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An ecological study of an Australian dung beetle, *Onthophagus granulatus* Boheman (Coleoptera: Scarabaeidae), using physiological age-grading techniques

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Abstract

The distribution and seasonal activity of *Onthophagus granulatus* Boh. was studied at two sites in eastern Australia. It is a univoltine species, with peaks of activity in spring and early summer. Breeding cycles and periods of stress were demonstrated by the proportions of newly emerged, nulliparous and parous beetles and those resorbing oocytes. The optimum temperature for brood production was 25°C. The threshold of development was 11·3°C, and 495 day-degrees C were required for development from egg to adult. Dung quality and drought were important factors affecting survival and brood production in the field. The distribution of the species in south-eastern Australia is limited by summer rainfall and temperature.

Introduction

The dung beetle fauna of Australia is represented by nearly 200 described species (Matthews, 1972). Most of these are found in the natural forest or heathland environments, but some have adapted well to the changes brought about by man and are able to maintain dense populations in cleared farmlands and in the large dung pads dropped by domestic cattle and horses.

In south-eastern Australia, two species which seem to have tolerated the changes better than others are *Onthophagus granulatus* Boheman and *O. australis* Guérin-Méneville. Hughes (1975) showed that these two species at times reached high densities in cow dung and dispersed or buried large quantities very rapidly. In so doing, they probably influenced the breeding of other organisms in the dung including the bushfly, *Musca vetustissima* Walker, which is so troublesome to man over almost the whole of the Australian continent.

Effective dung dispersal and control of the bushfly are two of the principal aims of the CSIRO dung beetle introduction programme begun in 1968 (Bornemissza, 1976). That project originated partly on the assumption that native dung beetles were ineffective and poorly adapted to the large dung pads of cattle. However, it is now clear that some of those beetles are not only attracted to cow dung but may develop very large populations in it. Thus it is important that their roles should be defined more precisely so that introduced beetles can be fitted more effectively into the already complex fauna of the dung pad.

Tyndale-Biscoe (1978) has shown that age-grading techniques based on the examination of the reproductive organs of dung beetles can be used to define stages in the life-cycles of the beetles. Those techniques were applied and expanded in these investigations and proved invaluable in elucidating the seasonal activity patterns of the beetles.

Field studies

Methods

Experimental sites.—Most field observations were carried out at a field station at Uriarra, 20 km west of Canberra. The experimental area was located in an 18-ha paddock permanently grazed by cattle. Average annual rainfall is 600 mm uniformly distributed throughout the year. However, the area is prone to frequent short term droughts varying from 1 to 3 months in duration.

Other observations were carried out near Armidale, on the northern tablelands of New South Wales. The experimental site was within the CSIRO Experiment Station at Chiswick, 20 km south of Armidale, where the annual rainfall is slightly higher than at Uriarra (736 mm) and most of the rain falls during the summer months from November to March.

Activity.—Dung beetle activity was measured every week for three years (Uriarra) and two years (Armidale) using standard pit-fall traps as illustrated in Fig. 1. The trap consisted of a cylindrical pit 30 cm deep and 20 cm in diameter. A wide-mesh (30 mm) metal grid rested on top of the pit. One litre of fresh dung wrapped in thin gauze was placed on the grid. Beetles attracted to the dung fell through the grid via

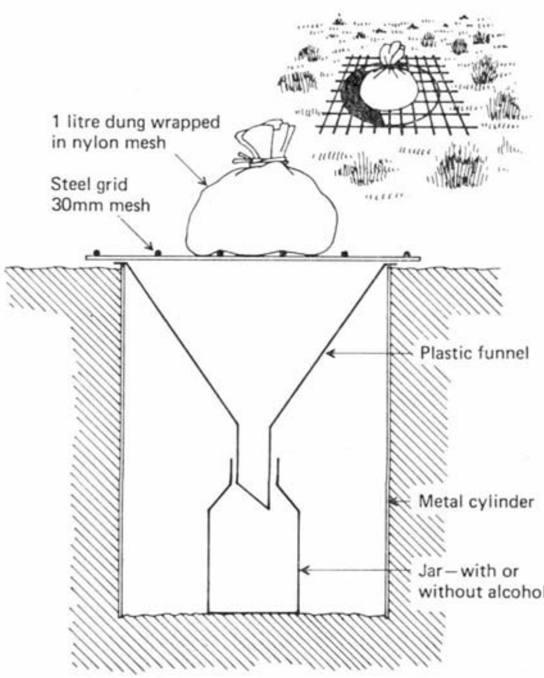

Fig. 1.—Construction details of the pit-fall trap.

a plastic funnel leading into a collecting jar. The traps were set at 16.00 h on one day each week and left out for 24 h. The 16.00 h setting time ensured that the pad was fresh and attractive to the beetles flying that night and retained its attractiveness through to the following morning when the day-flying beetles were active. On each occasion, five traps had alcohol in the containers and five had dry jars to provide beetles for subsequent dissection.

Dissections.—Each week a sub-sample of 30 female beetles was taken from the traps for dissection. If the total catch in the trap was less than 30 beetles, all the beetles were dissected. The beetles were killed in 70% alcohol and dissected in Ringer solution (Tyndale-Biscoe, 1978).

The ovary of *O. granulatus* is similar to that of *Euoniticellus intermedius* (Reiche) (Tyndale-Biscoe, 1978), and the same age-grading techniques apply to both species of beetles. The age-grade categories and their abbreviations are as follows:

Nulliparous—N_1 = Newly emerged beetles, soft cuticle, no fat-body, undeveloped reproductive system, unworn tibiae.

