic. This wind system was reproduced approximately by a computer program, Subroutine WIND, which calculated the windspeed and direction for any time and place along the eastern seaboard of Africa and Europe.

The simplest algorithm was used in Subroutine WIND to obtain a computed track which approximated the back-track of Corbey (Rainey 1963) rather than put emphasis on meteorological accuracy. Since about 250 runs of the simulation were envisaged each with between 10^4 – 10^6 'locusts' flying and calling for wind strength and bearing up to about 100 times, the number of calls of the subroutine was expected to be of the order of 10^9 . Clearly the number and complexity of instructions to compute windspeed and direction had to be minimized.

The Subroutine WIND uses coordinate geometry to resolve forces of two stylized wind fields representing the depression in the Atlantic and the coastal winds of the N. African and European mainlands. The depression, centred 800 km NNW of the Azores on 13 October 1954, moved slowly in the direction of the U.K. In the simulation it moves N80E at the rate of 10 kph. The winds near to the centre rotate with a tangential velocity of 100 kph diminishing at a constant rate of 8 kph per 100 km from the centre. Probably a more realistic model for the rate of decline in wind speed from the centre of a depression would be a negative exponential, but the important feature is that the wind speed near the proposed track of the locusts be realistic. The simplification is apparently satisfactory. A belt of offshore winds was proposed to simulate the conditions near the land masses. This wind on a bearing of N60W, loses intensity at a rate of 4 kph per 100 km. At the release point the wind speed is 30 kph. Both the anticyclone and offshore winds have a minimum speed of 1.0 kph.

The simplicity of the program creates two deficiencies. Firstly, the computed track does not duplicate exactly the backtrack given by Corby. The fit at the early part of the course is quite good but a substantial deviation occurs in the southerly airflow especially in the region of the Iberian peninsula where the computed track crosses the NW corner (Fig. 1(a)). Although no locusts were reported from Spain or Portugal that year, this feature is not regarded as a serious flaw.

Secondly, the transit time of the air mass is 30% greater than Corby's estimate. This fault is probably more serious as it affects directly the probabilities obtained. One of the reasons for the increased transit time in the simulation is the low wind flux in the region of the Canaries. At this point the tails only of both the offshore wind and the anticyclone overlap, with very low wind speed and in nearly opposite directions. As a result, a large proportion of locusts 'flown' in the simulation are lost in these light winds (Fig. 1(b)). This feature is probably not unreasonable since the Canaries are reported to have been invaded by a large number of locusts at this time, although it is only assumed that they came from these same swarms (Rainey 1963).

Each locust as it started from a point on the African mainland opposite the Canaries was given an upper limit for total flight time. This integer variable, called NSTEPS represents the locust's maximum potential flight time. In the air, the locust was subjected to a mortality factor, called MINSTEP, the minimum speed for it to remain airborne. If NSTEPS is reckoned in hours, MINSTEP has units of kph and is equivalent to the ground speed.

The locust's heading (THETA) and flight speed (SPEED) were taken from random number

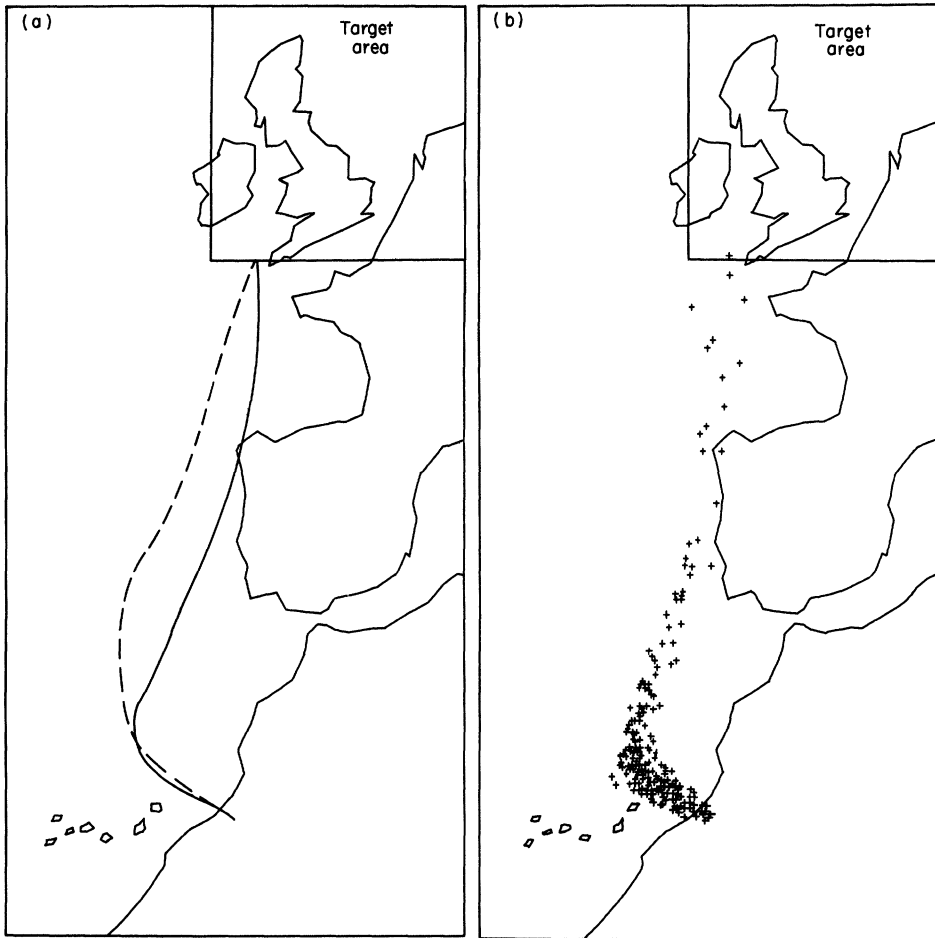


FIG. 1. (a) Map showing the trajectory obtained by backtracking the wind at 100 m (Rainey 1963) --- and the track of a typical successful locust in the simulation——. The early part of the simulated track coincides with the proposed geostrophic trajectory but afterwards diverges. The tracks converge at the target area (the area north of 50th parallel and east of 8th meridian). (b) Distribution of mortality of one simulation showing one successful to approximately 100 unsuccessful locusts. The majority of deaths occurred in the vicinity of the Canary Islands where the two convergent winds met nearly head on.

generators at the beginning of each step (hour) until either NSTEPS had elapsed or the resultant ground speed fell below MINSTEP. The resultant ground speed during any hour was calculated from the wind speed and direction for that place and time and the current air speed and heading. If a locust's displacement during any hour was less than MINSTEP, then it was assumed dead. The procedure was then repeated for another locust. At the end of a run, the proportion of successes was recorded with their average transit time and distance travelled. Between 10^4 – 10^6 locusts were flown in each run and small as this figure is compared to a natural swarm, it is sufficiently large to enable reproducible estimates of the probability of survival to be made. It does however emphasize the difficulty of doing laboratory experiments adequate to obtain real estimates of field population probabilities.

The parameter MINSTEP has no behavioural analogue, however some reasonable interpretations can be made. It was conceived as the minimum speed which the insect must travel in order to remain airborne. Obviously, if an individual were to fly into the wind at exactly the same speed as the wind, its ground speed would be zero, resulting in a waste of valuable energy. If this behaviour were kept up for long, fatigue would force a landing. If an individual were to cease beating its wings for any length of time, it would lose height (unless in an ascending air current of at least 1 ms^{-1}) and eventually reach the ground. Both these components are built into MINSTEP by ensuring that a certain minimum number of kilometres are traversed each hour. Because it is possible for a locust to fly very slowly and still travel further than MINSTEP by being blown on the wind, MINSTEP also incorporates a vertical component: a locust at say 1000 m is likely to remain in the air longer while gliding than one at 100 m, all other considerations (windspeed, lift, etc.) being equal. A flow diagram of the computer program is given in Appendix A, and Appendix B gives a summary of all results.

SIMULATION EXPERIMENTS

The effect of potential flight time

The innate potential for continuous flight called NSTEPS in the model, fixed in the individual as the ratio of its fat reserves to its rate of consumption, determines the maximum number of hours flight it can achieve under its own ideal conditions. This state variable was selected from a variety of frequency distributions.

The simplest distribution is the rectangular distribution in which all real values between A and B are equiprobable. The expected value is then the arithmetic average $(A + B)/2$ and variance is $(B - A)^2/12$. According to laboratory experiments, the mean continuous flight time is less than 15 h, in other words, if this were the parent distribution of potential flight time of desert locusts, the maximum possible time would be only 30 h, half the estimated flying time to the British Isles. In order therefore to achieve some success in flying from West Africa to the U.K. a range of zero to about 100 h is necessary.

The uniform distribution is rare in nature, although it is sometimes assumed in theoretical work. It cannot seriously be considered as the model for potential flight time because with each value as probable as any other, many more extreme individuals would have been detected in the laboratory experiments. It is included therefore only for comparison.

