ESTABLISHMENT OF EXOTIC DUNG BEETLES IN QUEENSLAND : THE ROLE OF HABITAT SPECIFICITY

B. M. DOUBE [1] & A. MACQUEEN [2]

[1] CSIRO Division of Entomology, G.P.O. Box 1700, Canberra, A.C.T. 2601, Australia
[2] CSIRO Division of Entomology, Private Bag No. 3, Indooroopilly, Qld 4068, Australia

Between 1968 and 1983, 22 species of dung beetles from southern Africa were released into pastoral regions of Queensland in northern Australia. Seven species have become widespread and abundant and the others either occur in isolated patches, are rare or have failed to establish self perpetuating populations. These species all occur in the Hluhluwe district in southern Africa which has a climate similar to that of coastal central and southern Queensland. The numerical abundance and habitat associations of the 22 species were examined at Hluhluwe to seek an explanation for their performance in Australia. It was concluded that habitat specificity and the adequacy with which habitat was matched in Australia were critical factors. Species which established in Australia were relatively common in cattle dung in Africa where they showed a preference for grassland on clay-loam soils.

KEY-WORDS : dung beetle, exotic species, invasion, habitat specificity.

Habitat specificity has long been recognized as a fundamental characteristic of species and is a major determinant of the distribution of organisms in a heterogeneous environment (**Begon** *et al.*, 1986 ; **Southwood,** 1987). Appreciation of this is essential to the success of classical biological control programs, where poor habitat matching of donor and target areas may result in refuges in which the pest largely escapes control by its natural enemies.

Monitoring the deliberate (and accidental) invasion of land masses by exotic species has allowed analysis of the factors which determine (i) whether an introduced species will be successful (i.e. establish and become widespread and abundant), and (ii) whether a successful introduction will have an impact on the community it invades (**Pimm,** 1987 ; **Crawley,** 1987 ; **Robinson & Dickerson,** 1987). It is the first question we wish to consider here in relation to the introduction of dung beetles to Australia.

Dung beetles, predators and parasitoids have been introduced to Australia to improve the level of biological control of dung-breeding pest flies (**Waterhouse,** 1974 ; **Bornemissza,** 1976 ; **Doube,** 1986). Between 1968 and 1982 CSIRO imported 55 species of dung beetles for release in Australia. Of these, 37 were intended for the summer rainfall regions of northern Australia. Nine species were not reared in numbers sufficient to justify releasing them in the field, but the remaining 28 species were released in at least one locality in northern Australia ; 22 of these occur in southern Africa. In recent times (1980-87), a substantial body of information about the distribution and abundance of these species was collected in southern Africa and provides a basis for an analysis of factors which influenced their chance of establishing in specified habitats in Australia.

In northern Australia, the release of exotic dung beetles and monitoring of their populations was concentrated in the pastoral regions within 200 km of the eastern coastline, mainly between Brisbane and Townsville (fig. 1). This region has a similar climate to that of the coastal lowlands of Natal, South Africa between Durban and the Mozambique border. The Hluhluwe district (about 150 km N of Durban) contains extensive pastoral areas and game reserves, and there the dung beetle assemblages have been monitored in a variety of habitats (**Doube**, 1983, 1986, 1987). It is clear that the abundance of many African species is strongly influenced by soil type, vegetative cover and the type of dung available (**Endrody-Younga** pers. comm. ; **Doube**, 1983, 1986).

The degree of success of the current suite of 22 African dung beetle species in coastal northeastern Australia now permits a retrospective evaluation of the criteria used in their selection. Here we show that most of those species which were relatively abundant in grassland on clay or loam soils of the Hluhluwe region also became abundant and widespread when introduced to homologous regions of Queensland. Species which were largely restricted to game reserves, bushland or deep sandy soil or were scarce or absent in the Hluhluwe district have so far failed to establish in coastal Queensland.

MATERIALS AND METHODS

ABUNDANCE AND HABITAT ASSOCIATIONS OF DUNG BEETLES IN AFRICA

Pitfall traps baited with 1 litre of fresh cattle dung were set at weekly intervals in 8 contrasting habitats between 5 April 1983 and 26 June 1984 in the Hluhluwe region of Natal, South Africa. At each site on each trapping occasion, 3 traps (> 10 m apart) were baited between 15.00 h and 17.00 h and the dung beetles trapped were collected 24 h later.

