a.m.r.c. reviews

The "Australian Meat Research Committee Review" is a bi-monthly publication. It will review and report recent research results that are relevant to the Australian livestock and meat producing industries. In doing this it will concentrate on, but will not be restricted to, those fields in which the Australian Meat Research Committee has sponsored research.

The intent of the publication is to keep the rural consultant and the extension officer informed about what is happening in meat research, and through them to promote the application of research findings.

In the pursuit of this aim, the Committee welcomes comment and suggestions for improving the publication.

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Work Copy

The Australian dung beetle project 1965-1975

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The viability of every pasture ecosystem is based on the normal functioning of its nutrient cycle, and this is a very complex process with a great number and variety of components. Each of these components, including the grazing animal[40], plays its part in keeping the system running productively. Should any of the components malfunction or disappear, or should the system be invaded by extraneous elements, there may be repercussions within the pasture ecosystem or even throughout the entire biome. Some of the effects are harmful. The avoidance of others would increase productivity and/or improve environmental quality.

The Australian grassland ecosystems were profoundly disturbed by the arrival of domestic stock. Prior to that the nutrient cycling is thought to have functioned smoothly in that the dung of the principal herbivores, the marsupials, was relatively unimportant and probably never accumulated in polluting quantities. A portion of the marsupial dung was buried by the native dung beetles. This burial speeded up decomposition and returned essential nutrients to the soil.

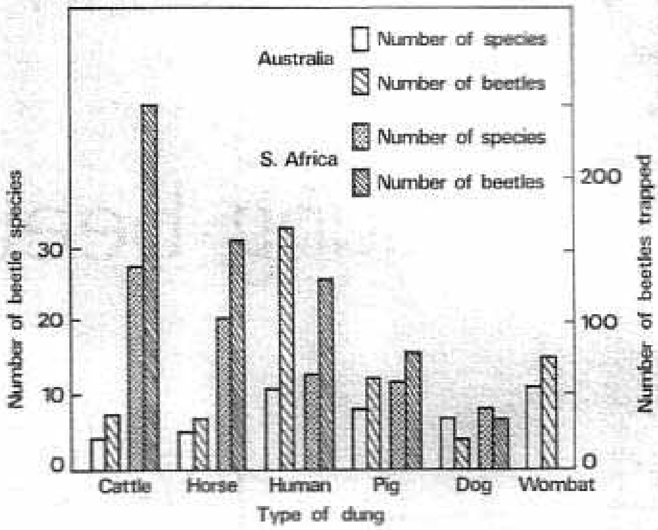
The introduction and rapid increase in the numbers of domestic grazing animals progressively upset this primitive cycling. As the large, voluminous droppings of horses and cattle accumulated, a pollution problem arose in many areas through the extensive fouling of valuable pasture land. The problem of pasture wastage and production loss through fouling by dung has long been understood by agrostologists in and outside Australia[15,25,38,42,50,67] but usually with resignation, as no alternative was envisaged. During the 1950's the possibility of an ecological approach to improve this unfavourable situation in Australia was recognised, and the suggestion of using dung beetles to disperse the dung was first put forward in 1960[6,12].

Concept and rationale

In Australia, most of the dung of domestic herbivores remained on the soil surface, dried and hardened[23,34]. In some places it remained for several years[6]. In contrast, in Africa, the Mediterranean region, and India, where cattle and other herbivores have existed for thousands of years, much of the dung was rapidly buried during the warm months by a great variety of dung beetles. Dung accumulation, pasture fouling, and wastage were slight. The dung was incorporated into the soil and speedily decomposed, and the dung beetles played an important role in the nutrient cycle of pasture ecosystems[10].

To explain why this did not happen in Australia, where there are many endemic species of dung beetles[45,46], calls for an examination of the dung problem of the entire continent. Dung beetles, or coprids[11], are highly specialized insects. Most of them are adapted to dung from the particular kinds of animals that are endemic to their region. Accordingly, Australian native dung beetles had adapted to the coarse-textured, pellet-like droppings of kangaroos and other marsupials. In contrast, their African or Indian counterparts had adapted to the droppings of the large

Figure 1: A comparison of the food habits of dung beetles from two continents show the greater preference of the African fauna for the droppings of large herbivores. The data were collected under comparable conditions in Gippsland, Victoria, and in Pilgrims Rest area, South Africa.



native herbivores, among them those of buffaloes, zebras, cattle, and horses (Figure 1). Although some Australian species are attracted to cattle and horse dung they seldom dispose of it; rather they use it in a limited way for short periods of the year[34]. It is easy to appreciate that the size, structure, water content and the microbial components of a large cattle pad confront an Australian dung beetle with conditions that are strikingly different from – and probably more complex[44] than – those of the marbles of a kangaroo.

One remedy for this problem of species to dung adaptation appeared to be to introduce to Australia selected bovine beetles from other continents. Tentative assessments of the extent of losses in production, and other harmful effects from the unburied dung, made the proposition appear attractive[6,12].

Pastures and rangelands in Australia are polluted with cattle dung at the rate of some 350-450 million pads each day. If these pads are not removed they will foul and render useless for up to a year 1/25 of a hectare for each cow or steer[21,23]. The loss in pasture and carrying capacity may be increased by the rank growth around the pads, which cattle shun[6,42,50,67].

Furthermore, some of the volatile nitrogenous components are lost from the unburied dung. One calculation is that a steer excretes 13.6 kg of nitrogen during the summer and that only 2.7 kg of this is returned to the soil if the dung remains unburied[26].

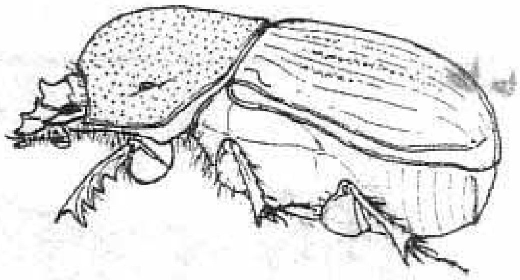
Unburied cattle dung is also the principal breeding site of two of Australia's most important live stock fly pests; the ubiquitous and obnoxious bushfly, *Musca vetustissima*[28,33,51,53], and the tropical blood-sucking buffalo fly, *Haematobia irritans exigua*, which is a close relation of the hornfly of the northern hemisphere, *H. irritans irritans*[13,48,60,69].

Other pests that breed in cattle dung include other cattle flies[25]; *Culicoides brevitarsis*, a blood sucking midge which transmits the virus of ephemeral fever to cattle, and which could become a vector of bluetongue[49]; and some parasitic gastro-intestinal worms of cattle and sheep[14,20,19,36].

In addition to the production losses, chemical control of these pests costs millions of dollars each year. The costs have been further increased by the need to use non-persistent insecticides that will leave no residues in the meat[66]. The continued use of insecticides against the buffalo fly may also result in the emergence of resistances, as it did with the hornfly in the USA.

The appreciation of the severity of these adverse conditions created by dung accumulation led, in 1964, to the birth of the Dung Beetle Project in the CSIRO Division of Entomology[22], under the financial sponsorship of the Australian Meat Research Committee.

This article is an account of dung beetle biology, of the organization and implementation of the project, and of the results of its first ten years of operation.



Biology of dung beetles

Dung beetles occur in all tropical and warm temperate climates, but they become scarce in high latitudes, and are absent from permanently cold or frosty regions. They belong to the subfamily Scarabaeinae (of the family Scarabaeidae) which contains 4,000 recognized species. Most of these species are found in Africa, India, and South East Asia (Figure 8). They live almost exclusively on the excrement of many different species of animals. In the tropics and sub-tropics, and during the warmer and moister months in the temperate areas, beetles are normally very active. They can be found in great numbers in the droppings of the large herbivores. For example, in Tsavo National Park, Kenya, a total of 22,746 beetles was collected from a 7 kg lump of elephant dung 12 hours after it had been dropped (T.J. Kingston, personal communication).

Dung beetles come in a wide range of sizes. Some species are only 2 mm long. Some, like the *Heliocopris* species, may be up to 60 mm long (Figure 2). Most are black or brown in colour although many species have brilliant metallic colours, varying from golden-green and all shades of blue to bronzy-red. The males often have characteristic ornamental horns, whereas the females generally lack ornamentation and have stouter and more powerfully developed front legs, which are adapted for digging.

Figure 2: Dung beetles vary greatly in size, shape, and coloration. Seven of the species that have been recovered after release in Australia are illustrated here (see Table 3) together with the giant *Heliocopris* species. *Heliocopris* is drawn life size and the other beetles twice life size.

