Adult cattle:

Beef cattle: Treat occasionally strategically. Dairy cows are rarely treated; if so it is at drying off.

Since cattle need to be kept at high densities in the vicinity of greater horseshoe bat breeding sites to boost *Aphodius rufipes* and *Geotrupes* spp. beetle availability at certain critical times of year. High densities of cattle/sheep/horses are likely to lead to increased risk of heavy nematode parasite burdens, especially in young animals. These burdens need reducing by effective measures if a healthy herd is to be maintained. Young animals need more anthelmintic treatments than adult livestock, as they are immunologically naive and highly susceptible to parasitic infections at first. Ewes need treatment at lambing as they show rising levels before birth, as do mares.

Ivermectin is a broad-spectrum anthelmintic which is currently approved for cattle excluding milking herds, as pour-on and injection formulations. Most (98%) of the drug lost from the body does so in the dung. It takes several weeks for all ivermectin to be excreted from a single dose treatment, but peak levels normally occur within 2 days of treatment, followed by a slow decline.

Ivermectin-treated cattle dung has been shown to have ecotoxic effects on dung inhabiting insects, especially cyclorrhaphous dipterans and larval *Aphodius* (Strong 1993). It probably also has similar effects on *Geotrupes*. Further studies by Strong and his collaborators have shown that ivermectin-contaminated cow pats are at least as attractive to adult beetles as control pats, and that they lay eggs in it. The eggs hatch into larvae which are unable to complete development to pupae. Hence the life cycle is terminated by ivermectin, although the adults show low sensitivity to ivermectin poisoning. With drench and injection treatments all dung produced remains toxic to larval development for at least 10 days, and structural defects have been noted in larvae growing in pats 16 days post treatment. Furthermore ivermectin in large cow pats degrades very slowly with no significant losses after 45 days. Possibly in the smaller, thinner pats from young animals degradation is more rapid through the action of sunlight penetrating the surface. Sunlight causes rapid breakdown of ivermectin. In comparison to pats, degradation in soils is more rapid, and it binds strongly to particles, reducing its toxicity. In water it also binds to particles which reduce the likelihood of damage to wildlife generally, though it is highly inadvisable to dispose of empty containers directly into water habitats as fish and water fleas (*Daphnia*) are especially vulnerable.

Clearly cattle fitted with a rumenal bolus designed to release ivermectin slowly over 120 days would produce dung which is unusable for the life-cycle of dung beetles and other insects. If routinely fitted to livestock herds on a widespread basis it would potentially do enormous damage to dung fauna populations in time, and have wide effects on the ecosystem. The use of ivermectin boluses in cattle should not be permitted anywhere, not only on the grounds of damage to wildlife, but also since their use will promote the rapid development of drug-resistant parasites (Herd 1993).

Management objectives to sustain high densities of <u>Aphodius rufipes</u> near roosts

1) Promote the development/retention of permanent grazing pastures within 1 km of maternity roosts (the young sustenance zone) at a 50 % level, which is 157 hectares. Some of these pastures should be as close to the roost as possible, subject to the need for some close woodland cover to comply with flight behaviour needs. Improved or semi-improved pastures of low conservation value should be improved by non-hazardous methods, to provide high levels of grass productivity. This is needed to cope with high densities of livestock in August.

2) Stock the young sustenance zone pastures with cattle, sheep and possibly a few horses at up to 1.4 cattle/ha, or 8 sheep/ha early in the season as weather permits and rotate between cattle and sheep in specific fields (March -May). This represents up to 220 cattle or 1256 sheep, but mixtures of both are preferred. They should be enough to keep the grass sward short, without serious pasture damage in wet or cold conditions. Rest fields in June for grass growth recovery, and do not permit silage or hay cutting. Graze at 2-3 cattle/ha or cattle mixed with at least 11-16 sheep/ha (level depending on quality/quantity of grass), from the first of July until late August at least. Continue at lower levels if necessary into October as the grass state permits. In July and August these figures mean 314-471 cattle or 1727-2512 sheep (or pro rata mixtures of the two). If weather permits, continue grazing at lower levels to suit grass growth into early October.

   NB stocking levels will always have to be adjusted in the light of climatic conditions influencing the growth of grass. Numbers of livestock assume 157 hectares of pasture are available within the young sustenance zone. These figures are estimated to be required to sustain a colony with 100 young (see Part 1).

3) Ensure that cattle used from July onwards are primarily mature animals, as small ones produce small pats which dry rapidly and cannot sustain *Aphodius* larval development to viable pupae.

4) Promote the grazing of cattle at further distances up to roost sustenance zone limits (up to 3-4 km, but especially 3 km) to generate high productivity of surrounding beetle populations. At 3 km range, and about 50% grazing levels this means about 1760 cattle or about 10,000 sheep should ideally be present in the roughly 2,500 hectares of land beyond the young sustenance zone. Stocking levels and patterns will have to be more flexible enough to allow the logistics of 2) above. Livestock will need to be moved between the outer roost sustenance zone and the young sustenance zone.

5) Prohibit the use of avermectins as anthelmintics to treat livestock kept within the young sustenance zone. Recommend alternative drugs such as the milbemycin **moxidectin** (sold as Cydectin^{R}, Cyanamid), the benzimidazoles **fenbendazole** (sold as Panacur^{R}, Hoechst) or **oxibendazole** as alternatives, together with rotation of cattle with sheep, as part of a coherent programme to control parasites, without

generating drug resistance. Moxidectin and fenbendazole have been shown by Strong, Wall and colleagues to permit successful completion of the life-histories of both *Aphodius* and cyclorhaphous flies.

6) Prohibit the use of bolus, slow-release, avermectins on livestock in the wider roost sustenance zone beyond (and elsewhere), and recommend the alternatives above in 5). Allow injections, pour-on and drench formulations of avermectins if strongly recommended by vets as part of a mixed programme to control parasites and avoid resistance to these drugs developing. If used at all, avermectin treatments near bat roosts should be carried out only in the spring at recommended frequencies.