The normal distribution with mean μ , and variance, σ^2 , is included because it is the distribution assumed by most statistics and therefore assumed by experimenters analysing their data. It has the advantage over the uniform distribution that the majority of points are clustered around the mean with few at extremes. It shares, however, with the uniform distribution the disadvantage of being symmetrical about the mean and therefore biologically improbable.

A distribution which satisfies the requirements, that the majority of variables be below 20 h but a small proportion be greater than 60 h is the lognormal distribution with parameters μ and σ^2 : the median is given by e^μ , the mean by $\exp(\mu + \frac{1}{2}\sigma^2)$, and variance by $\exp(2\mu + \sigma^2)(\exp(\sigma^2) - 1)$. In fact, with parameters set to $\mu = 2.3$ and $\sigma^2 = 1.4$, the median flight time is about 10 h with 6% capable of flying 60 h or more. A proportion of this magnitude is unlikely to be detected in the laboratory, especially with experimental material from cultures many generations old.

The model was used to investigate the effect of the distribution of potential flight time on the proportion of hypothetical locusts reaching the British Isles for a range of values

of MINSTEP. This was achieved by varying in turn the value of MINSTEP from 0 to 15 km for each of three distributions. The distributions for flight time (NSTEPS):

- | | |
|-------------------------------|---|
| (i) Rectangular distribution— | $A = 0, B = 120$ |
| (ii) Normal distribution— | $\mu = 30, \sigma = 20$ |
| | $\mu = 60, \sigma = 20$ |
| | $\mu = 60, \sigma = 10$ |
| (iii) Lognormal distribution— | $\mu = 2.3-3.4, \sigma^2 = 1.4$ |
| | $\mu = 2.3-3.4, \sigma^2 = 1.96$ |
| Flight speed (SPEED) | Distributed normally $\mu = 15, \sigma = 9$ |
| Minimum steplength (MINSTEP) | Variable, 1.0–15.0 kph |
| Size of swarm (LOCUSTS) | Variable from 10^4 – 10^6 |

It is obvious that testing all possible combinations of the variables over a reasonable range would be prohibitively expensive. Fourteen distributions of potential flight time were used in conjunction with each of seven values for MINSTEP, and in each case, the proportion of hypothetical locusts lost increased with increase in MINSTEP. However, there is a difference in the form of the relation between mortality and MINSTEP for the three distributions, and also with the parameters of the distributions.

To show the effect of mean and variance on performance, the normal distribution was used for endurance because of the simple relationship between its parameters and the sample statistics. The effect on success rate of variations in both mean and variance of the normal distribution is shown in Fig. 2. The mean obviously has an effect since an increase from 30 to 60 h, with standard deviation at 20 h, results in more success than an increase in standard deviation from 10 to 20 h, given a mean of 60.

Figure 2 also shows how three dissimilar distributions with the same mean can have similar success rates over a wide range of minimum step-lengths. The parameters of the three distributions were chosen to show this effect. The three distributions, with parameters $U(0, 120)$, $N(60, 20)$ and $L(3.4, 1.4)$, have the same mean of 60, but widely different variances of 1200, 400 and 11 000 respectively. From this we can see how important it is to determine the distribution of endurance and that estimates of mean and variance alone are insufficient. This is less important when simply using a variable in a simulation of this sort unless the simulation is intended to be used to relate the physiology to ecological requirements because the interpretation of the distributions are very different. Clearly, not only the sample statistics but also their distributions must be specified if the physiological data are to be useful.

It was suggested above that the distribution of potential flight time may have characteristics of the lognormal and this distribution will be used in the rest of the paper. It has been shown how mean and variance can affect the outcome of the simulation. The effect of varying the lognormal parameters (μ, σ^2) is now investigated.

The effect of varying μ (while keeping $\sigma^2 = 1.4$) was investigated for a series of values of MINSTEP. Predictably, the probability of survival decreased with decreasing mean for a given value of MINSTEP. The probability of survival and mean flight speed are approximately linearly related but the gradient increases as the value of MINSTEP increases (Fig. 3).

Except at the lower levels ($P < 10^{-6}$), the probabilities are all self-consistent and form quite a smooth surface. The unevenness in the surface at the lower probability level is the result of the stochastic variation about a true mean: only with a large number of successes

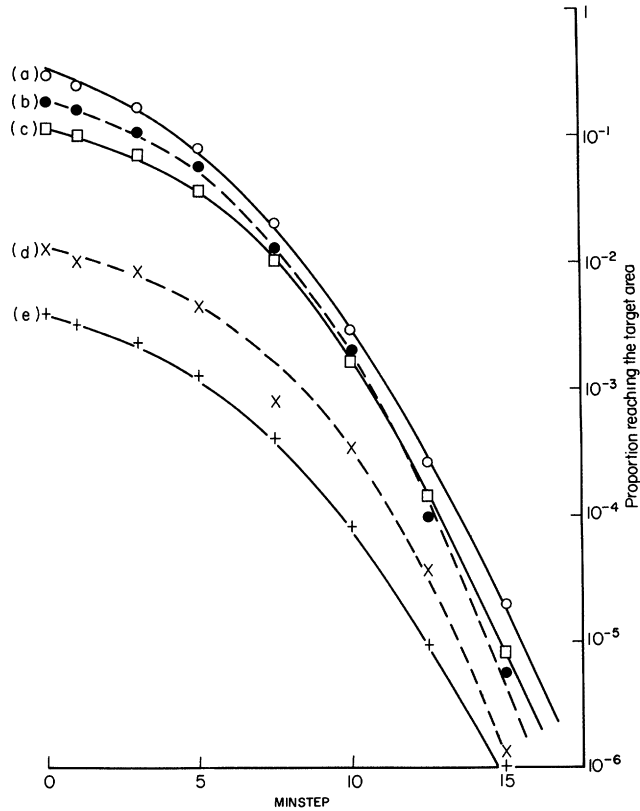


FIG. 2. The proportion of successful arrivals at the target area against minimum step-length (\equiv ground speed) for five distributions of potential flight time. Three different distributions ((a), (b), and (c)) with the same mean ($m = 60$) have similar response curves, their vastly different variances compensating for their different shape (see Fig. 10). Curves (c), (d), and (e) are the same distribution but with different sample statistics. The distributions of potential flight time are: (a) uniform between 0 and 120, mean = 60, S.D. = 35, (b) lognormal, parameters, $\mu = 3.4$, $\sigma^2 = 1.4$, mean = 60, S.D. = 100, (c) normal, mean, $\mu = 60$, S.D. $\sigma = 20$, (d) normal, mean, $\mu = 60$, S.D. $\sigma = 10$, (e) normal, mean, $\mu = 30$, S.D. $\sigma = 20$.

(not less than 100) would the probability settle down to near a constant value. In engineering terminology, the signal-to-noise ratio is low. Aside from the poor signal-to-noise ratio at the lower levels the probabilities are consistent with the rest of the results.

To investigate the effect of σ^2 , the foregoing analysis was repeated with $\sigma^2 = 1.96$ instead of 1.4. The increase in both mean and variance of the lognormal results in an increased number of successful flights. The increase was about 25% whatever the other parameter values and the effect was to raise slightly the level of the surface in Fig. 3. The increase is small so that the two surfaces cannot be distinguished. However logarithmic regression of proportion of successes with $\sigma^2 = 1.4$ against the corresponding proportion with $\sigma^2 = 1.96$ shows that there is a near linear increase in success rate by increasing σ^2 . The regression equation is $Y = 0.78X^{0.8}$ ($r = 0.981$, $t_{38} = 14.1^{***}$) where X is the proportion of successes with endurance having parameter $\sigma^2 = 1.96$ and Y is the corresponding proportion when $\sigma^2 = 1.4$.

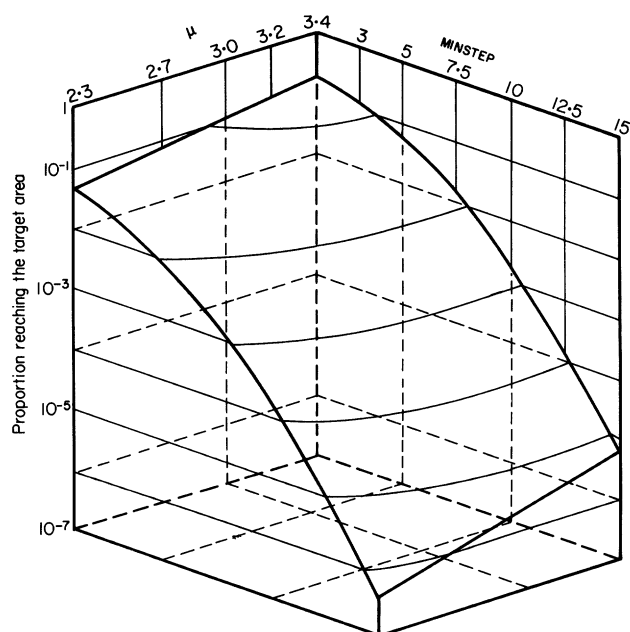


FIG. 3. Response surface of proportion of successes against minimum steplength and potential flight time. The potential flight time was distributed as a lognormal variate with parameter $\sigma^2 = 1.4$ and $\mu = 2.3-3.4$. Flight speed was distributed normally with mean 15 and S.D. 9 kph. Downwind bias was zero.