N_2 = Young beetles, hard cuticle, some fat-body, undeveloped or slightly developed reproductive system, slightly worn tibiae.

N_3 = Young beetles, hard cuticle, developed fat-body, developed reproductive system, slightly worn tibiae.

Parous —P_1–P_3 = Older beetles, similar to N_3 but with increasing accumulations of yellow body at the base of the ovarioles; increasingly worn tibiae.

Resorbing —R = Beetles of any age from N_2 to P_3, with visible signs of oocyte breakdown, or extrusion of oocyte sideways through the ovariole wall. Visible signs of past resorption are yellow granules attached to the outside of the ovariole base.

Weather records.—A thermohygrograph in a standard Stephenson screen provided a continuous record of temperature and humidity, and rainfall was measured each week.

Results

Seasonal activity, Uriarra.—Trapping and dissection results are summarised in Fig. 2*a*, *b* & *c*. Beetle activity commenced in September each year and continued throughout the summer until April, with peaks during October and early in the following year. Few, if any, beetles were trapped from May to early August. Beetles were exceptionally active in 1976–77, often reaching more than 1000 per trap. In the following two years, associated with drought conditions at crucial periods of their life-cycle, numbers were substantially lower.

Changes in the age-composition of the population showed up clearly in the dissections. Thus in September 1976 when the beetles first became active, up to 80% were nulliparous and developing their eggs (N_{2-3}) and the remainder were parous in the process of producing broods (P_{1-3}). The relative numbers of parous beetles increased during October and November. The population density decreased sharply in November and then consisted almost exclusively of actively breeding parous beetles (P_{1-3}), with little change in December except that late in that month, following good rains on 24 December (15 mm), some newly emerged beetles (N_1) appeared. Earlier in the month when conditions were hot and dry, increasing numbers of beetles were resorbing their eggs and some were clearly old beetles probably incapable of further breeding.

In January and February, a mass emergence of beetles occurred and the beetle numbers increased dramatically so that on 9 February over 3000 came to each trap. Dissections indicated that during that period 70–75% of the beetles were newly emerged. The numbers had begun to decrease again by mid-March, with a decrease in new emergences and increasing age of the population. Most beetles were developing eggs, but some were ovipositing and a substantial proportion were resorbing eggs.

Activity began again in September 1977. The population consisted almost entirely of breeding beetles, indicating a survival of adult beetles over the winter period. A severe drought from late September to late December was associated with large numbers of beetles which were resorbing eggs. Despite good rains during January, there was no mass emergence of new beetles as had occurred the previous year. However, small numbers of newly emerged beetles appeared in February, and the proportion increased

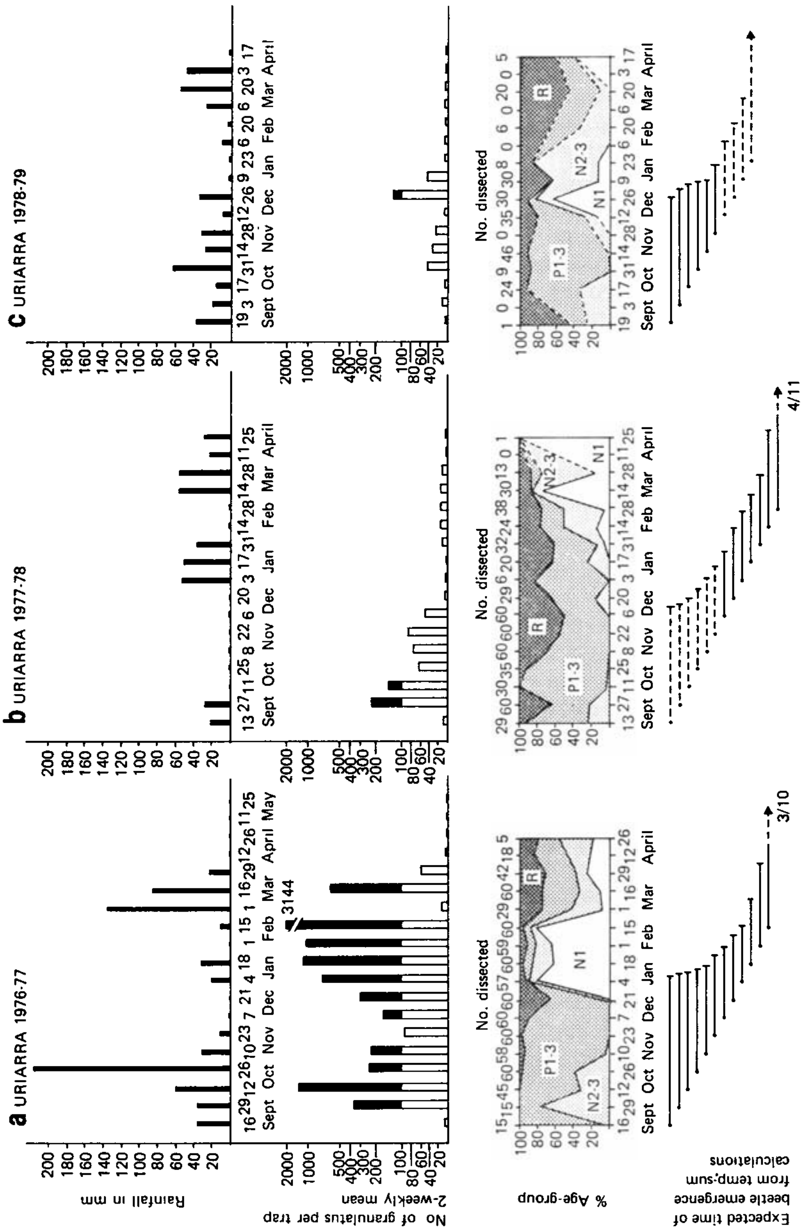

Fig. 2.—Field data from the Uriarra site. The expected times of beetle emergence from temperature summation calculations are shown as solid lines when beetles did emerge, and interrupted lines when emergence failed to take place.

in March and April. At the same time, the proportion of resorbing beetles (R) decreased and were considerably fewer than during the equivalent time the previous autumn. By April, there were hardly any beetles caught in the traps; the only one dissected was newly emerged.

