Chapter 7: Discussion

Validity of the model

The relevance of this discussion of the practical and theoretical implications of the responses of *G. m. morsitans* and *G. pallidipes* to vegetation depends on the extent to which the modelling of movement in relation to bushes and baits can be used to supplement results of field experiments. The model simplifies the real patterns of movement, uses crude maps and employs rough estimates for important parameters, i.e. *f*, *k*, interval duration and hop length. No variations are made to the rate or pattern of cell evacuation, to cover the possibility that tsetse take longer, faster or straighter hops in certain vegetation types, because there is no experimental evidence to show whether they do. Moreover, the model seems unable to predict the assessed distribution of tsetse between vegetation types, perhaps because of no allowance for effects of the uneven distribution of hosts and dry-season resting sites. There is no experimental indication of how to allow for these matters. The problems identify important matters for further research.

Despite the problems, the model does highlight some of the simpler ways in which bushes can contribute to tsetse distribution and invasion. For example, it seems that movement is impeded mainly at the junction of dense and lightly bushed habitats, not by resistance within the main expanse of the dense habitat. This suggests that invasion could be restricted most in areas where flies must cross many narrow bands of alternating vegetation types, i.e. where there are many junctions. Furthermore, the field data available as checks on the modelling of sampling suggest that the model is not far wrong in its indications for matters involved in this, i.e. persistence, catching-out, and the effects of odours, hedges and site manipulation for both species. The modelled rate of removal of flies by traps and targets fits well with the rates observed in the field. The model’s demonstration of the concentration of tsetse at the junction of paths matches Nash’s (1933) field evidence for *G. m. morsitans*, albeit that he studied paths through tall grass, not bushes. Since the model gives fair approximations for those sampling matters that can be checked, it seems reasonable to accept its indications for other sampling matters, provided the emphasis is on the principles exposed, rather than precise quantitative interpretations.

Practical implications for bait siting

Site selection

The choice of site to maximize catches from traps and targets depends on the following considerations.

Stimulus

To ensure a strong dose of odour, the site must get direct insolation to warm the dispensers, during and immediately before the periods of tsetse activity. This means that the site should not receive oblique shade from distant trees in the late afternoon. Catches of *G. pallidipes* can improve if the site has a dark log, about the same size as the trap, to supplement visual attraction. However, given the problem of selecting just the right sort of log, it is wisest to avoid such objects, especially since any sort of log is likely to reduce the catches of *G. m. morsitans*.

Since traps and targets seem not to be seen at distances greater than c. 15 m, there is little point in choosing clearings of greater radius than this. Moreover, there is warning in the fact that catches from traps in large clearings were greater when the clearing contained a few scattered bushes – very large, perfect clearings may be less productive.

Access

Gaps for access should account for at least a third of the clearing’s perimeter, and are most beneficial when downhill. Suitable access is provided by paths at least 1 m wide, preferably with no leafy bushes overhanging. If overhang cannot be avoided completely, it should be at least 1 m above the soil or any ground cover. A few leafless stems across the access are no serious hindrance, but passage can be halved when the stems form a 15 × 15 cm lattice. Since a narrow band of densely bushed vegetation appears to restrict tsetse movement severely, baits placed in a line along riverine thickets should be alternated between each side.

Capture efficiency

To ensure efficient trapping, the entrances to traps should face downwind. Plenty of light must pass down through the trap. This requires the absence of a canopy directly above the site. If a canopy cannot be avoided, it should be the smallest, highest and sparsest available, restricting no more than 50% of through light. The site must be clear of bushes, shrubs and fallen trees – even when only 25 cm tall the bushes can be limiting.

Trimming

In some vegetation types there will be no site which, in its natural state, meets all of the above requirements. It could then be beneficial to trim the nearby vegetation, to remove or thin a low and dense canopy, reduce the extent of bushes within a few metres around the trap, and create, lengthen or widen paths to the site. 

