

M 1606

## PER CENT EMERGENT WEIGHT: A ROADMAP TO ADULT RHINOCEROS BEETLE, *ORYCTES RHINOCEROS*, BEHAVIOUR

ROBERT K. VANDER MEER\*

University of the South Pacific, Suva, Fiji Islands

(Received 16 June 1986; revised 30 September 1986)

**Abstract**—Adult rhinoceros beetles, *Oryctes rhinoceros* L., leave their pupal chambers, take their first flight, and die at well-defined ratios of their wet weight and their adult emergent weight. In addition, the beetles feed in a cyclical manner that is variable with time; however, each feeding event is well defined by a constant ratio of their weight just prior to feeding and their adult emergent weight. The ability to accurately estimate the emergent weight of field collected beetles, and therefore calculate the percentage emergent weight at the time of capture, makes these correlations useful in ecological studies and may be extended to other insects.

**Key Word Index:** *Oryctes rhinoceros*, emergent weight, flight, feeding, behaviour, death, physiological age, temporal age, Coleoptera, ecology, lifecycle

### INTRODUCTION

Coconut rhinoceros beetles, *Oryctes rhinoceros* L., are an important pest of coconut palms in India, Southeast Asia, and several areas of the South Pacific (Catley, 1969; Bedford, 1980). Female beetles lay eggs in decaying vegetable matter where the larvae develop and pupate after making a small compacted pupal chamber. The newly eclosed adult remains in the pupal chamber for a variable length of time, then leaves the chamber for its first flight to a host palm tree. Palms are damaged when the beetles burrow into the growing point of the palm and feed on exudate from the macerated tissue. After feeding, the adults of both sexes fly back to decayed vegetable matter breeding sites where they mate, and the females deposit eggs. The feeding-mating-oviposition cycle occurs several times during a beetle's lifetime (Gressitt, 1953; Cumber, 1957; Cherian and Anantanarayanan, 1939). There have been no published reports of correlations between quantifiable morphometric properties of *O. rhinoceros* and several readily identifiable behaviours associated with the beetle's life cycle, although Zelazny and Neville (1972) reported a relationship between beetle endocuticle layer formation and its temporal age.

Correlations between behavioural changes and an insect's flight activity have been reported for an ambrosia beetle, *Trypodendron (Xyloterus) lineatum*, (Graham, 1959) and the bark beetle *Dendroctonus pseudosugae* (Southwood, 1962). In both examples, young adults showed different behavioural responses

to host material depending on the amount of flight exercise. In addition, the inclination for *D. pseudosugae* to fly was positively correlated to the fat content of individuals, and Atkins (1966) suggested that the decline in lipids during aging, starvation, or flight might induce behavioural changes. This paper reports extraordinary relationships between *O. rhinoceros* weight loss relative to adult emergent weight and a series of behavioural events beginning shortly after adult emergence and ending with the beetle's death.

### MATERIALS AND METHODS

Adult beetles for this study were reared from field-collected late 3rd-instar larvae. They were placed individually in glass quart jars filled with a rearing media of decomposed sawdust and cow dung (Schipper, 1976). Most of the advanced larvae constructed their pupal chamber directly on the side of the glass container, which made it possible to view their activity inside the chamber. Adults were large enough (4-12 g, Vander Meer and McLean, 1975) so that weight losses and gains could be readily measured on a balance (Dial-O-Gram, sensitivity = 0.01 g). Their life span (4-6 months) and episodic feeding habits made single daily weighings adequate for monitoring weight loss and food uptake. When beetles were placed together for long term studies they were identified by scoring a number code on their elytra.

#### *Pupal chamber egress*

Just prior to pupation, rhinoceros beetle larvae form a chamber in the decaying vegetable matter in which they pupate. After the adult ecloses it remains in the pupal chamber for a variable length of time

\*Current address: Insects Affecting Man and Animals Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, FL 32604, U.S.A.

(Zelazny, 1975). To avoid disturbing newly eclosed adults in their pupal chambers, their emergent weight was estimated from previously developed correlations between pupal weight and emergent weight (Vander Meer and McLean, 1975). The top of the pupal chamber was carefully broken and the pupa removed and weighed. The pupa was returned to its chamber and its top first covered with a small piece of wood and then with rearing medium. The pupal chamber was monitored daily for adult eclosion and subsequent movement out of the pupal chamber. Immediately after observing pupal chamber egress, the beetle was weighed and the time noted.

