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Reproductive activity of *Onthophagus granulatus* Boheman (Coleoptera: Scarabaeinae) in New Zealand: Implications for its Effectiveness in the Control of Pastoral Dung.

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ABSTRACT

Reproductive condition and breeding cycles of adult female *O. granulatus* were demonstrated in field collected insects using physiological age-grading techniques to assess the proportions of newly emerged, nulliparous and parous beetles and those resorbing oocytes. Northern New Zealand populations of the dung beetle were univoltine. Breeding and dung burial started in early September and was maintained continuously until March with a late January peak in brood ball production (nidification) coinciding with the greatest abundance of adults. Adults ceased reproductive development at the onset of winter, during which females maintained ovariole condition at nulliparous stage two (N_2). Brood mortality was greatest in early spring and late autumn, resulting from the effects of low soil temperature and high soil moisture. Nidification activity of *O. granulatus* and its effect on the amount of dung remaining on the surface of pasture is discussed in terms of its efficacy of removal of livestock dung.

KEY WORDS

dung, oocyte, maturation, resorption, nidification, over wintering, dung burial, development

INTRODUCTION

Onthophagus granulatus Boheman (Figure 1) and *O. posticus* Erichson, are native Australian dung beetles that have been established in New Zealand for approximately 130 years (Anon 1878; Emberson & Matthews 1973). *Onthophagus granulatus* populations appear to be widespread in New Zealand, although *O. posticus* is restricted to the North Island (Dymock & Forgie 1993). At least 20 other species of coprophagous beetles, including aphodiines, hydrophilids and members of the endemic canthonine genera, *Saphobius* Sharp and *Saphobiamorpha* Brookes, occur in a variety of habitats throughout New Zealand. None of the *Saphobius* or *Saphobiamorpha* species have been reported to utilise the dung of livestock. The Mexican coprine, *Copris incertus* Say, was introduced by the Department of Scientific and Industrial Research (DSIR) into New Zealand during the 1950's with establishment of breeding populations in Whangarei, and recently in South Kaipara. To date, the introduction *C. incertus* remains the only deliberate attempt to import dung beetles to address the problem of pastoral dung accumulation and dung breeding flies in this country.

During peak seasonal activity in Australia, populations of *O. granulatus* often exceed 100 beetles per pad, and can bury large quantities of dung rapidly (John Feehan, SOILCAM, pers. comm.). In contrast, New Zealand populations of *O. granulatus* rarely achieve high densities per pad during favourable seasonal conditions. With an estimated 113 million beef and dairy pads alone deposited each day on New Zealand pastures (Dymock & Forgie 1993), the existing dung fauna appear to have little effect in the rapid assimilation of pastoral dung.

The Onthophagini are one of several scarabaeine tribes in which highly fecund females provision subterranean burrows with sufficient dung to allow the development of numerous larvae, and which in many countries, contribute favourably to the pastoral ecosystem by increasing plant yield (Bornemissza & Williams 1970; Fincher *et al.* 1981), pasture productivity (Bornemissza 1960; Fincher 1986), nutrient cycling (Gillard 1967), and pastoral irrigation (Fincher 1981). The rapid burial of fresh dung results in significant reductions of dung-breeding pest flies (Bornemissza 1970; Ridsdill-Smith *et al.* 1987; Ridsdill-Smith & Hayles 1990) and the eggs and larvae of gastrointestinal helminths (Bryan 1973; Fincher 1975).

The objectives of this paper are: i), to document the reproductive physiology of *O. granulatus* in northern New Zealand pastures; ii), quantify its efficacy in dung removal from pasture; and iii), discuss the potential for augmenting this species with additional dung beetles and the economic value dung beetles have through the ecological services they provide.