Effect of flight speed

To investigate the effect of flight speed, the endurance was fixed as lognormal with parameters $\mu = 3.4$, $\sigma = 1.4$. The uniform distribution was used, in the range zero to B, where B takes values 0, 5, 10, 20, 30 to determine the interaction between flight speed and minimum steplength. The uniform distribution, an unlikely parent distribution for speed, was used because it has effectively only one parameter, thus simplifying comparisons.

Comparison of the normal and uniform distribution (Fig. 4) shows that at least at lower minimum steplengths there is little difference in success rate but as MINSTEP increases above 10, the uniform distribution becomes relatively more advantageous. This is probably because of the shape of the two distributions: the extremes are less well represented by the normal distribution than by the uniform, thus enabling relatively more locusts to overcome the higher minimum steplengths. The similarity in results obtained with the two distributions reemphasizes the need for caution in interpreting results of laboratory experiments. The two distributions have similar means and variances and lead to similar overall results but have different proportions of fast flyers.

Figure 5 shows the success surface for a range of flight speeds at seven values of MINSTEP. At zero MINSTEP, 20% of locusts eventually successfully reach the target area. Increasing the minimum steplength when flight speed is zero imposes no mortality on the swarm below 7.5 but suddenly reaches 100% between 7.5 and 10.0. Increasing flight speed increases the steplength at which 100% mortality occurs. The sudden jump to 100% mortality exists because the uniform distribution was used. It has a maximum value set

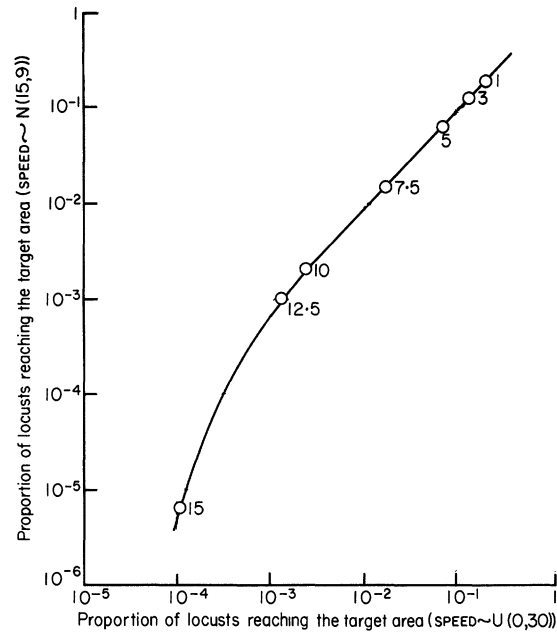


FIG. 4. Comparison of the uniform and normal distribution for flight speed. Each point is the proportion of successes at one of seven values of MINSTEP. The two distributions are exactly equivalent at the lower minimum step lengths.

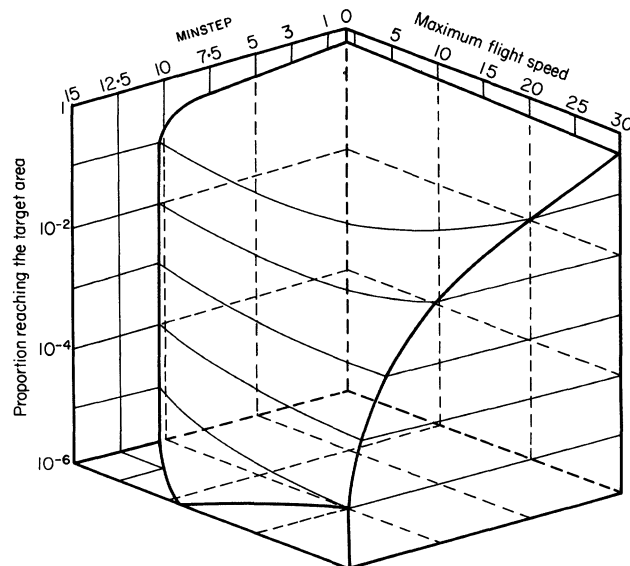


FIG. 5. Response surface of proportion of success against minimum steplength and flight speed. Flight speed was distributed as a uniform distribution between 0 and B for B = 0-30 kph, and potential flight time was distributed as a lognormal variate with parameters $\mu = 3.4$, $\sigma^2 = 1.4$. Downwind bias was zero.

by the parameter B , which, if less than the difference between the minimum steplength and the minimum windspeed causes all locusts to get caught at the point where wind speed is least. No such discontinuity exists with a distribution without an upper limit (e.g. normal) although, if the distribution is narrow enough, the success rate approaches zero so rapidly that it appears to be discontinuous. When flight speed is zero, the 80% mortality is the result of the lack of potential flight time to complete the course.

Increasing $MINSTEP$ increases the mortality, as expected, but increasing flight speed does not compensate for losses except by raising the steplength at which the discontinuity occurs. This is because at high flight speeds orientation in any direction other than downwind must result in large deviations from course, and thus lost time. This is especially true when flight speed is high compared to wind speed. In fact, raising the flight speed does nothing to improve the chances of reaching the target because the average ground speed only increases slowly by comparison. The ground speed and displacement of successful locusts are both directly proportional to flight speed, so that the transit time increases, reducing the number potentially able to reach the target. Thus there is little advantage in locusts flying fast, except when there is no wind, or they are flying downwind. There may thus be a selection pressure for oriented flight downwind as this would enable locusts to potentially make longer migrations and would be selected for if there is an ecological advantage in traversing a larger area (Taylor, French & Macaulay 1973).

Effect of bias

As flight speed increases so the locust must become less dependent on the wind for motion while orientation becomes more important since more energy will be wasted by deviations from downwind. Clearly downwind orientation would ensure that less energy is wasted at higher flight speeds.

On the assumption of random (or near random) orientation, there is good reason for keeping the flight speed low and allowing the air to do the work of displacement; the expected displacement of a random walk is only the square root of the distance traversed, the locus of the expected final positions being described by the perimeter of a circle. Obviously in a moving medium the circle becomes displaced in the direction of travel of the medium. The best strategy then must be to face downwind and fly at such a speed that will just maintain the flyer in the air, but the value of downwind orientation increases with speed while increase in speed means a smaller proportion of work done by the wind. There should be an optimum combination of flight speed and orientation.

If a locust flies downwind at a speed just fast enough to keep it airborne, it is most likely to maintain its position in the swarm, and will conserve its fuel resources as it rides on the wind. If, however it flies too fast using energy too quickly it must land prematurely. This must happen more often on average to an individual which persists in flying into the wind, or upwards, while lateral flights may result in a zig-zag pattern at the boundary as it attempts to maintain contact with its fellows.

Recent evidence from radar surveys (Roffey 1972; Schaefer 1976) seems to suggest that there may be a tendency, when the entire swarm is considered, to face downwind, although Riley (1975) reports instances of night flights in which orientation appeared to be upwind. If the proportion that 'preferred' a downwind direction were known, a cardioid such as Salla & Shappy (1962) used could be defined. The basic form of the cardioid model is,

$$R = P + Q \cos \theta \quad (1)$$

where R is a step vector in the direction θ (\equiv THETA in the simulation). An alternative parameterization yields,

$$R = P(1 + A \cos \theta) \quad (2)$$

where $A = Q/P$ and is the ratio of directed to non-directed movement. When $A = 0$, the expected position after one step of a particle in a stationary medium lies on a circle of radius P , the steplength (\equiv SPEED). After n steps, the expected position lies on a circle of radius $P\sqrt{n}$. The range that Sailer & Shappert investigated was $0 \leq A \leq 1$ where the expected position lies on a cardioid with a small bias for one direction and no forbidden orientation. And it is this condition which may best describe locust movement in the absence of a transport medium. If $A > 1$, the expected position lies on a folded ellipse. Estimation of A is most simply made by finding the ratio of the excess number of orientated flights over the expected number on the assumption of no orientation: if we chose a small quadrant ψ° on either side of the downwind direction in which the expected proportion of downwind orientation is $\psi/180$, and the actual proportion is p , the degree of bias,

$$A = (180p - \psi)/\psi. \quad (3)$$

The proportion of the swarm facing downwind does not seem to have been estimated although Schaeffer (1976) has drawn attention to the fact that radar could be used to make such estimates.