There were 4 trap sites in pastoral regions and 4 inside game reserves. The distance between the most widely separated trap sites was about 30 km. In both pastoral and game reserve environments, 2 sites were located in a track of clay-loam soil (one in grassland, the other in bushland) and 2 were located in a track of deep sand (one in grassland, the other in bushland). Thus there was an orthogonal set of data based on the 3 habitat dimensions examined ; namely vegetative cover (4 grassland and 4 bushland sites), soil type (4 clay-loam and 4 sandy soil sites). and management (4 pastoral and 4 game reserve sites). The number of each species trapped in grassland, in clay-loam soils and in pastoral situations was expressed as a percentage of the total number trapped overall to give a measure of its habitat associations. For example, in the case of *Onthophagus gazella* (F.), 89.7 % of 715 individuals were trapped in grassland, 67.6 % were trapped on clay-loam soil and 57.6 % were trapped in pastoral habitats (table 1).

RELEASE AND BREEDING PERFORMANCE OF DUNG BEETLES IN AUSTRALIA

All release sites were in pasture grazed by cattle on clay-loam or sandy loam soils. Beetles were not released in areas of deep dune sand equivalent to the African sandy soil sites. Most of the early releases in northern Australia comprised 300-500 insectary-reared beetles placed on a number of fresh dung pads at each of several or many sites ; later, the strategy was to release more beetles (up to several thousand per site) at fewer sites.

The release sites of all species were visited at irregular intervals during the summer wet season in the years following the initial release. During each visit, numerous dung pads were examined for the presence of the introduced species. For the first two years after release, specimens of newly recovered species were examined, when appropriate, for

TABLE 1

The numerical abundance and habitat associations of 22 dung beetle species trapped in the Hluhluwe district of lowland Natal, South Africa, with their performance following release in the field in Queensland, Australia

Species	Habitat associations in Natal					Status in Australia	
		Percent of total catch in each category					
	Beetle Length (mm)	Grassland (vs Bushland)	Clay-loam (vs sand)	Pastoral (vs Game Reserve)	Total Number	First released	Current status/distribution
Abundant and widespread							
Euoniticellus intermedius	8	79.3	68.1	49.1	9 980	December 1971	Near distributional limits
Onthophagus gazella	11	89.7	67.6	57.6	715	January 1968	Near distributional limits
Liatongus militaris	9	84.4	85.2	38.4	2 852	June 1968	Dispersal continuing
Sisyphus spinipes	9	69.1	58.4	27.9	3 101	March 1972	Dispersal continuing
Sisyphus rubrus	8	91.5	96.0	45.3	6 585	August 1973	Dispersal continuing
Onitis alexis	15	72.9	33.0	68.5	203	August 1972	Dispersal continuing
*Onitis viridulus**	16	—	76.9	—	65	September 1976	Dispersal continuing
Established but not widespread							
Onitis pecuarius	16	—	—	—	0#	November 1976	Established in one locality
Onitis caffer	15	42.9	42.9	64.3	14	May 1983	Established in one locality
Copris elphenor	19	97.5	9.5	6.5	200	October 1978	Established in one locality
Not known to be established							
Euoniticellus africanus	9	—	—	—	0#	December 1973	Apparently absent
Onthophagus binodis	10	—	—	—	0#	August 1973	Apparently absent : recovered 1975
Sisyphus mirabilis	10	12.3	65.5	15.3	1 283	April 1972	Apparently absent : low numbers released
Sisyphus infuscatus	8	63.9	75.9	39.3	1 005	October 1976	Apparently absent : recovered 1982
Allogymnopleurus thalassinus	11	98.2	4.8	22.5	2 186	March 1979	Apparently absent : bred for several generations in field cages then low numbers of survivors released
Onitis tortuosus	16	—	—	—	0#	November 1976	Apparently absent
Onitis westermanni	12	—	—	—	0#	January 1977	Apparently absent
Onitis deceptor	19	81.3	1.7	49.8	235	December 1979	Apparently absent
Onitis uncinatus	18	87.5	62.5	68.8	16	December 1979	Apparently absent
Copris diversus	10	—	—	—	0#	October 1976	Apparently absent
Copris bornemisszai	20	—	—	—	0#	January 1977	Apparently absent
Copris fallaciosus	21	79.4	47.1	67.6	34	January 1977	Apparently absent : recovered 1978

* Only 3 individuals caught in 1983-84. Data presented are for 1982-83 from pastoral grassland on clay and sandy soil only.

These species are known to be present in the Natal region of South Africa but were not trapped in 1983-84.

— No data available.