In general, the present work with odour-baited devices extends and explains the siting rules of Swynnerton (1936)
for odourless traps, without altering most of his advice. The extent to which the recommended policy of trap orientation, site selection and trimming can increase catch depends on the policy it replaces. If it replaces the random orientation of traps, and hiding traps and targets in leafy ‘caves’, catches will increase about ten times. Teaching the rules of optimal siting to field staff could make the difference between dismal failure and signal success in efforts to detect or eradicate tsetse.

Appendix C suggests simple rules to teach. It might also be helpful to give trainees an even simpler take-home message, like that which the author found effective when teaching the positioning of artificial refuges for the fly. The maxim was: ‘Put the refuges where you yourself would shelter on a scorching day’. For the distinctive instruction needed to site traps or targets, the staff should imagine a man wandering by convenient routes through the bush and gazing around for a bait whose location he has forgotten. The man sees further and from higher than tsetse, and does not use odour, but the places where each creature discovers baits readily seem similar. Hence, the dictum might be: ‘Put the bait where a short man would easily rediscover it’. This advice meets the convenience of personnel and the behaviour of flies, even if the author had hoped for something less prosaic to cap five years of toil.

Site management

Continued use

The catching-out experiment (fig. 14) showed that the catch of G. m. morsitans on the first day of trapping was about 50% greater than on subsequent days. The effect was not significant but it was strongly suggestive and has often been observed in other trapping experiments with G. m. morsitans (R.J. Phelps, personal communication). However, it is difficult to attribute the effect to catching-out since the model’s simulations suggested that catches would decline only slightly and gradually (fig. 35, f = 0.002). Some effect might have been expected due to the relatively high level of human activity on the day that the trap was erected – flies attracted to the site by the men may have rested nearby and entered the trap when the men left. This accords with the known effects of men on trap catches of G. m. morsitans (Vale, 1982b). The catch of G. pallidipes was not high on the first day, agreeing with the fact that men do not enhance the trap catches of this species (ibid.). Moreover, for both species there was no effect of time after Day 1. Hence, it seems unnecessary to move traps in order to sustain catches, at least in cases such as the present, where highly mobile species of tsetse occur in large areas (Vale et al., 1984). For tsetse such as Glossina brevipalpis Newstead, which occur in small pockets (Swynnerton, 1936), a catching-out effect could be severe. Presumably, it is the low mobility of the palpalis group of tsetse that produces catching-out effects with these flies, even when the traps are localized in large blocks of uniform vegetation (Green, 1994).

Upkeep

Artificial sources of host odour will not, on their own, have much impact on the survival of tsetse populations. The flies seem not to persist near such sources and the brief time needed to move up the plume appears a small loss. Moreover, even when the flies are at the odour source or in the plume, they divert to visual baits further away (Vale, 1984; Torr, 1989). Hence, the responses to the odour do not preclude responses to natural baits, and the flight up the artificial plume might even lead to the location of a host. The implication is that the site must be furnished with a well maintained trap, or a target with an effective deposit of insecticide.

Spacing

The spacing between baits must allow for the fact that fly movement towards a bait relies largely on diffusion, so that the time taken for the movement depends on the square of the distance to be covered. For bait control that is expected to eradicate tsetse in a year, a suitable spacing is provided by baits that are at 100–250 m intervals along lines about 2–3 km apart, to give a target density of about 4/km² for control of G. m. morsitans and 2/km² for G. pallidipes (Vale et al., 1988a). Hence, virtually all of the population between the target lines seems to diffuse at least 1.5 km in a year. However, the probability of flies diffusing to the baits in that time could decline drastically if the distance between the lines is increased. Moreover, if greater densities of targets are deployed to achieve faster control, the targets must be spaced more evenly. More lines of targets should be deployed, instead of increasing the frequency of targets within the lines. Target spacing cannot be increased in linear habits because the rate of diffusion is not increased in such places (fig. 28, Path).