To investigate the effect of bias on migration performance the interaction with MINSTEP was first established. The introduction of bias involved a small modification to the simulation program, namely, the insertion of the cardioid term before the computation of the resultant between wind and powered flight. The direction of the wind (α) is returned by Subroutine WIND and the flight speed and direction (θ) were determined from random generators as before. The step R in the direction θ is given by the cardioid eqn (2) adjusted for the direction of the wind:

$$R = P(1 + A \cos(\alpha - \theta)) \quad (4)$$

where P is the flight speed and is greater or less than R depending on the value of $A \cos(\alpha - \theta)$. If orientation happens to be exactly downwind and bias $A = 1.0$ then $R = 2P$ and when direction of orientation is upwind $R = 0$. This form of bias does not require the use of a complicated distribution for orientation like the von Mises or circular normal distributions (Kendall 1974), but has a very similar outcome when the whole population is considered.

To investigate the interaction between BIAS and MINSTEP, potential flight time (NSTEPS) was distributed lognormally with parameters $\mu = 3.4$, $\sigma^2 = 1.4$ and flight speed (SPEED) distributed normally with mean 15 and standard deviation 9 kph.

Figure 6 shows the proportion reaching the target as a surface in response to values in MINSTEP in the range 0 to 10 and values of BIAS from 0 to 3.0. The plane of zero bias in Fig. 6 matches the plane in Fig. 3 where $\mu = 3.4$. Comparison of Figs 3 and 6 shows clearly the action of bias in maintaining a high success rate as MINSTEP increases.

Three topographical features can be clearly identified in Fig. 6, namely plateau, rim and valley. The plateau has a slight slope in the direction of increasing MINSTEP but is nearly horizontal in the plane of BIAS. There may also be a slight ridge (see below).

The general level and slope of the plateau are determined by the choice of distribution

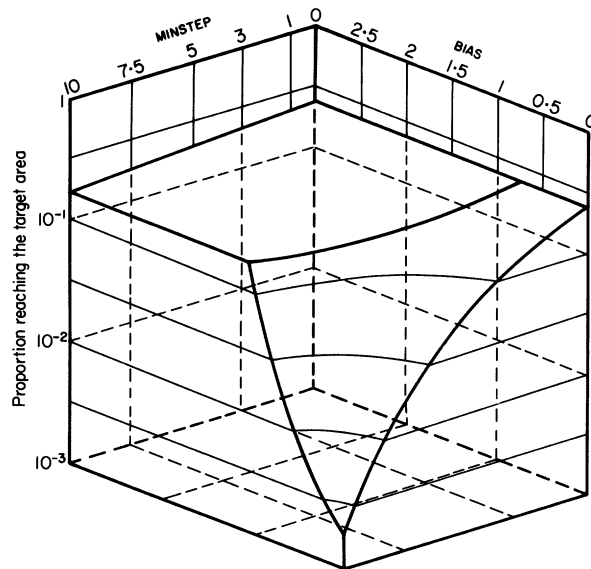


FIG. 6. Response surface of proportion of successes against minimum steplength and downwind bias. Potential flight time was distributed as a lognormal variate with parameter $\mu = 3.4$, $\sigma^2 = 1.4$ and flight speed was distributed normally with mean 15 and S.D. 9 kph.

of potential flight time. Specifically, the general level is determined by the value of σ^2 (of the lognormal distribution) while the slope is controlled by the value of μ . Figures 3 and 6 show how these parameters operate to control the success response surface with respect to MINSTEP. Decreasing the value of μ would result in an increase in the gradient of the slope while increasing μ sufficiently would make the plateau exactly horizontal. A sufficiently large increase in σ^2 would reduce the mortality to near zero except for that determined by flight speed.

The rim of the success surface is due to flight speed. Increasing flight speed reduces mortality (Fig. 5) to a level determined by the potential flight time. In Fig. 5 the rapid transition from high to low levels of success has its analogues in Fig. 6 at the rim to the valley. The locus of the rim reflects the interaction between speed and MINSTEP; increasing flight speed increases the proportion of success. Thus decreasing the flight speed reduces the area of the plateau.

TABLE 1. Proportion of locusts successfully reaching the target area for combination of downwind bias and minimum steplength: * mark the maxima

BIAS	MINSTEP				
	1.0	3.0	5.0	7.5	10.0
0.0	0.181	0.123	0.601×10^{-1}	0.135×10^{-1}	0.200×10^{-2}
0.2	0.190	0.128	0.621×10^{-1}	0.156×10^{-1}	0.258×10^{-2}
0.4	0.201	0.152	0.809×10^{-1}	0.275×10^{-1}	0.462×10^{-2}
0.6	0.210	0.196	0.137	0.533×10^{-1}	0.113×10^{-1}
0.8	0.223	0.216	0.208	0.134	0.347×10^{-1}
1.0	0.226	0.220	0.213	0.211	0.104
1.5	0.232*	0.229*	0.222*	0.214*	0.176*
2.0	0.231	0.228	0.217	0.207	0.174
2.5	0.223	0.221	0.207	0.200	0.170
3.0	0.217	0.213	0.197	0.186	0.169

The transition from unbiased to maximum effect of bias becomes more rapid as MINSTEP increases and this deepening valley marks the parameter space in which selection pressure for bias is strongest. Of course it is not independent of flight speed as the rim has a curvature which is probably a characteristic of the distribution of flight speed.

Figure 6 with its logarithmic scale for success rate shows little variation in the surface features of the plateau but inspection of the actual values (Table 1) suggests that there may be a slight ridge approximately corresponding to a BIAS of 1.5. This ridge, if it exists and is not simply the result of stochastic variation, shows that the *optimum* BIAS is not dependent on MINSTEP.

However BIAS is probably not independent of speed and Figs 7, 8 and 9 show the results of a series of runs in which the degree of BIAS was incremented from 0 to 3 for each of five distributions of flight speed: uniform distribution in range 0 to B with B = 1, 5, 10, 20, 50. The outcome of this experiment is far from simple. The naive expectation would be a uniform increase in the probability of success for each increment of BIAS. Figure 7 shows that this is not so; that there may be an optimum BIAS \times SPEED interaction. Inspection of the effect on transit time suggests the possibility of an optimum while average speed increases with BIAS and the rate of increase with flight speed.

In an evolutionary sense the important criterion is survival, which in this simulation is measured by the probability of arriving at the target. It can be seen from Fig. 7 that the survival rate is highest when BIAS is about 2.3 while the average flight speed is between 9.0 to 10.0 kph. However, fitness (which is essentially what survival amounts to) measured

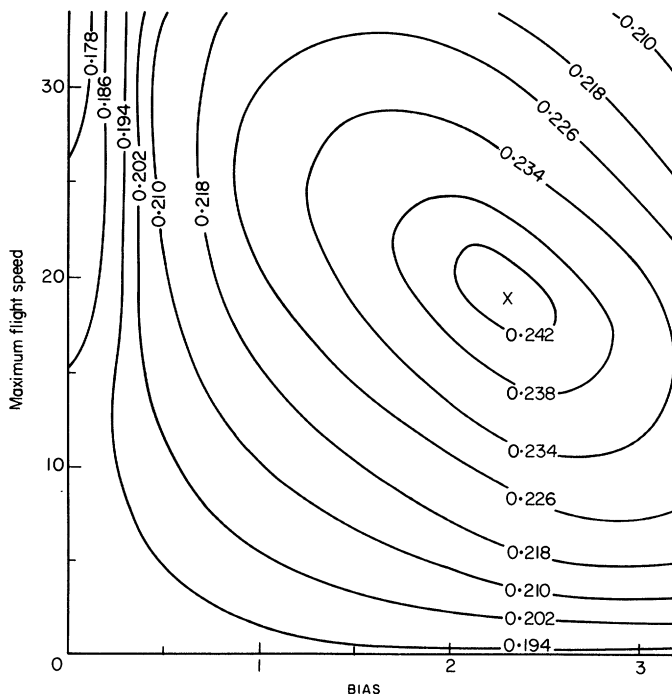


FIG. 7. Contours of proportion of success for a range of flight speeds and downwind biases, showing a peak at SPEED = 19 kph and BIAS = 2.3. Flight speed was distributed uniformly between 0 and B for B = 0–30 kph, and potential flight time was distributed log-normally with parameters $\mu = 3.4$, $\sigma^2 = 1.4$. MINSTEP = 1.0 kph.