Beetles were trapped weekly at 8 sites in Africa over 15 months (April 1983 to June 1984). Trap sites were located in each of the following 3 pairs of contrasting habitats, with 4 sites per habitat : grassland and bushland ; clay-loam soil and deep sand ; pastoral and game reserve. The data shown are the percentages of the total number of beetles overall on grassland, clay-loam soil and in pastoral situations.

indications of age (e.g. tibial wear) in an attempt to distinguish parent beetles from their progeny. Most of the species released have several generations per year and even the long-lived species e.g. *Copris elphenor* Klug, do not live beyond 2 years (**B. M. Doube,** unpublished).

RESULTS

Between 1968 and 1988, only 7 of the 22 species released have become abundant and widespread in pastoral regions of coastal southern and central Queensland (table 1) and these can be regarded as successful colonists. Of the remaining 15 species, 3 species are present only in one locality : *C. elphenor* is established near Biloela, central Queensland, while *Onitis pecuarius* Lansberge and *Onitis caffer* Boheman are established in the southern highland area near Toowoomba, which has a much cooler climate than most regions between Brisbane and Townsville. Three species, *Sisyphus infuscatus* Klug, *Onthophagus binodis* Thunberg and *Copris fallaciosus* Gillet, were recovered some years after their release in central Queensland but have not been seen since then, despite repeated searching, and are unlikely to have established. Nine other species are now presumed to have failed to establish breeding populations since none has been recovered following their release 10 years ago or more.

There is a strong association between the affinity of the species for a particular habitat (as given by the African data in table 1) and whether it established in Australia. The 7 most successful species showed a positive association with grassland and were relatively common in pastures on clay-loam soil ; most were relatively abundant in Africa. *Copris elphenor* has established on sandy loam and showed an association with sandy soil in Africa (table 1). Although this species was rare in South African pastoral sandy soil sites in 1983/84, it was common at one site in previous years and was a dominant element in other pastoral sandy soil systems in the summer rainfall regions of South Africa (**B. M. Doube,** unpublished). Two of the 12 unsuccessful species (*Onitis uncinatus* Klug and *C. fallaciosus*) have habitat associations which are similar to those of the successful group of species. These species were difficult to rear in the laboratory because of larval (*O. uncinatus*) or adult reproductive (*C. fallaciosus*) diapause. They also had to contend with lower than average summer rainfall for several years after release.

Six of the 12 species which have failed to establish between Brisbane and Townsville, and also *O. pecuarius,* were not trapped in the Hluhluwe study although all have been collected in the Natal lowlands. Of the other six species, which were trapped in the Hluhluwe region but failed to establish in the pastoral areas of southern Queensland, 2 (*Onitis deceptor* Peringuey and *Allogymnopleurus thalassinus* (Klug)) showed a strong association with deep sand and were rare at the clay-loam sites. *Sisyphus mirabilis* Arrow, which also failed to establish in Queensland, shows a preference for bushland and was common only in the game reserve environment : in addition only 53 individuals were released due to breeding problems.

DISCUSSION

Successful establishment of an exotic species requires that a sufficient number of breeding individuals be released into a habitat in which they can reproduce and that favourable conditions persist for long enough to allow their progeny to develop, breed and disperse. The need for climatic matching of donor and target areas (fig. 1) has long been recognized but definition and matching of the precise habitat requirements of many species