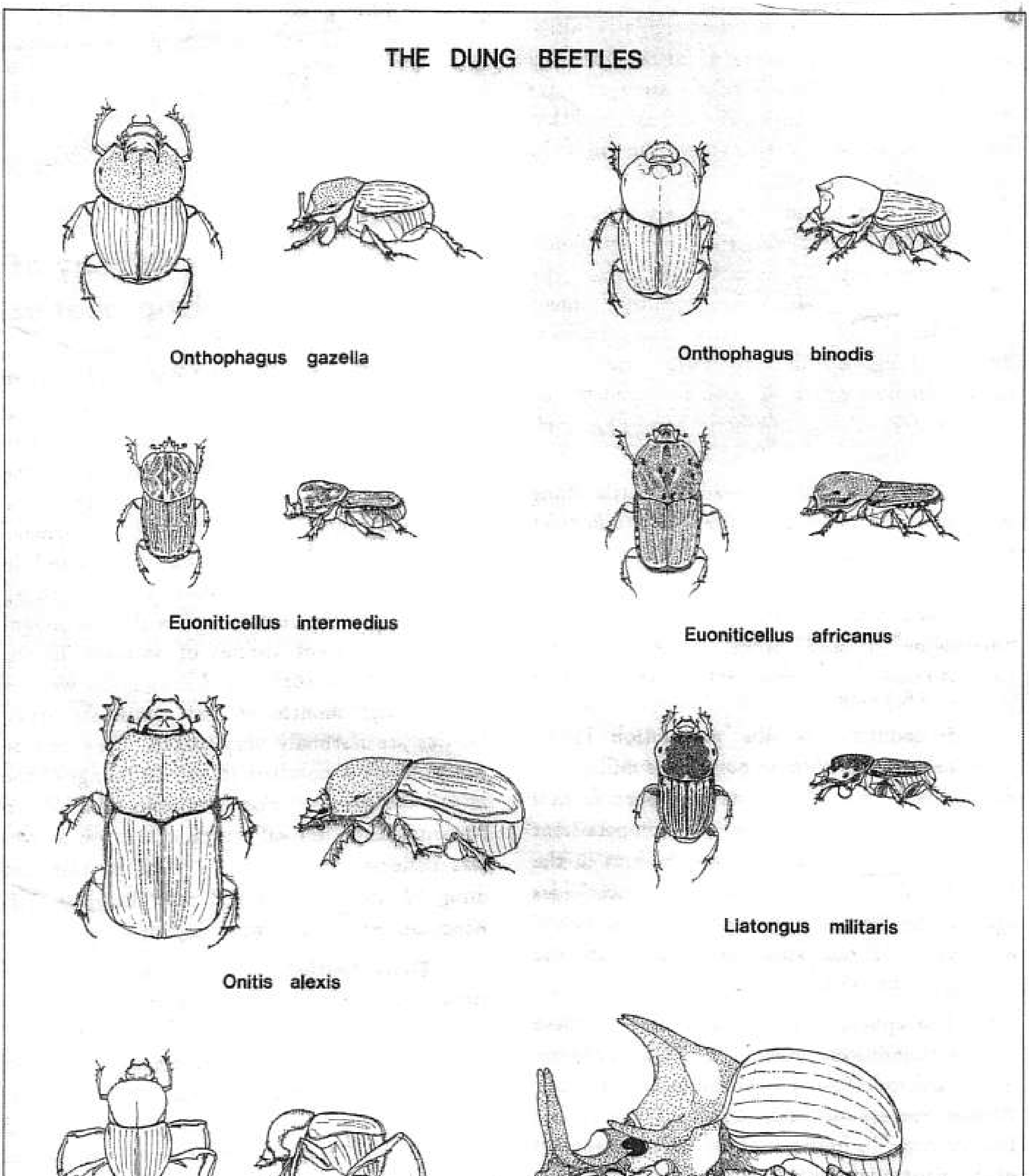
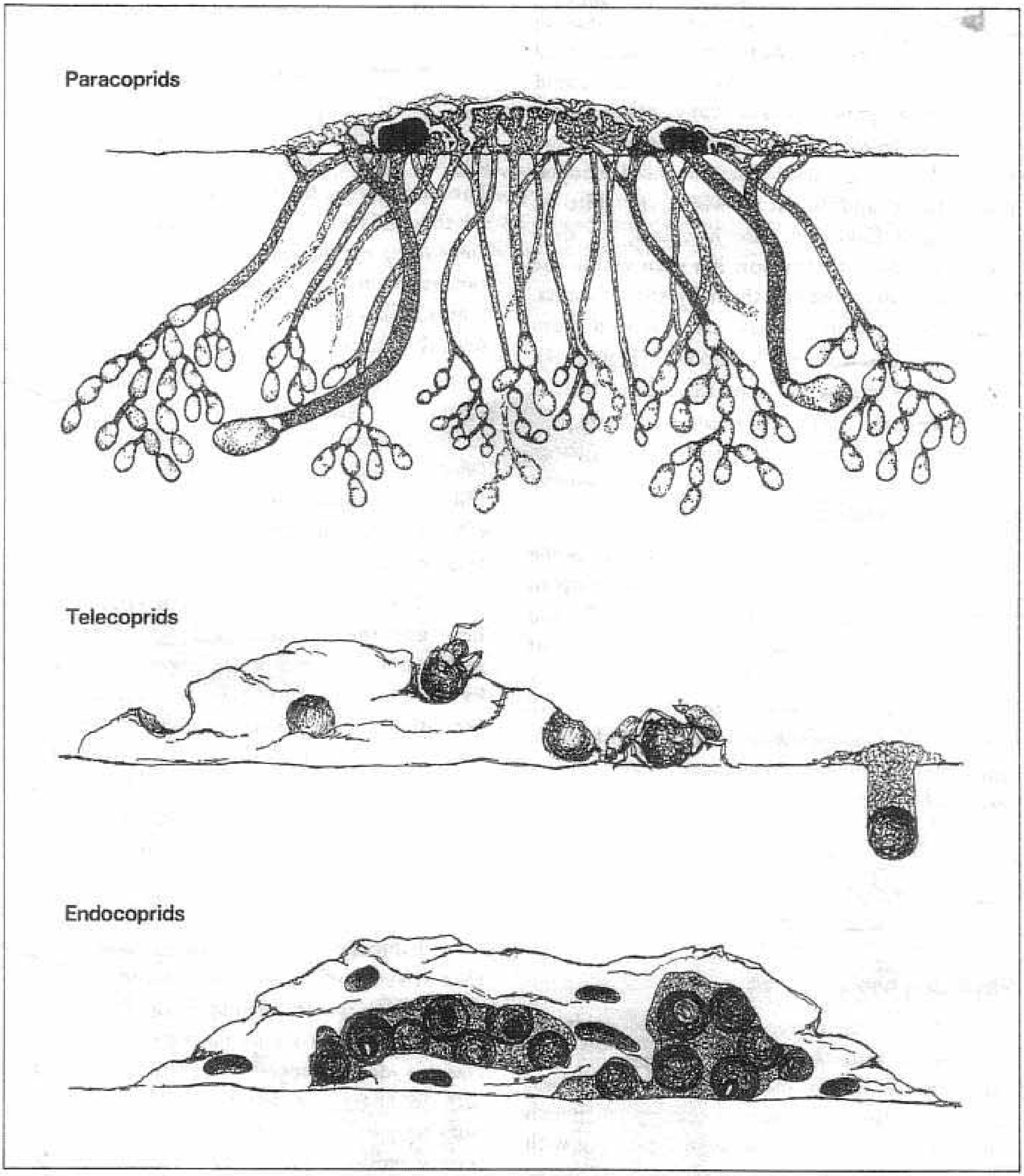


Figure 3: The most common dung beetles are the paracoprids, which bury dung beneath or around dung pads. The ball rollers or telecoprids carve chunks of dung out of the pad, knead them into balls and roll them away for burial. The least known and least effective beetles are the endocoprids, which build their nests inside dung pads during the dry warm periods when the other types are inactive.



Feeding habits

Adult coprids have soft membranous mouthparts that are modified to ingest only the liquid constituents of the dung and the minute particles that are carried in suspension, leaving the coarse parts, plant fibres and seed behind[22,29,47]. Thus, adult coprids could never chew grass roots or any other undecomposed tissues. Their larvae, however, can bite off dung with their well-developed mouthparts, and ingest it whole. In spite of this, coprid larvae are also harmless, for they are confined for their whole life span within the dung balls prepared for them by their parents. They soon perish if they are removed from their "food-and-shelter" abodes (Figure 4). Thus, there seems no way that dung beetles could become pests in Australia. Moreover, their ultimate numbers will always be regulated by the availability of dung – the only food supply they can use.

The adults are proficient fliers. Some species have made recorded traverses of up to 50 km over seas. Most species are twilight and night fliers, but there are still many hundreds of species, especially the ball rollers, that fly during the day in search of fresh dung. All coprids have a well developed sense of smell, and often arrive at dung almost as soon as it is dropped.

Breeding habits

According to their breeding habits, coprids can be classed into three major groups[8], though with many variations[29]. Perhaps the best known are the ball rollers or telecoprids, which knead balls out of the dung and, pushing with their hind legs, roll them away for burial some distance from the dung source (Figure 3). More widespread and numerous are the paracoprids, which dig tunnels under and away from the dung to serve as their nests, which they stock with round, ovoid or sausage-shaped brood balls (Figure 3). The group that makes least impact on the environment is the endocoprids, which make their nests inside the dung pad (Figure 3).

Most dung beetles work in conjugal pairs, and in many species the sexes meet and identify one another by sophisticated chemical communication[63].

Once beetles land on a pad some may quickly burrow into or under the dung to feed. The majority of the telecoprids remain feeding on the surface. The males rough out the balls. Depending on the size of the beetle, these balls can be as small as a peppercorn or as large as a tennis ball, and can take from sixty seconds to several minutes to make. The balls are rolled away and buried in short shafts (Figure 3), where the females excavate a neatly formed brood chamber in the ball and lay a single egg in it. In favourable situations in Africa and India, ballrollers can be so numerous and efficient that they can remove a cow pad in less than an hour.

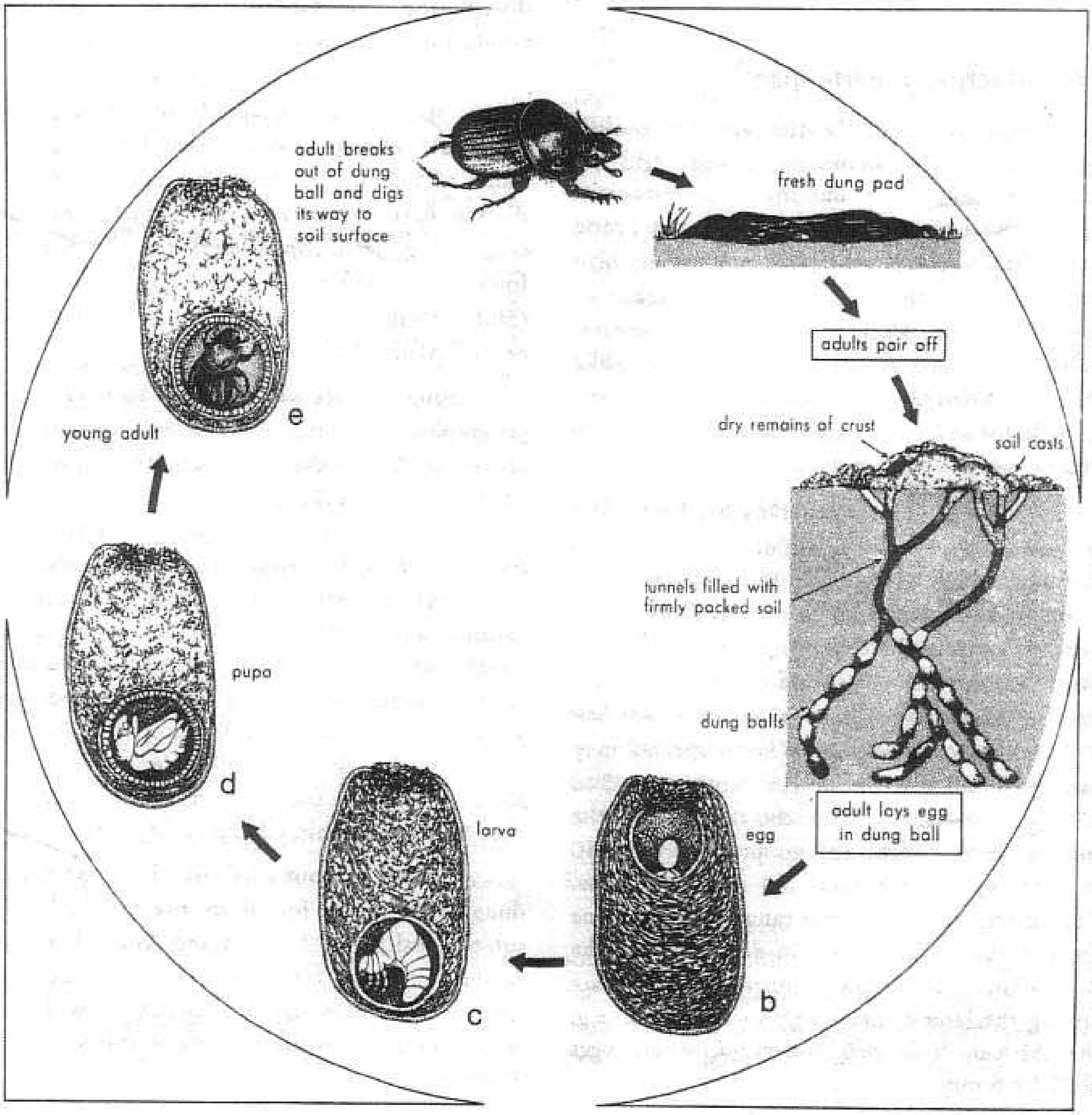
The female paracoprid beetles dig tunnels, and the males bring dung from the pad and pass it to them. It is progressively formed by the females into falls of various shapes according to the species. Each ball intended for brood has a chamber (Figure 4) excavated into it and a single egg is laid in this chamber. The number of brood balls in a single nest made under or near a cowpad by one female may vary from 1 to 15, according to the species and the intensity of competition for the dung.

Paracoprids are probably less dependent than telecoprids on suitable weather, being less affected by rain or drying of the surface crust of the pad. They are by far the most important class of dung dispersers, yet they are seldom seen by the casual observer. The signs of their burying activities, which have long been recognized by entomologists[39,59], are the push ups of soil that the females bring up to the surface in and around the droppings.

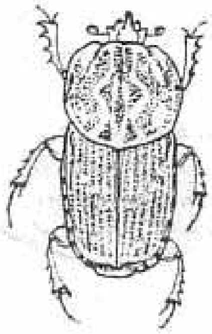
Competition between beetles of both classes is often quite fierce. At its peak a large cow pad may totally disappear within three or four hours, though usually it takes one or two days. Paracoprids may also have to compete for tunnelling and nesting space below ground, but the ball-rolling habits of the telecoprids largely save them from this pressure.

The endocoprids are most active during the dry season or when other coprids are inactive through other reasons. They thus escape severe competition. By tunnelling through the dung and excavating chambers in it to receive their clutch of brood balls (Figure 3),

Figure 4: The life history of *Onthophagus gazella*, which may be completed in 30 days during the summer. The adults work in conjugal pairs to build their nest under a pad. In each ovoid dung ball an egg is elaborately encased (b). The egg hatches in 2-3 days and the larvae feeds for about 16 days in the ball (c). As it feeds it works downwards and pupates at the bottom of the ball (d). The pupal stage lasts for only a few days before turning into a young adult (e), which takes a further 3-4 days to harden its wing cases and legs and break out of its cocoon and emerge on the surface in search of fresh dung.



they weaken the pads and hasten their disintegration at the beginning of the wet season. This benefits the flush of plant growth that commences at that time.