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[1] *This work was carried out while employed by AgResearch (New Zealand Pastoral Agricultural Research Institute) in Auckland in 1992-93.*

Figure 1. *Onthophagus granulatus* Boheman, 1858. Habitus, male (major morph). Scale bar = 1mm

MATERIALS AND METHODS

Field study site

The majority of the field study was carried out at the Pearce organic farm, Shelly Beach, South Kaipara (36°35'S, 174°21'E) from October 1992 to November 1993. The experimental area was located in three wind-sheltered paddocks in the centre of the farm. Soil beneath the pasture was predominantly a sandy loam. These paddocks were permanently grazed by sheep and cattle and were therefore the areas of highest dung beetle activity. Climate data for Shelly beach over 30 years reveals average and average maximum summer (December-February) air temperatures of 17.7°C and 26°C respectively, and average and average maximum winter (June-August) air temperatures of 10.5°C and 17.7°C respectively (Figure 2a; Shearer 1973). The average annual rainfall is 1,346 mm, and except between the wettest months (June - September), is relatively uniform in distribution throughout the year (Figure 2b). The soil temperature at 10 cm beneath the pasture during summer averages 18.8°C and reaches a minimum of approximately 9.6°C during winter (Figure 2c; *NZ Met. S. Misc. Publ.*109, 1976-1984).

Physiological age-grading

The ovary of *O. granulatus* consists of a single telotrophic ovariole comprising a germarium, a vitellarium containing 5 to 7 sequentially developing oocytes, a calyx and oviduct leading to a vagina. The ovariole of newly emerged females shows no differentiation between the germarium and the vitellarium (Halffter & Lopez 1977). The period of reproductive maturation (the differentiation between germarium and vitellarium resulting in the sequential development of oocytes) to reach sexual maturity varies considerably in dung beetles and depends among other things on the amount of feeding by the newly emerged adult (Halffter & Lopez 1977).

To obtain a reasonable assessment of the beetle population at any one time, sub-samples of 100 beetles collected each fortnight from around the farm were dissected in insect physiological saline. Each beetle was examined for cuticular hardness and the amount of tibial wear. The abdominal sternites were then removed and the fat-body and reproductive system examined using a dissecting microscope.

Female age-grading using ovarian physiology has been used to determine the reproductive potential (and hence the number of generations per year) in several phenological studies of scarabaeinae (e.g., Tyndale-Biscoe 1978; Lumbreras *et al.* 1991; Gonzalez -Vainer & Morelli 1999; Gonzalez Megias & Sanchez Pinero 2004). In this Kaipara study, age-grade categories were based on those developed by Tyndale-Biscoe (1978) and included **Nulliparous (N):** N_1, newly emerged beetles, no fat-body, undeveloped ovariole (no oocyte development), soft cuticle and unworn tibiae; N_2, young beetles, some fat-body, slightly developed ovariole (partially developed oocytes in vitellarium), moderately hard cuticle and slightly worn tibial teeth; and N_3 young beetles, developed fat-body, developed ovariole (full sequential development of oocytes), completely hard cuticle, increasingly worn tibiae (teeth no longer sharp or pointed), **Parous (P)**: older beetles, similar to N_3 but with the presence of a yellow body between the calyx and the basal oocyte in the vitellarium, seen as a slight deposit (P_1), or a moderate deposit (P_2) or a thick ring or plug (P_3). Parous females also had moderate to severely worn tibial teeth. **Resorbing (R)**: Beetles from N_2 to P3, with visible signs of basal and sometimes sub-basal oocyte breakdown, or extrusion of oocyte through the ovariole (calyx or vitellarium) wall into the haemocoel. Yellow granules (if present) attached to the outside of the calyx are evidence of past resorption(s).

Male reproductive development was categorised as either 'developed' (testis enlarged and iridescent-white in appearance; two ectadenia accessory glands with white coloured swollen proximal and distal areas) or 'undeveloped' (testis clear and not enlarged and ectadenia glands hardly recognisable and void of any swollen areas).

Broods were categorised as eggs, first-, second-, third-instar larvae, pupae and teneral adults for brood production, development and survival experiments. A stereomicroscope fitted with an eye-piece micrometer was used to determine larval developmental stage by measuring head capsule widths of 1st instar (1.35 mm), 2nd instar (1.62 mm) and 3rd instar (1.90 mm) larvae. Third instar larvae have a distinct yellow head capsule and yellow/green skin colouration, becoming pale in the pre-pupal phase following evacuation of the gut contents. Teneral adults in broods are those that have soft cuticles and have not emerged from pupal cocoons at time of sampling.