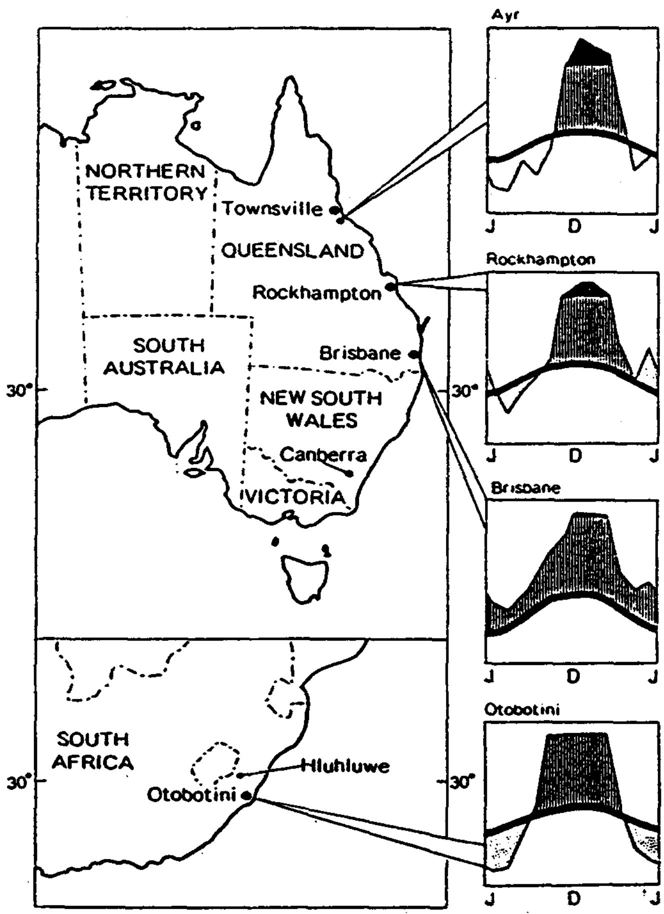

Fig. 1. Climatic similarities between the study area near Hluhluwe in South Africa and dung beetle release sites in coastal and subcoastal Queensland. The climatic diagrams (from **Walter & Lieth,** 1964) show mean monthly temperature (thick line) and rainfall on a common scale: dry periods (precipitation < evaporation) are shown as dotted areas and moist periods (precipitation > evaporation) as vertical lines. Black areas denote months receiving in excess of 100 mm rainfall, on a scale reduced to 1/10 of the original.

needs also to be considered in the selection of biocontrol agents (**Doube,** 1986; **Kirk & Ridsdill-Smith,** 1986). In Australia, most species of exotic dung beetles were released into environments which were highly modified by man and where the indigenous herbivores and bushland had been replaced by domestic stock and pasture. There were few competitors for the alien dung in this habitat (**Waterhouse,** 1974).

Our criterion for judging establishment is that adult progeny of a species should be found at a site on more than one occasion at least 2 years after release. Most species which established were fecund and multivoltine, and establishment was self-evident within a few years of release. We considered that fecund species had failed to establish if they were not found 3-5 years after release and, in the case of univoltine species of low fecundity, after 5 to 10 years. In some instances the probability of establishment was reduced by a succession of dry seasons following release of the beetles.

Seven species of dung beetles are now well established and widespread in Queensland (table 1). Two of these (*O. gazella* and *Euoniticellus intermedius* (Reiche)) are considered largely to have reached the limits of their natural distribution, extending over most of northern Australia. Three other species (*C. elphenor, O. caffer* and *O. pecuarius*) are now present in such numbers that they are unlikely to become extinct.

Whether the ball-roller *S. infuscatus* has persisted since 1982 is unknown, but it may be present at low densities, since *Sisyphus* species are cryptic. They smear themselves with dung and leave no tunnels beneath the dung pad and so can easily be overlooked. Adult progeny of 2 tunnelling species (*C. fallaciosus* and *O. binodis*) were recovered respectively 1 or 2 years after release but were not collected during subsequent checks. We consider that these, plus a number of other species which have not been recovered at all in the years following release, have failed to establish.

The number of individuals which constitute a viable founder population varies widely and will be influenced by the physical environment, the biology of the species and the quality of specimens released. Furthermore, the life history characteristics of species affect both the size of the founder colony required and the time taken for the species to become well established. It is apparent, *a priori,* that fecund, dispersive, multivoltine species (e.g. *E. intermedius, O. gazella*) will have the potential to establish from a small nucleus over a short period of time, whereas univoltine species of low fecundity and wide dispersal power will require more individuals and a much longer time span. This may be the case for some of the K-selected coprine species (e.g. *C. elphenor*).

Eight of the 12 species which failed to establish were difficult to rear in the laboratory because of larval or adult diapause (*Onitis westermanni* Lansberge, *Onitis tortuosus* Boheman, *O. uncinatus, O. deceptor, Copris bornemisszai* Ferreira, *C. fallaciosus, Copris diversus* Waterhouse and *A. thalassinus*). As a result, only low numbers of these species were released in the field and some of these were slightly deformed individuals, possibly with low viability. It appears likely, on the basis of habitats available in Australia and habitat preferences shown in Africa, that some of these species (e.g. *O. uncinatus* and *C. fallaciosus*) could be successful colonists if laboratory rearing problems were overcome.