Reproduction and life span

As insects go, dung beetles are not prolific breeders. The numbers of eggs laid are relatively low[29,31], but this is compensated for by the meticulous provisioning and brood care that ensures the survival of a high proportion of the offspring. The number of eggs laid per female lifetime varies from species to species. Some lay as few as 25; others, like the Afro-Asian *Onthophagus gazella* that is now so widespread in the Australian tropics, may lay 200 or more.

The large coprids generally live longer and lay fewer eggs than the medium (10-25 mm) or the smaller (less than 10 mm) species. For example, the larger species such as those of the genera *Copris* and *Heliocopris* can live through three seasons (2½ years) and lay some 50 to 80 eggs. Similarly, the females of the larger ball rollers, like *Scarabaeus* and *Kheper* species, may live up to two years, producing from about 5 to 25 eggs per season[31]. On the other hand, the smaller *Onthophagus* species produce from 80 to 200 eggs during their 3-4 month lifetime. Coprid eggs come in a wide range of sizes. Some are less than a millimetre in diameter, e.g. the Australian *Onthophagus sydneyensis*; others are among the largest insect eggs in the world, e.g. the African *Helicopris andersoni*, whose eggs are 12 x 6 mm.

Physical and biotic requirements

Apart from having preferences for certain types of dung, coprids also have specific climatic and edaphic requirements, e.g. for extremes and means of temperature, for amounts and distribution of rainfall, for types of soil, and for vegetation formations. These factors shape the distribution pattern and range of each species. Many species are adapted to tropical or temperate climates. Many have fairly narrow limits of tolerance of temperature and rainfall. A few have remarkably wide tolerances and ranges, e.g. *Heliocopris hamadryas*, which is found from the temperate areas of south Africa (500 mm rainfall) to the equatorial highlands of central Africa (5000 mm rainfall).

Some species are confined to very small geographical areas, e.g. several Australian species of *Onthophagus*, which are found only on the Atherton Tableland[45,46]. Others, such as *Onitis alexis, Liatongus militaris* and *Euoniticellus intermedius*, occur across enormous areas of Africa, and parts of southern Europe and Arabia. *Onthophagus gazella* is equally at home in most parts of Africa and Arabia, India, and south-east Asia, and has adapted so well to new environments in Hawaii and Australia. *Sisyphus schaefferi* is found in North Africa, southern and central Europe, Asia Minor, Kashmir, China, and Korea.

However, about a half of all the species of dung beetles are found in the tropical and sub-tropical belts of Africa and Asia, where the rainfall is over 1000 mm. A few such as *Onthophagus alquirta* are restricted to desert areas where the rainfall is erratic and less than 250 mm.

Seasonal distribution

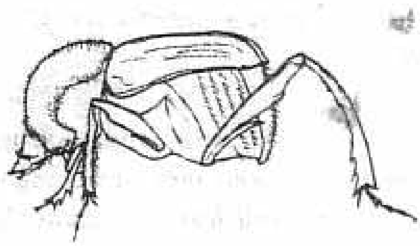
Most species, even those with the extremely wide ranges of distribution quoted above, are not uniformly dispersed throughout their range. Rather, they are distributed in a mosaic pattern that is influenced by climatic factors, soil and vegetation types. Their occurrance, activity, and abundance are further influenced by seasonal variations in temperature and rainfall.

For their normal dung burial activity they require reasonable moist soil for ease of digging, and temperatures within the 15-40°C range. In the tropics and subtropics in Africa, peak activity is reached soon after the onset of the rains, and is sustained for many weeks or months. In temperate areas, the increase in soil and air temperatures in spring is probably the factor triggering high dung beetle activity.

There is also a lot of difference in the numbers and variety of species to be found at one site throughout the year. In both the tropics and temperate areas an early spring, a mid-summer, and an autumn fauna can be recognized within one area. This basic grouping can be further modified by the appearance of the progeny of the spring fauna in late summer or autumn. These spring-autumn progeny, however, seldom breed, but overwinter as adults. However, they do bury dung or shred it to pieces as they feed.

Within one season there may be from one to several generations, according to the species. In the tropics, *O. gazella* can develop from beetle to beetle in 28 days, and may have four or five generations in a season. At the other extreme there are species, like some African *Onitis*[52], or the European *Chironitis furcifer*, that need at least 18 months for one complete generation[27].

Fluctuations in seasonal conditions from year to year at any one site may result in certain species being very abundant in one year, yet scarce in the following year.



Natural enemies

Unlike most other groups of insects, coprids have few recorded natural insect enemies, such as parasitic wasps and flies. Parasitic mites and nematodes may be of some importance. Microbial diseases, due to viral, bacterial, or fungal infestations, have never been observed to reach epizootic proportions. This is of great advantage to the beetles. It is of even more advantage to the project, because under mass propagation in congested quarantine conditions, a virulent micro-organism could wipe out entire cultures in a matter of a few days. Although fungi, especially the ubiquitous *Beauveria bassiana*, have often been observed to attack larvae, pupae, and adults, the number of infected individuals has been very few. Probably the fungal infestations that were seen were secondary invasions of coprid cadavers.

Predators, both vertebrate and invertebrate, are, perhaps, the most widespread enemies of dung beetles. In Africa moles, mongooses, meerkats, and jackals have been seen devouring dung beetles. During the winter on the highveld of southern Africa it is common for nests of the large *Helicopris* species to be excavated by these predators, who crack open the huge brood balls and eat the larvae.

Birds also take their toll. Many species, such as the hornbills, attack ball rollers during the day, and others, such as owls, do so at night. Flocks of guinea fowl often feed on beetles in dung pads in Africa, and several species of ibis have been observed to do so in both Africa and Australia. Lizards and toads also eat dung beetles. None of these predators seems to pose a serious threat to any species of coprid.

The spiders and solfugids that have sometimes been seen attacking dung beetles are probably even less important. In dung pads on the other hand, the predacious staphylinid and historic beetles actively seek out coprids and attack their unsclerotized areas to gain access to the soft internal organs. Large histerid beetles have been seen feeding on *Onthophagus gazella*, or on even larger kinds, such as *Copris* spp.. Staphylinids, on the other hand, mainly attack the smaller beetles (1-8 mm), and only a few species are large enough to prey on dung beetles. One such species is the 20 mm hairy *Emus hirtus*, which occurs in parts of Europe.

Apart from a few species of birds, marsupials and lizards, and the introduced fox, Australia has fewer and less aggressive predators than those in Africa. Thus there seems to be no serious biological threat to introduced dung beetles, with the possible exception of predation by the cane toad, *Bufo marinus*. These large toads were introduced from South America via Hawaii in the early 1930's and released in the cane fields of North Queensland. The have already spread along an 1800 km coastal strip as far south as northern New South Wales[18]. Introduced originally to control root-infesting beetles of sugar cane, an objective which seems unlikely to be achieved, the toads have become predators on noxious and beneficial insects, including dung beetles. Since the introduced beetle *O. gazella* became established along the Queensland coast, it has frequently been reported that the toads have adopted a new habit; that they sit on or around fresh cow pads at night, and intercept large numbers of incoming *O. gazella*. Dissections have shown that the gut of a toad may contain up to 80 beetles at a time, but it is not known whether meals of this size are taken daily.

Dusk-flying species, such as *O. gazella*, seem to face the greatest risk, for they undertake their main dispersal flights just at the time when the toads are emerging to forage. In paddocks, away from sites of dung concentrations (e.g. troughs, paths, cattle camps) the chances of toads locating fresh dung pads are reduced. At the moment there is little possibility of combatting the toads by any economical means, but there is still no clear evidence that they are having a serious effect on dung beetle populations.

I have seriously considered the possibility, should it be necessary, of taking counter measures against *Bufo marinus* by introducing certain *Heliocopris* species that are too large for the toads to swallow, or others (such as *H. faunus* and *H. hermes*) that would either break their way through the body wall of the toad, or at least rupture the stomach wall before death and otherwise lacerate the viscera with their sharp and spiny legs. This would, of course, ensure that the toad had taken his last meal.

Benefits from dung beetles

Improving the soil

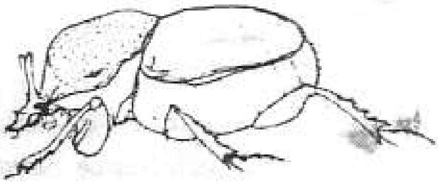
In African and Asian countries where bovines are endemic there is usually a versatile beetle complement which rapidly removes their droppings from the soil surface and incorporates them into the soil, so accelerating the rate of circulation of nutrients and increasing the productivity of grassland ecosystems[6].

It has been pointed out that, near Canberra, ungrazed pastures have a higher requirement for added phosphorus than those grazed by stock[43]. It appears that some nutrient cycling process is set up at higher stocking rates which is absent, or much less efficient, in ungrazed or lightly grazed pastures. This happens in spite of the heavily stocked pastures becoming littered with local concentrations of immobilized nutrients[32].

In one experiment in South Africa, dung beetles returned to the soil over 13 kg. or 90 per cent, of the faecal nitrogen (and presumably almost all of the phosphorus) excreted by each steer during the summer grazing season[26], and it could be expected that a comparable dung beetle fauna would do the same in Australia. Nutrients in the dung returned in this way are more readily available to the plant growth through more rapid decomposition and humus formation[37]. The effect is comparable with the action of earthworms in some countries[4].

The uptake of nitrogen, sulphur, and phosphorus by plants was measured in a controlled experiment in a Canberra glasshouse[10]. The results (Table 1) show that where coprids were active, the yield was over 80 per cent higher than where, in the absence of beetles, the dung was left unburied.

These improvements also occur in pastures grazed by large herbivores, although obviously, in a spotty, mosaic-like pattern. In those African grasslands where vast herds of game still graze[61] and are attended by a



multitude of dung beetles, this self-manuring process can proceed on an impressive scale, and helps to sustain carrying capacities that can be surpassed only by modern and costly farming techniques[62].

Enough has been said to indicate that in improved pastures, the use of chemical fertilizers, which is generally necessary[5,43], could be effectively supplemented by the activity of dung beetles. In rangelands – unimproved native pastures – the effects of any legume contributions to soil nitrogen, plus the slow return of nutrients through decomposition of dung and plant detritus, and the contribution of urine to fertility, can also be supplemented by the activity of dung beetles. To press theory to its limit, in either situation, if the pads of one grazing cow were always dropped in a different position, and if beetles were active all the year round, then in ten years (or a few years longer according to some

Table 1 : The yield of Japanese millet and the uptake into the plant tops of nitrogen, phosphorus and sulphur in pot culture. (Reference 10).

All values are means of ten replicates (pots) for each treatment

Treatment	Yield		Uptake		
	Tops	Roots	N	P	S
No dung, no beetles (control)	13.6g	10.1g	105mg	11.5mg	14.9mg
Beetles alone	13.1	10.6	106	10.8	11.8
Dung alone	17.3	12.7	127	14.8	15.7
Dung mixed by hand	37.0	18.4	253	52.3	28.6
Dung + beetles	31.3	14.7	206	40.7	24.9
Control + N+P+S	37.5	14.2	207	57.3	46.8
L.S.D.					
P = 0.05	2.9	2.7	24	4.2	3.8
P– 0.01	4.0	3.7	33	5.6	5.1

estimates[41]), every square centimetre of an area of 0.4 hectares would, at some time or other be efficiently cultivated and manured at no cost to the grazier.

At this point it is desirable to draw attention to the difference between the action of dung beetles and of harrowing, which has often been used to disperse dung pads in intensively grazed pastures. The value of harrowing is now in question, for it has been shown to reduce immediate plant yields by up to 15 per cent through mechanical damage, and to increase the area of grazing shunned by cattle by spreading fresh dung over a much wider area than that covered by the original pad[67]. Harrowing is essentially superficial, and has little cultivating effect on unploughed soil.

By contrast, the action of dung beetles does not damage the plants at all, and the rapid removal of fresh dung reduces the need to shun any area for long. The tunnelling produces effective, cumulative cultivation of the soil.