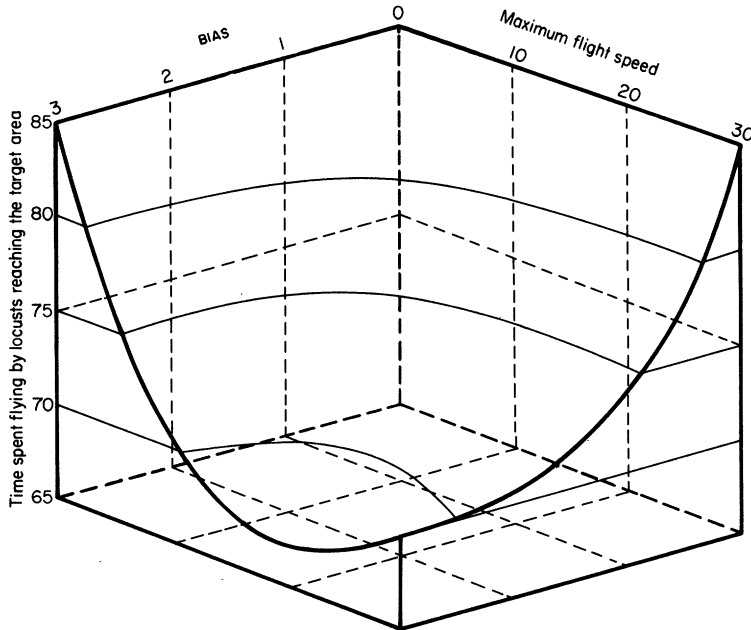


FIG. 8. Response surface of transit time of successful locusts against flight speed and downwind bias. Flight speed was distributed uniformly between 0 and B for $B = 0-30$ kph, and potential flight time was distributed lognormally with parameters $\mu = 3.4$, $\sigma^2 = 1.4$. $\text{MINSTEP} = 1.0$ kph.

in terms of the ability to cross a given expanse of water is a rather artificial criterion; possibly distance travelled or transit time, or even average speed are better criteria. An inert particle, with neither orientation nor speed, travels the minimum distance. In consequence powered flight, biased or not, cannot reduce this except by the ability to navigate; a possibility which we need not consider for locusts. Because of the way the cardioid model operates, too much orientation can result in large deviations from course. This is because the course is curved and the wind direction changes with place and time; even if a locust is orientated downwind at the beginning of a step, it is unlikely to be facing downwind at the end and the longer the step the larger the deviation will be. Consequently it is possible for successful locusts to have flown considerably further than the minimum distance (e.g. successful locusts with $\text{SPEED} = U(0, 30)$ and $\text{BIAS} = 3.0$ fly two-thirds as far again as inert particles—see Appendix B).

In Figure 8 the transit time of successful locusts is plotted as a surface against SPEED and BIAS . It has the appearance of a corrie, but over the range of input values used, no minimum can be identified. If there is a minimum transit time it would seem to be at about 10 kph with $\text{BIAS} 3.0$. It is clear that as BIAS increased, the successful locusts travelled further in their allotted time (NSTEPS) and completed the trip in less time than an inert particle.

Figure 9(a) shows the ground speed as a function of BIAS for six flight speeds. At lower flight speeds the increase in ground speed with BIAS is indistinguishable from linearity but as SPEED increases a curvature becomes visible, but the major effect of increase in SPEED is an increase in the rate of increase of ground speed with BIAS .

The effect of BIAS is obviously very complex and this is most likely attributable to the

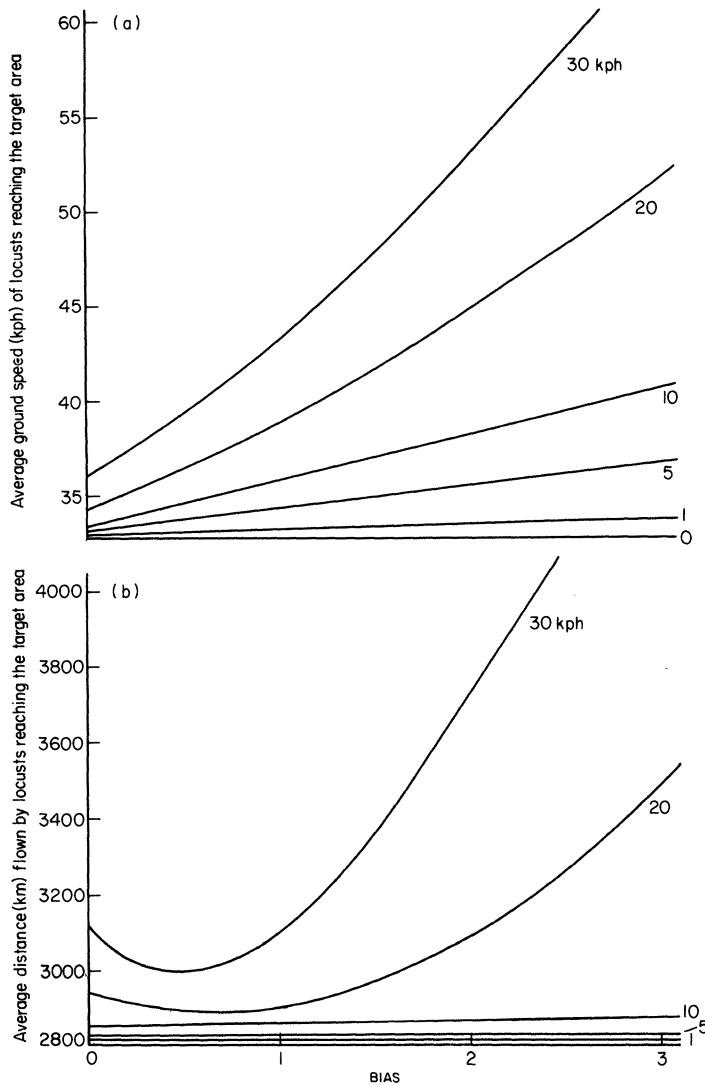


FIG. 9. (a) Average ground speed of successful locusts increases monotonically with downwind bias for six distributions of flight speed; the slope increases with flight speed. (b) Average distance flown of successful locusts has a minimum curve as downwind bias increases; the curvature increases with flight speed. The distance is given with 2791 km as the baseline, the distance flown by an inert particle blown on the wind (see first entry in Appendix B). Flight speed was distributed uniformly between 0 and B where $B = 0-30$ kph, and potential flight time was distributed lognormally with parameters $\mu = 3.4$, $\sigma^2 = 1.4$, and $\text{MINSTEP} = 1.0$ kph.

exact geometry of the course and the choice of the cardioid as the model. With the bias parameter, A , constrained to be between zero and one, as Saila & Shappy (1963) had it, the cardioid is well behaved and ideal for the purpose of investigating migratory successes. But when $A > 1.0$, the great enlargement of the step vector locus in the direction of bias has certain logical disadvantages. The great increase in displacement due to deviations from the course is a serious drawback. Figure 9(b) shows how for a given flight speed the

displacement declines to a minimum and then rises sharply again. The minimum displacement also increases with flight speed, confirming that high flight speed is a disadvantage as decided earlier.

We see now why there should be an optimum combination of downwind bias and flight speed, as shown by Fig. 7. The particular combination of 9.5 kph and $A = 2.3$ is, of course, conditional on the value of MINSTEP ($= 1.0$). Exactly what effect increasing the value of MINSTEP would have is uncertain, but in view of the effects of MINSTEP on success in Figs 3 and 6, it seems likely that the optimum BIAS would remain unchanged but that the shape of the surface, and steepness, would change as optimum flight speed increases to overcome the trapping effect of MINSTEP.

DISCUSSION

This simulation model is necessarily complex as it attempts to elucidate some of the factors affecting survival of insects, specifically locusts, during migration. Migration is known to be a hazardous occupation, although as Taylor & Taylor (1979) have pointed out it is not so much the act itself that is dangerous as the inability to find a region of lower risk. In this episode the safe place was the only dry land downwind from the locusts' breeding grounds in West Africa, which happened to be the Canary Islands and the British Isles. Consequently the migration was not successful in an evolutionary sense.

However, this lack of success provided an ideal situation to investigate some of the factors affecting a locust's migratory prospect. These factors are; (a) the time available for flight, which can be equated to the product of fuel supply and rate of consumption; (b) the flight speed, related to rate of consumption; (c) the ability to orientate in a particular direction and thus conserve fuel. The investigation of these factors was facilitated by the use of a variable which imposed an artificial mortality on flyers and which could be manipulated to permit comparison of the effect of the factors on survival.

Three points emerge from the investigation which, although applying particularly to locust migrations do have greater generality. The first point became apparent during the search for estimates of locust performance. According to the laboratory studies of Wies-Fogh and his collaborators the survival of locusts originating in N.W. Africa and reaching the British Isles by powered flight alone would be impossible. It is not that the observations themselves were wrong, but that the distribution of the flight performance was not measured and so the proportion of exceptional insects (which would not be detected in the laboratory) could not be deduced: this is a pernicious effect of any experiment using cultured animals. It is the rogue individuals in the tail of the distribution which may be important. The majority of 'average' locusts are the ones which cause such devastation to vegetation and it is upon these that applied biologists concentrate their attention. But it is the exceptional individuals which are the material of evolutionary change, especially under conditions of environmental manipulation by man; e.g. resistance to chemical pesticides.

Not only is it important to determine how the distribution of physiological properties within the population but precise estimates of the parameters are needed since small differences in some parameters can lead to comparatively large differences in performance.