The 7 species which have become well established all occur towards the r-end of the r-K continuum and most are found in moderate numbers in pastoral grassland on clay-loam soil in the Hluhluwe region (table 1) and in Hluhluwe Game Reserve (**Doube**, 1983). The beetles *O. caffer* and *Onitis viridulus* Boheman were relatively scarce in the Hluhluwe trap catches (baited for 24 h), but these species preferentially colonise older dung (3-7 days old) (**Doube** *et al.*, 1988) and are much more abundant in Hluhluwe than is suggested by the data in table 1. In contrast, there are other r-selected species which have not been successful in Australia. A knowledge of their habitat associations, obtained after their release in Australia, indicates that they are unsuited to much of the pastoral country between Brisbane and Townsville. As already mentioned, *O. deceptor* and *A. thalassinus* occur almost exclusively on deep sandy soils, while *S. mirabilis* appears to prefer bushland in game reserves. During the early stages of the dung beetle program there was minimal information on the broadscale habitat associations of dung beetles and, as a result, management decisions on which species to introduce were influenced strongly by localised high levels of abundance of species in Africa which were not necessarily representative of the regional patterns identified later on.

Ten species were scarce ($n < 50$) or absent from the Hluhluwe trap data and, although present in coastal Natal, all have failed to establish in coastal Queensland. A number of these species have been abundant at times in summer rainfall regions of southern Africa (e.g. *O. westermanni*) but were scarce or absent from pastures near Hluhluwe during the period 1981-86 (**B. M. Doube**, unpublished). It therefore seems unlikely that their climatic tolerances are so strict that they cannot establish in regions of Queensland with a strong climatic similarity to the Hluhluwe region, but we cannot be certain of this. The breeding stocks for most species were not collected in Hluhluwe but in other summer rainfall regions of South Africa (**Bornemissza**, 1979). For example, stocks for a number of species were derived from beetle populations in pastoral areas near Pretoria in the Transvaal highlands. A number of these have spread over much of northern Australia. Other species have a broad geographic distribution in Africa, and 2 of these (*O. caffer, O. binodis*) are relatively common in pastures in the mediterranean-type climate areas of the Cape Province (**Davis**, 1987). They were introduced to Australia from the Cape Province and are now established in pastures in the mediterranean region near Perth, W.A. The summer rainfall strain of *O. caffer* introduced from the Pretoria region of South Africa, is now also established in Queensland (table 1).

The species which became widespread and abundant in cattle pastures in Australia were predominantly r-selected species found in pastures in the clay-loam soil regions of equivalent climate in South Africa. K-selected species which can be reared readily in the laboratory (e.g. *C. elphenor*) should also be successful, but may take a long time to become widespread and abundant. Species which are rare in a particular habitat in Africa appear to have a low probability of becoming established in the corresponding habitat in Australia. However, this was far from clear when the initial selection of species was made and it is quite possible that in Africa there are constraints upon beetle distributions, such as competition and predation, which do not apply in Australia. From this *a posteriori* analysis we conclude that climate and habitat matching are significant factors influencing the probability that subtropical African dung beetles will establish in northern Australia, provided that a sufficient number of healthy individuals are released.

The same rationale has been extended to other dung beetle assemblages from other climatic regions, e.g. the mediterranean-type climatic areas of Europe and Australia (**Ridsdill-Smith & Kirk**, 1985). Climate-matching followed by habitat-matching has permitted the selection and successful introduction of species, provided that they can be reared readily in the laboratory (**Doube** *et al.*, in press). The same principles are likely to yield beneficial results when applied to the selection and introduction to Australia of predators and parasitoids of dung-breeding pest flies because they also show strong habitat affinities (**Davis** *et al.*, 1988). For example, species which are common in the Hluhluwe pastoral regions and which parasitise or prey upon dung breeding *Haematobia* (**Doube & Huxham**, 1987) are prime candidates for introduction to subtropical northern Australia.

ACKNOWLEDGEMENTS

The Australian Meat Research Committee supported this work. We thank the Natal Parks Board of South Africa for assistance.

RÉSUMÉ

Etablissement de bousiers exotiques dans le Queensland : le rôle de la spécificité de l'habitat

Entre 1968 et 1983, 22 espèces de bousiers originaires du sud de l'Afrique ont été lâchées dans des régions d'élevage du Queensland, dans le nord de l'Australie. Sept espèces se sont bien dispersées et sont devenues abondantes : certaines vivent dans des zones discontinues, d'autres enfin sont rares ou n'ont pas réussi à s'établir de façon durable. Ces 22 espèces sont présentes dans le district d'Hluhluwe, dans le sud de l'Afrique, où le climat est analogue à celui de la partie centrale et méridionale de la

Côte du Queensland. L'abondance numérique et les caractéristiques du biotope de ces espèces ont été examinées à Hluhluwe pour essayer d'expliquer le résultat de leur introduction en Australie. Il s'avère que la spécificité dans le choix de l'habitat et la convenance du nouvel habitat sont les facteurs critiques du succès. Les espèces qui se sont établies en Australie étaient relativement communes dans les bouses du bétail d'Afrique, où elles montraient une préférence pour les prairies sur sol lourd-argileux.