As suggested elsewhere[6], the tunnelling of paracoprid beetles should improve the physical condition of the soil by incorporating organic matter, and by bringing the soil of deeper layers (mostly from 10 to 30 cm depth) to the surface where it can cover plant detritus that is ignored by the beetles, and so speed its incorporation into the soil. This process should also improve the aeration, friability, water penetrability, and water holding capacity of the surface layers of the soil, and in this be comparable in effect with the work of certain earthworms in some damp pastures in temperate areas[58].

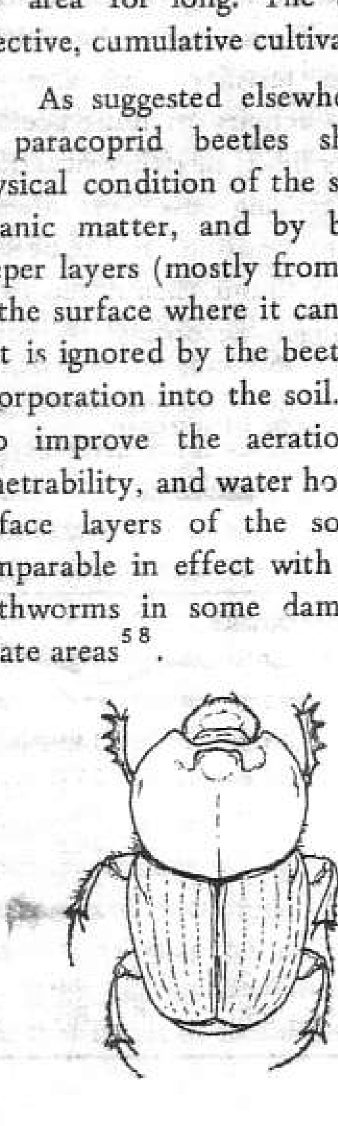
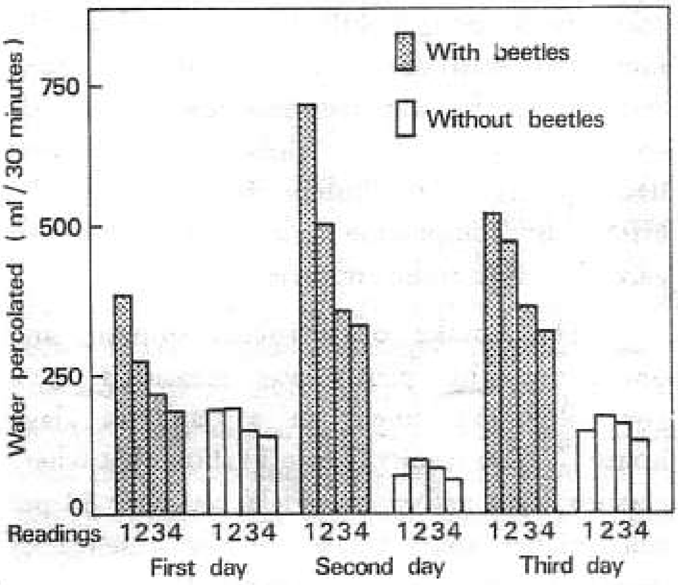


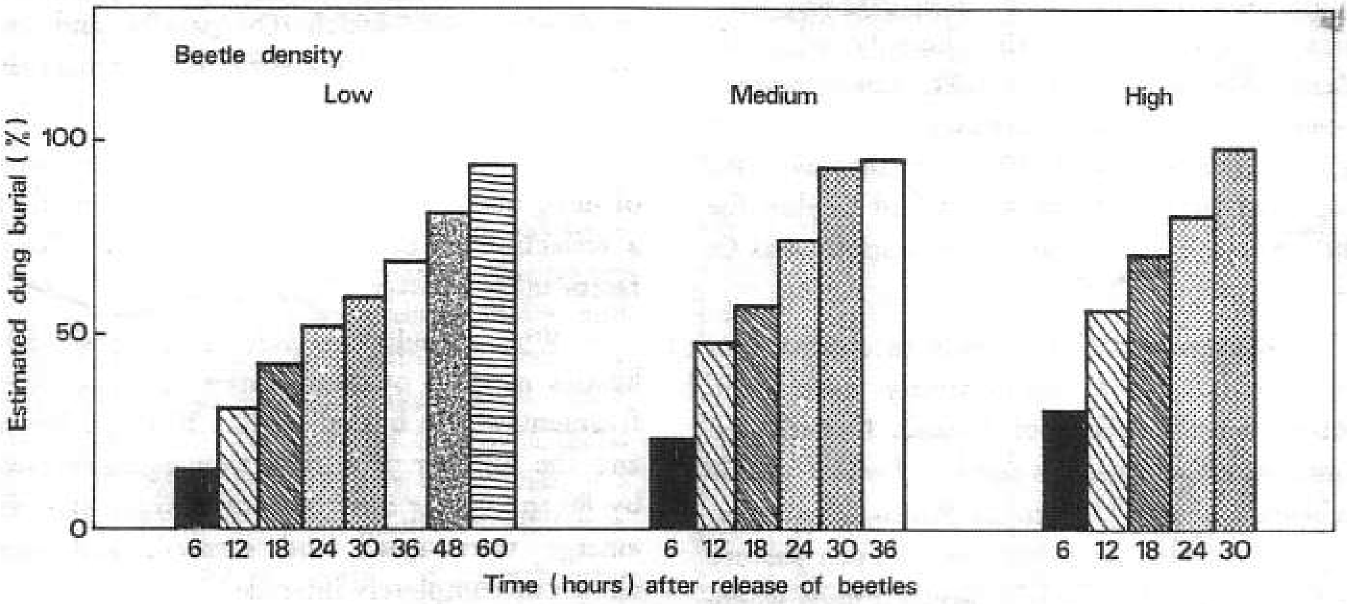
Figure 5: The way in which the burying dung beetles can improve aeration, water permeability, and water holding capacity of soils is illustrated by the results of one laboratory experiment. The beetles were placed with dung on the surface of soil packed into 30 cm long drainage pipes. The pipes were watered each day. The values are means of ten pipes "with beetles" and five pipes "without beetles" and show how water penetration increased in the "with beetles" pipes over the first three days.



However, the shallowness of some Australian soils poses problems. Deep tunnelling beetles that bury their dung balls very deep may place them out of reach of shallow-rooting pasture plants, and they may also bring to the surface subsoil which would have been better left down below.

Although these claims for improvement in soil structure due to the activities of dung beetles seem reasonable, there is only my own unpublished data to support them. In the experiments illustrated in Figure 5 several breeding pairs of *O. australis* increased the volume of water required to saturate a loam type soil before waterlogging occurred by five times higher than in the controls. The percolation rate in a loam was increased by 30 per cent and in a clay soil by 20 per cent. Although in the field any such improvements would again occur in a mosaic, their cumulative beneficial effect on grazing land could be quite large.

Figure 6: The volume of dung buried by *Onthophagus gazella* in an insectary in Canberra. The beetles were released at one of three densities (10, 20, and 30 pairs per sample) on one litre dung pads containing bushfly eggs. No bushflies emerged from any of the medium and high density pads. In the four replicates at low density, emergence was nil, nil, 27 and 2.



reduction coincided with extremely dry conditions, and the lowered numbers were not maintained for the rest of the season nor during succeeding years.

There seems, therefore, to be some difference between the impact of the beetles in Hawaii and Australia. One reason may be that certain mesostigmatid mites, which are usually carried by coprids[17,30,66], were quarantined out of Australia (see below) but probably accompanied beetles of the same species into Hawaii, where the quarantine precautions would not have excluded them. These mites cling to the beetles and use them as means of transport. They stay close to the beetles in the dung, and some infest them as soon as they show signs of leaving in search of a fresh pad. Through this phoretic association, such mites gain free access to new sources of food which comprise nematode worms, fly eggs, and small maggots[17].

It is known that some macrochelid mites are effective predators on house fly eggs[2,3] that are laid in farmyard manure. At this stage, however, only a thorough scientific investigation can clarify whether this coprid-mite association is as important in fly control in cattle dung as it is known to be for certain carrion-burying beetles, such as the European *Necrophorus* species. These beetles bury small dead vertebrates for their larvae somewhat as coprids bury dung[54]. The mites, which arrive at the carcase attached to the adult beetles, enter the brood chambers prepared for the beetle larvae. Here they feed on any blowfly eggs and maggots with which the carrion may have been infested before burial. In the absence of these mites, the *Necrophorus* larvae could not survive, because their food supply would be destroyed by the blowfly maggots[57]. Present knowledge does not conclusively demonstrate any such vital association between coprids and mites, but the phoresy certainly seems to benefit the mites[16,17].

Australia has many species of macrochelid and other phoretic mites that are carried by native dung beetles, and again only further research will reveal what, if any,

Fly control

Hawaiian entomologists were the first to try coprids for the control of dung-breeding flies, such as the blood-sucking hornfly of cattle *Haematobia irritans irritans*. The attempt began around the turn of the century[13,25,48]. But it was only during the 1950's that the Hawaiians imported beetles from Africa and Ceylon for the same purpose. Among the imports was *O. gazella*.

The potential of coprids to control flies was not measured quantitatively until 1966 (when, on the island of Hawaii, I conducted some investigations, the results of which will be published shortly). Then, at Puako, Hawaii, an experiment was carried out in an open pasture and in surrounding heavily wooded parts where cattle regularly sheltered from the midday tropical heat. In both situations, fresh cow pads were exposed to oviposition by flies and to colonization by dung beetles. The control pads were covered with a fly screen to exclude the beetles after the flies had oviposited. The four species of coprids that had established in the area were *L. militaris* and *O. gazella*, both from Africa, and *O. incensus* and *Copris incertus* from Mexico.

The results (Figure 7) were clear-cut. Ninety six per cent fewer flies emerged from pads in the open pasture than from the corresponding controls. In the heavily wooded area the advantage was only 21 per cent. The disparity between the two situations seemed to be due to the failure of *O. gazella* and *L. militaris* to colonize the pads under the trees. The two Mexican species could bury less than half of the pads dropped under the trees, whereas in the open pasture all pads were buried within 30-36 hours.

Although *O. gazella* was clearly a very efficient species in the open, the results served as a warning that one or two kinds of beetles, however excellent, cannot be relied upon to achieve total dung dispersal, and that it may be necessary to build up a small fauna consisting of a complex of at least several efficient species.

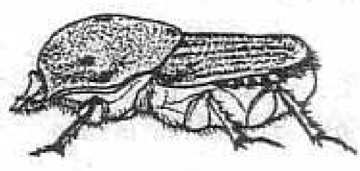
These Hawaiian results were later confirmed and extended in laboratory experiments in Canberra in which *O. gazella* and the Australian bushfly, *Musca vetustissima* were the test species[9].

In these experiments (Figure 6) the speed of dung burial, which at a given temperature is a reflection of beetle density, was the crucial factor in fly control.

When populations were of the order of 20 beetles per litre of dung, entire cow pads were fragmented and buried within 30 to 40 hours, and the number of bushflies emerging reduced by 80 to 100 per cent. Moreover, those that did emerge were small and stunted, and were almost or completely infertile[64].

Since no traces of fly eggs or larvae are to be found in the brood balls buried by the beetles, it is presumed that they are destroyed during the elaborate processes of constructing balls, or die in the unfavourable remains of the pad. Nor have eggs and larvae been found in food balls, though these receive less meticulous attention. It seems likely that the few flies that do emerge manage to complete their feeding in small fragments of dung that were neglected by the beetles.

Following the release of *O. gazella* in north Queensland (see below) a marked reduction in abundance of buffalo flies and other dung-breeding flies was reported[1,22,66], especially in the Townsville area. However, the



relationship develops between these organisms and introduced dung beetles in Australia, and whether deliberate introductions of African mites will reduce the pest status of dung-breeding flies.

Perhaps the most convincing evidence for the vital role that a coprid fauna can play in suppressing dung breeding flies was obtained from a field experiment carried out near Pretoria, South Africa. The results (Figure 7) supplement those recorded in Canberra and Hawaii. The greatest impact on fly numbers was obtained from pads that were exposed to the full complement of the local dung beetle fauna. A total of 25 species (6 genera) removed all pads in no more than 24 hours, and reduced the numbers of flies emerging by an average of 98 per cent.