Other key prey species

At certain times of the year some *Geotrupes* species, Cockchafers (*Melolontha melolontha*), tipulid and ichneumonids become important prey items. They may be significant for relatively short periods between April and September, but their densities could have important implications for the survival of bats in the spring or autumn and pregnancy in adult females. Tipulids and ichneumons may enhance the growth of the young if *Aphodius rufipes* populations are reduced by drought or cold weather.

Since the recommendations for moths and *Aphodius rufipes* populations largely determine the overall nature of roost sustenance areas, there is a danger that specific additional recommendations for alternative prey items will overcomplicate advice to landowners. However, a mixed woodland/permanent heavily grazed ecosystem is likely to promote the populations of all of the other key prey species.

The following accounts of each key prey item are brief summaries of their ecology, inasmuch as the information may be useful as background for advisory bodies.

Geotrupes

1) *Geotrupes* is a tunnelling genus of dung beetle digging 30 cm below the soil surface to bury dung. The genus is seasonal, appearing in spring and autumn, and is relatively scarce compared with *Aphodius*, with only 1-2 individuals per cow pat. Very large adult insects (13-25 mm length) with strong spiky legs. It is important in the diet of greater horseshoe bats in spring, but not so much in the autumn, when other prey, such as *Aphodius*, are available. It may be more important in winter when other prey do not fly, in which case cattle grazed pastures near hibernacula may be important for winter feeding (Ransome, 1968, 1971).

Three common species, others rarer. All are nocturnal.:

(a) *G. stercorarius* (L) (16-23 mm; up to 1 g wet mass); common and widespread. Some authors say it prefer horse dung but others say cow dung. It breeds in spring, during April and May, flying from February until May. Two adults per pat maximum.

(b) *G. stercorosus* (=*G. sylvaticus* of Fowler; = *Anoplotrupes stercorosus* Scriba); (13-17mm). Uses cow, human, horse and sheep dung. Spring to summer breeder. Common and widespread, and is said to be forest loving.

(c) *G. spiniger* (Marsh) (16-25 mm; up to 1g wet mass) Common; autumn breeder, flying from late August until late December, but does not breed for 2 months. Its flight period suggests it could be important to feeding during hibernation. It prefers cow dung in semi-shaded sites towards field edges or in sparse woodland. One adult per pat maximum. It has been shown to colonise up to 44.4% of pats in the breeding season. It overwinters as larvae, pupae or as adults.

Life history of Geotrupes

On emergence adult beetles are very frail and light, and must feed for several weeks or months. This period has been called the 'maturation feeding period' (Halffter & Matthews 1966). This may be due to the fact that the protected nest contains only a limited amount of food, enough for larval and pupal development, but not enough for egg maturation. *Aphodius* sp. show the same delay.

Dung is found by olfaction, by flying for unknown distances. During maturation feeding, high nitrogen content of dung may be more important than carbohydrate, and explains the habit of visiting omnivore dung at this time in some species, whereas breeding takes place using herbivore dung. Protein is needed to build up muscles in both sexes, and eggs in females. At the end of the maturation feeding period the body mass has increased substantially, and females would be especially nutritious. Possibly greater horseshoe bats wait until then before feeding on Geotrupes - would be in late October or April according to species.

Cockchafer: *Melolontha melolontha*

Adults are very large beetles (20-25 mm long); males: mean mass = 872 mg wet mass; range 695-1055 mg (n = 11); females even larger). Its large size and thin chitinous skeleton makes this a highly profitable prey species as it is also highly nutritious (Hoese and Schneider, 1988). Greater horseshoe bats seem to prefer this species to *Geotrupes* or moths when numbers are high.

Life history of cockchafers

Adults fly from May to June normally, but only for a brief period of a few weeks. Exceptionally fly in mid April. In some years they may swarm. Adults feed on deciduous tree leaves, cutting large holes in the margins, and females fly to pastures with short grass to oviposit and return to woodland to feed again. Bats catch them in transit, swarming near trees or close to the ground when ovipositing. A clumsy flier which is probably easy to catch by bats. Eggs take 5-6 weeks to hatch, and larvae feed on roots of grass, herbs, shrubs and trees, taking four years to develop (Linssen 1959).

Tipulids

In order of frequency in a continuous study over four years by Robertson (1939), who incorporated data previously collected by R.D. Pinchin and J. Anderson, the species over grassland are:

Tipula paludosa (57.4%); *T. obsoleta* (14.4%); *Pales maculata* (7.6%); *P. flavescens* (6.7); *T. pagana* (5.7%); *T. marmorata* (3.7%); *T. oleracea* (3.3%); rest (10 other species.) <1%. each and never more than 2.6% of totals captured.

Life history of tipulids

All species winter as larvae underground. No adults were caught between mid November (16th) and early May. Earliest dates were: 6, 20, 5 and 22 May in sequence of 4 years. Coulson (1962) found that 90% of female *T. paludosa* oviposited within 18 hours of emergence, and daily mortality was high at 29-71% for males; 55-88% for females, so both are very short lived. Barnes (1937) found that *T. paludosa* males lived for 7 days and females 4-5 days, and that about 75% of females mated and oviposited within 24 hours of emergence. All species need short grass for oviposition. Egg hatching and larval success rates benefit from damp conditions, and some species have aquatic larvae.

Robertson (1939) showed a minor maximum peak of populations occurs in May, and a major peak in September. The May peak was due to *P. maculata*, and the September peak to *T. paludosa*. The two extra years converted the May peak to June, but they had no effect on the September peak. The change was due to the reduction in catches of the May-flying *P. maculata*, and the much greater abundance of *P. flavescens*. This seems to be the normal pattern, as only in 1933 was there a May peak. October was the only month in which females predominate over males. This was due to the fact that *T. marmorata* and *T. obsoleta* fly then, and both show a preponderance of females attracted to light traps.

Phenology

Tipula oleracea - flies from early May/early June to end September, or late October. Evidence of 2 broods/year in either May/June or August/September each lasting about 6 weeks.
Pales maculata - first species to fly each year - from early May to end of June mostly.
P. flavescens - flies from early June to late July/early August.
T. paludosa - a few in late June to the end of July, then an increase throughout August and a peak through September (max.- 14th) and a rapid fall in October with a few specimens up to early November. Of 1949 caught only 101 were outside the

August/September period. Possibly two-brooded, but no evidence for a break in adult numbers.