When simulating events to predict a possible outcome, the exact distributions used for some variables may not matter, since different distributions can sometimes produce the same overall result. In such circumstances the sensitivity of the model to a particular

state variable will usually be considered to be low. But equating two particular distributions may only be valid over a fixed range beyond which a discontinuity may arise under certain circumstances. Such flaws in models only become crucial when the model is to be used to investigate the biology of the system, since the assumptions built into the model are likely to differ between distributions. For example, the uniform distribution for flight speed was used to simplify the investigation of certain interactions but, having a fixed upper limit to flight speed, its use resulted in discontinuities in the response surfaces.

The distribution of potential flight time is probably the most important and least measured variable controlling locust migratory flight. It is the time spent in the air which ultimately governs how far and how many locusts travel. The survival curves in Fig. 2 shows three similar curves generated from three different distributions (the parameters were chosen so that the curves would be similar). The shapes of these distributions are also shown in Fig. 10(a), (b), (c)) and it can be seen that although the results they produce are comparable, the uniform and normal distributions could not describe laboratory data without it being obvious that locust flight potential is not sufficient to account for Rainey's maritime migration. The lognormal distribution has far fewer rogue individuals with the majority agreeing well with the laboratory material.

The data in the literature for potential flight time place an upper limit to continuous powered flight of about 20 h. If we consider the median potential flight time to be half that then apply it to the three distributions, it is easily seen (Fig. 10(c), (d), (e)) that the uniform and normal distribution are unable to account for any long distance flight. With a median of 10 only the lognormal distribution has a sufficiently large proportion above 60; even so it may not be ideal since its mean and variance are much higher than the uniform and normal distributions. However, until the actual distribution of flight potential is known, the median is probably the best description of central tendency and the lognormal the best distribution to assume.

The other point of the exercise was to find behaviour to conserve fuel. This was done by relaxing the assumption of random walk in a moving medium to investigate the effect of down-wind orientation. It is fairly obvious that migratory mortality and ability to orientate will be inversely related, but it is not obvious that there may be a limit to the advantage of orientation. Sailer & Shapp (1963) pointed out that precise orientation could be a disadvantage without the ability to compensate for drift off course. Their use of the cardioid as a model for bias was a fortunate one since bias makes no assumptions about the ability of the migrant or orientation in a particular direction. Bias thus is a property of the population rather than of the individual. Their model was adopted for this reason since the only known behavioural adaptation for orientation of locusts is away from the edge of the swarm, and the take-off reaction (into the wind) when the edge of the swarm passes overhead of alighted individuals.

Sailer & Shapp's view of the advantage of bias over precise orientation is well borne out by their own model's feature of increasing the total displacement by increasing the deviation from the shortest route. This is particularly evident when the course is curved as in this case. The increased displacement can be interpreted in terms of the habit locusts apparently have of 'rolling' within the swarm. Downwind bias confers some advantage on the individual but, if it leads to too fast forward motion, it may result in a motion away from the leading edge (backwards relative motion). According to Rainey (1963) only about 10% of swarms travel faster than the wind, thus the higher ground speed of some individuals must be absorbed by the rolling motion. In this simulation the decrease in transit time from Africa to the target only represents a maximum of 10%

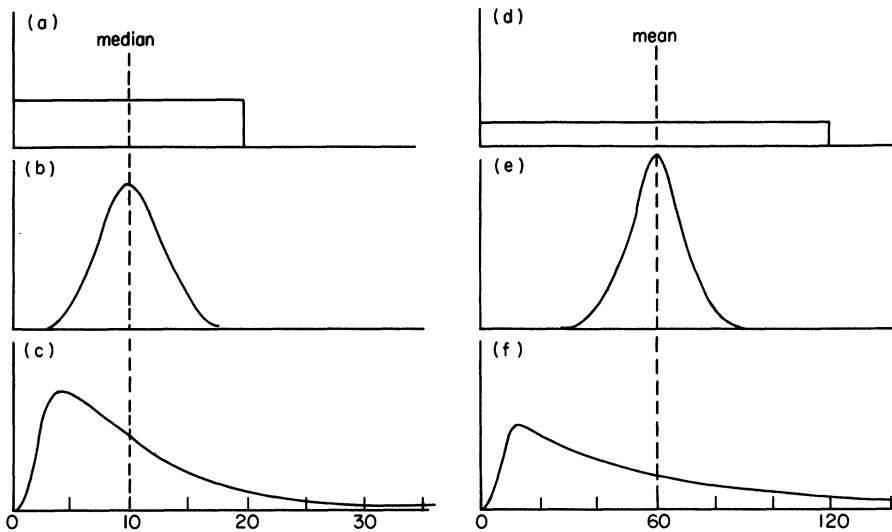


FIG. 10. Sketches of the three distributions used for potential flight time. (a), (b) and (c) have the same median; (d), (e) and (f) the same mean. Characteristics of these distributions are:

Type	Median	Mean	S.D.	$P(x > 60)\%$	Parameters	
(a) uniform	10	10	7	0	0	20
(b) normal	10	10	7	$\sim 10^{-5}$	10	7
(c) lognormal	10	20	35	6.4	2.3	1.4
(d) uniform	60	60	35	50	0	120
(e) normal	60	60	20	50	60	20
(f) lognormal	30	60	100	23	3.4	1.4

increase in speed for the swarm but corresponds to a 100% increase in speed of some individuals.

The simulation experiments on bias indicate the existence of an optimum speed-bias interaction. This is a conclusion which might have been reached from an engineering view-point but does not seem to have been considered in mathematical models of migration, especially those models derived from random physical processes (diffusion). Taylor (1978) found that migration and dispersal could not be treated as a random process: the random model was inadequate to describe the dispersal of seven out of eight insect species. The models which he found to be adequate had parameters which could be interpreted in terms of behaviour and which specifically excluded random processes. Even with the assumption of random walk, the end product is non-random distribution of deaths (see Fig. 1(b)). The non-randomness is provided by the moving medium and it is clear that locusts are well adapted to travel towards and with the Intertropical and other Convergence Zones (Rainey 1951). It seems likely that the speed-bias interaction is mediated in this instance by the behaviour which maintains swarm cohesion and is an adaptation to keep the maximum number of individuals in an airstream with the best chance of taking them to extensive, albeit temporary, areas of vegetation. This habit concentrates locusts in the most favourable regions, consequently the spatial distribution is highly aggregated (on the ground as well as in the air) as is expected from dispersive processes which do not rely on diffusion. L. R. Taylor (1961) speculated and has since

demonstrated convincingly (Taylor, Woiwod & Perry 1978) that random spatial distributions are rare in nature; *S. gregaria* is no exception, and it is clear that it is its adaption to flight towards convergence zones that make it so.

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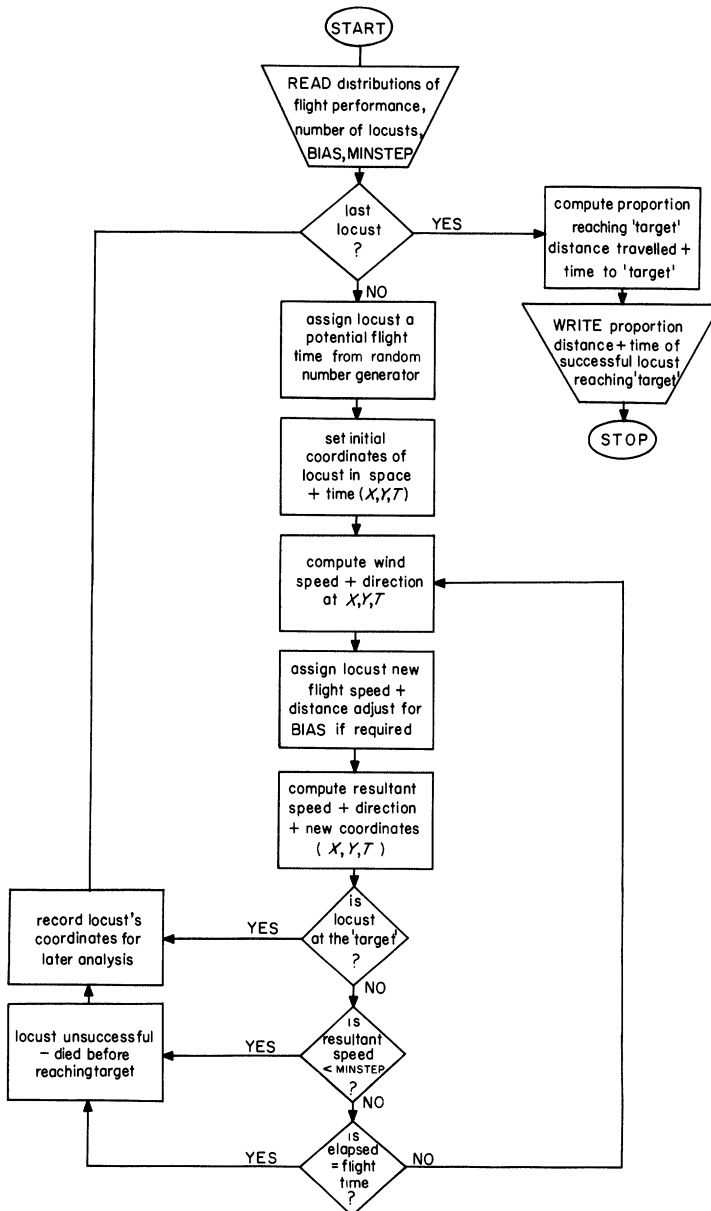
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APPENDIX A

Flow diagram of the computer program simulating a migration of *Schistocerca gregaria*.