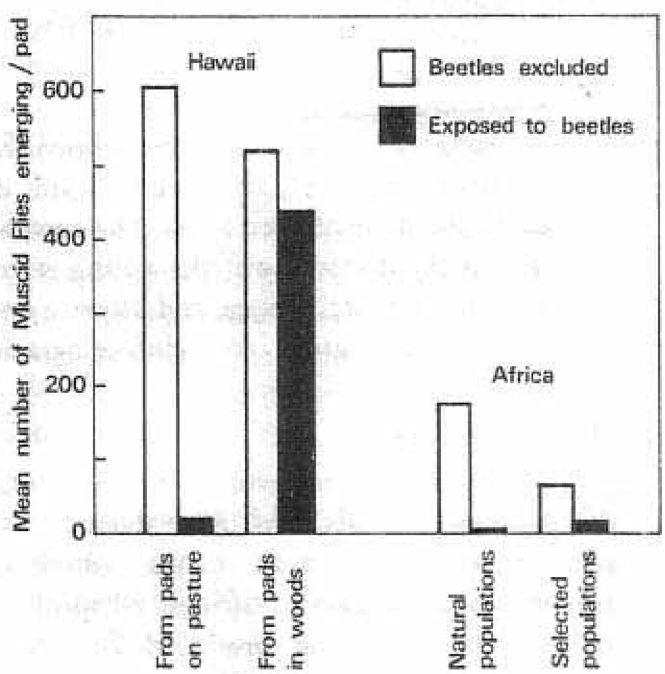
The three experiments show that dung beetles can control some dung-breeding flies. This may be why flies that breed in cattle droppings are relatively scarce in Africa. For example, there is an African fly so closely related to the Australian bushfly that it can inter-breed with it[53], yet it is rarely as abundant in Africa as its sibling is in Australia. There are also several species of bloodsucking flies in Africa that are closely related to the still-troublesome buffalo fly in Australia, but they are of little consequence to animal husbandry. The relative scarcity of these flies throughout Africa might be attributed to the frequent dipping of cattle to control disease--bearing ticks. However, such chemical control is practised only in intensively farmed areas. The range cattle and those of the small village farmers and herdsmen are seldom or never dipped.

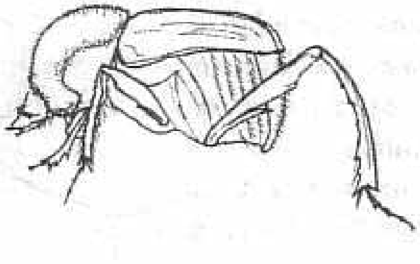
Distinction must be made between flies which breed in fresh droppings of grazing herbivores, and the synanthropic or filth flies that frequent and breed in rubbish dumps, excreta, and other sorts of organic waste that accumulate in and around unsanitary habitations. Coprids do not frequent such situations, but confine their attentions to fresh excreta in open spaces.

In the unsanitary peri-domestic situations, filth flies are completely unhindered by dung beetle activity.

Figure 7: Other experiments that illustrate the possibility of fly control by dung beetles were done near Puako in Hawaii and Pretoria in South Afica. In Hawaii the African beetles *Onthophagus gazella* and *Liatongus militaris* almost completely suppressed fly emergence from one-litre cowpads placed in open pasture but not from similar pads in a mesquite thicket nearby. In the thicket only two minor species of beetle from Mexico were active, and then in a desultory way.

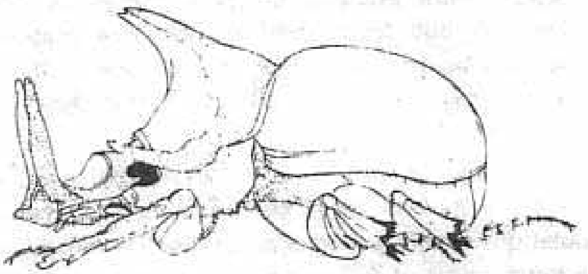
Near Pretoria, in similar experiments, both natural populations of the local beetle fauna and selected populations of a few species suppressed fly emergence. The lower levels of fly numbers in the control pads in Africa is almost certainly due to the efficient dung beetle fauna that is operating all the time.





Organization of the project

Objectives



Worm control

Eggs or larvae of some strongyline worms that are intestinal parasites of livestock are deposited in the dung of their hosts. The cowpads then act as incubators until the young worms develop into their active stage and disperse onto the surrounding grass to reinfect grazing animals[20,36].

Control of these worms by rapid dung disposal by coprids was first demonstrated experimentally in South Africa, where the activity of a complex of at least 20 species of coprids in cow dung produced an average reduction of 85 per cent of infective worms on pasture[55,56]. In Australian experiments with captive populations of the Afro-Asian *Onthophagus gazella*, infective larvae were reduced by from 50 per cent on irrigated pastures to 93 per cent on non-irrigated pastures[14].

Sheep worms can also be reduced by dung beetle activity. The eggs and the ensheathed larvae of the small parasitic worm, *Haemonchus contortus*, were destroyed by the activity of the native beetle, *O. australis*[19]. There is also some evidence that the mouthparts of dung beetle larvae can destroy eggs and larvae of worms[47].

The overall aim of the Australian dung beetle project is to establish a bovine dung beetle fauna on the Australian mainland and in Tasmania. This will be done by selecting a range of coprids from among the thousands of species found in Africa, Europe, and Asia.

The selection strategy is to assemble minifaunas of highly efficient species for every major climatic area of the Australian continent, including the tropics, subtropics, and temperate areas. The species selected for each area will be co-adapted as far as possible; that is, in their activities they will complement one another, rather than compete.

The word minifauna is used here to refer to a combination of species that will be selected from the array of the complete fauna of a region overseas. The components of each minifauna must be ecologically compatible to achieve the most efficient dung disposal possible in terms of speed, quantity dispersed, and seasonal duration of activity. Furthermore, each minifauna should have a potential for dung disposal, during peak seasonal periods, such that pads are dispersed in no more than 48 hours.

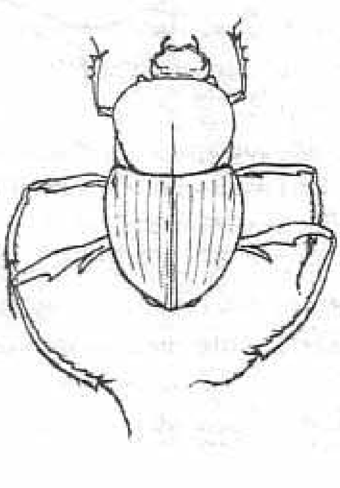
It is intended that each minifauna should be structured in the same fashion as the complete fauna from which it is drawn. In considering structure, the coprid fauna of an area is viewed as consisting of a heirarchy of a few central or keystone species of major importance, some secondary species to contribute very material supplementary activity, and an array of tertiary species, of lesser importance. Minifaunas are to be assembled by selecting the outstanding members from each rank of the heirarchy from each fauna.

The plan for the first few years was to locate in Africa and India as many central species as possible, with the emphasis on species suited to as many climatic areas as possible, so as to get the Australian program under way.

It was assumed that the early recognition of species having a potentially central role in the Old World would be relatively easy, and that, once this was done, and the species were transported to Australia, other species could be selected to supplement them.

On the basis of the known ecology and distribution pattern of the Australian and European coprid faunas[29,45,46], it was estimated that perhaps as many as 160 species would be needed in Australia. Such an array of beetles could provide a good coverage from the desert or semi-desert conditions of central Australia to the high rainfall areas of north Queensland, and from the cold highland areas of Tasmania to the tropical lowlands around Darwin.

A project with such comprehensive objectives could only be operated on an intercontinental basis; with a centre in Australia and another overseas. An operational centre for the Australian program was set up during 1964 at the headquarters of the CSIRO Division of Entomology in Canberra. For the overseas program a research and collection centre was established in 1970, at Pretoria, South Africa, with the cooperation of the Plant Protection Research Institute.



Quarantine aspects

Although it appeared most unlikely that dung beetles could become pests in Australia there was the possibility that, along with the adult beetles, would come such fellow travellers as mites and rhabditid nematodes or, worse still, pathogenic organisms such as the virus that causes foot-and-mouth disease of bovines[65]. Direct importation of beetles into Australia from Africa or Asia was, therefore, not feasible.

A partial solution to the problem was offered by the Hawaiian Islands, where *O. gazella* was firmly established. The only parasite or disease of stock or man in Hawaii that is not already present in Australia is the giant liver fluke, *Fasciola gigantea*, which infests cattle in wet or marshy situations. Investigations in Hawaii showed, however, that *O. gazella* and other dung beetle species then present in the islands could not ingest fluke eggs that had been mixed into dung: the eggs were too large to survive the fine grinding action of the beetle's mouthparts[47]. Moreover, the beetles had shown no adverse features of any kind during the eight years since their establishment in the Hawaiian islands. Thus the islands offered a safe source for launching the project, and direct importation of adult beetles into Australia was commenced in early 1966.

Large stocks of *O. gazella* were held in quarantine in Canberra and kept under observation preparatory to release. It was soon discovered that the beetles were infested with supposedly harmful pyemotid mites. Large numbers of these minute mites were clinging by their mouthparts to the soft inner surfaces of the hard wing cases of the beetles, and there had escaped the acaricidal powder applied in Hawaii before shipment.

In view of this finding, not even the Hawaiian islands could be considered a safe source of dung beetles for Australia. Field collected *O. gazella* were, therefore, never released in Australia. Instead, stocks for release were bred in the insectary under conditions that precluded the mites from infesting the Australian generations, and research was commenced on methods of importing that would entirely eliminate the risks of introducing any parasites and pathogens of man, beetles and livestock.

The method developed involved the surface-sterilization overseas of the beetle eggs in 3 per cent formalin solution for three minutes before despatch. In Canberra, these eggs were then implanted into cavities in dung balls that had either been hand made from dung collected in Canberra, or had been removed from specially maintained cultures of breeding dung beetles. In these balls the eggs developed through to adult beetles.

In the overseas program these measures have now been made even more rigorous. The procedures before the eggs are dispatched to Australia are carried out in a specially designed and equipped sterilizing room. The surface-sterilized eggs are placed in sifted and dampened peat moss from sterilized stocks from Australia. The moss is then packed in sealed containers and despatched to Canberra. Thus, once the coprid eggs have been surface-sterilized in Pretoria, they are in contact only with sterile materials of Australian origin throughout their 36-hour air journey to Canberra. On arrival at the quarantine laboratory, the eggs are implanted into suitably sized dung balls, either hand made or taken from cultures of donor beetles.

These strict safety measures have proved to be effective, yet have not so endangered the viability of the eggs of most species as to jeopardise transplantation. With modification to suit particular species, the method opens the way to the safe importation of a wide variety of dung beetles, irrespective of their geographic origin.

The pilot beetle

In the Afro-Asian beetle, *O. gazella*, which may be considered to have experienced eight years of natural quarantine since its establishment in Hawaii, Australia gained an excellent beetle to use for the development of the techniques, and performance of biological studies that were required as a basis for subsequent introductions.

These studies encompassed the feeding and nesting behaviour, reproduction, life cycle, various methods of egg-sterilization, and, above all, techniques of transplantation of the eggs from the maternal brood balls into others. Methods of mass-propagation and of large-scale beetle release also had to be developed and put to practical test. In all these respects, *O. gazella* served the project well. The experience gained was then expanded to include several other coprid species also introduced from Hawaii, and was also applied in part to the predacious histerids (Table 2).

Reference should perhaps be made here to the introduction of predacious histerid beetles to complement the coprids in the control of dung breeding flies. Histerids are shiny beetles, mostly black, and ranging from 2-15 mm in length. They are naturally attracted to many kinds of rotting organic matter, where they prey on the immature stages of flies or other insects.

It was thought at first that coprophilic histerids could be useful agents in suppressing the fly larvae in cow pads, especially at times when dung-burying by coprids is reduced by spells of drought. Histerids are less sensitive than coprids to the level of soil moisture, because their whole life cycle takes place inside the dung pad, or at the interface of dung and soil which is sufficiently moistened by the pad. This moistness, in fact, may extend to a depth of about 2 cm, and it provides a zone of conditioned soil where the beetles can pass their pupal stage.