T. marmorata - few from mid September increasing in late September and lasting until late October (32 days activity); single brooded.

T. obsoleta - starts in v. late September and peaks throughout October, suddenly ceasing in early November (30 days activity).

T. pagana - builds up in early October to a short peak in mid-late October and tails off in early November (26 days activity).

Data on the effect of temperature on flight activity is poor, but few seem to fly below 10 °C. All tipulids fly low over the ground, and are clumsy fliers, so are likely to be easily caught by hunting greater horseshoe bats.

Ichneumonids

Only one type of ichneumon was identified in faecal samples, the Yellow Ophion, *Ophion luteus*. It may not be a single species, but a parasitic complex. It is a large ichneumonid (15-20 mm long) which is thought to parasitise noctuid moth larvae. These larvae are subterranean and nocturnal, feeding at ground level from mid summer until late December, before diapausing overwinter. They continue development in the following spring. Hence the parasites are especially active in late autumn, early winter, and in spring. They appear to be able to fly at very low climatic temperatures (Part 1). In order to parasitise their prey females must hunt them at ground level. This may make them vulnerable to greater horseshoe bat predation in a similar manner to tipulids.

Management objectives to promote these key prey species

The management objectives already proposed to sustain high densities of moths and *Aphodius rufipes* provide good conditions for high densities of *Geotrupes*, Cockchafers, and tipulids by either providing dung or tree-leaf food supplies, or short grass on permanent pastures which aid oviposition. High noctuid moth densities will promote the levels of the Yellow Ophion. There are therefore few additional objectives to propose.

They are as follows.

1) Encourage the retention of permanent pastures in order to permit the long life-cycle of the cockchafer to be completed, as well as those of tipulids and *Aphodius rufipes*. Pasture ploughing should be strongly discouraged, at least within the young sustenance zone. In the wider roost sustenance zone permanent pastures should be encouraged as much as possible. Furthermore, no insecticide treatments should be permitted to control cockchafer larvae, leatherjackets (tipulid larvae) or wireworms (larval click-beetles) in pastures. These would seriously affect important prey items for greater horseshoe bats.

2) As tipulid larval development is favoured by damp conditions, any aquatic environments and/or marshes should be retained, or their development encouraged. This would be particularly advantageous fairly close to the roost. Aquatic environments will also favour the production of adult caddis flies (Trichoptera) in certain months, particularly May and late August/September, when other food supplies may be erratic.

PART 3: IMPORTANT FEATURES INFLUENCING BAT MOVEMENTS BETWEEN ROOSTS AND FORAGING AREAS

Introduction

The provision of rich foraging areas within the roost sustenance zone will be of little use if the behaviour of the bats does not permit access to them. Observations of greater horseshoe bats leaving to forage from maternity roosts show that this species strongly adheres to regular flight paths which may extend for considerable distances. Flights are close to the ground and mostly beneath vegetational cover. Paths may be changed during a summer season, such as when the bats switch from woodland to pasture feeding, but recur annually with a similar pattern unless vegetational features change substantially.

Roost exit flight paths are never directly out into open areas unless bats have no alternative routes. This behaviour is in contrast to exit flights of many vespertilionid bats which emerge out directly into open areas at high levels, and disperse rapidly in many directions. The flight behaviour of greater horseshoe bats may result from predation pressure (Speakman, 1990, 1991), and would account for the tendency for this species to emerge later than pipistrelles. Pregnant greater horseshoe bats, which progressively lose agility as pregnancy progresses, emerge when it is almost completely dark just before giving birth. In contrast, early in the spring and when in mid to late lactation, they often emerge in much lighter conditions (*pers. obs.*). These periods are both times of nutritional stress, and indicates that these bats are constantly having to choose between the risks of predation and those of starvation. Certainly, exits from roost buildings always shows frequent circling behaviour by the first individuals which leave, suggesting that light-sampling behaviour is taking place. When in the field they fly fast across open well-lit spaces and head for cover.

Habitats around roosts should therefore reflect these behavioural restraints, which may restrict or prevent access to favourable foraging sites. Since in my experience practical problems vary with roost distance, I will consider habitat features in two sections; those close to the roost, and those away from it.

Important habitat features close to roosts

Jones *et. al.*(1995) found that emergence times of bats from two maternity roosts separated by about 2 km varied by from 5 to 37 minutes in the summer. The earlier emergence occurred at the site within woodland, which was much darker than the one located in the roof of a house. If this also affected returns at dawn, it would mean that bats may lose up to an hour's foraging a night as a result of high natural light levels at roost exits. Since darkness only lasts about 5 to 6 hours in late June, this may have serious consequences by delaying births of pregnant bats. Birth-timing has been shown to be crucial to the long-term survival of cohorts of greater horseshoe bats, and bat populations

(Ransome, 1989, 1995). Clearly no artificial lighting should be present around roost exits since they would make emergences even later.

Outside the roost exit, suitable cover should be present to provide darkened flight paths to assist safe departure into the wider habitat. Problems are most likely to arise at roosts located in occupied buildings, especially if extensive open lawns surround them. Lines of trees, tall shrubs or fences and buildings may all be suitable for cover.

Important habitat features away from roosts

Jones and Morton (England), Duvergé (England), Bontadina (Switzerland) and Pir (Luxemburg) have all carried out serious and extensive radio-tracking studies of greater horseshoe bats. The behavioural features of travelling and hunting bats they describe, both published and by personal communication, are remarkably consistent. They are briefly summarised in the following account.

Greater horseshoe bats travelling away from the roost towards foraging grounds (commuting) at distances of up to 4 km radius from the roost, do so along distinct flight paths. Up to three main flight paths radiating in different directions can be used by a single colony, with varying proportions of the colony using different ones through a single summer, possibly as different foraging areas became profitable. The majority (about 70%) of flight paths run along the edges of woods, woodland rides or tall hedges, only rarely crossing open fields. When they do cross open fields, it is normally well after dusk, and rarely on clear moonlit nights. In all cases commuting bats keep close to vegetation or buildings, some of which are used as night roosts, or resting perches for culling insects. They travel at about 1 metre height above the ground or away from vegetation edges.