The 1978–79 season was characterised by a moist and highly favourable spring. Small numbers of overwintering beetles became active in September, and brood production proceeded without restriction. There was a substantial emergence of new beetles from mid-December to January, but then a severe drought again intervened. No effective rain was received from late December to early March, and many broods were desiccated. New emergences decreased during January and ceased in February and March, and an increasing proportion of beetles resorbed their eggs. Substantial rains fell in March and April, but this did not reduce the proportion of resorbing beetles in the population. However, beetle numbers were so low at this time of year that dissection data must be treated with some caution. No more newly emerged beetles were trapped until April, and these possibly arose from broods which had survived the drought and completed their development following the breaking of the drought in March.

Seasonal activity, Armidale.—The results of trapping and dissection are summarised in Fig. 3*a* & *b*. Seasonal conditions were in general much more favourable than at

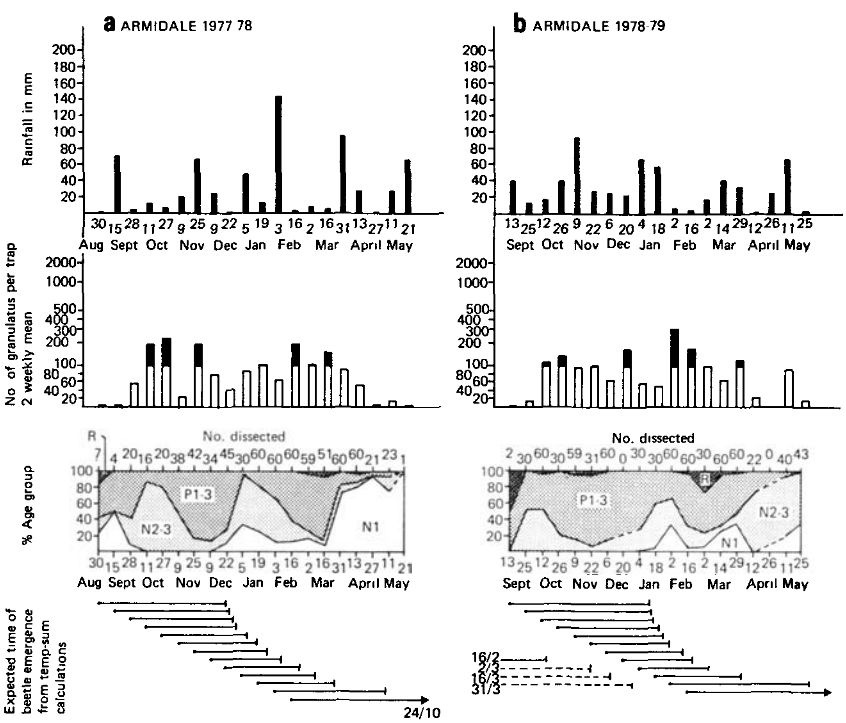

Fig. 3.—Field data from the Armidale site.

Uriarra. Rainfall was adequate and consistent throughout both the 1977–78 and 1978–79 summers, February 1979 being the only month in which less than 10 mm fell. Large numbers of beetles were trapped throughout both seasons, although the exceptional activity seen at Uriarra in 1976–77 was not reached. The spring and summer peaks of activity which occurred at that site were also apparent at Armidale in 1977–78 but not as marked in 1978–79.

An unusual feature of the Armidale early spring populations was the presence of a few newly emerged beetles at that time, in contrast to the situation at Uriarra. This probably indicates some survival of broods over the winter period in that area, where mean and minimum temperatures from May to July are on average about 1 °C warmer than at Uriarra.

Very few beetles were found to be resorbing eggs at any time during either season at Armidale, indicating that conditions were indeed generally favourable throughout. This again was in sharp contrast to the situation at Uriarra, where rainfall fluctuated widely from month to month, resulting in periods of severe stress for the beetles, especially during the 1977–78 and 1978–79 seasons.

Experiments under field conditions

Survival of broods in winter

Methods.—Four categories of broods were taken from laboratory cultures in May 1979. These were 0–3 days old, containing eggs; 1–7 days old, containing early-instar larvae; 8–14 days old, containing early- and late-instar larvae; and 15–28 days old containing late-instar larvae, pupae and teneral adults. Broods in each of these categories were placed in gauze-bottomed cylinders filled with vermiculite and sand. The cylinders were then dug into the ground at Uriarra to a depth of 30 cm and covered with a gauze lid to contain any emerging beetles and to allow natural rainfall to reach the broods. Samples of broods were removed and examined at monthly intervals from May onwards until early spring when the beetles again became active in the field. All broods with white, healthy looking eggs were placed at 27 °C in the laboratory to check for hatching, which would indicate that they were still viable.

Results.—The oldest group of larvae and pupae survived until July, but by August they were all dead (Table I). All the younger larvae had died by June. Empty broods indicate that death had probably occurred either in the egg stage or during the first larval instar, leaving no trace of a head capsule in the brood. All eggs were dead from June onwards.