As it turned out, very little success followed the introduction and release of histerids (see Tables 2 and 3), and doubts arose about their value in Fiji[7]. A continued program seemed unjustified, and introductions were discontinued in 1971.

The different breeding habits of the few species of beetles from Hawaii provided a basis for evolving flexible methods that were to serve in handling the wide variety of beetles to be introduced later from Africa and elsewhere.

First successes

January 30, 1968 was a red letter day in the program. Then the first stocks of the bovine-dung beetle, *O. gazella*, to be released in Australia were distributed at Lansdown, near Townsville. In the next few years a further 300,000 *O. gazella* were released on sites about 100 km apart, as were many thousands of the other Hawaiian species (see Table 2).

During the first rainy season after the first releases, five species were recovered in the coastal areas of North Queensland. Some of these species spread slowly, but within two seasons, *O. gazella* had exploded in literal millions. It spread at the rate of some 50 to 80 km per season, and quickly closed the gaps between the six original release points. It colonised two off-shore islands, Magnetic Island and Palm Island, that were respectively 10 and 30 km from the Queensland coast.

By April 1970, at the end of the third rainy season, *O. gazella* was continuously dispersed and firmly established over an area that extended inland 120 km, and north and south of Townsville a total distance of about 400 km[1,22,66]. By June 1975, *O. gazella* was established virtually throughout the tropics, inland roughly to the 500 mm isohyet, and it was also gaining a foothold in areas further south (see Figure 10).

Where conditions were favourable, the effect of the beetles on cow pads was dramatic. In the Townsville area, beetles were so numerous that pads disappeared within a day or so of being dropped.

This spectacular success of *O. gazella* gave Australian graziers their first opportunity to see what a dung beetle, well adapted to bovine pads, could do on their pasture-lands. *O. gazella*

Table 2 : Adult histerid beetles and dung beetles introduced from Hawaii into quarantine in Canberra during 1966-67.

Species	Climatic Zone	Origin	Performance class	Year of first release	Present status
Hister chinensis †	Tropical	Java	Tertiary	1967	Spreading
Hister nomas	Warm-temp.	Africa	Tertiary	1967	Spreading
Hister caffer	Wt-T	Africa	Tertiary	1968	Recovered(?)
Onthophagus gazella	Tropical	Africa	Central	1968	Exploding
Liatongus militaris	Wt-T	Africa	Secondary	1968	Spreading
Onthophagus sagittarius	Tropical	Ceylon	Secondary	1968	Spreading
Copris incertus	Wt-T	Mexico	Secondary	1969	Recovered(?)
Canthon humectus	Ct - Wt	Mexico	Secondary	1969	Recovered(?)
Onthophagus incensus	Warm temp.	Mexico	Tertiary	--	-----
Oniticellus cinctus	Wt-T	Ceylon	Tertiary	--	----

T = tropical, Wt = warm temperate, including sub tropics, Ct = cold temperate.
† Breeding stocks obtained in Fiji.

Table 3 : Histerid and dung beetles sent from Africa to Australia between November 1970 and August 1975.

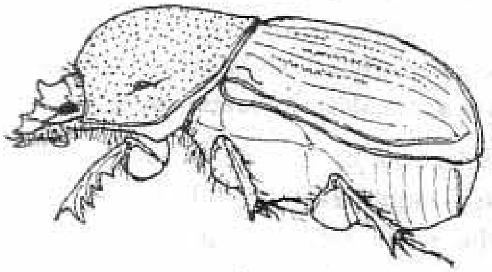
Species	Climatic zone	Performance class	Eggs sent Date number	Present status
Hister calidus	Wt-T	Tertiary	Nov. 70 1362	Released
Hister cruentus	Ct	Tertiary	Jan. 71 225	Released
Sisyphus miriabilis *	Wt-T	Tertiary	Dec. 70 154	Released
Sisyphus rubris ‡	Ct-Wt	Secondary	Dec. 70 903	Recovered
Onthophagus binodis SRS	Ct-Wt	Central	Jan. 71 1143	Recovered
Onthophagus bubalus	Ct-Wt	Secondary	Feb. 71 567	Released
Euoniticellus africanus	Ct-Wt	Secondary	Mar. 71 857	Recovered
Euoniticellus intermedius ‡	Wt-T	Secondary	Mar. 71 2600	*Exploding*
Chironitis scabrosus	Ct	Tertiary	Apr. 71 855	Released
Sisyphus spinipes ‡	Wt-T	Secondary	Oct. 71 2920	*Spreading*
Onthophagus binodis WRS ‡	Ct	Secondary	Nov. 71 1050	Released
Onitis alexis CHS ‡	Ct	Secondary	Dec. 71 5613	*Spreading*
Onthophagus gazella CHS	Ct	Tertiary	Jan. 72 3670	*Spreading*
Onitis westermanni	Wt-T	Central	Mar. 72 2580	Cleared
Onitis caffer SRS ‡	Ct-Wt	Central	Jun. 72 3435	Cleared
Chironitis scabrosus GP	Ct	Tertiary	Jun. 72 350	Released
Onitis alexis TS	Wt-T	Central	Nov. 72 5691	Recovered
Onthophagus gazella GP	Wt-T	Central	Dec. 72 3945	*Exploding*
Sisyphus rubrus	Ct-Wt	Secondary	Feb. 73 3185	Recovered
Heliocopris andersoni *	Wt-T	Central	Feb. 73 196	Quarantine †
Sisyphus spinipes GP ‡	Wt-T	Central	Mar. 73 483	*Spreading*
Onitis deceptor	Wt-T	Central	Apr. 73 677	Quarantine †
Onthophagus nigriventus	Wt-T	Secondary	Sept.73 1066	Recovered
Onitis vanderkelleni	Wt-T	Central	Oct. 73 2162	Recovered
Allogymnopleurus thalassinus	Wt-T	Secondary	Dec. 73 693	Quarantine †
Garreta nitens *	Wt-T	Secondary	Dec. 73 320	Quarantine †
Copris elphanor *	Wt-T	Secondary	Jan. 74 341	Quarantine †
Copris bornemisszai *	Wt-T	Tertiary	Feb. 74 183	Cleared
Copris hispanus	*Ct	Central	May 74 79	Quarantine †
Copris lunaris *	Ct	Central	Jun. 74 26	Quarantine †
Onitis belial *	Ct	Secondary	Jun. 74 25	Quarantine †
Bubas bison *	Ct	Central	Jun. 74 384	Quarantine †
Onthophagus vacca	Ct	Central	Jun. 74 845	Quarantine †
Onthophagus taurus	Ct	Central	Jun. 74 1730	Released
Onitis crenatus	Ct-Wt	Central	Dec. 74 3731	Cleared
Sisyphus fortuitus	Wt-T	Tertiary	Dec. 74 1077	Quarantine
Sisyphus infuscatus	Wt-T	Secondary	Dec. 74 324	Quarantine
Allogymnopleurus thalassinus ‡	Wt-T	Secondary	Jan. 75 404	Quarantine †
Garreta nitens	Wt-T	Secondary	Jan. 75 248	Quarantine
Copris elphanor ‡	Wt-T	Secondary	Jan. 75 1866	Quarantine
Onthophagus foliaceus ‡	Wt-T	Secondary	Jan. 75 4730	Released
Onitis uncinatus	Wt-T	Secondary	Feb. 75 1658	Quarantine
Onitis caffer ERS	Ct	Central	Apr. 75 2176	Quarantine
Onitis caffer SRS	Ct-Wt	Central	May 75 6067	Quarantine
Onitis caffer WRS	Ct	Central	Jun. 75 3056	Quarantine
Onitis anthracinus	Ct	Secondary	Jul. 75 1189	Quarantine

Abbreviations: CHS: Coldhardy strain. TS: Tropical strain. ERS: Even rainfall strain
SRS: Summer rainfall strain. WRS: Winter rainfall strain. GP: Gene pool additive.
T: Tropical. Wt: Warm temperate. Ct: Cold-temperate.

*Trial shipment. † Breeding stock died out in quarantine

‡ Species potentially capable of attaining central status in parts of Australia.

was a spectacular performer after it became established in Australia, both in terms of its capacity for dung removal and its abilities to reproduce and spread. However, as illustrated in the Hawaiian experiments, even beetles like *gazella* have limitations that are imposed by environmental conditions. This means that *O. gazella* will not be uniformly effective in all areas where it occurs (Figure 10). It means that it will require a number of other efficient species to supplement its activities, or fill the gaps that might occur in its distribution.



The overseas program

The operations in Africa began with the establishment of headquarters in Pretoria in July 1970. After a critical study of the literature on the taxonomy and distribution of the 2,500 or so species of coprids of the Old World, supplemented by inspection of museum collections, a restricted list of about 600 species was compiled to provide flexible guidelines to the most suitable type of beetles to seek, and the localities where they might be found.

The dung beetle project is a bilogical control project, but in some essential respects it differs from almost all other attempts at biological control undertaken. In its attack on a breeding medium as a primary target, its only precedents are the Hawaiian campaign against the hornfly[25], and a similar but abortive attempt in Puerto Rico[30]. In its selection of a non-living target (with the objective of pasture and soil improvement) it is unique.

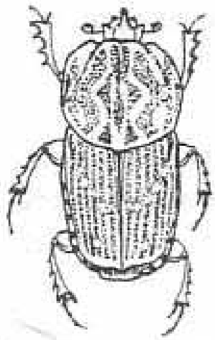
Another very unusual feature is the tremendous reservoir of potentially useful candidate beetles – for all practical purposes inexhaustible. Many biological control projects require the operators to undertake thorough and protracted search for safe and effective agents. We, by contrast, find that there is "un embarras du choix". Particularly for the warmer areas of Australia, the problem in selecting species to introduce is not what or where, but which.

Selection criteria

In spite of the rich choice available, the selection of species with characteristics appropriate to the Australian pasture ecosystem is relatively complicated, calling not only for expertise, but, unavoidably, also for a blend of caution and arbitrary judgment. In selecting species for Australia the following criteria are applied:

1. *Genuine dung-breeder.* This primary requirement is that the beetle must be an obligatory breeder in dung, with no alternative food materials at any stage of the life cycle. Fortunately, about 98 per cent of the coprids of the Old World are known to conform to this requirement, so that little time need be spent in considering the few undesirable species before discarding them.

2. *Predominantly bovine dung breeder.* Many species of coprids feed as adults on a variety of dungs, but have a distinct preference for a certain kind for use in breeding. The occurrence of adult beetles on bovine dung is, therefore, not an adequate criterion. Tests must be done to establish that they prefer to use bovine dung (that of cattle or buffalo) in breeding, before the species gets a high rating for further screening.



3. *Dung burial efficiency.* Among the paracoprids, beetle species of medium or large size should be able to bury at least 25 ml of dung per pair in a day or, if they bury slowly, to attain great abundance.

Smaller species, and especially the telecorprids, such as species of *Sisyphus* or *Gymnopleurus*, are also acceptable – in spite of a much lower rate of burial per pair – if they are usually found on cow pads in large numbers.

4. *Ease of handling.* To ensure that an effective, on-going program is maintained, immediate efforts are concentrated on those beetles that are easily reared. Coprids are easy to collect, and many are easy to breed in the laboratory, but there are also many species in such genera as *Scarabaeus*, *Kheper* or *Catharsius* that have not responded readily or at all to indoor conditions (Table 3). When their field performance is outstanding, such species are reserved until time or facilities permit more intensive study.

5. *Fast breeder.* Currently preference is given to species with a high fecundity and rapid larval development. This criterion is, however, difficult to apply rigidly (see below).

6. *Compatibility.* Beetles that are selected should be compatible in habits, properties, and preferences so as to exclude, or at least minimize, interspecific competition. The degree of their co-adaptation is assessed in the field, partly by their abundance and consistency of occurrence, and, where they occur together, partly from subjective observation of their interactions. The beetles' daily and seasonal patterns of activity give some clues to their compatibility with one another.