Hence contiguous lines of vegetation of sufficient height and thickness to provide darkness in the early part of the night, and before dawn, when light levels are still relatively high are highly desirable for commuting bats. These lines should link up important foraging areas to ensure bat accessibility to them. As bats may travel up to 4 km radius from the roost, and woodland blocks are relatively small in many parts of this country, the most effective method of linking such blocks is by tall hedgerows or tree lines.

Features promoting successful foraging by bats

Greater horseshoe bats capture prey by two main methods; continuous hunting on the wing (hawking), and by flycatching from a perch (Jones and Rayner, 1989). Hawking over pasture occurs at low levels, usually between 0.6 and 1.5 m and close to woodland edges or hedgerows. About 95% of all hawking occurs within about 10 metres of hedgerows or woodland edge (L. Duvergé, *pers. comm.*). Perch feeding involves hanging from a suitable projection, such as the end of a bare branch. This is usually at about 1.5-2 metres from the ground, and sheltered by an overhead screen, such as the leaf canopy above it. This behaviour seems to confirm the predator avoidance behaviour seen at roost exits. The bat scans the area in front of it with long constant-frequency ultrasonic pulses, whilst rotating its body axis through 360 °. The short distance from the ground of feeding perches may be set by the minimum detection distances of a range of prey size (Walters *et. al.*, 1995), and also the higher concentrations of many of its prey species close to ground level (referred to in Part 2). The bat intercepts detected prey as it flies past, returning to its perch, where it may cull captures of large prey with inedible or less edible parts.

All radiotracking studies confirm the extensive use made of woodland edges. Duvergé notes, in addition, the use of hedgerows as perching sites, in which case they almost always use the leeward side. Hedgerows are also features along which bats hunt on the wing. It is well known from the work by Lewis (1969a, 1969b, 1970) that hedgerows have important effects upon the distribution of aerial insects. These effects include reduction of windspeed, concentration of insects from adjacent habitats into regions of drag, particularly on the leeward side, during winds, and the generation of substantial numbers of insects from hedgerow plant biomass. These benefits require the hedgerow to be sufficiently broad and thick. The advantages increase with taller and thicker hedges.

Livestock make good use of the shelter provided by hedgerows, woodland edges and specimen trees in park land. They tend to rest near or below such features, and their dung concentrates at these places. This behaviour means that concentrations of dung beetles are likely to form near sites favoured by hunting or perching bats.

The edge effect, which results in high concentrations of fauna at the junction of any two different habitats, is well known. A tall thick hedge is a very efficient method of generating a maximum level of insect prey items using a minimum area of land. Besides promoting access to major foraging areas for commuting bats, hedgerows can be important creators of the physical conditions that enhance insect concentrations and reduce windspeeds for economical hunting flight.

Management objectives to promote early emergence from roosts, safe access to foraging areas, and successful foraging

1) Promote the development of dark regions around the immediate roost exit by restricting the use of artificial lights, and encouraging the development of light screens. These may usefully include evergreen trees and shrubs.

2) Promote the development of shaded flight pathways leading to the nearest wooded areas. These may also be achieved by the use of tree and/or tall shrub lines. They should include species of trees which produce overhanging branches low down in an umbrella-like cover, such as beech, apple or plum trees, not trees like poplar, with vertical branches, which can be spaced out so that their canopy just overlaps. Many small ornamental species would be suitable if the variety has the right shape, and houseowners insist on attractive trees in their gardens.

3) Promote the planting of hedgerows and tree lines across large tracts of fields and pastures to create smaller fields so that hawking bats can utilise a larger proportion of the field area. Convert existing highly trimmed, square-shaped hedgerows into a more bat-friendly state. Hedgerows should be broad (3-6 m across), and at least 3 metres mean height, and include specimen trees at intervals which also grow in an umbrella-like fashion in open conditions. This structure will allow safe perch-hunting over adjacent pastures, and a safe refuge for those that hawk when moonlight levels are high.

4) Promote the replacement of wire fences with hedgerows as in 3).

5) Promote the development of park land, by planting large specimen trees, and groups of smaller ones, on the grazed permanent pastures. If orchards occur with a grazed understorey, they should be retained, with suitable advice on restrictions in pesticide use to prevent insect removal or possible bat poisoning via the food chain. This habitat will also permit sheltered perch-feeding and hunting on the wing.

6) Promote the development of grazed meandering grassy woodland rides with occasional wider glades leading towards other foraging areas, such as pastures. Also create some scalloped indentations into long straight woodland edges. These changes will greatly add to available wind-sheltered edge zone between woodland and pasture, which is highly favoured by foraging bats.

PART 4: LAND MANAGEMENT PRESCRIPTIONS INTEGRATING WITH CURRENT FORESTRY AND FARMING SYSTEMS TO MAINTAIN OR ENHANCE FORAGING AREAS

These prescriptions are divided into three sections. The first section covers prescriptions common to the whole roost sustenance area (up to 3 km around the roost). Sections two and three cover the young sustenance zone (up to 1 km around the roost) and the wider roost sustenance zones separately, since the nature of the desirable livestock management regime of the desirable habitat varies between them.

Prescriptions within the whole of the roost sustenance zone

1) Support the retention of all mature ancient semi-natural deciduous woodland, old orchards and park lands.

2) Support the development of further extensive blocks of deciduous woodland up to about 50% of the total area.

3) Support the replacement of coniferous plantations with deciduous trees gradually over a period of time, avoiding extensive clear-felling.

   NB All woodlands should be permeated by grassy rides, contain grassy glades and be surrounded by regions of permanent pasture, especially close to roosts. They should be managed without insecticide treatments. Glades probably need to be 10 - 15 metres across before they will be used by the bats for feeding.

4) Support the retention of existing hedgerows and tree lines linking areas of woodland. Encourage hedgerow improvement to become 3-6 m wide, mean 3 m high, with frequent standard emergent trees.

5) Support the development of new hedgerows or tree lines, as in 4) above, to divide up large grazed pasture areas to create many smaller fields and link up with blocks of woodland.

6) Support the retention of all grazed permanent pasture, subject to the need to create sufficient woodland and hedgerows.