TABLE I. *The survival of broods of* O. granulatus *in the field at Uriarra between May and September 1979*

Age in days, and date when placed in field	Date examined	No. examined	Brood contents		
			Living	Dead	Empty
14–28 days, 8 May	8 May	10	10	—	—
	6 June	6	6	—	—
	3 July	8	7	1	—
	28 Aug.	10	—	9	1
8–14 days, 8 May	8 May	10	10	—	—
	6 June	7	—	5	2
	3 July	10	—	9	1
	31 July	10	—	9	1
	28 Aug.	10	—	8	2
1–7 days, 8 May	8 May	10	10	—	—
	6 June	4	—	2	2
	3 July	10	—	10	—
	31 July	10	—	8	2
	28 Aug.	10	—	2	8
0–3 days, 23 May	23 May	10	10	—	—
	6 June	4	—	4	—
	3 July	5	—	5	—
	31 July	9	—	9	—
	28 Aug.	10	—	1	9

Survival of adults in the winter

Methods.—Newly emerged (N_1) and developing (N_2) beetles from the laboratory culture were placed out in the field at Uriarra in April 1978, in cylinders dug into the ground as described above. Fresh dung was placed on top of the vermiculite and sand every two weeks. Samples of beetles were removed at intervals throughout the winter, and the females were dissected.

Results.—At the time of sampling it was noted that there were small numbers of dead and decomposing beetles, indicating that some mortality (about 30%) had taken place during the winter. However, a large number survived, the majority having overwintered in the N_2 stage (Table II) with hard cuticle, some fat-body, and no visible development of the ovary. However, by October, several beetles had begun to develop their eggs. On three occasions (9 August, 30 August and 13 October), one female in each sample had a small quantity of yellow body visible, which would indicate resorption of partially developed oocytes.

TABLE II. *Development of newly emerged females of* O. granulatus *in the field at Uriarra between April and October 1978*

Date examined	No. examined	Physiological age-category			
		N_1	N_2	N_3	P_1
18 Apr.	4	—	4	—	—
1 June	3	—	3	—	—
20 July	11	4	7	—	—
9 Aug.	13	—	12	—	1
30 Aug.	12	—	11	—	1
19 Sept.	13	—	13	—	—
13 Oct.	18	—	13	4	1

Brood production and survival in the field

Methods.—Every two weeks throughout both the 1977–78 and 1978–79 summer seasons, cylinders similar to those described above were dug into the ground at Uriarra. One litre of fresh locally produced dung was placed on the vermiculite in each cylinder and left exposed for one week. During that time beetles, if they were present in the field, were attracted to the dung either to feed or produce broods. At the end of the week, when most beetles had left, the vermiculite was searched for broods. These were counted but left in place in the cylinder and the gauze lid replaced. At fortnightly intervals thereafter, a subsample of broods was examined until there was no longer any living material remaining in the cylinder, or the beetles had pupated or emerged.

Results.—In 1977–78, brood production commenced in September and continued through until early January, the numbers of broods depending upon beetle activity at the time (Table III). No more broods were produced during the remainder of the season, apart from some in February. None of the broods produced up to October survived, whereas at least some of those deposited on and after 9 November developed successfully and pupated. This implies that beneath the newly deposited dung pad soil moisture is adequate for the early larval instars to survive a short dry period. However, in a prolonged drought, the later larval instars may succumb to desiccation.

In 1978–79, beetle numbers were exceptionally low and no broods were produced from experimental dung pads until early November. Good numbers were then produced throughout November and in December, but numbers declined in January–February when drought conditions prevailed. There was a late production of broods in March following the breaking of the drought on 4 March.

Broods deposited in November and December developed successfully to emerge as

TABLE III. *Survival of broods of* O. granulatus *laid naturally in the field at Uriarra during the active seasons of 1977–78 and 1978–79*

Date pad exposed	No. of broods	Sampling date	Brood Live	Contents Dead
1977				
31 Aug.	0			
14 Sept.	21	28 Sept.	10	—
		12 Oct.	2	2
		26 Oct.	2	1
		9 Nov.	—	4
28 Sept.	13	12 Oct.	3	—
		26 Oct.	2	—
		9 Nov.	2	1
		23 Nov.	1*p*	1
		7 Dec.	—	3
12 Oct.	50	26 Oct.	7	3
		9 Nov.	1	—
		7 Dec.	—	39
28 Oct.	3	9 Nov.	2	—
		7 Dec.	—	1
9 Nov.	6	23 Nov.	2	—
		7 Dec.	2	—
		21 Dec.	1*p*	—
23 Nov.	7	7 Dec.	3	—
		31 Dec.	1	—
		4 Jan.	1*p*	—
		1 Feb.	2	—
7 Dec.	1	21 Dec.	—	1
21 Dec.	3	18 Jan.	2	—
		15 Feb.	—	—
		1 Mar.	1*a*	—
1978				
4 Jan.	9	14 Jan.	3	—
		1 Feb.	2	—
		15 Feb.	—	2
		1 Mar.	1	—
18 Jan.	0			
1 Feb.	10	15 Feb.	3	—
		1 Mar.	3*pa*	3
		15 Mar.	1*a*	—
15 Feb.	0			
1 Mar.	0			
15 Mar.	0			
1978				
13 Sept.	0			
27 Sept.	0			
10 Oct.	0			
24 Oct.	0			
7 Nov.	21	28 Nov.	1	—
		12 Dec.	—	—
		8 Jan.	20*pa*	—
21 Nov.	38	28 Nov.	2	—
		12 Dec.	—	—
		8 Jan.	36*pa*	—
6 Dec.	44	8 Jan.	2*p*	—
		30 Jan.	42*a*	—
18 Dec.	6	8 Jan.	1	2
		30 Jan.	3*pa*	—
1979				
9 Jan.	0			
23 Jan.	2	30 Jan.	1	—
		20 Mar.	—	1
6 Feb.	0			
21 Feb.	0			
1 Mar.	0			
7 Mar.	5	20 Mar.	1	—
		3 July	—	4
20 Mar.	0			