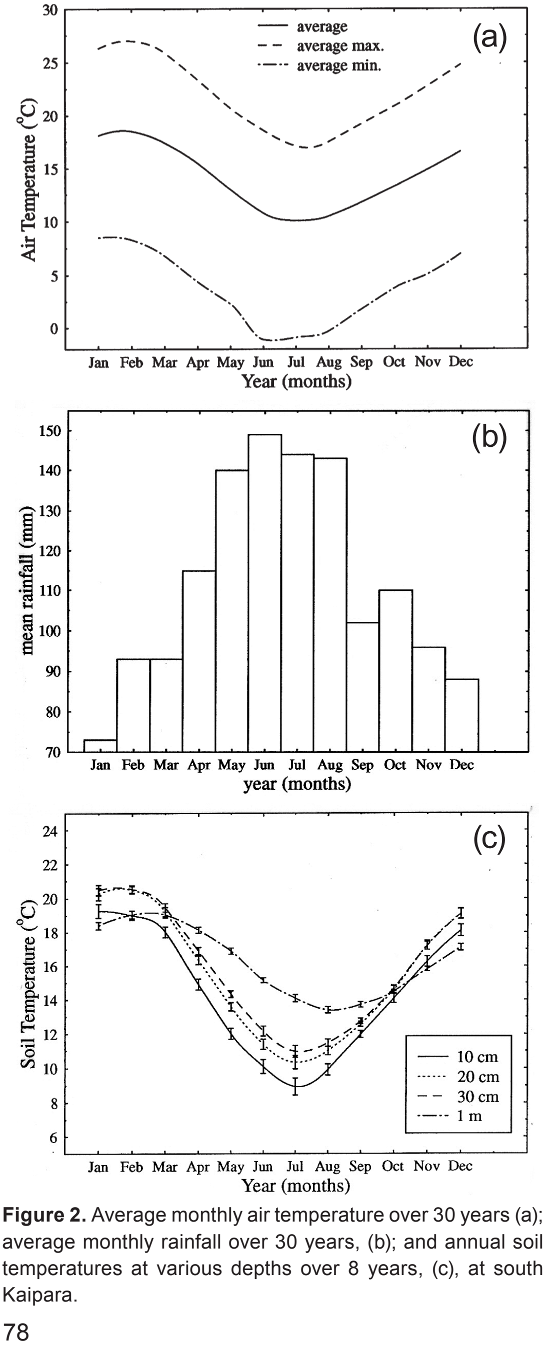

Figure 2. Average monthly air temperature over 30 years (a); average monthly rainfall over 30 years, (b); and annual soil temperatures at various depths over 8 years, (c), at south Kaipara.

Reproductive status

(1) Spring-Autumn: Each fortnight, 100 beetles were collected by hand and dung-baited pitfall traps in the experimental area. Both methods of sampling give similar patterns of seasonal abundance of beetles and have been equally effective in population sampling (Doube & Giller 1990).

(2) Winter: To determine reproductive status during winter, 43 undeveloped males and an equal number of N-P females from a laboratory culture were placed out in the field in late April in 4 gauze-bottomed cylinders (Ø=20 cm x 35 cm deep) three-quarters filled with vermiculite, sand and soil. Cylinders were dug into the ground and covered with a gauze lid. One litre of fresh dung was added to the cylinders every two weeks. Removal and dissection of 6-12 beetles encountered in the cylinders (and selected without bias) was carried out once a month throughout the winter, and more frequently as spring approached. These results were incorporated into Figure 3a.