7) Support the development of further grazed permanent pasture up to 50% of the total area. These pastures should ideally be developed as mixed park lands and small fields separated by substantial hedgerows.

   NB. All grazed pasture should be permanent, and managed without any insecticide use at all. Both are crucial to avoid disrupting supplies of cockchafers and tipulids.

8) Support the retention or creation of marshy or aquatic habitats if feasible.

Prescriptions for grazing regimes within the young sustenance zone

1) If permanent grazing pasture is present at a 50 % level, 157 hectares should be available within 1 km of the roost. Substantial areas of grazed pastures, as park land or small fields with hedgerows, should be as close to the roost as possible. Where there is no other conservation interest, they should be managed to be improved by non-hazardous methods, to provide high levels of grass productivity. This is needed to cope with high densities of livestock between July and September. Unimproved pasture or semi-improve pasture with a high conservation interest should not be improved by the addition of fertiliser.

2) Support the stocking of these pastures with cattle, sheep and possibly a few horses at 1.4 cattle/ha, 8 sheep/ha early in the season as weather permits and rotate between cattle and sheep in specific fields (March -May) to keep a short, but not seriously damaged, sward. This represents 220 cattle or 1256 sheep, which should keep the grass sward short, without serious soil disturbance in wet conditions. Mixed grazing at say 110 cattle and 628 sheep, rotated to reduce parasite problems, is an advantage long term.

   Rest fields in June to allow grass growth recovery which is likely to be necessary, and do not permit silage cutting.

   Graze at 2-3 cattle/ha or cattle mixed with 11-16 plus sheep/ha (maximum level depending on quality/quantity of grass), from the first of July until mid September at least. This represents 314-471 cattle or 1727-2512 sheep if 157 hectares of improved pasture is available. Mixed grazing with sheep, with cattle dominant, is also desirable. If weather permits, continue grazing at lower levels into early October.

4) Support grazing from July onwards using primarily mature cattle; either beef or milking herds.

   NB stocking levels may need to be adjusted in the light of climatic conditions influencing the growth of grass in a particular summer. Numbers of livestock assume 157 hectares of pasture are available within the young sustenance zone. These figures are required to sustain a colony with 100 young (see Part 1).

Prescription for grazing regimes outside the young sustenance zone in the wider roost sustenance zone

1) The roost sustenance zone limits may be up to 3-4 km, but especially 3 km. At 3 km range, and about 50% grazing area levels this means about 1414 hectares of grazed land, of which 1257 ha are outside the young sustenance zone. 1257 cattle, at 1/ha,

or about 6285 sheep at 5/ha, should ideally be present. Mixed grazing of cattle and sheep with rotation among pastures should aid parasite control. At these lower grazing levels longer swards should be freely available to the larvae of noctuid moth species. Stocking levels and patterns of grazing will have to be more flexible than in the young sustenance zone to allow the logistics of the regime specified for that zone.

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APPENDIX A: MOTH POPULATION ESTIMATIONS

There is no method currently available which accurately measures population levels of moths in an area. The problem is exacerbated by two major factors as follows.

1) The moths present in an area consists of resident individuals which have developed locally, and varying proportions of immigrants which may soon move on. The proportions vary with the moth sp. eg Scarlet Tiger moth (*Callimorpha = Panaxia dominula* (L)). lives in discrete residential colonies, the Silver-Y moth (*Plusia gamma*) is largely migratory, moving NNW in spring & summer, and S in autumn (Williams 1958, Baker 1978). The main difference between species is the length of time each spends in its particular habitat before once more leaving to travel across country (Baker 1969). A result of this is that the mosaic dispersion of a species over large geographical regions through time is forever changing (Taylor & Taylor 1977). Despite this mobility, within-habitat stability of numbers of 263 sp. caught at 53 sites was shown over six years (Taylor and Woiwod 1980). Baker 1984 suggested this happens because mobile individuals each make the best decision when to leave an area.

   A consequence of long-distance migration is the smoothing of regional differences in morph frequency of polymorphic species. Large Yellow Underwings (*Noctua pronuba*) has a more or less constant morph frequency throughout Britain (Cook & Sarsam 1981); are long-lived in laboratories (55 days males; 75 females; Singh & Kevan 1965); and probably travel at least 100km (Baker 1985). Baker made this claim partly from the very low recapture rates of moths at Woodchester Park.

2) Traps have different efficiencies in capturing moths, and the relationship between catch numbers and population levels is usually unclear.

   There is a debate about the effective range of light traps. Baker & Sardovy 1978 argue from mark-recapture experiments that the range of attraction is just 3 m to a trap 0.6 m above ground level, and that the angle of elevation is more important than brightness. Other workers argue that the attraction range near the ground is from 100-500m, and that brightness and contrast with background illumination are the critical factors (Hartstack *et al.* 1968; Bowden and Morris 1975). Gregg *et al.* (1994) report personal communication with V.A.Drake and R.A.Farrow who observed radar views around ground-level light traps which showed plumes of insects extending up to 200m from the traps. However, Muirhead-Thomson (1991), after crosswind trapping experiments argues that, although light traps are perceived and influence flight behaviour at much greater distances, they are not effective at catching moths over more than 10-25m. This distance is similar to the findings of Sotthibandhu (1978), who tethered moths and exposed them to a 125 W mercury-vapour lamp raised 9m above ground level. They responded between 10 and 17m.

   Baker (1985) argues that light traps are highly selective to moths, even when they have the right spectral composition (Mikkola 1972), and intensity (Bowden &

Morris 1975). In addition, for a moth to make a mistake and enter the trap its lamp must satisfy critical elevation and vertical dimension criteria. These must mimic the moon's size and position in the sky, so that it affects the dorsal ommatidia of the eyes. Even these factors were not sufficient, as he argued the moth must also be in a physiological state to make use of moon orientation (i.e. in a migratory phase). Supporting evidence for his views included: there appears to be a better correlation between light-trap catch and volume of migration as shown by radar (Schaefer 1976) than between light and suction-trap catches (Taylor & Carter 1961); light-traps are ignored by adjacent nectar-feeding moths (Baker unpubl. data); males, which are probably more migratory than females (Baker 1978) predominate in light catches. Exceptions to the latter include *Noctua pronuba*, in which females have a long pre-ovulatory period (Singh & Kevan 1965) and are probably more migratory.