Numbers of brood with no following letter = larvae.
p = pupae.
a = adults.

adults. However, of the two broods deposited in January, the one examined in March had died during the drought period, which continued until early March. This is in marked contrast to the previous year when the December–January broods developed successfully when regular rains maintained high soil moisture levels. Although the eggs deposited in early March hatched and developed for a short time before temperatures fell, all died during the early winter months.

Laboratory experiments

General methods

A laboratory culture of *O. granulatus* was maintained to ensure a ready supply of beetles of known age. The methods used were similar to those described by Hughes et al. (1978) for *E. intermedius* except that instead of a soil mixture, a mixture of fine vermiculite and sand was prepared in the proportions 2:1. Samples of *M. vetustissima* reared in cattle dung showed profound differences in survival and reproductive potential, depending on the source of the dung and the time of the year it was collected (Greenham, 1972). In this paper, the dung used in examining the influence of temperature was good-medium quality dung collected from an irrigated pasture at Fyshwick, Australian Capital Territory. The dung used in the dung quality experiments was collected from various sources as described below. After collection, the dung was kept deep frozen until required.

Effect of temperature on rate of development from egg to adult

Methods.—

Unit: 50 broods, 0–2 days old in vermiculite and sand, watered 3 × per week to constant weight.
Treatments: 15, 20, 25 and 30°C.
Replication: 1.
Duration: until all broods had emerged or died.
Observations: Emergence of beetles recorded 3 × per week.

Results.—The mean rate of development from egg to adult increased with increasing temperatures (Table IV). However, the low survival at 30°C made the rate estimate

TABLE IV. *Rate of development of broods, survival and size of emerging adults of* O. granulatus *at different temperatures*

Temp. (°C)	No. of broods	Day of emergence			No. surviving	Mean thoracic width (mm)
		Earliest	Mean	Latest		
15	50	138	139	149	29	3·71
20	50	54	56	62	44	4·08
25	50	33	36	42	44	4·00
30	50	30	30	30	4	3·58

at that temperature dubious, and when plotted, it fell below the linear regression line drawn through the rate estimates at 15, 20 and 25°C . It was therefore excluded from the calculations. The regression line drawn through the rates of development at the other three temperatures intersects the base line at 11·3°C. This is considered to be the threshold temperature for development. It was calculated that to complete development from egg to adult, *O. granulatus* requires a total of 495 day-degrees above this threshold temperature i.e. $495 = D\ (T-11{\cdot}3)$ where D is the number of days taken to develop from egg to adult at temperature T.

Temperatures at both extremes tested (15 and 30°C) had an adverse effect not only on the survival of the eggs and/or larvae but also on the size of the emerging adults.

Effect of temperature on brood production and life-span of newly emerged beetles

Methods.—

Unit: 1 pair (male + female), 0–1 day old in moist, compacted vermiculite and sand, at LD 14: 10 h with 0·25 litre of good quality dung changed weekly.

Treatments: 15, 20, 25, 30°C.

Replications: 10.

Duration: Until all females had died.

Observations: Broods counted weekly; mean life-span in weeks.

Results.—The mean number of broods was clearly highest at 25°C (Table V) and significantly different from the mean numbers produced at both 20 and 30°C ($P < 0{\cdot}05$). No broods were produced after eight weeks at 15°C, though partial development was observed to take place (all beetles at the N_2 stage).

TABLE V. *The effect of temperature on the numbers of broods produced by females of* O. granulatus *during their life-span*

Temperature (°C)	Mean no. of broods per female ± s.e.	Life span (weeks)	
		Mean	Range
15	0 (after 8 weeks)	—	—
20	26·0 ± 6·60	23·50	6–46
25	70·0 ± 11·14	16·26	5–23
30	25·8 ± 4·75	7·2	3–12

The life-span of beetles was very variable within each temperature treatment; however the mean life-span decreased with increasing temperatures.

Effect of temperature on brood production of sexually mature beetles

Methods.—

Unit: 1 pair (male + female) 4–6 weeks old in moist, compacted vermiculite and sand at LD 14: 10 with 0·25 litre of good quality dung changed weekly. Prior to the commencement of the experiment, these beetles were kept at 27°C under conditions which allowed ovarian development but minimised brood production.

Treatments: 15, 20, 25, 30, 35°C.

Replications: 10.

Duration: 6 weeks.

Observations: Broods counted weekly.

Results.—The influence of temperature on brood production in these older beetles (Table VI) was similar to that seen in the newly emerged beetles (Table V). A one-way analysis of variance of the data yielded significant differences between the treatments ($F_{(4-45)} = 18{\cdot}0008$; $P<0{\cdot}001$). The data were submitted to a multiple range test, which showed no significant differences between mean brood numbers at 20 and 25°C. However, at both extremes of the temperature range tested, production was significantly reduced over the six-week period. At 35°C, only a few broods were produced during the first week and all beetles were dead within three weeks.

Some broods were produced at 15°C, but only during the week or so after transfer to that temperature, indicating a residual influence of their prior exposure to 27°C.