#### First flight

Young adult beetles (4–6 days old) whose emergent weight had been directly measured were marked for identification and placed in a holding cage large enough to allow flight (Garlovsky and Zelazny, 1971; Vander Meer *et al.*, 1979). The beetles were weighed daily and observed for flight each evening between dusk and 2:00 a.m. Beetles observed flying were immediately weighed. During this, and subsequent experiments, food (sugar cane and very ripe bananas) was always available for the beetles to eat.

#### Feeding periodicity and death

Adult beetles (female and male) of known emergent weight (directly measured) were maintained in holding cages (Vander Meer *et al.*, 1979), which allowed for the normal activities of flight, feeding, mating, and female ovipositioning. The weight loss and gain of adult beetles was monitored 6 days a week until the individual's death. In this way, feeding activity was easily discovered through weight increases. The weight at a beetle's death was determined as its weight on the day of death.

#### Determination of lipid content

Beetles that had just emerged as adults or had just died were immediately analysed for total lipids by the gravimetric method of Bligh and Dyer (1959). Three beetles of each sex were sampled for each of the two categories.

## RESULTS

#### Pupal chamber egress

A plot of the adult emergent weight versus beetle weight at pupal chamber egress (Fig. 1) shows a strong linear correlation ( $r^2 = 0.933$ ,  $n = 26$ ). Adult beetles weighed 90–94% of their adult emergent weight ( $92.9 \pm 2.7\%$ , Mean  $\pm$  SD,  $n = 26$ ) when they exited from their pupal chambers. In these tests the beetles left their pupal chambers 2–13 days ( $8 \pm 3$  days, Mean  $\pm$  SD,  $n = 26$ ) after eclosion.

#### First flight

Although the beetle's feeding and breeding cycle, consisting of flight to a host palm tree followed by flight to a breeding site, occurs many times during a beetle's lifetime, only flight behaviour during the first cycle was investigated. Figure 2 shows a strong correlation ( $r^2 = 0.926$ ,  $n = 22$ ) between a beetle's

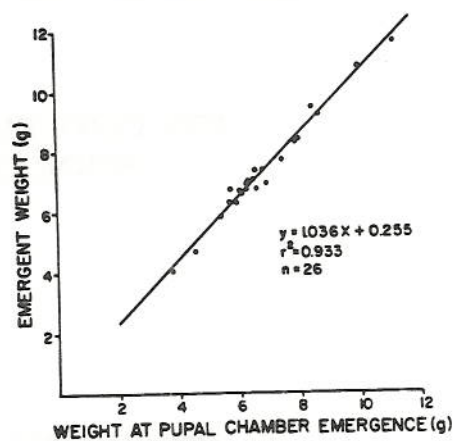


Fig. 1. The linear correlation between an adult beetle's emergent weight and its weight at the time of egress from the pupal chamber.

emergent weight and its weight at the time of its first flight. Flight weights ranged from 58 to 74% of a beetle's emergent weight ( $67.1 \pm 4.5\%$ , Mean  $\pm$  SD,  $n = 22$ ). The time of first flight after adult emergence ranged from 17 to 28 days ( $21 \pm 3$ , Mean  $\pm$  SD,  $n = 22$ ). Food was accessible to the beetles at all times during the study; however, none of the individuals fed (no detectable weight gain) prior to their first flight.

#### First and subsequent feeding

A strong linear correlation ( $r^2 = 0.953$ ,  $n = 47$ ) existed between an individual beetle's adult emergent weight and its weight at first feeding (Fig. 3). The percentage adult emergent weight at this stage of a beetle's physiological life ranged from 51 to 65.9% ( $58.1 \pm 2.9$ , Mean  $\pm$  SD,  $n = 47$ ). The time from emergence as an adult to the time of first feeding was  $26.2 \pm 3.4$  days (Mean  $\pm$  SD,  $n = 47$ ). Percentage emergent weight is a remarkable predictor of an individual beetle's feeding behaviour when plotted against time (Fig. 4). It is apparent that the feeding relationship is applicable throughout the adult's several feeding cycles. For a typical individual (Fig. 4) the time intervals between feedings are variable (Mean  $\pm$  SD =  $22.4 \pm 11.1$  days;  $n = 5$ ); however, the

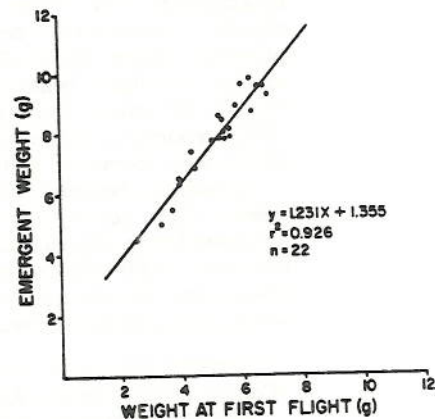


Fig. 2. The linear correlation between an adult beetle's emergent weight and its weight when it takes its first flight.