Most moth migration occurs at heights of tens or hundreds of metres above ground level (Schaefer 1976; Riley *et al.* 1983). If it is the migrant population that is being caught it is likely to be during the low-flying phase at the start or end of migration (Baker & Sadovy 1978). This would be consistent with the findings of Taylor & Carter (1961) that moths fly lower at low densities, and higher at higher densities, if high densities reflect additional concentrated migrating individuals.

I offer the following hypothesis in an attempt to explain these conflicting views. Some species of moths are affected by similar circumstances to locusts when in the larval phase. They remain solitary and resident in an area normally, but become migratory if overcrowded as larvae, possibly in response to low food supplies dwindling in certain 'outbreak areas'. Migratory moths, since they are physiologically programmed to orientate by a distant light source, normally the moon or stars, are most vulnerable to capture in light traps.

Trap capture likelihood, and distance of effective attraction, even in migratory individuals, is also influenced by at least the following factors.
(a) The lamp intensity and vertical size; (b) prevailing contrasting illumination intensities; (c) its elevation from the moth's flight path; (d) competing point sources of light which may distract; (e) screening by obstacles especially nearby, which allow escape; (f) levels of cross-wind. The flight power of the moth species is also likely to be a factor in its capture rate.

Clearly some moth species are always resident (eg Wood Tiger), and others highly migratory (eg Large Yellow Underwing and other noctuids), but not completely so. If the migratory urge is variable as suggested, and related to population densities in outbreak areas, probably to the south of Britain, in continental Europe, the great variation in migration levels observed may be explained.

APPENDIX B: FACTORS INFLUENCING POPULATIONS OF SOME IMPORTANT MOTH SPECIES

(Data mainly from Carter & Hargreaves, 1986 and South, 1961)

1) *Noctua pronuba* **(L.) (Large yellow underwing)**
Habitat: agricultural land, gardens, waste ground, open country, moorland where suitable plants grow. **Food plants:** dandelion (*Taraxacum officinale*), chickweed (*Stellaria media*), dock (*Rumex*), grasses and a wide range of herbaceous plants, - wild and cultivated. including dog violet (*Viola riviniana*) and primrose (*Primula vulgaris*), present in woodlands. **Life-history:** one generation per year; eggs laid in compact flat masses on underside of leaves in July and August. Hatch in August. Feed until mid-winter before diapausing, completing growth in spring. Eat leaves and stems. Active at night, sheltering in soil by day. Pupate in May in subterranean cocoons. Emerge in June or July and fly until late August; rarely September and October.

2) *Noctua (=Euschesis) comes* **(Hübner) (Lesser yellow underwing)**
Habitat: meadows, gardens, waste ground, hedgerows, open woodland, heaths. **Food plants**: as for *N. pronuba*, but also foxglove (*Digitalis purpurea*), heather (*Calluna vulgaris*), sallow (*Salix*), hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*) and silver birch (*Betula pendula*). **Life-history**: one generation per year. Eggs laid in August and hatch in September. Larvae feed for a short time on low plants before diapausing over winter. In spring they become active and feed on low plants again, but also ascend tree trunks to feed on newly emerged foliage after bud-break. Mainly nocturnal activity shown. Pupate in underground cocoons in May, and adult moths normally fly from July to August.

3) *Agrotis exclamationis* **(L). (Heart and Dart)**
Habitat agricultural land, meadows, gardens, waste land and other places where suitable food plants grow. **Food plants:** dock (*Rumex*), plantain (*Plantago*), chickweed (*Stellaria media*), fat hen (*Chenopodium album*), turnip (*Brassica rapa*), sugar beet (*Beta vulgaris*), and many other herbaceous plants. **Life history**: one generation per year; eggs laid on leaves and stems in June, caterpillars hatch in July. They feed at night on roots, stems and leaves, hiding under soil by day. Fully grown by autumn; burrow into soil and diapause as larvae overwinter; pupate in spring and emerge as adults flying in June and July; sometimes in September as well.

4) *Apamea (= Xylophasia) monoglypha* **(Hufnagel) (Dark Arches)**
Habitat: meadows, moorlands and other grassy places. **Food plants**: cocksfoot (*Dactylis glomerata*), couch grass (*Agropyron repens*) and other grasses eaten, including their roots. **Life-history**: eggs laid in July; hatch in about ten days; caterpillars August-April/May. They feed at night at the base of stems. Pupate in May under soil. Emerge as adults flying from June to August; and sometimes also in September and October.

APPENDIX C: THE ECOLOGY OF *APHODIUS RUFIPES*

Aphodius is a very ancient genus, having been found in Baltic amber from the Lower Oligocene, 40 million years ago. Its distribution is virtually world-wide, as long as there are large grazers present. *A. rufipes* is known from Pleistocene deposits found at Isleworth, Middlesex, 43,000 years ago, and at Barton Court, Oxfordshire in late Roman times, 1,600 years BP (Cambefort, in Hanski and Cambefort 1991). Hence nocturnal *Aphodius* species have been potential prey items for bats over major time periods, and possibly since *Rhinolophus* evolved at least 35 million years ago.

Research findings relevant to comments made in Part 2.

Adult features:

1) Its relatively large size (93 mg live mass), and the fact that most of it is eaten (*pers. obs.*) means that between 50 and 70 beetles permit a full feed for one bat. In an hour a bat could easily catch and consume these numbers as this allows a detection, capture, handling and consumption time of 51 to 67 seconds/beetle caught, if they were freely available.

2) *A. rufipes* was the most sensitive to desiccation out of 8 species tested. Death provoked in 10 hrs at 0% RH and 20 °C. (Landin 1968).

3) Adults avoid temperatures <9 and >19 °C; preferred range is 14-17 °C. Cold stupor sets in below <6 °C, and convulsions & death >38 °C. Flight can occur above 9 °C. (Landin 1968), which is one of the lowest levels for the genus.