TABLE VI. *The effect of temperature on the numbers of broods produced by sexually mature females over a six-week period*

Temperature (°C)	Mean no. of broods per female ± s.e.
15	$1 \cdot 5^{b} \pm 2 \cdot 4$
20	$22 \cdot 3^{a} \pm 11 \cdot 1$
25	$28 \cdot 8^{a} \pm 13 \cdot 0$
30	$10 \cdot 1^{c} \pm 9 \cdot 4$
35	$0 \cdot 4^{b} \pm 0 \cdot 7$

Means followed by the same letter are not significant ($P > 0 \cdot 05$)

Effect of dung quality on maturation feeding period

Methods.—

Unit: 10 pairs (male + female) 0–1 day old in moist, compacted vermiculite and sand in insectary glasshouse in October–November 1978 with natural photoperiod at 27±2°C.

Treatments: (1) with 0·5 litre good quality dung collected in October from an improved pasture at Uriarra, Australian Capital Territory; (2) with 0·5 litre poor quality dung collected at the end of the dry season at Rockhampton, Queensland.

Replications: 10.

Duration: 4 weeks.

Observations: samples of 10 males and 10 females dissected each week.

Results.—Beetles fed on good quality dung (Greenham, 1972) developed rapidly, and the first broods were produced within two weeks and nine out of the ten females had produced broods within three weeks (Table VII). Beetles fed on poor quality dung failed to produce any broods, and 70% had died within four weeks.

TABLE VII. *The influence of dung quality on the maturation feeding period of newly emerged females of* O. granulatus *and on the rate of accumulation of fat-body (FB) in males*

Time (weeks)	Number and physiological age-category of beetles			
	Good quality dung		Poor quality dung	
	♀	♂	♀	♂
0	10 N_1	10 FB−	10 N_1	10 FB−
1	6 N_2 3 N_3 1 dead	9 FB+ 1 dead	8 N_1 2 dead	9 FB− 1 dead
2	5 N_3 1 parous 4 dead	10 FB+	6 N_1 4 dead	8 FB− 2 dead
3	1 N_3 9 parous	10 FB+	5 N_1 6 N_2	8 FB− 2 dead
4	2 N_3 8 parous	Not sampled	3 N_2 7 dead	10 dead

Males responded in a similar way, with large quantities of fat-body being produced when fed on good quality dung and none being visible in those fed on poor quality dung.

The effect of dung quality on brood production in sexually mature beetles

Methods.—

Unit: 20 pairs (male + female) 1–2 weeks old in moist, compacted vermiculite and sand in insectary glasshouse in July 1977 with natural photoperiod at 27 ± 2°C.

Before the commencement of the experiment the beetles were fed on medium quality dung.

Treatments: (1) good quality dung as in last experiment; (2) medium quality dung collected on irrigated pasture near Canberra; (3) poor quality dung prepared from (2) by adding extra fibre (peat); (4) poor quality dung collected towards the end of the dry season from south-western Australia. Each unit was provided with 0·5 litre dung changed twice weekly.

Replications: 3.

Duration: 5 weeks.

Observations: broods counted weekly.

Results.—There was a clear-cut relationship between dung quality and numbers of broods produced, at least during the five-week period of the experiment (Fig. 4).

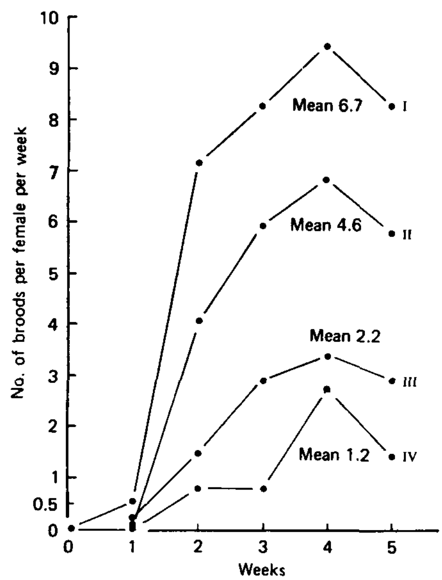

Fig. 4.—The effect of dung quality on brood production of sexually mature females of *O. granulatus*. (I, good quality dung; II, medium quality dung; III, medium quality dung plus peat; IV, poor quality dung.)

Except for a few isolated broods during the first week, brood production began in the second week increasing to a peak in the fourth week. On average, the beetles on the good quality dung produced more than five times as many broods as those on the poorest quality dung.

The experiment also showed that dung quality could be lowered by adding fibrous material, such as peat, to the mixture, perhaps by decreasing the availability of the liquid nutrients to the feeding beetles.

Discussion

Physiological age-grading criteria developed by Tyndale-Biscoe (1978) were applied for the first time to a field study of the native Australian dung beetle *O. granulatus*.

Through regular dissections of the reproductive organs of beetles caught in the field it was possible to outline in detail the changes in composition of the population during the year and to examine the influence of varying seasonal conditions on the activity of the beetle.