Brood production and development

Two methods were used to determine brood production and survival in the field. For the first, gauze-bottomed plastic cylinders (Ø=20 cm x 20 cm deep) were filled with a compacted soil mixture and dug into the ground flush with the pasture surface. On every sample occasion, one litre of fresh dung was placed on the soil of 4 unused cylinders in each of the experimental areas and left exposed for two weeks to dung beetle reproductive activity. At the end of two weeks the cylinders were searched for broods which were counted and then returned to the cylinders. Any adult still in the cylinders or dung were removed. Sub-samples of broods were removed each subsequent fortnight until no broods remained in each cylinder and teneral adults had emerged. Gauze lids were placed over cylinders after the two week exposure period to prevent escape of newly emerged adults and prohibit entry by other breeding adults to the dung in the cylinders. Cylinders were re-used once they had been completely emptied of brood balls/emerged teneral adults. Determination of larval instar was made using measurements of head capsule width.

Secondly, 45 brood balls were also collected each fortnight from the soil beneath cow pads distributed around the experimental area for comparison with those in the cylinders. Brood balls were dissected and their contents age-graded.

Brood survival over winter

To determine to the fate of the small proportion of broods in balls prepared by adults in Autumn, laboratory colony brood balls containing eggs and first instar larvae (n=43), second instars (43), third instars (36), and pupae or teneral adults (38), were placed outdoors in gauze-bottomed cylinders (as above) in mid–late May. Cylinders were covered with gauze lids to prevent the escape of emerging beetles and to allow rainfall and light to enter. Broods (and emerged beetles) were destructively sampled each month through winter until spring by which time no broods remained in the cylinders.

Growing day degree calculations

A temperature threshold of 11.3 ºC for the development of *O. granulatus* from egg to adult was calculated by Tyndale-Biscoe *et al.* (1981). Australian *O. granulatus* require 495 day degrees above this threshold for development from egg to adult during an active season that is compounded by summer droughts. As a comparison, day degree calculations for the south Kaipara *O. granulatus* population was derived using a growing day degree calculator (ex. Michigan Agricultural Experimental Station (MSU)) that incorporates the averaging method or the sine wave (Baskerville-Emin) method depending on minimum daily temperatures above or below the threshold temperature (11.3 ºC) of development respectively.

RESULTS

Longevity of *O. granulatus* adults in Australia ranges from 6 to 46 weeks (mean = 23 weeks) at 20°C in the laboratory (Tyndale-Biscoe *et al.* 1981). The life span of *O. granulatus* adults in the Auckland laboratory colony was similar to that recorded by Tyndale-Biscoe *et al.* (1981). Physiological age comparisons and tibial wear between wild caught versus laboratory reared beetles indicates adults collected from the field survive for at least 16 to 20 weeks during the active season.

Reproductive status

(1) Spring-autumn: Sampling in the first spring season commenced in October 1992. A full range of reproductive age of beetles were present in the female population comprising N_1 (10%), $N_{2\text{-}3}$(60%), P (10%) and R (20%) (Figure 3a). The proportion of females resorbing eggs declined through November and December of the first season. Thereafter, resorption persisted in a relatively small proportion of nulliparous and parous beetles until the beginning of winter. Up until mid-December, most females were N_3, P and developed males, with small proportion of the sampled population comprising newly emerged and N_2 beetles.

After December, beetle densities increased rapidly with a continual presence of beetles at all reproductive stages occurring in the samples until late March, after which most of the samples consisted of a new generation of beetles undergoing reproductive maturation to $N_{1\text{-}2}$. These beetles ceased reproductive development at the N_2 stage which comprised 100% of the female population by mid-May. Proportions of older N_3, $P_{1\text{-}3}$, and NR+PR beetles dwindled away through autumn. Dissections revealed that oocyte resorption was to an N_2 level of reproductive development, indicating their preparation to over winter along with the new N_2 beetles. Dissections of adults from April onwards revealed increasing accumulations of fat-body in the abdominal cavities of the male and female beetles. There was then a marked resurgence in oocyte maturation during the early spring of the following season, with 70% of the female population at N_3 reproductive stage by September 20, 1993 (Figure 3a). The majority of males were also reproductively developed at this time. By October (Figure 3a, 4.10.93), all reproductive ages were present in the population including a small cohort of 'undeveloped' males and $N_{1\text{-}2}$ female beetles. A higher number of resorbing females (up to 45% in mid-October, 1993) were present in the population during spring than summer (means: 18.3% and 8.6% respectively) in the first active season. Rainfall during this period was greater and air temperature lower than recordings for the previous spring (data not presented).