4) Normal flight direction is against the wind as it uses olfaction to find dung (Landin 1968). High winds are thought likely to suppress flight. Low winds assist in fresh dung location using the antennae and possibly maxillary palps (Landin 1968).

5) No activity was observed outside dung in heavy rain - possibly due to lack of olfaction clues (Landin 1968).
"It should be presupposed that extremely strong winds and continuous heavy precipitation constitute definite impediments to all activity, particularly flight, outside the droppings." (Landin 1968).

6) The membranous structure of the mouthparts of adults and the narrow channels of the mandibles force them to feed on fluids (Landin 1961). Hence fresh cow pats are a preferred diet. This is especially true in exposed habitats as dung dries rapidly. Less so in shaded habitats where horse dung is often used.

7) Eggs laid in dung; rarely in soil, in batches of about 5 (White 1960, Holter 1979). About 20-25 laid altogether (Schmidt 1935). Smaller Aphodius species are claimed to produce about 100 eggs per female (Holter 1979, Yasuda 1987). As ovaries

contain only 3-6 ovarioles, a period of recovery is needed between laying phases (Schmidt 1935). When females emerge from pupae they have immature ovaries (Madle 1934, White 1960) - need 1-6 weeks period to develop eggs and mate. A further period of 1-2 weeks or more elapses before females lay eggs (data from isolated females - Landin 1961).

8) As all dung rapidly dries out, especially in exposed positions (Landin 1961), points 5) and 6) above mean that adults are constantly forced to leave their dung supply and fly in search for fresh ones. Furthermore its nutritional value may deteriorate rapidly. Most adult *Aphodius* have left cow pats by the second day (Laurence 1956). This means they concentrate in regions with fresh pats and are repeatedly exposed to predation by bats. *Aphodius* females move longer distances and/or move more often than males (Hanski 1980a) and so disperse widely. Foraging greater horseshoe bats are known to follow cattle moved into new fields on the day the cattle are moved and feed on dung beetles attracted by the new dung (L. P. Duvergé *pers. comm.*). Maximum distance of attraction in the field is not known, but in experiments adults responded to dung from at least 40 cm in still air (Landin 1961). Landin refuted the claim of previous authors (such as Warnke 1931, 1934, and Madle 1934) who were of the opinion that their olfactory capabilities were very small. He argued that winds attract beetles from considerable distances, and stated that fresh dung placed in a field without other droppings would attract beetles within minutes. He also quoted a situation where fresh dung was placed on an isolated island 10 km from the nearest grazed island, and beetles arrived to feed on it. Furthermore Hanski attracted large numbers of *A. foetidus* to a dung trap in the centre of Oxford, several kilometres from the nearest cattle pastures.

9) Emigration rates from dung are density dependent at high densities (Landin 1961). Rates increase if they have < 25-70 times their volume of dung available per adult. An average cow pat of 1500 cm3 volume could support from 178 to 500 adults (max. = 63/pat observed by Holter 1975).

10) Denholm-Young quotes mean figures from 15 studies as follows. Grazing season = 188 days; average stock level (cattle) = 1.4 per ha; pats/cow/day = 11.9.

This translates into 16.7 pats/ha/day, and a maximum of 1052 adult beetles/ha/day. At 93 mg wet mass/adult this represents about 98 g/ha/day, or about 0.1 kg/ha/day of adult beetles. Adult bats eat about 3-4 g of wet mass of insect food/feed, or 6-8 g/bat/day. Juveniles eat from 0 to 3 g/bat/day between 29 and 45 days of age whilst they feed close to the roost at a distance of up to 1 km. This covers an area of 314 ha. If all the area was grazed pasture 0.1 x 314 = 31.4 kg of adult beetles could arrive at fresh pats per day. 100 pre-weaning young bats eating 3 g/day would consume 0.3 kg adult beetles/day if they ate no other food. This represents about 1% of available beetles if they were at maximum densities in the pats.

In practice stocking levels of 2-3 cows/ha can be maintained from mid July to late August in most years, so only 50% of the close surrounding habitat (157 ha) of a roost needs to be grazed pasture to keep predation levels at about 2%. There are allowances for lower levels than the maximum in the pats, since predation levels can probably reach 5%. Furthermore, since juveniles are normally born over a three week period, and since they steadily increase their foraging range after they are 30 days old, several hundred juveniles may be supported by these stocking levels.

If 157 ha of the land around a roost up to a distance of 1 km (50%) is grazed by cattle at 2-3/ha it means that 314-471 cattle should be kept to sustain a bat colony with 100 young. Smaller colonies may require lower stocking levels, but it is probably inadvisable to drop much below 100 cattle within the young's sustenance range (0.7 km). This is because low densities of fresh dung from grazers are much less attractive to colonising dung beetles than high ones, and population levels of adult beetles may fall disproportionately.

11) Adult greater horseshoe bats travel much further than pre-weaned young - up to 4 km; mean 2.84 + 0.91 km (Jones et al. 1995). At 3 km range they may feed over 2828 ha. If 50% of the area outside the young sustenance zone is grazed pasture (1257 ha) with 1.4 cows/ha and adult beetles = 0.1 kg/ha/day available it should generate 126 kg of adult beetles. A colony of 700 adults eating g/bat/day within this range would consume 5.6 kg beetles/day if they ate nothing else. This represents about 4.4 % of those in the area. Since fresh dung may attract beetles from a distance of many kilometres (see 8) above in Research Findings) the removal of a part of the local population by bat predation may promote immigration from further afield, if grazers are abundant there. Furthermore, in most years adult bats feed mainly on moths (Part 1) so the densities of cattle could be lower than 1.4 /ha without serious risk of shortages, especially as moths are only likely to be in short supply in cold wet summers. Such weather promotes the levels of *Aphodius rufipes*.

The key requirement may be the presence of abundant grazers, especially cattle and horses, within the 1 and 3 km radii. The most crucial for juvenile growth and survival, as well as helping reduce commuting distances for lactating females, will be 2-3 cows/ha in the 157 ha of grazing pastures which should be available (50% of 314 ha @ 1 km radius from roost). This area can support 314-471 cows for a short period between July and August, and up to 220 long-term.