The state variables include the distributions and parameters for potential flight time (NSTEPS) and flight speed (SPEED) the minimum ground speed required for continuous flight (MINSTEP) and the degree of bias to downwind orientation (BIAS). Coordinates X , Y , T represent the position of a locust, given as latitude and longitude at time T hours after the start. The proportion reaching the target (see Fig. 1), the average distance flown and the time taken to reach it are output when the desired number of locusts (10^4 – 10^6) have 'flown'.



APPENDIX B

Results of 243 simulation runs.

The first entry gives the distance flown and time taken for an inert particle to be transported in the wind field. Experiments are arranged in blocks with the same distributions for NSTEPS and SPEED which are random variables distributed as uniform $U(A, B)$, normal $N(\mu, \sigma)$, or lognormal $L(\mu, \sigma^2)$ variates: the numbers in brackets are the parameters of the distribution used e.g. $U(0, 5)$ represents a variate distributed uniformly between 0 and 5. MINSTEP is the minimum ground speed and BIAS is the degree of down-wind orientation. The results, given in the last three columns, are the *proportion* of locusts successfully reaching the target (see Fig. 1), the average *distance* travelled by successful locusts and their transit *time*. The sample sizes are not given but were not less than 10^4 , and for very small proportions of successes were in excess of 10^6 .

MINSTEP	BIAS	Proportion	Distance (km)	Time (h)
NSTEPS = $U(120, 120)$; SPEED = $U(0, 0)$				
0.0	0.0	1.000	2791	85.00
NSTEPS = $U(0, 120)$; SPEED = $N(15, 9)$				
0.0	0.0	0.301	3096	84.90
1.0	0.0	0.291	3079	83.65
3.0	0.0	0.197	3092	83.58
5.0	0.0	0.870×10^{-1}	3062	81.63
7.5	0.0	0.228×10^{-1}	3059	81.32
10.0	0.0	0.292×10^{-2}	3024	78.56
12.5	0.0	0.270×10^{-3}	3023	76.41
15.0	0.0	0.196×10^{-4}	2961	72.89
NSTEPS = $N(30, 20)$; SPEED = $N(15, 9)$				
0.0	0.0	0.370×10^{-2}	3064	82.44
1.0	0.0	0.344×10^{-2}	3033	80.93
3.0	0.0	0.257×10^{-2}	3017	80.02
5.0	0.0	0.140×10^{-2}	3020	79.64
7.5	0.0	0.440×10^{-3}	3010	78.89
10.0	0.0	0.740×10^{-4}	2963	75.81
12.5	0.0	0.100×10^{-4}	2962	74.60
15.0	0.0	0.700×10^{-6}	2993	74.50
NSTEPS = $N(60, 20)$; SPEED = $N(15, 9)$				
0.0	0.0	0.116	3063	83.21
1.0	0.0	0.112	3058	82.39
3.0	0.0	0.791×10^{-1}	3055	81.88
5.0	0.0	0.365×10^{-1}	3042	80.95
7.5	0.0	0.111×10^{-1}	3041	80.37
10.0	0.0	0.190×10^{-2}	3008	78.29
12.5	0.0	0.130×10^{-3}	2946	74.54
15.0	0.0	0.800×10^{-5}	2994	74.00
NSTEP = $N(60, 10)$; SPEED = $N(15, 9)$				
0.0	0.0	0.110×10^{-1}	2997	79.57
1.0	0.0	0.980×10^{-2}	3011	79.74
3.0	0.0	0.940×10^{-2}	2991	79.01
5.0	0.0	0.460×10^{-2}	2982	77.74
7.5	0.0	0.700×10^{-3}	2956	75.86
10.0	0.0	0.270×10^{-3}	2962	75.78
12.5	0.0	0.400×10^{-4}	2948	75.00
15.0	0.0	0.100×10^{-5}	2985	74.00

MINSTEP	BIAS	Proportion	Distance (km)	Time (h)
NSTEPS = L(3.4, 1.4); SPEED = U(0, 0)				
0.0	0.0	0.193	2791	85.00
1.0	0.0	0.193	2791	85.00
3.0	0.0	0.193	2791	85.00
5.0	0.0	0.193	2791	85.00
7.5	0.0	0.193	2791	85.00
10.0	0.0	0	0	0
12.5	0.0	0	0	0
15.0	0.0	0	0	0
NSTEPS = L(3.4, 1.4); SPEED = U(0, 5)				
0.0	0.0	0.193	2823	85.40
1.0	0.0	0.193	2823	85.40
3.0	0.0	0.193	2823	85.40
5.0	0.0	0.193	2823	85.40
7.5	0.0	0.180	2822	85.35
10.0	0.0	0.543×10^{-1}	2821	85.03
12.5	0.0	0.100×10^{-3}	2816	83.80
15.0	0.0	0	0	0
NSTEPS = L(3.4, 1.4); SPEED = U(0, 10)				
0.0	0.0	0.193	2844	85.41
1.0	0.0	0.193	2844	85.40
3.0	0.0	0.190	2844	85.37
5.0	0.0	0.150	2843	85.29
7.5	0.0	0.625×10^{-1}	2841	84.80
10.0	0.0	0.970×10^{-2}	2836	83.95
12.5	0.0	0.100×10^{-3}	2816	82.14
15.0	0.0	0.200×10^{-5}	2751	79.24
NSTEPS = L(3.4 1.4); SPEED = U(0, 20)				
0.0	0.0	0.192	2939	85.45
1.0	0.0	0.182	2940	82.98
3.0	0.0	0.124	2943	85.28
5.0	0.0	0.623×10^{-1}	2931	84.26
7.5	0.0	0.144×10^{-1}	2920	83.21
10.5	0.0	0.210×10^{-2}	2896	81.44
12.5	0.0	0.800×10^{-3}	2957	82.00
15.0	0.0	0.600×10^{-5}	2898	78.33
NSTEPS = L(3.4, 1.4); SPEED = U(0, 30)				
0.0	0.0	0.191	3111	85.69
1.0	0.0	0.180	3115	85.82
3.0	0.0	0.122	3124	85.53
5.0	0.0	0.635×10^{-1}	3093	84.23
7.5	0.0	0.168×10^{-1}	3075	82.63
10.0	0.0	0.200×10^{-2}	3031	80.33
12.5	0.0	0.120×10^{-3}	3034	79.17
15.0	0.0	0.100×10^{-4}	2924	76.33
NSTEPS = L(2.3, 1.4); SPEED = N(15, 9)				
0.0	0.0	0.345×10^{-1}	3125	85.47
1.0	0.0	0.367×10^{-1}	3115	84.46
3.0	0.0	0.253×10^{-1}	3112	84.03
5.0	0.0	0.123×10^{-1}	3070	82.24
7.5	0.0	0.300×10^{-2}	3055	80.74
10.0	0.0	0.310×10^{-3}	3230	80.71
12.5	0.0	0.340×10^{-4}	3023	76.65
15.0	0.0	0.774×10^{-6}	2965	78.00
NSTEPS = L(2.7, 1.4); SPEED = N(15, 9)				
0.0	0.0	0.707×10^{-1}	3106	85.05
1.0	0.0	0.682×10^{-1}	3124	84.79
3.0	0.0	0.441×10^{-1}	3123	84.31
5.0	0.0	0.200×10^{-1}	3134	83.72