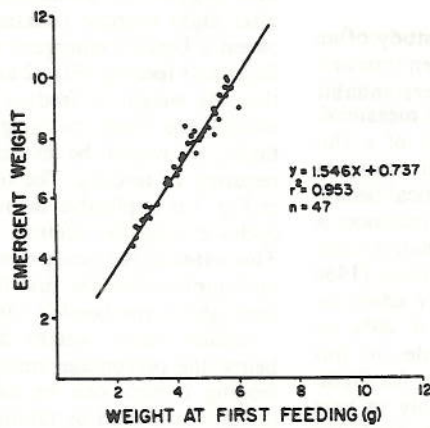


Fig. 3. The linear correlation between an adult beetle's emergent weight and its weight just prior to its first feeding.

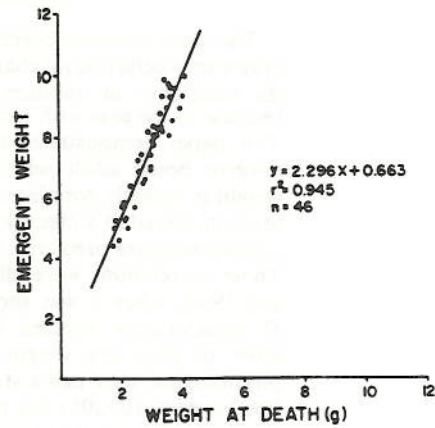


Fig. 5. The linear correlation between an adult beetle's emergent weight and its weight at death.

beetle's percentage emergent weight just prior to feeding is remarkably consistent (Mean  $\pm$  SD =  $60.1 \pm 1.1$ ;  $n = 6$ ). No significant differences were found between the mean percentage emergent weight just prior to feeding for males and females ( $n = 10$  each) across the several feeding sequences per adult beetle lifetime (female =  $58.7 \pm 1.87\%$ ; male =  $58.4 \pm 2.22\%$ ; mean  $\pm$  SD). There was little variation of percentage emergent weight within the multiple feedings of each individual. The mean and standard deviation of the standard errors from the twenty male and female examples above was  $1.0 \pm 0.3\%$ . The mean number of feedings per individual was  $6.7 \pm 1.9$  (SD).

#### Death

Weight at death is also highly correlated ( $r^2 = 0.945$ ) with adult emergent weight (Fig. 5). The percentage adult emergent weight ranged from 35.1

to 44.2 ( $39.7 \pm 2.7$ , Mean  $\pm$  SD,  $n = 46$ ). Adult longevity, the time from adult emergence to death, was variable ( $134.8 \pm 29.2$ , Mean  $\pm$  SD,  $n = 46$ ).

#### Lipid content

No significant differences in total lipid (Bligh and Dyer, 1959) were observed between the sexes in newly emerged adults (female =  $50.5 \pm 9.2$ ; male =  $67.0 \pm 29.0$ ; mean  $\pm$  SD mg/g emergent weight,  $n = 3$  each,  $P > 0.05$ , Newman-Keuls test). Their combined mean and standard deviation was  $58.7 \pm 21.1$  mg/g. Similarly, males and females that had just died were analyzed for total lipid. There were no differences in the sexes (female =  $1.9 \pm 0.9$ ; male =  $1.6 \pm 0.9$ ; mean  $\pm$  SD mg/g emergent weight,  $n = 3$  each), and the combined results were  $1.7 \pm 0.8$  mg/g. Newly emerged adults had over 33 times more total lipid than beetles that had just died.