7. *Distribution range.* It is desirable to select species with a wide geographic distribution, for this normally implies availability of stock with a wider range of climatic adaptation than would be expected in a species with restricted or spotty distribution.

8. *Taxonomy.* The first seven criteria deal with critical biological and ecological characteristics, but the importance of sound taxonomy should never be overlooked. The research workers engaged in the project naturally find it a great advantage to work with readily distinguishable species. Unfortunately this is not always possible. In several genera there are valuable species that are difficult to separate without dissection, especially as females. However, such problems are not allowed to override the basic requirements of securing the most efficient assemblage of beetles possible.

The selection of beetles is an involved process, with innumerable ramifications that should all be taken into account to secure a balanced minifauna. However, there are occasions when it may be an advantage to overlook some of the criteria. For instance, a rigid adherence to the search for fecund beetles with short life cycles, such as *O. gazella*, would exclude many efficient species such as some of the genus *Heliocopris* which may not lay more than 20-30 eggs within a season and have only one generation a year. To offset these disadvantages they are long-lived, and one pair can bury a large cow pad in a few hours.

As already mentioned, caution is exercised in assessing the preference of a species for a certain kind of dung. We have given thought to the desirability of conserving the Australian dung beetle fauna, which is entitled to as much consideration as any other element of the native biota. African species that show particular interest in the pellet-type droppings of antelopes from arid regions could, in theory, show comparable interest in marsupial droppings, and so jeopardize the survival of the Australian coprids by out-competing them. In fact, one species that was tested preferred the droppings of hand-fed marsupials (obtained from an African zoo) to that of antelopes. Its despatch to Australia has been postponed while the situation is reconsidered.

Many species of coprids from arid areas of India and Africa would be valuable for burying domestic animal droppings (including those of sheep) in the arid parts of Australia. There, where rainfall does not exceed 250 mm, only two species of native *Onthophagus* are known. However, it seems unlikely that these or other native species would be exterminated. They have evolved in the ecosystem and would probably have some competitive advantage over imported species that would enable them to survive.

Nature of surveys

Two types of survey trip are conducted to find suitable beetles and assess their usefulness to Australia.

The first type is the stock-taking trip to assess the broad potential of an area, often remote from Pretoria (Figure 8). On such journeys note is taken of the distribution of livestock, collecting conditions, facilities for transport, means of despatch of beetles, and the potential co-operativeness of administrative authorities, health inspectors and custom officials.

Figure 8: Although dung beetles are distributed naturally over a large part of the old world, the Australian search has only covered a small part of the potential area and examined a few of the 2.5 thousand species.

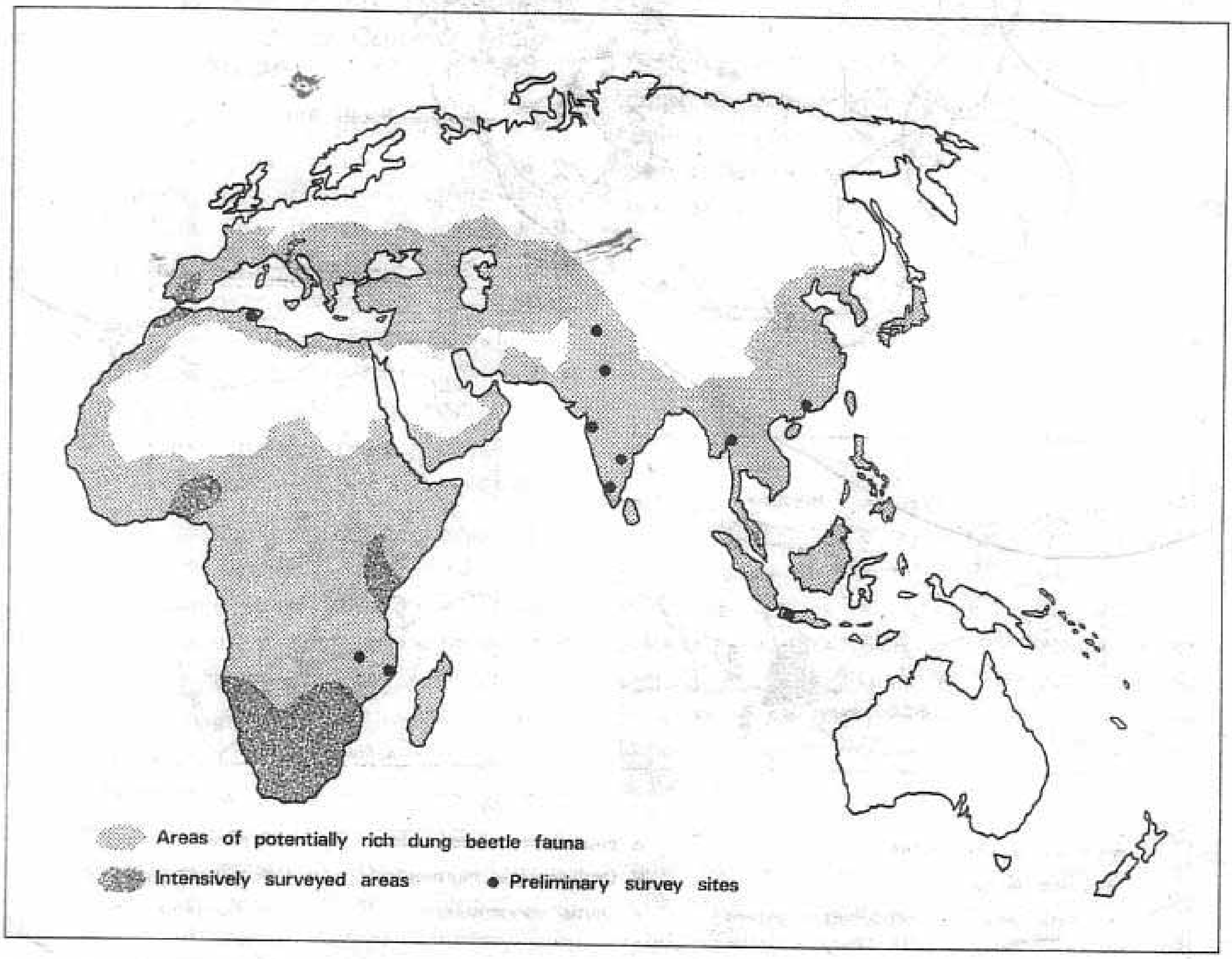
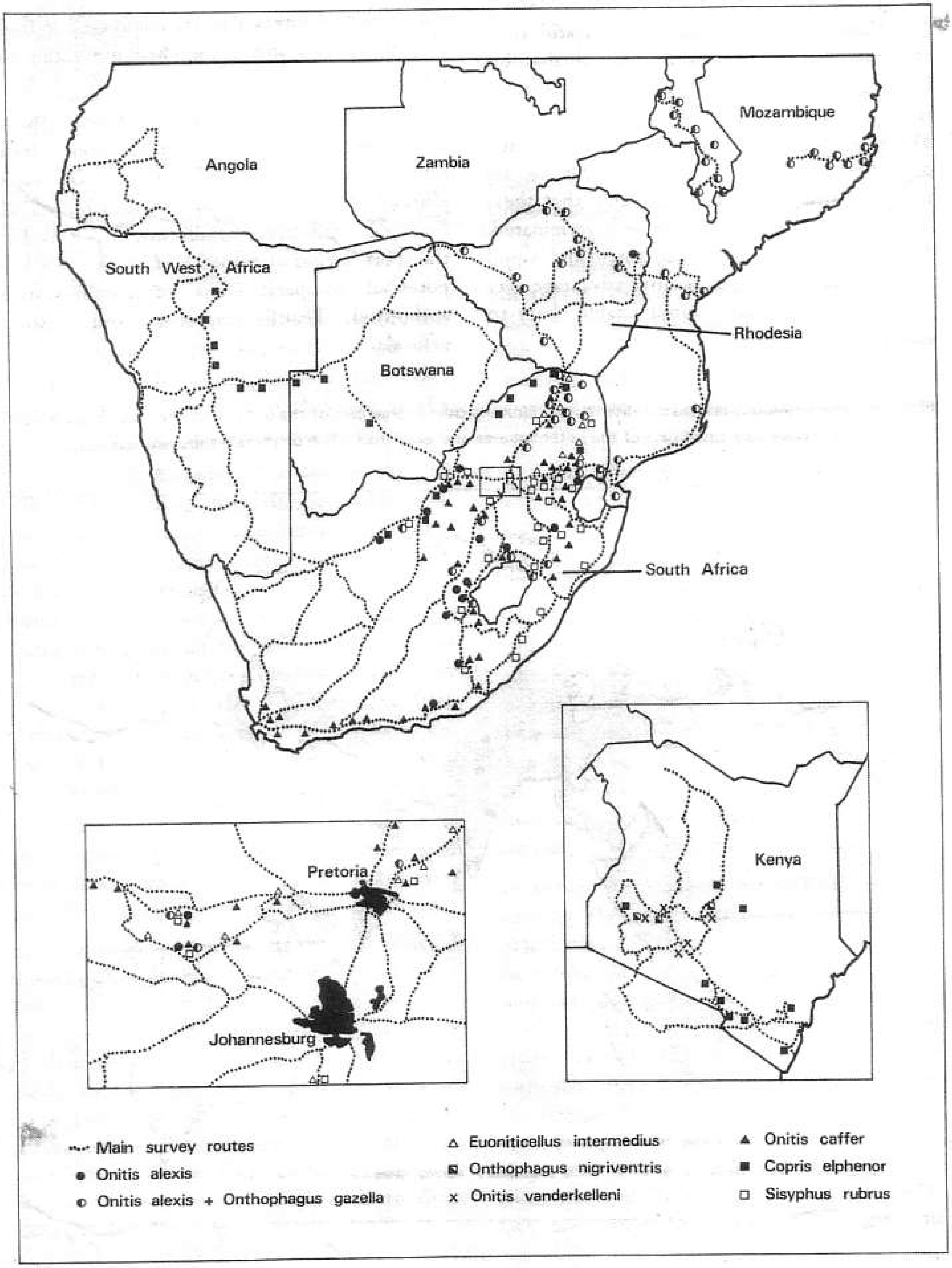


Figure 9: The breeding stocks of species selected for transplanting to Australia are based on pooled stocks from a wide range of ecological situations. This is done to ensure genetic diversity and provide the flexibility needed to adapt to a variety of situations. This map shows the areas over which stocks of a few of the species have been collected.



First and foremost, however, a concentrated effort is made to size up the coprid fauna of an area or country by collecting all available species, and preserving them for identification and future reference. Relevant habits, patterns of activity, and capacities for dung disposal are also noted. The promising species are then listed as targets for study during future visits. At Pretoria the preserved specimens are mounted, labelled, identified and stored in the reference collection which, even now, is probably the largest coprid collection in existence, and certainly is the most representative for Africa.

Whenever possible on these stock-taking trips, some live specimens of promising species are sent back to Pretoria to provide material for preliminary study of culture methods and to test methods of despatch and avenues of transport. Such trial shipments have sometimes led to egg-production in Pretoria and subsequent transplantation to Canberra without further collecting.

These stock-taking trips are usually brief, and often encompass several countries in a climatic region. They are usually followed up by further visits. The aims of these follow-up trips are primarily to collect the living beetles of target species over a wide ecological range, and to study the biology, habits, phenology, and dung-disposing capacities of species on the target list. Other species, that were not observed or were not at their peak activity during the stock-taking visit, are also studied.

Back at headquarters the beetles are kept under observation in pairs in the insectary, or in quarantine if they come from outside South Africa. Their habits, biology, and reproductive potential are assessed. If they are rated as suitable candidates, mass propagation begins and finally eggs are sent to Australia.

An effort is made to ensure genetic diversity of the species by collecting the breeding stock throughout its full ecological range, especially as this is reflected by temperature and rainfall. This is important for providing a broad basis for adaptability of the species within its new environment, and for furthering rapid establishment and wide dispersal[68].