(2) Winter: All N_3, $P_{1\text{-}3}$, and NR+PR beetles placed in the cylinders had undergone oosorption to N_2 stage of development by late May, and thereafter all sampled females were N_2 (Figure 3a, 17.5.93). All young and old males sampled from the cylinders were categorised as undeveloped from late May and maintained this state of reproductive diapause through winter. Although beetles remained reproductively dormant over winter, average maximum temperatures were mild enough to allow adults to feed (Figure 2a). Winter feeding was confirmed by the presence of food in the guts of most of the beetles recovered from the cylinders and beetles infrequently collected from beneath dung in the field. Additionally, beetles sampled from the cylinders always contained high levels of fat-body.

On each sampling period, up to 10.5% of the population of over wintering beetles in the cylinders were dead. Without exception, mortality occurred in old beetles i.e. beetles with well worn tibiae and with resorbed oocytes in N_3 and $P_{1\text{-}3}$ stage of reproductive development prior to the onset of winter.

Brood production and development

Sampling for brood balls began in early November 1992. All pre-imaginal stages were present in the samples. Early nidification was evident from 10 September 1993 when broods from dung balls constructed in soil beneath pasture revealed 88% of the pre-imaginal beetles were eggs and 12% were 1st to 2nd instar larvae.

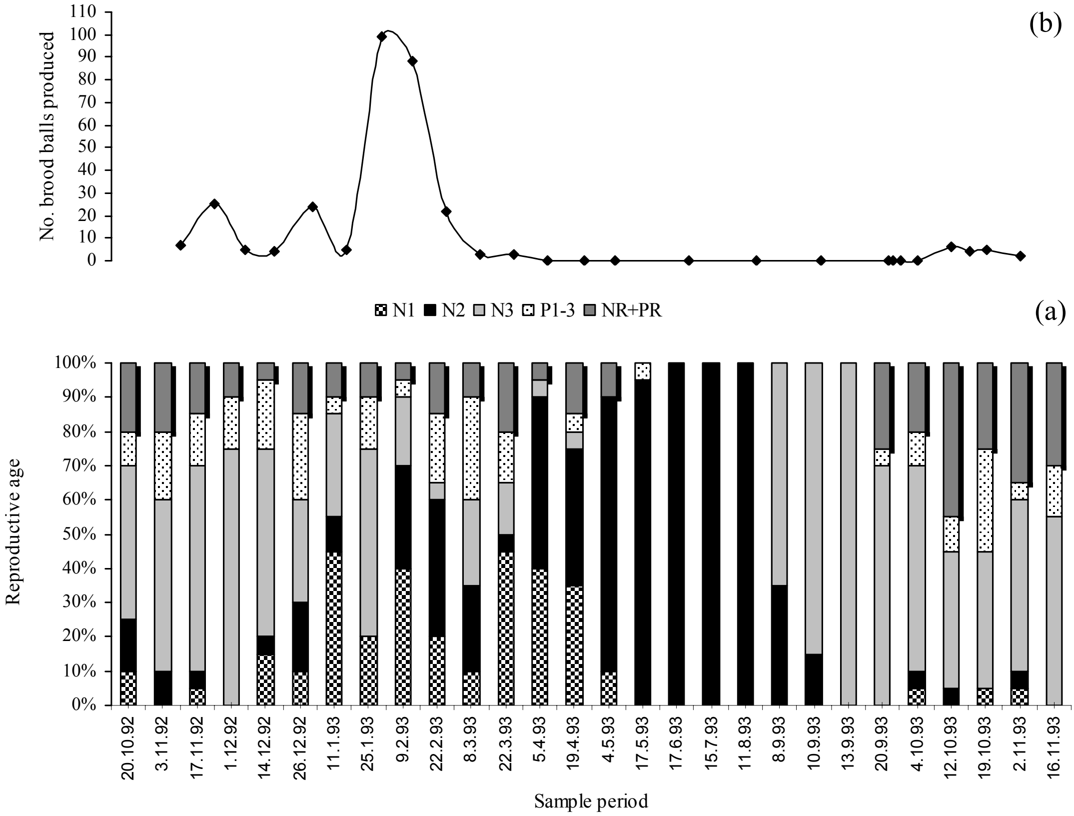

Figure 3. Seasonal reproductive state, a); and brood ball production, b), of *Onthophagus granulatus* females, at Shelly Beach farms, South Kaipara during October 1992 to November 1993.