The number of grazers in an area is crucial to the level of populations of dung beetles. In southern France in the mid nineteenth century, tens of thousands of sheep and goats used to be driven from the Garrigue to Mont Aigoual for the summer. Rural depopulation of grazers followed at the end of the century and intensified in the twentieth century. Many species of dung beetle became rare or extinct in this region, whereas in other regions where grazers did not decline, a rich fauna of dung beetles persisted (Lumaret and Kirk 1991). Similar losses of dung beetle populations are now occurring in northern Italy and Spain as grazers are removed.

12) To ensure against climatic disasters, a mixture of habitat types should be provided. These must include exposed cattle-grazed fields, preferably of different

topographical orientation (south and north-facing), surrounded by suitable hedges for perch-feeding, cattle-grazed parkland and/or grassy orchards, and deciduous woods or forests criss-crossed with woodland rides. The latter two habitats are particularly suitable for horse grazing.

Such a habitat range, suitably arranged in mosaics, should offer a large edge zone, and regions of woodland with a rich diversity of herb-layer plants. These woods should allow feeding in spring and autumn at critical marginal climatic temperature levels (Jones et al. 1995), and promote good supplies of maybugs (*Melolontha melolontha*) in May/June, and moths from June onwards. In mid to late summer adult bats usually feed on large moths whenever they are abundant, in preference to *Aphodius rufipes*. Juveniles appear to be unable to feed on moths until they are at least 40-45 days old, possibly because they are unable to compensate for Doppler-shifts in echolocation. Moths are much faster fliers than *Aphodius* beetles. Hence juveniles are critically dependent upon *Aphodius rufipes* (usually) or other small weak-flying insects.

13) Although different types of grassland have different dung insect faunas (eg Merritt and Anderson 1977), this factor is not so important to *Aphodius* sp. This is because almost the whole life cycle occurs within the dung.

Requirements of the larvae of *Aphodius rufipes*.

1) The average population of larvae of about 100 passes 40% of its pat through their gut (Holter 1975).

2) A single pat can have up to 9 *Aphodius* species adults and 1 *Geotrupes*, but only 3 larval species at any one time (Denholm-Young 1978). This is because adults can feed on a variety of fresh dung in many habitats, but adults are much more selective in both before laying eggs. Eggs are much less aggregated than adults (Holter 1979). Second instar larva needs from 200-400 times its volume of dung for optimal development, and 3rd instar larvae from 60-150 times (Landin 1961), or 2-3 cm^3 dung per 2nd instar larva, $5cm^3$ per half-grown 3rd instar larva. Densities of larvae can average 100 per cow pat, passing 40% of pat through their gut (Holter 1975). Larvae migrate vertically through the dung to obtain their preferred temperatures (Landin 1961) and so may compete for food supplies at high densities. If the densities of larvae exceed the requirements listed above, the larvae either force each other out of the dung, or bite each other to death (Landin 1961). This is especially likely to occur in the field as densities of all *Aphodius* species may reach several hundreds (Merritt 1974) or even thousands (Mohr 1943) per pat. Competition between species within dung in Landin's experiments gave no indication of one species being superior to another. Larger species, such as *A. rufipes* were not superior to smaller ones. However, in competition with dipterous larvae, Aphodius larvae are superior, since the former lack biting mandibles. High densities of dung beetles in dung are known to suppress populations of dipterans.

3) Larvae are more susceptible to desiccation than adults, and as they are unable to leave the pats before completing their larval life history, dehydration of the dung leads to major mortality. They have 3 larval instars and a pupa. The first larval instar is most vulnerable to desiccation. The third instar larva hibernates over winter within the pat in Sweden (Landin 1961) when desiccation is unlikely. It leaves the pat and pupates in the surface layers of the soil in spring. White (1960) states that adults also can hibernate in England.

4) Time needed for development is temperature dependent. In summer complete larval development can occur in 4 weeks (Landin 1961).
Landin's timings: Eggs hatch in 3-5 days; 1st instar = 2-4 days; 2nd instar = 3-8 days; 3rd instar = 3-5 weeks when hibernation starts. Third instar larvae must finish development before hibernating as it is incapable of feeding on dung in the spring. This may be due to dung quality deterioration over winter.

5) The pupae of *Aphodius* generally last from 1-4 weeks (Landin 1961, Holter 1975, Stevenson and Dindal 1985), but specific details for *A. rufipes* are not available. It may last much longer as adults do not usually start to fly until late May, or early June (Hanski 1979).

6) Larvae are capable of feeding on the coarser fibres of cattle dung because they have powerful sclerotised mandibles, and larger mouths than the adults (Landin 1961).

7) Dung characteristics allowing the completion of larval life history include:
(a) retention of enough water to prevent desiccation
(b) remaining within the thermal range (-4 to 46 °C, (Landin 1961)).

8) Larvae can develop in cow, horse or sheep dung. Landin (1961) experimentally tested adult *Aphodius* beetles' response to cow, horse and sheep dung. He found all species were attracted by all kinds of dung, but less so to horse dung with the exception of *A. rufipes*. This attraction may reflect the feeding requirements of the adults (see above), rather than their suitability for larval development. He felt that generally it was not the kind of dung that mattered, but the climatic conditions of the environment, particularly affecting the microclimatic conditions within the dung, which restrict dung beetles to a certain habitat.

9) Different types of grassland have different dung insect faunas (eg Merritt and Anderson 1977), but such differences are not so important to *Aphodius*, which breed within the dung. Hence *Aphodius* sp. are less affected by soil type and vegetation cover. These factors may exert small effects via their influence on dung desiccation rates.

10) The abiotic environment in which the dung is dropped has a profound effect on the composition of its fauna (Mohr 1943) as it controls its desiccation rate and temperature range, and each *Aphodius* species has its own characteristic tolerance ranges (Landin 1961). So does seasonality since each species has its own period of

activity (Hanski 1980b, 1986, Holter 1982). Landin (1961) classified Aphodius into 3 groups as follows:

i. Eurytopic - wide range of habitats selected
ii. Oligotropic - reasonable range
iii. Stenotopic - narrow range. *A. rufipes* is eurytopic.

11) The key to successful completion of larval development is the retention of sufficient water within the dung (see comments on species survival above - points 3) and 9).