At Uriarra, *O. granulatus* basically has a univoltine life-cycle. Newly-emerged beetles first appear in mid-summer and then go through a maturation feeding period 'Reinfungsfrass' of Halffter & Matthews, 1966), which may continue until the autumn. As temperatures decrease, the beetles cease activity and remain throughout the winter either in shallow burrows or beneath ageing dung pads. In the spring, adult beetles become active again as temperatures rise. Their ovaries are in various stages of development (N_2–P_3), and some may even have yellow body present, indicating either breeding during the previous autumn or resorption due to stress. The former is possible because there were at least some parous beetles in the population in April at both sites in each year studied. The second alternative is also possible, with slow partial development of the oocytes during warmer days alternating with rapid degeneration of successive follicles on cold days throughout the winter. This has also been reported to occur in the Dytiscidae (Joly, 1945; Bell & Bohm, 1975). In the spring, dung quality is generally good (Greenham, 1972) and the beetles require only a brief feeding period before producing their first broods. Depending upon seasonal conditions, brood production then continues on good quality dung until December or even early January, ceasing at about the time when the first new beetles of the next generation begin to emerge. Some late-summer or early-autumn broods may be deposited, but these are generally fewer in number since they are produced at a time when dung quality is no longer at its peak.

The proportion of beetles with resorbing oocytes varied at different times of the year, between years and between sites. There was a clear correlation with periods of drought as shown at Uriarra in December 1976, October–December 1977, and January–February 1979, and at Armidale in February 1979. Oosorption was less frequent at Armidale where the average annual rainfall (736 mm) is higher than at Uriarra (600 mm). More importantly, rainfall is more consistent during the summer months, with 53% falling from November to March. The exception, as already noted, was the peak of resorption on 2 March 1979, following a three-week period when only 4·7 mm of rain fell.

Drought could induce oosorption by drying out and hardening the soil, making oviposition difficult; lack of oviposition sites is known to induce resorption in *E. intermedius* (Tyndale-Biscoe & Watson, 1977). Drought could also induce oosorption through haying-off of the pasture and the production of poor quality dung by the cattle, thus causing a nutritional deficiency in the adult beetle (Bell & Bohm, 1975; Tyndale-Biscoe & Watson, 1977). Moisture stress is one of the many factors promoting oosorption in insects (Bell & Bohm, 1975), and in the case of *O. granulatus* it appears to play a substantial role in the life-system of the beetle.

The influence of drought was confirmed in analysis of the dissection data from Uriarra. There was also evidence of some correlation between oosorption and age of the beetles, older beetles tending to show higher rates of resorption than younger ones. However, the data available were insufficient to allow a clear separation of this age effect from other possible factors (e.g. rainfall and season).

The population density of beetles at Uriarra, as revealed by trap catches, fluctuated greatly during and between seasons. The enormous activity encountered in the first year of observation (1976–77) was probably due to the consistent rainfall in the area during the two previous summer seasons when there was only one month (December 1974) with less than 10 mm. The short-term droughts of October–December 1977 and January–February 1979 caused high mortality of larvae and pupae and reduced beetle numbers dramatically during those two years. At Armidale, on the other hand, with no substantial droughts during the two years of observations, beetle numbers remained consistently high, indicating there was very little brood mortality in the field.

From the calculation that *O. granulatus* requires a total of 495 day-degrees above the threshold of 11·3°C to develop from egg to adult, it was possible to predict the approximate expected dates of emergence of broods laid in the field at any time throughout the season. These are shown in Fig. 2*a–c* & 3*a–b*. At Uriarra in 1976–77, temperature summation calculations from broods laid in the spring showed that they should emerge from early January onwards and continue during February and March. The dissections showed that that indeed occurred. In 1977–78, similar calculations indicated that the new emergence should begin in December. However, the drought experienced at that time caused high mortality in the broods and the first newly emerged beetles did not appear until the end of January from broods laid from December onwards. In 1978–79, broods laid from September to November emerged when expected but those laid on 12 December and later failed to emerge due to their desiccation in January and February. At Armidale, there were no drought periods causing detectable mortality in broods and thus the new generation in both years appeared at the predicted times.

O. granulatus has thus evolved a life-cycle which ensures maximum brood production in the spring when dung quality is at its peak. The medium to poor quality dung present in the field in late summer and autumn (Greenham, 1972) over a large part of its distribution range allows only limited breeding to take place, and the broods which are produced fail to survive the winter at Uriarra. Some do survive at Armidale, but the proportion is so low that it does not greatly alter the univoltine nature of the population.

Seasonal variation in population density is strongly influenced by rainfall. This was indicated during periods of drought by high mortality of larvae and high resorption rates in the adult beetles.

The dependence of *O. granulatus* on adequate summer rainfall and its inability to tolerate temperatures higher than 30–35°C provide useful indicators of the factors likely to restrict the distribution of the species in Australia. Matthews (1972) examined all the specimens then available to him and outlined the broad distribution limits of the species in south-eastern Australia. During the course of the studies described in this paper, additional surveys were carried out and many new locality records obtained. The full range of the species can now be defined more precisely (Fig. 5).

Since immature *O. granulatus* suffer heavy mortality during hot dry periods, the amount of rain falling during the summer months could be expected to be a major factor limiting the distribution of the species into the low summer rainfall areas of southern and inland Australia. In fact, the southern and western distribution into the Mediterranean type winter rainfall regions of South Australia is well-defined by the 75-mm summer (December–February) isohyet. The specimen collected near Euston was probably from a population sustained by additional moisture from either irrigation or natural seepage associated with the Murray River.

Although *O. granulatus* is a summer active species requiring adequate rainfall, its distribution northwards into the predominantly summer rainfall regions of Australia is also limited.