From mid-November onwards, all pre-imaginal stages were represented in the population including the empty pupal cocoons of emerged teneral adults. Proportions of broods containing eggs remained between 50-60% both in the pastoral sampling and those laid in cylinders from December until the end of March. In mid May, a single brood ball containing a fertile egg (reared through to hatching in the lab) was recovered from beneath sheep dung.

Two small and one large peak in brood production occurred during the active season (Figure 3b). Both smaller peaks were approximately 5 weeks apart and the large peak spanned a 6 week period of increased nidification, coinciding with a peak in adult abundance in the population.

Broods sampled early in September 1993 suffered 50% mortality. Twenty to thirty percent mortality occurred in eggs and first instar larvae up to December. Brood survival was greatest from December to February. During this period, brood production reached a peak with only 11-14% brood mortality. From late February to April, when most brood production had finished, mortality was evident in approximately 30% of the broods sampled.

Brood survival over winter

All but one of the eggs and 1st- 3rd instar larvae in brood balls placed in the cylinders had died by mid-August. One egg or first instar larva had further developed to 3rd instar larva and was still living at the time of sampling on 13 August. Six newly emerged adults were found on 15 July in the cylinder containing pupae and teneral adults. On the same date, 6 of the 10 brood balls sampled contained live teneral adults. However, by late August all remaining pupae and un-emerged teneral adults had died.

Growing day degree calculations

A total of 1019 day degrees above a threshold of 11.3 ºC were available for *O. granulatus* development from mid-September to the end of March. During the peak period of brood production in January-February, it took 8-10 weeks from the time fresh dung pads were placed on each of the cylinders (25 January) to the emergence of new adults, and 6-8 weeks from egg to adult following dung placement on 9 February. Growing day degree calculations corresponding to these actual development time frames were 385–517 and 296–428 day degrees respectively.

DISCUSSION

Combining reproductive status with brood production

Numbers of ovipositing *O. granulatus* in south Kaipara peaked in late January - early February. Dung burial activity for brood ball construction also peaked and eggs laid at this time developed into to the new generation of adults from March. The two smaller peaks in brood production in spring may have reflected variable environmental conditions (such as temperature) that determined flight activity of the same (and recently recruited) adults, and equally, developmental time of the pre-imaginal stages.

From April onwards, the new population of adults consisted mainly of $N_{1\text{-}2}$ females and reproductively undeveloped males (Figure 3a), all feeding to accumulate fat body for the onset of winter. A small proportion of parous and resorbing females and reproductively developed males remained in the population which would account for the dwindling proportion of brood balls occurring in the field until the end of March. Late season broods continued to develop at very low rates of growth during late autumn-early winter, but the over wintering experiment indicated that virtually all had died by late winter. Nonetheless, potential exists for a small cohort of broods (perhaps those in brood balls buried by adults in sheltered pastoral locations) to survive and continue developing through mild winter (see Tyndale-Biscoe & Walker 1992). Old beetles tended to not survive the winter.

Maturation feeding for reproductive output commenced in early spring when the over wintering beetles again became active. The maturation phase varies considerably among dung beetles, ranging from weeks to months depending upon species, dung availability, the quantity of dung fed on by newly emerged adults (Halffter & Lopez 1977) and dung quality (Greenham 1972; Ridsdill-Smith & Hayles 1990). Tyndale-Biscoe *et al.* (1981) found that newly emerged *O. granulatus* adults in Australia feeding on good quality dung reached sexual maturity and began nidification in approximately 2 weeks, compared with beetles fed on poor quality dung which failed to breed and the majority dying after 4 weeks. Male beetles produced large amounts of fat-body when fed on good quality dung and none in males fed on poor quality dung. Temperature was also found to affect the length of the maturation-feeding period. For *O. australis* Guerin- Meneville, the maturation feeding period lasted up to 34 weeks at 20°C and 2-9 weeks at 25°C (Tyndale-Biscoe & Walker 1992).