Even a well established beetle such as *O. gazella* was considered to be in need of genetic enrichment, because the Hawaiian strain originated from only two areas – Beira in Mozambique, and Mombasa in Kenya. Both of these are on sandplains and have similar climates and annual rainfalls of 1,000-1,250 mm. To secure the full potential of *gazella* for Australia, it seemed advisable to seek extra stocks in southern Africa (see Figure 9). This genetically enriched strain was seeded into established populations throughout tropical Australia in 1973-74 and was also sent to Hawaii, thus recognizing Australia's debt to the islands.

Attention is also paid to establishing cultures of recognized varieties of a species from different climates, especially when the range covered is wide. This sometimes means maintaining two or more strains separately throughout the production line until they are released in Australia (Table 3).

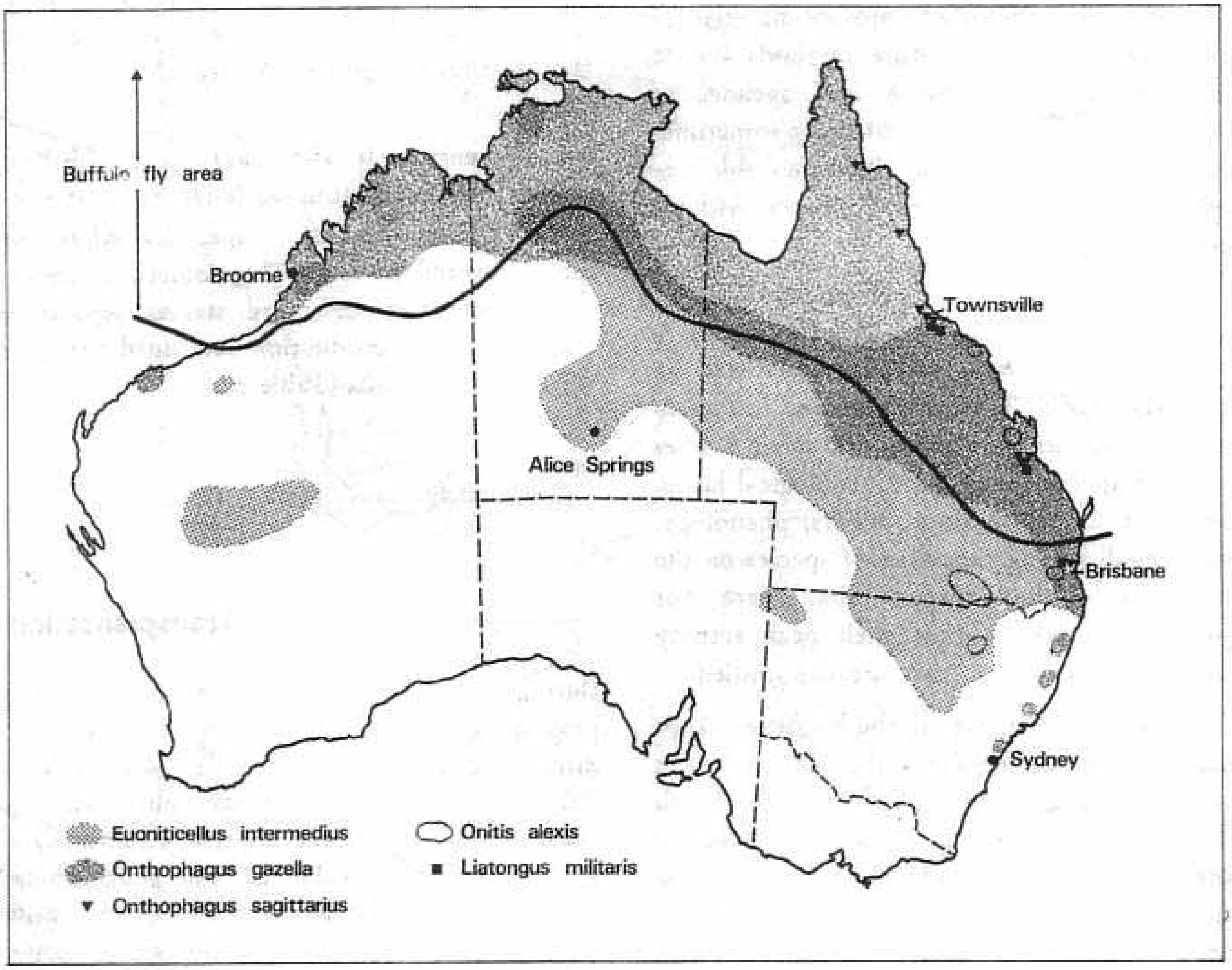
Transplantation

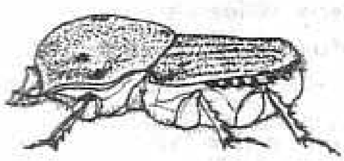
During the first five years of the overseas program a total of 139 species of coprids and three species of histerid beetles was studied. Fortyone species of coprids, plus ten climatically or genetically diverse strains, were sent to Australia (Table 3). The geographical progress as at July 1975 of five of the most important species released in Australia is shown in Figure 10.

Many of the species of beetles studied could not be induced to breed at all. Others were rejected because of various undesirable habits. Those species that could be bred and showed promise in other respects were listed for transplantation when adequate material became available.

In the five years since the inception of the overseas program an average of eight species of beetles has been introduced into Australia each year. The figure will increase from 1975-76 onward. Particular attention will be paid to species likely to be adapted to southern areas. Thus, seasonal conditions in all critical regions permitting, the next 10 or 12 years should see the transplantation to Australia of some 160 species. This is our estimate of the numbers required to meet the needs of the entire continent.

Figure 10::*Onthophagus gazella* and *Euoniticellus intermedius* are by far the most successful species of dung beetles yet released in Australia. *Onitis alexis*, a slower breeder, is also showing promise of early establishment. *Onthophagus sagittarius* from India and *Liatongus militaris* from Africa, which were both released in 1968, are also slow breeders, but are probably more widely spread than this map indicates. Other African beetles, released in the cooler southern areas, have been less successful.





The Australian program

The Canberra centre receives all material sent from Africa and elsewhere. The tasks there are to implant imported eggs into artificial or foster-parent brood balls, to mass breed beetles, and to organize their release in the chosen areas. As opportunity offers, the spread of the beetles and their effect on cow pads and fly populations are assessed, albeit on a more limited scale than desirable. As the overseas program has expanded, the facilities at Canberra have been built up to deal with the increased flow of material and the multitude of diverse tasks the unit has to perform.

Quarantine and mass breeding

During the first ten years, a total of 48 species of coprids, including climatic and genetically diverse strains, and five species of histerids, was processed in quarantine in Canberra. The relatively simple breeding habits of histerids, involving no brood care, permitted the early release of all five (Tables 2 and 3). Despite the drastic quarantine procedures to which the coprids were subjected, 31 species came through the process successfully. Most of those that failed in the processing, such as *Onitis caffer*, *O. deceptor* or *O. westermanni*, were found to have obligatory dormancy periods during larval or adult stages. The same applied to a large number of telecoprids (Table 3). Climatic chambers are now being installed in the quarantine rooms, and this will allow simulation of different seasonal conditions, and should reduce these problems.

Once out of quarantine, beetles are mass produced in insectaries to supply the numbers needed for rapid establishment in the field. They are propagated in large breeding pens equipped with subsoil heating to ensure continuous and rapid breeding.

Strategy of releases

Once the beetles are breeding well and the seasonal conditions in their intended release areas are favourable, a release site is selected from among those chosen as suitable according to the climatic and edaphic requirements of the species. The beetles are packed in damp peat moss in ventilated plastic containers in strong cardboard boxes. Under these conditions they can survive journeys of three or four days without harm. They are then despatched by air to graziers or State Department of Agriculture of CSIRO staff for release. At their destination they are simply tipped out onto fresh cow pads in a pasture. Normally the beetles burrow immediately into the dung.

Up to the present, 23 species of coprids, i.e., almost half the number introduced, have been released. Among these 23 are two climatic strains of each of three species and genetically diverse strains of three other species (see Table 3). The beetles have been distributed in hundreds of thousands, at several hundred release points, all over the mainland of Australia and Tasmania. About two-thirds of those released were bred in the insectary, but thousands of *O. gazella* and *E. intermedius* were also cropped from former release sites where they had become abundant. *O. binodis*, *O. sagittarius*, *L. militaris*, *E. africanus* and *S. spinipes* are now becoming numerous enough to permit similar field collections.

In the last seven years the Canberra team has released nearly 800,000 beetles at 900 sites. In the same time, over 12,000 quarantine-bred coprids and 1500 histerid beetles were exported – most of them to the USA, Hawaii or Melanesia.

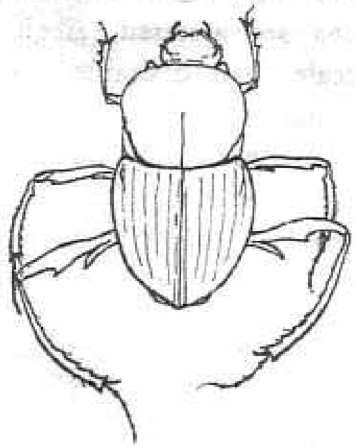
Hundreds of requests for beetles are received at Canberra each year. Regrettably, there are insufficient stocks to meet most of these requests. But there is still a lot of unofficial trafficking in *Onthophagus gazella* and *Euoniticellus intermedius*, taken from sites where they are well established.

Follow-up studies

Perhaps the most rewarding phase of the whole project is the recovery-surveys to check on the fate of beetles released. Shortages of personnel and the enormous distances involved have restricted these surveys, but there is some regular monitoring to measure beetle activity, spread, abundance, and effect on cow pads and fly populations. An area under close observation near Rockhampton is the main evaluation site at present. Monitoring is also being done at the Q.D.P.I. Swan's Lagoon Station at Millaroo, at sites near Brisbane, and at Narrabri in north-central New South Wales.

From the observations at these centres, from a few cross-country surveys, and from reports from graziers that are substantiated by specimens, it has been possible to compile a map (Figure 10) showing the distribution of the two most successful species as at July 1975. From these reports it appears that the spectacular success of *O. gazella* is now being surpassed by *E. intermedius*, both in rate of spread and speed of population build-up. Where it has been possible to check, *E. intermedius* has established within a year at almost all release points north of latitude 32°. In contrast with *O. gazella* which is most successful within the 500 and 1,000 mm isohyets, *E. intermedius* promises to be most effective within the 300-600 mm rainfall zones of warm inland areas, and also to destroy at least some pads in large areas on both the wet and dry sides of this most favoured zone.

An evaluation unit was established near Brisbane in late 1973. It was later transferred to Rockhampton, where the environmental conditions and the array of established beetles appear more appropriate. One of the tasks of this unit is to follow up the dispersal and establishment of the various species released, and to study natural enemies that beetles might encounter in their new environment. Also important will be the monitoring of the population build-up, and the study of the effect of the beetles on the status of pest flies that breed in cattle dung.



Conclusions and prospects

The Australian dung beetle project already has substantial achievements to its credit.

At the two major research centres, over 150 species of coprids have been studied during the first ten years. About half of the 48 species transplanted to Australia have been released. At least eleven of them have established, and probably more of the releases will prove to have been successful.

The spectacular successes of *O. gazella* and *E. intermedius* have provided encouraging evidence of the viability of the project. Although other species may take much longer to prove themselves, *O. alexis* and several other species could soon initiate explosive multiplication similar to that of *O. gazella* and *E. intermedius*. The distribution of three central species (*O. gazella, E. intermedius* and *O. alexis*) has recently overlapped, or will shortly do so, in several areas in south and central Queensland, and the opportunity will then arise to observe the combined effects of these beetles, whose individual performances have been impressive.

In the extensive areas of Australia where African dung beetles have attained sufficient numbers, there is abundant visual evidence that the objective of dung dispersal is achieved during favourable times of the year. There is evidence of an impact on bushfly breeding in one key area, and there is a suggestion of an occasional reduction in the numbers of buffalo fly, though not sufficient as yet to meet the requirements of the cattle industry.

The full potential of the dung beetle resources of the Old World has not yet been tapped, and there is still a long way to go to meet all of Australia's needs. It is, after all, a continent of 7½ million square kilometres, with annual rainfalls ranging from 100 to 5000 mm. There are many ecosystems that have not yet been considered, and many features of secondary importance calling for attention within the ecosystems that have been studied.

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