Theoretical implications

Interpretation of catches

Intuitive or subjective interpretations of catches have been important in setting our notions of tsetse ecology and behaviour, and in dictating research priorities. Such interpretations have been so misleading in several spheres that the dangers are worth illustrating from present work. For example, since odour-baited traps have been developed from an understanding of host-orientated behaviour, one might think that we should regard traps as host-like objects. This in turn suggests that attempts to improve the poor efficiency of traps should concentrate on further study of responses to hosts. However, the effects that odours, wind direction and fly species have on the passage of flies into a trap are much the same as the effects of these factors on passage through gaps in vegetation. Consequently, do traps simulate a host, or do they in part represent a bush in which a host is hidden? In any event, the further improvement of trap efficiency may benefit most from study of responses to vegetation, not hosts alone.

Intuitively, the explanation for the reduced catches associated with hedges is that fewer flies arrive, due to a blocking of attractive stimuli or restricting the access of flies. Such effects were indeed important. However, of almost equal importance was the less expected reduction in the efficiency of catching the flies that arrived. Even when this efficiency change is recognized, there is danger in explaining it intuitively by only the changed stimuli received when the flies have reached the trap. Important factors that affect the probability of entry may occur further away. For example, if the trap is placed so that flies arriving by it must have passed through gaps in distant hedges, and if such passage is comparable to entering the trap, then the samples of flies that arrive may be pre-selected for individuals that have the
greatest propensity to enter. Pre-selection for tsetse that fly over hedges could lead to an arriving sample that travels over the top of the trap, and hence away from the trap’s entrance. Present work shows that G. m. morsitans are more likely than G. pallidipes to fly over a bush in order to get to an odour-baited trap, and other work (Vale, 1982a) shows that G. m. morsitans flies relatively high when it has arrived.

Perhaps the most intriguing way in which subjectivity seems to invade our interpretations involves the long-held belief that a trap left in one place for a few days causes the local population of G. pallidipes to be greatly reduced (Swynnerton, 1936). However, the present data show that on about 50% of occasions the catches increase after the first day. The tendency then is merely to blame the weather for altering the availability of flies, whereas on the remaining occasions when catches decline, there is the more memorable and exciting suggestion of catching-out.

**Distribution and seasonal abundance**

Present work illustrates the difficulty of defining the area sampled by a bait and so highlights a group of problems in using catch data to map tsetse infestations and to decide where self-sustaining populations need to be controlled. The sampled area could be a few hectares or many thousands, depending on whether one wishes to cover the area from which 50% of the catch came in an afternoon, or from where all of it could have originated in a month. In simple theory, the smaller the catch the more likely that all of it came from nearby. In practice, however, small catches are often discounted as consisting of stray flies arriving unusually quickly from a population established far away, e.g. flies borne by road traffic (Hursey & Allsopp, 1984; Allsopp & Hursey, 1986). Even where no flies are caught it is uncertain whether sampling was sufficiently long and intense to detect tsetse. Problems like these emphasize the abstraction of regarding tsetse as ‘present’ on one side of a mapped line and ‘absent’ on the other (Robinson et al., 1997a,b). It is more realistic to conceive an infestation as a set of contours of the probability of catching a fly per unit of sampling effort (Rawlings et al., 1993), and to strive for the interpretative powers that will allow catch data to be translated into contours of the true density of tsetse. Even then, there remains the problem of not knowing what population densities and sizes are required for self-sustainability under various circumstances, so we do not know what density contour, if any, could alone circumscribe the areas where self-sustaining populations occur.

Turning to the distribution of tsetse between vegetation types, present experiments show that if a good sampling site were chosen in one vegetation, and a poor site in another, the comparison between the apparent density of tsetse in different vegetation types could change by at least one order of magnitude at certain seasons. Even if indices of abundance were produced by the average catches at a large number of randomly selected sites in each vegetation, there is still the problem that in some vegetation types, and at certain seasons, randomly chosen sites will have relatively large numbers of leafy bushes and shady trees. Such features affect important responses to baits, so that catches are likely to differ between vegetation types, irrespective of any differences in population levels. To overcome these difficulties, there are two options: (i) use any site and compensate for the estimated sampling biases there; or (ii) choose or create a site and bait to avoid bias. These options are discussed below.