Experiments described in this paper showed that although newly emerged beetles are able to complete their maturation feeding period and produce some broods at 30°C, their life-span was greatly reduced and total brood production was severely restricted. Similarly, in mature beetles, exposure to 30°C again reduced brood production, and exposure to 35°C resulted in all beetles dying within three weeks. Thus it is unlikely that *O. granulatus* is able to establish a population in the field if temperatures between 30 and 35°C are encountered for prolonged periods during the summer months. In fact, the northern limits of the species in Queensland and the inland western limits in northern New South Wales are defined reasonably well by the average summer maximum temperature from December to February of 32·5°C. The isolated occur-

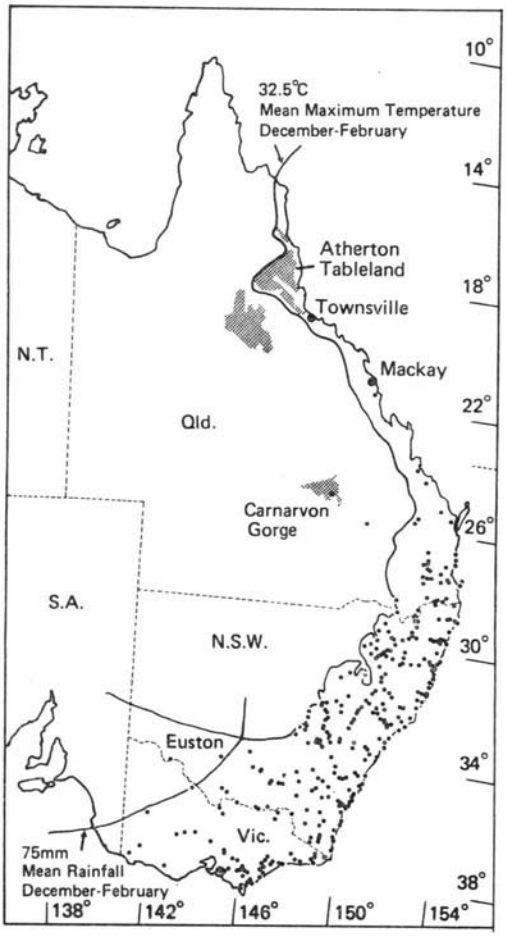

Fig. 5.—Records of the occurrence (●) of *O. granulatus* in eastern Australia in relation to summer temperature and rainfall. (Hatched areas indicate elevations > 600 m.)

rence at Carnarvon Gorge in south-western Queensland is probably due to the lower average temperatures there associated with higher altitudes (>600 m).

The most northerly record of the species is near Mackay on the central Queensland coast, but it seems possible that careful search may reveal isolated populations as far north as Townsville on the coast and possibly on the cooler Atherton Tablelands.

The influence of *O. granulatus* on the dispersal and/or burial of cow dung is limited by its overall distribution, by its seasonal activity patterns and by seasonal conditions. The latter may affect population density, either through inhibition of brood production when dung quality is poor or through mortality of the immature stages. Drought at strategic times in two successive years decimated the population at Uriarra, although in some nearby districts where the moisture stress was less severe large numbers of beetles were observed and dung dispersal was often substantial.

The contribution of *O. granulatus* to the control of *M. vetustissima*, which breeds in dung pads, is likely to vary widely from year to year and from district to district.

At times of great activity, as occurred in 1976–77, complete control of breeding of the fly was achieved in individual pads (unpublished data). At lower densities, the control achieved was correspondingly less (Wallace, Tyndale-Biscoe & Holm, 1979).

Clearly *O. granulatus* plays an important role in dung dispersal in south-eastern Australia. However, as already noted by Hughes (1975), additional species of beetles are needed to help in that task.

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References

BELL, W. J. & BOHM, M. K. (1975). Oosorption in insects.—*Biol. Rev.* **50**, 373–396.

BORNEMISSZA, G. F. (1976). The Australian Dung Beetle Project 1965–1975.—*Australian Meat Research Committee Review* **30**, 1–30.

GREENHAM, P. M. (1972). The effects of the variability of cattle dung on the multiplication of the bushfly (*Musca vetustissima* Walk.).—*J. Anim. Ecol.* **41**, 153–165.

HALFFTER, G. & MATTHEWS, E. G. (1966). The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae).—*Folia entomologica Mexicana* no. 12–14, 312 pp.

HUGHES, R. D. (1975). Assessment of the burial of cattle dung by Australian dung beetles.—*J. Aust. ent. Soc.* **14**, 129–134.

HUGHES, R. D., TYNDALE-BISCOE, M. & WALKER, J. M. (1978). Effects of introduced dung beetles (Coleoptera: Scarabaeidae) on the breeding and abundance of the Australian bushfly, *Musca vetustissima* Walker (Diptera: Muscidae).—*Bull. ent. Res.* **68**, 361–372.

JOLY, P. (1945). La fonction ovarienne et son contrôl humoral chez les Dytiscides.—*Archs Zool. exp. gén.* **84**, 49–164.

MATTHEWS, E. G. (1972). A revision of the scarabaeine dung beetles of Australia. I. Tribe Onthophagini.—*Aust. J. Zool. Suppl. Ser.* no. 9, 330 pp.

TYNDALE-BISCOE, M. (1978). Physiological age-grading in females of the dung beetle *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeidae).—*Bull. ent. Res.* **68**, 207–217.

TYNDALE-BISCOE, M. & WATSON, J. A. L. (1977). Extra-ovariolar egg resorption in a dung beetle, *Euoniticellus intermedius*.—*J. Insect Physiol.* **23**, 1163–1167.

WALLACE, M. M. H., TYNDALE-BISCOE, M. & HOLM, E. (1979). The influence of *Macrocheles glaber* on the breeding of the Australian bushfly *Musca vetustissima* in cow dung.—pp. 217–222 *in* J. G. Rodriguez (*Ed.*). Recent Advances in Acarology, Vol. 2.—569 pp. New York, Academic Press.

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