Model of locust migration

MINSTEP	BIAS	Proportion	Distance (km)	Time (h)
7.5	0.0	0.466×10^{-2}	3113	81.71
10.0	0.0	0.770×10^{-3}	3133	80.35
12.5	0.0	0.380×10^{-4}	3000	76.26
15.0	0.0	0.122×10^{-5}	2916	71.50
NSTEPS = L(3.0, 1.4); SPEED = N(15, 9)				
0.0	0.0	0.111	3107	85.24
1.0	0.0	0.108	3115	84.40
3.0	0.0	0.702×10^{-1}	3124	84.02
5.0	0.0	0.334×10^{-1}	3104	83.03
7.5	0.0	0.890×10^{-2}	3046	80.65
10.0	0.0	0.810×10^{-3}	3442	84.42
12.5	0.0	0.580×10^{-4}	3723	86.38
15.0	0.0	0.400×10^{-5}	3012	74.00
NSTEPS = L(3.2, 1.4); SPEED = N(15, 9)				
0.0	0.0	0.149	3115	85.52
1.0	0.0	0.140	3124	84.57
3.0	0.0	0.967×10^{-1}	3105	83.63
5.0	0.0	0.452×10^{-1}	3072	82.48
7.5	0.0	0.107×10^{-1}	3045	80.69
10.0	0.0	0.930×10^{-3}	3250	82.29
12.5	0.0	0.780×10^{-4}	3001	76.85
15.0	0.0	0.465×10^{-5}	2966	75.83
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
0.0	0.0	0.196	3114	85.54
1.0	0.0	0.181	3120	84.43
3.0	0.0	0.123	3130	84.28
5.0	0.0	0.601×10^{-1}	3107	83.02
7.5	0.0	0.135×10^{-1}	3087	81.18
10.0	0.0	0.200×10^{-2}	3173	80.68
12.5	0.0	0.100×10^{-3}	3117	77.88
15.0	0.0	0.583×10^{-5}	2902	72.14
NSTEPS = L(2.3, 1.96); SPEED = N(15, 9)				
0.0	0.0	0.659×10^{-1}	3106	85.16
1.0	0.0	0.579×10^{-1}	3125	84.55
3.0	0.0	0.393×10^{-1}	3122	84.37
5.0	0.0	0.180×10^{-1}	3157	83.79
7.5	0.0	0.582×10^{-2}	3127	81.80
10.0	0.0	0.630×10^{-3}	3035	79.70
12.5	0.0	0.533×10^{-4}	3038	78.00
15.0	0.0	0.327×10^{-5}	2946	72.60
NSTEPS = L(2.7, 1.96); SPEED = N(15, 9)				
0.0	0.0	0.112	3115	85.34
1.0	0.0	0.103	3104	84.51
3.0	0.0	0.724×10^{-1}	3094	83.66
5.0	0.0	0.320×10^{-1}	3147	83.78
7.5	0.0	0.718×10^{-2}	3056	81.06
10.0	0.0	0.870×10^{-3}	3024	79.21
12.5	0.0	0.400×10^{-4}	3092	80.50
15.0	0.0	0.397×10^{-5}	3051	76.33
NSTEPS = L(3.0, 1.96); SPEED = N(15, 9)				
0.0	0.0	0.158	3127	85.68
1.0	0.0	0.151	3132	84.85
3.0	0.0	0.100	3139	84.45
5.0	0.0	0.482×10^{-1}	3123	83.36
7.5	0.0	0.109×10^{-1}	3156	82.13
10.0	0.0	0.157×10^{-2}	3127	81.40
12.5	0.0	0.140×10^{-3}	3214	80.50
15.0	0.0	0.667×10^{-5}	3070	76.15

MINSTEP	BIAS	Proportion	Distance (km)	Time (h)
NSTEPS = L(3.2, 1.96); SPEED = N(15, 9)				
0.0	0.0	0.184	3111	85.55
1.0	0.0	0.176	3136	84.76
3.0	0.0	0.123	3128	84.10
5.0	0.0	0.515×10^{-1}	3110	83.33
7.5	0.0	0.137×10^{-1}	3112	81.57
10.0	0.0	0.152×10^{-2}	3081	79.70
12.5	0.0	0.130×10^{-3}	3546	83.54
15.0	0.0	0.795×10^{-5}	3090	76.00
NSTEPS = L(3.4, 1.96); SPEED = N(15, 9)				
0.0	0.0	0.225	3142	85.95
1.0	0.0	0.223	3125	84.83
3.0	0.0	0.155	3104	83.83
5.0	0.0	0.696×10^{-1}	3165	83.92
7.5	0.0	0.167×10^{-1}	3102	81.45
10.0	0.0	0.219×10^{-2}	3075	79.72
12.5	0.0	0.100×10^{-3}	2959	75.50
15.0	0.0	0.984×10^{-5}	2965	73.80
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
1.0	0.2	0.190	3121	81.53
1.0	0.4	0.201	3105	78.74
1.0	0.6	0.210	3132	76.69
1.0	0.8	0.223	3188	74.91
1.0	1.0	0.226	3333	74.44
1.0	1.5	0.232	3387	70.10
1.0	2.0	0.231	3723	69.59
1.0	2.5	0.223	4090	69.55
1.0	3.0	0.217	4495	70.32
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
3.0	0.2	0.128	3097	80.98
3.0	0.4	0.152	3092	78.41
3.0	0.6	0.196	3111	76.25
3.0	0.8	0.216	3168	74.69
3.0	1.0	0.220	3311	74.10
3.0	1.5	0.229	3432	70.60
3.0	2.0	0.228	3767	70.26
3.0	2.5	0.221	4083	69.49
3.0	3.0	0.213	4634	72.06
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
5.0	0.2	0.621×10^{-1}	3089	80.08
5.0	0.4	0.809×10^{-1}	3096	77.63
5.0	0.6	0.137	3132	76.06
5.0	0.8	0.208	3181	74.73
5.0	1.0	0.213	3288	73.78
5.0	1.5	0.222	3396	70.13
5.0	2.0	0.217	3752	69.67
5.0	2.5	0.207	4081	69.61
5.0	3.0	0.197	4450	70.10
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
7.5	0.2	0.156×10^{-1}	3110	78.95
7.5	0.4	0.275×10^{-1}	3099	76.61
7.5	0.6	0.533×10^{-1}	3165	75.71
7.5	0.8	0.134	3222	74.80
7.5	1.0	0.211	3168	72.57
7.5	1.5	0.214	3387	69.97
7.5	2.0	0.207	3799	69.91
7.5	2.5	0.200	4074	69.28
7.5	3.0	0.186	4431	69.49

Model of locust migration

MINSTEP	BIAS	Proportion	Distance (km)	Time (h)
NSTEPS = L(3.4, 1.4); SPEED = N(15, 9)				
10.0	0.2	0.258×10^{-2}	3024	75.86
10.0	0.4	0.462×10^{-2}	3122	75.34
10.0	0.6	0.113×10^{-1}	3262	75.74
10.0	0.8	0.347×10^{-1}	3189	73.19
10.0	1.0	0.104	3352	73.95
10.0	1.5	0.176	3408	70.07
10.0	2.0	0.174	3755	69.59
10.0	2.5	0.170	3998	69.01
10.0	3.0	0.169	4489	70.05
NSTEPS = L(3.4, 1.4); SPEED = U(0, 1)				
1.0	0.2	0.192	2804	85.07
1.0	0.4	0.193	2809	85.01
1.0	0.6	0.191	2816	84.99
1.0	0.8	0.194	2823	84.95
1.0	1.0	0.195	2824	84.84
1.0	1.5	0.190	2810	84.32
1.0	2.0	0.195	2811	84.02
1.0	2.5	0.198	2818	83.80
1.0	3.0	0.192	2811	83.02
NSTEPS = L(3.4, 1.4); SPEED = U(0, 5)				
1.0	0.2	0.190	2821	84.73
1.0	0.4	0.195	2818	84.09
1.0	0.6	0.192	2821	83.48
1.0	0.8	0.196	2820	82.88
1.0	1.0	0.195	2821	82.26
1.0	1.5	0.204	2821	80.81
1.0	2.0	0.211	2822	79.40
1.0	2.5	0.214	2824	78.10
1.0	3.0	0.219	2827	76.77
NSTEPS = L(3.4, 1.4); SPEED = U(0, 10)				
1.0	0.2	0.195	2841	84.06
1.0	0.4	0.195	2840	82.92
1.0	0.6	0.209	2839	81.71
1.0	0.8	0.205	2839	80.54
1.0	1.0	0.210	2839	79.44
1.0	1.5	0.211	2840	76.79
1.0	2.0	0.228	2844	74.46
1.0	2.5	0.235	2855	72.25
1.0	3.0	0.235	2861	70.17
NSTEPS = L(3.4, 1.4); SPEED = U(0, 20)				
1.0	0.2	0.192	2925	82.97
1.0	0.4	0.200	2909	80.60
1.0	0.6	0.206	2910	78.57
1.0	0.8	0.217	2897	76.43
1.0	1.0	0.231	2904	74.55
1.0	1.5	0.240	2927	70.59
1.0	2.0	0.242	3071	68.59
1.0	2.5	0.240	3274	67.61
1.0	3.0	0.236	3468	67.00
NSTEPS = L(3.4, 1.4); SPEED = U(0, 30)				
1.0	0.2	0.187	3060	81.93
1.0	0.4	0.199	3064	79.15
1.0	0.6	0.221	3048	76.32
1.0	0.8	0.226	3080	74.22
1.0	1.0	0.225	3149	72.62
1.0	1.5	0.232	3359	69.95
1.0	2.0	0.226	3753	70.04
1.0	2.5	0.213	4125	70.19
1.0	3.0	0.208	4453	70.35