**Compensate for bias**

Attempts to compensate for sampling biases are exemplified by the interpretation of catches at Sites 1–6 (figs 38 and 39). The example is not perfect because the sites were partly chosen to minimize bias – all sites were in a small clearing, near a track and not densely shaded overhead, so that the compensations for bias did not change enormously the apparent distribution of the flies. Nevertheless, the compensations for bias led to important changes in principle in the estimated distribution of tsetse. For example, if one was worried about where to place baits to stop a wet season invasion of tsetse across the transect that linked the sites, then the actual catches would suggest that most attention should be given to the south end. After compensation it appears that much or most attention should be given to the opposite end. Unfortunately, the compensation for sampling biases involves the tenuous use of the model in a highly quantitative way. All that can be said for certain is that with the current modelling ability, the compensation for site effects will change the indications for tsetse distribution and invasion routes, without guaranteeing that the indications are much better.

**Avoid bias**

One of the most important suggestions from the model is that the safest indices of tsetse abundance are the catches at those sites which, in their natural or altered states, are the most productive. This leads to the counter-intuitive indication that in certain vegetation types the most typical sites should be avoided. For example, in landscapes covered mainly by large blocks of dense bush, the least fair site is one in its natural state inside one of the blocks. The fairest site would be on a junction of natural paths between the blocks, with perhaps one or two artificial paths cut to improve access from other natural paths nearby. However, caution is required: if many long paths are cut the sampled area will be so opened as to encourage a concentration of active flies.

Even if the site chosen is on a path there is the possibility that nearby bushes and shady trees can affect the capture efficiency of a trap there. This problem seems largely avoidable by sampling with targets, whose capture efficiency depends relatively little on vegetation in the immediate vicinity. However, there still remains the problem that the sampling efficiency in various vegetation types will be affected by factors for which no allowance has been made, such as the abundance of natural hosts. Thus, although some means of reducing bias are apparent, there is certainly no assurance that bias can be avoided completely.

**New tools**

The many difficulties in present investigations emphasize the need to develop a variety of tools. At the simple, practical end of the range, it would be helpful to have odour dispensers which deliver a standard dose at all temperatures, e.g. a bimetallic strip might regulate the aperture through which odour diffuses. At the opposite end of the range there is a need for new models of tsetse movement which, like the present model, allow movement in restricted space but which, unlike the present model, are comprehensive and convenient. For example, with the
present model a pentium computer took ten days to process the 280,000 intervals (1 s) involved in the simulation of a week of catching-out. The present model does not address those large, very open areas such as grassland and fields into which tsetse may not venture far (Vale, 1980; Brightwell et al., 1997). The fly seems restricted as much by the complete absence of bushes and trees as by dense vegetation. It seems, therefore, that the model needs further refinement but it does offer a start on a new way of predicting the movement of *G. m. morsitans* and *G. pallidipes*, to complement existing models and additional experiments. Present work suggests that once the impedances of various vegetational patterns have been measured, the movement of flies in areas of mixed vegetation might be simulated most simply by electrical models of diffusion (Monteith, 1963).

The present model could be of wider help where suitable data are available. Its principles are applicable in two or three dimensions to any object which moves in only those directions that are recognized in advance as leading directly to places within physical bounds or 'preferred' segments of the environment at large. A gas molecule is not such an object because it collides 'blindly' with its bounds and returns to the space it was vacating. In contrast, most self-propelling forms of life seem to limit themselves to certain niches within the physical structure of their habitat, even when other niches are potentially accessible (Price, 1975). For some mosquitoes, such as *Mansonia fuscopennata* Theobald (Diptera: Culicidae), the niche at any one time of day seems to be a particular stratum in tall forests, but with transfer to other strata at other times (Haddow, 1961). However, these indications for 'distribution', like the indications for the distribution of many other biting flies, are produced by bait catches – in this case catches of flies feeding on a man at various levels on a tower. In related studies, the 'flight activity' of biting flies was measured by catches at light traps (Corbet, 1961). These types of catch, which reflect the sum of many separate responses, are subject to the same sorts of interpretative problems that bedevil the use of bait catches as indices of the abundance and activity of tsetse. If catches are to be used to elucidate such matters, and if they are to show the details of behaviour that can be modelled to account for distribution, it is necessary to adopt also some sampling tools that are more focused and objective. The electric nets employed in present work and in the studies of Phelps & Chapman (1980) with a tower might be useful as bare minima.