Throughout spring 1993, comparatively high proportions (up to 45%) of female *O. granulatus* were resorbing oocytes at south Kaipara. Two causes of oosorption during this period are hypothesised: Lush spring grass, which has a high moisture and low carbohydrate content, is highly digestible when eaten by cattle, resulting in liquid dung (Haynes & Williams 1993). While the fluid component of dung is the major source of nutrition for adult dung beetles (Aschenborn *et al.* 1989), dung of this consistency is unworkable by many dung beetles including *O. granulatus* for nidification. Beetles were always found breeding around the periphery of pads and where dung immediately beneath the crust was beginning to dry. There was also a substantial decrease in air temperature during November 1993 which may have contributed to the high proportion of oosorbing females. Abnormally low temperatures appear to increase the incidence of oosorption in insects (Bell & Bohm 1975).

Mortality of *O. granulatus* eggs and larvae at south Kaipara may have been due to a combination of lower temperatures (Tyndale-Biscoe *et al.* 1981), and excess soil moisture levels in the first 10 cm of soil beneath the dung pad. In turn, excess moisture levels may have resulted from a combination of relatively high spring rainfall, and liquid draining from dung (especially in spring), which strongly influences soil moisture beneath a dung pad (Barkhouse & Ridsdill-Smith 1986; Haynes & Williams 1993).

Growing day degrees and univoltinism

In Australia, low rainfall and high temperatures during the active season are known to limit *O. granulatus* populations to a univoltine lifecycle (Tyndale-Biscoe *et al.* 1981). The spring and autumn peaks of population activity in these beetles suggest univoltinism may be a facultative response to dry, drought-like conditions occurring in the summer (Tyndale-Biscoe & Walker 1992). The optimal temperature for *O. granulatus* reproductive activity and brood development is 25°C (Tyndale-Biscoe *et al.* 1981), a temperature regularly exceeded during the active season in Australia.

In New Zealand, *O. granulatus* populations appear also to be limited to a univoltine lifecycle. At the height of summer when climatic conditions in south Kaipara are blessed with relatively frequent rain spells and good soil moisture and temperature levels, observed development times from egg to adult ranged from 8-10 weeks and 6-8 weeks following dung placement in field cylinders in

25 January and 9 February respectively. Growing day degree calculations corresponding to these observed development time frames (i.e., 385–517 and 296–428 day degrees respectively out of a total of 1019 day degrees available during the active season), overlap with the 495 day degrees calculated for development from egg to adult in Australian populations of *O. granulatus* (Tyndale-Biscoe *et al.* 1981).

However, several key constraints limit New Zealand populations of *O. granulatus* to univoltism: Spring and autumn temperatures are comparatively low and rarely, if ever, exceed 25°C (Figure 2a). According to day degree calculations, eggs laid in early spring did not complete development to adults until mid-late January. Broods developing from brood balls prepared in autumn suffered virtually total mortality over winter. Apart from reproductive physiological constraints (including time taken to reach sexual maturity) that also effect Australian populations of *O. granulatus*, high soil moisture levels in spring and autumn, and dung quality contribute to maintenance of a univoltine population.

All these constraints limit the ability for *O. granulatus* populations in northern New Zealand to bury more dung.