MOTS CLÉS : bousier, espèce exotique, introduction, spécificité habitat.

Received : 12 October 1989 ; Accepted : 14 March 1990.

REFERENCES

Begon, M., Harper, J. L. & Townsend, C. R. — 1986. *Ecology : Individuals, Populations and Communities.* — Blackwell, Oxford.

Bornemissza, G. F. — 1976. The Australian dung beetle project 1965-1975. — *Aust. Meat Res. Comm. Rev.*, 30, 1-30.

Bornemissza, G. F. — 1979. The Australian Dung Beetle Research Unit in Pretoria. — *S. Afr. J. Sci.*, 75, 257-260.

Crawley, M. J. — 1987. What makes a community invasible ? In : Colonisation, Succession and Stability. (**A. J. Gray, M. J. Crawley & P. J. Edwards,** eds), pp. 429-453. — *Blackwell,* Oxford.

Davis, A. L. V. — 1987. Geographic distribution of dung beetles [*Coleoptera : Scarabaeidae*] and their seasonal activity in the southwestern Cape Province. — *J. S. Afr. Entomol. Soc.*, 50, 275-285.

Davis, A. L. V., Doube, B. M. & McLennan, P. D. — 1988. Habitat associations and seasonal abundance of coprophilous Coleoptera [*Staphylinidae, Hydrophilidae, Histeridae*] in the Hluhluwe Region of South Africa. — *Bull. Entomol. Res.*, 78, 425-434.

Doube, B. M. — 1983. The habitat preference of some bovine dung beetles [*Coleoptera : Scarabaeidae*] in Hluhluwe Game Reserve, South Africa. — *Bull. Entomol. Res.*, 73, 357-371.

Doube, B. M. — 1986. Biological control of the buffalo fly in Australia : the potential of the southern African dung fauna. — *Misc. Publ. Entomol. Soc. Amer.*, 61, 16-34.

Doube, B. M. — 1987. Spatial and temporal organisation in communities associated with dung pads and carcasses. In : Organisation of Communities : Past and Present. (**J. H. R. Gee & P. S. Giller,** eds), pp. 253-280. — *Blackwell,* London.

Doube, B. M. & Huxham, K. A. — 1987. Laboratory assessment of predation on immature stages of *Haematobia thirouxi potans* (Bezzi) [*Diptera : Muscidae*] by some beetles from the southern African dung fauna. — *J. Entomol. Soc. S. Afr.*, 50, 475-480.

Doube, B. M., Giller, P. S. & Moola, F. — 1988. Dung burial strategies in some South African coprine and onitine dung beetles [*Scarabaeidae : Scarabaeinae*]. — *Ecol. Entomol.*, 13, 251-261.

Doube, B. M., Macqueen, A., Ridsdill-Smith, T. J. & Weir, T. A. — In press. Native and introduced dung beetles in Australia. In The Ecology of Dung Beetles (**I. Hanski & Y. Cambefort,** eds). — *Princeton University Press,* N.Y.

Kirk, A. A. & Ridsdill-Smith, T. J. — 1986. Dung beetle distribution patterns in the Iberian Peninsula. — *Entomophaga,* 31, 183-190.

Pimm, S. L. — 1987. Determining the effects of introduced species. — *Tree,* 2, 106-108.

Ridsdill-Smith, T. J. & Kirk, A.A. — 1985. Selecting dung beetles [*Scarabaeinae*] from Spain for bush fly control in south-western Australia. — *Entomophaga,* 30, 217-223.

Robinson, J. V. & Dickerson, J. E. Jnr. — 1987. Does invasion sequence affect community structure ? — *Ecology,* 68, 587-595.

Southwood, T. R. E. — 1987. Habitat and insect biology. — *Bull. Entomol. Soc. Am.*, 33, 211-214.

Walter, H. & Lieth, H. — 1964. *Klimadiagramm-Weltatlas, Part 2.* — *Gustav Fischer,* Jena.

Waterhouse, D. F. — 1974. The biological control of dung. — *Sci. Amer.*, 230, 100-109.