Despite these demands for complex tools, there is a large group of insects for which some pertinent data can be produced simply with the notebook and stopwatch considered by Krebs & Davies (1984). The many species of relatively conspicuous butterflies approaching environmental structures can be watched, albeit with some difficulty, and show a variety of responses that relate to occupied space. For example, *Lepidochrysops variabilis* Hedicke (Lepidoptera: Lyceniidae) fly up sloping ground to get to mating areas on hilltops hundreds of metres higher than the feeding area, but they will not travel over trees, nor through or under them to get there (Cottrell, 1965). Unlike tsetse moving up an odour plume, the *Lepidochrysops* going up a slope stop and remain at vegetational barriers. Given further simple observations, on matters such as how long the butterflies wait, the effect of barrier dimensions and the use of gaps of various width, it might be possible to predict well the distribution of the mate-seeking population.

Returning to the smaller and drabber insects whose flight can be hardly watched at all, the catches of stomoxynines, non-biting muscoids and tabanids in present work (Appendix D) indicate the extent to which the movement of these flies can be simulated by the current, bush-based expression of the modelling principles. It seems that the flies are restricted by bushes, but differ from *G. m. morsitans* and *G. pallidipes* in flying more readily over leafy hedges. For those many species of tsetse which, unlike the present two, are seldom caught far from dense forest and riverine thickets (Swynnerton, 1936; Buxton, 1955), it seems that even moderately bushed vegetation may be restricted space. Adopting the previous hypothesis that the response to entrances in traps duplicates the reaction to gaps between bushes, then the performance of various traps against the different species of tsetse might give some preliminary clues for distinctions in bush-related behaviour. Hence, it is intriguing that the Biconical trap (FAO, 1992) performs well against riverine and forest tsetse (*Green*, 1994), despite having entrances which are so narrow and raised as to make the trap inefficient for savannah species (Vale, 1982a).

A fuller ability to explain and predict the movement and distribution of the various species of tsetse depends on obtaining information of greater precision and wider variety in answer to the two main questions of how many flies are in particular areas, and what the flies are doing. Sampling at baits cannot, on its own, provide this information. One alternative might be to isolate quickly a plot of a hectare or so, in each of a variety of vegetation types, blocking movement in and out of the plots. Intense use of a range of catching devices could then extract the enclosed populations in a few days, leading to samples of the true population density in each vegetation. Present results suggest that a wall of netting, several metres tall, would be an effective isolator. However, the data produced would indicate only the number of flies in the area at the instant of isolation. It is at least as important to know the dynamics, since these produce the distribution and set the invasion rates.

The main dynamic matters are the readiness with which tsetse move across the junction between vegetations, the birth and death rates in each vegetation, and the way that the movements of flies within each vegetation are affected by the physical features within a few metres of the ground and by the abundance of hosts and shady, dry-season resting sites. A detailed solution to most of these problems seems to be in tracking individual flies by radar. A radar system being developed for tsetse has already been miniaturized sufficiently for use with bees, bugs and moths (*Riley et al.*, 1996; *Reynolds & Riley*, 1997). With further miniaturization there is the promise of elucidating where an individual tsetse goes, when and by what pattern of movement it gets there, and how long it stays and survives after arrival – most of the missing detail needed to understand tsetse distribution, invasion and sampling. Moreover, the system offers the prospect of following more closely what the flies do at various stages of their trophic and reproductive cycles. Thus, armed with radar to supplement catches and to assist their interpretation, the study of the ecology and behaviour of tsetse, and of other agile minimi, could enter the next century with much greater confidence. We could ‘watch’ tsetse flies almost as closely as we can follow tortoises.