Brood ball production in terms of efficacy of pastoral dung removal

Onthophagus granulatus are slow burying, highly fecund onthophagines. Each female buries an estimated 131-196 grams (wet wt.) of dung for brood ball construction in her reproductive lifespan, as under favourable conditions (Tyndale-Biscoe *et al.* 1981), 70 eggs are oviposited in balls weighing an average of 2.34 ± 0.46 grams (dry wt.= 0.82± 0.32 grams). While relatively abundant in northern New Zealand pastures in late January-February, *O. granulatus* rarely if ever achieve densities exceeding 100 beetles per dung pad (pers. observ.), unlike Australia. Beetles exceeding a density of 100 beetles per dung pad could remove an average of 1-2kg of cattle dung over a relatively short period of time assuming conditions and dung quality are favourable for this species in New Zealand pastures, which may not be the case. The optimal temperature for *O. granulatus* activity is 25 °C (Tyndale-Biscoe *et al.* 1981) which is rarely achieved with consistency from spring to autumn in New Zealand pastures where *O. granulatus* are present. Other factors such as, dung quality (e.g., liquid dung) and high soil moisture levels, particularly in spring and autumn may also restrict a build up in population densities required to rapidly bury pastoral dung in New Zealand.

Onthophagus granulatus are relatively small (6-8 mm) beetles. Halffter & Matthews (1966) found a linear relationship between beetle size and size of brood balls suggesting larger beetles bury more dung per egg than smaller ones. For example, a female *Bubis bison* (L.) is 5 times heavier than *Onthophagus vacca* (L.), and buries 5 times the volume of dung per egg (Lumeret & Kirk 1987; Kirk & Wallace 1990). Dung beetle size is as much an important consideration in controlling levels of dung/forage foul on pasture surfaces as it is in the effective control dung breeding flies (Kirk & Wallace 1990). In Australia, Wallace and Tyndale-Biscoe (1983) found a 50% reduction in the number of puparia of the pest bush fly, *Musca vetustissima* (Walker) by only six *Onitis alexis* (Klug) beetles. The same percentage reduction was obtained by 940 *O. granulatus* beetles.

Equally, burial capacity of each species of scarab for food/brood ball production is, in part, a product of the level of development in nidification behaviour. The average brood ball weight of *Heliocopris dilloni* is 364 grams (Kingston & Coe 1977). The burial of 2 kilograms of dung by a pair of *H. dilloni* took 45 minutes (Coe & Kingston 1988). This species produce 1-2 generations a year depending on the rains and is reproductively active for up to 3 seasons. In comparison, a much smaller species of dung beetle, *Onthophagus gazella* Fabricius, may have 4-5 generations a season with each female producing 180-200 eggs in her 3-4 month reproductive lifespan (Ferrar 1973). At a density of one pair of beetles per 100 grams of dung, *O. gazella* can completely bury a dung pad within 48 hours (Bornemissza 1970).

Failing pastoral ecosystems are those which lack dung beetle communities comprising an abundance of many different species capable of burying large amounts of dung during the course of nidification. Many countries that lack dung beetles, and that are predisposed to the dung of artiodactyls like cattle, sheep, goats, and antelope in open pastoral environments, import the most suitable species to mitigate dung related problems (e.g., forage foul, reduced pastoral productivity, dung breeding pest flies, etc). Selection of the most suitable candidate species for release and establishment in New Zealand pastures will need to pay particular attention to many varying pastoral conditions throughout the country, including factors that limit seasonal activity and efficacy of dung burial in *O. granulatus.*

Economic benefits to dung burial

Drenches and fertilizers are among the highest cost outlays for conventional farmers working in pastoral environments lacking suitable dung-burying beetle communities. Significant coverage of pastures by unutilised dung reduces total available forage and negatively influences pastoral productivity (Bornemissza 1960; Fincher 1981) and with it reduced economic benefits to the farmer. By establishing populations of dung beetles there are significant financial benefits to both farmers and national economies. For example, the ecological services provided by dung beetles are worth an estimated US$380 million/yr to the US economy (Losey & Vaughn 2006). With an absence of dung beetles, beef losses in the US due to forage fouling alone would be ca. 244 million kg of beef per year. However, with current natural levels of dung beetles, 98 million kg of beef are potentially lost per year (Losey & Vaughan 2006). In contrast, NZ has approximately 9-10 million head of beef and dairy cattle in production per year (Statistics New Zealand, Agricultural Production Census/Survey:http://www.maf.govt.nz/statistics/pastoral/livestock-numbers/). Assuming equivalent benefits, establishing populations of suitable dung burying beetles into New Zealand could be worth US$38 million (NZ$60.8 million) per year to the NZ agricultural sector.

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