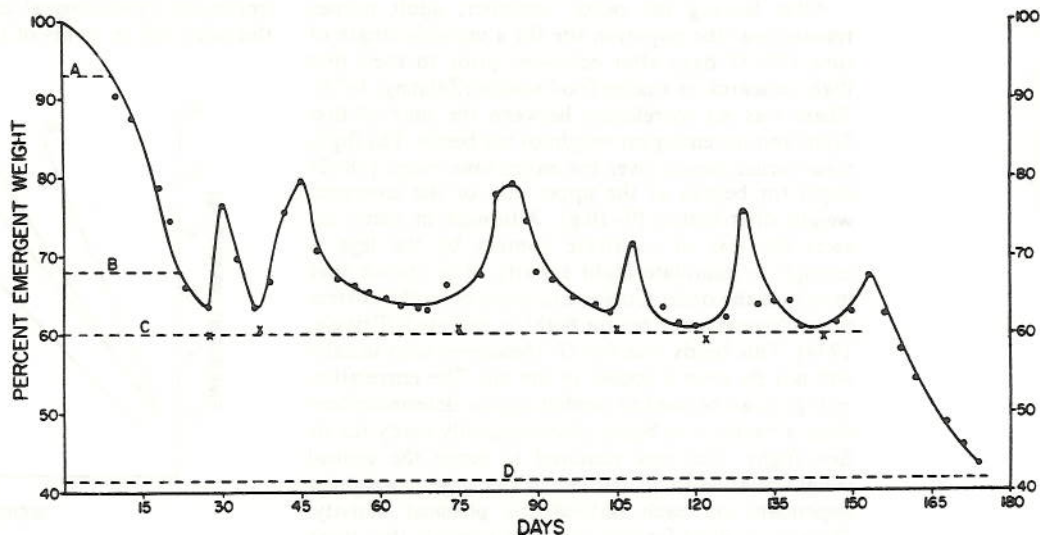


Fig. 4. An example of the adult life cycle for an *Oryctes rhinoceros* female in terms of percentage emergent weight versus time. Points represent 3 day running means of the percentage emergent weight. A = percentage emergent weight at pupal chamber egress. B = percentage emergent weight at first flight. C = percentage emergent weight just prior to initiation of feeding (x marks the lowest daily percentage emergent weight prior to feeding). D = percentage emergent weight at death.

## DISCUSSION

The most common correlations in the study of an organism's behavioural changes are between time and the behaviour in question. This is understandable because of the ease with which time can be measured. This paper demonstrates that the weight of a rhinoceros beetle adult relative to its adult emergent weight is strongly correlated to several critical behaviours in the adult's lifecycle and in some instances is a more accurate predictor of behaviour than is time. These correlations were alluded to by Atkins (1966 and 1969), when it was shown that female adults of *D. pseudotsugae* rejected host material if 20% or more of their dry weight was fat. Beetles in this physiological state had a strong propensity for flight. Beetles with 10–20% fat responded readily to host material, whereas, those with less than 10% fat failed to fly. The rhinoceros beetle's large size, long life span, and ease of handling made it an ideal candidate to test whether or not certain behaviours were directly correlated to the readily measured adult weight. The emergent weight of an adult is variable but is directly correlated to pupal weight and to the area of the elytra (Vander Meer and McLean, 1975). Any of these measurements—specific to each individual beetle—could be used in these correlation studies. The emergent weight was chosen as the primary fixed measurement because it was the easiest to obtain.

*Behavioural correlations*

The time of adult egress from the pupal chamber varied considerably in our studies (2–13 days) and in the literature (7–22 days; Gressitt, 1953; Cherian and Anantanarayanan, 1939; Vander Meer and McLean, 1975). In contrast, a very tight correlation (Fig. 1) exists between a beetle's adult emergent weight and egress from the pupal chamber. This behavioural event can be more accurately predicted and monitored using a beetle's percentage emergent weight than by its temporal age.

After leaving the pupal chamber, adult beetles remain near the pupation site for a variable length of time (17–32 days after eclosion) prior to their first flight in search of a palm food source (Zelazny, 1975). There was no correlation between the time of first flight and the emergent weight of the beetle. The flight time varied almost over the entire time range (18–28 days) for beetles at the upper end of the emergent weight distribution (9–10 g). Although in many insects the loss of substrate contact by the legs is enough to stimulate flight activity, it is known that insects in the order Coleoptera must be in the correct physiological state before flight is initiated (Pringle, 1974). This holds true for *O. rhinoceros* who usually will not fly even if tossed in the air. The correlation in Fig. 2 can be used to predict and/or determine how close a beetle is to being physiologically ready for its first flight. The time required to reach the critical weight relative to an individual's emergent weight is dependent on each individual's physical activity. Data on cyclical feeding activities indicate that these relationships may also apply to later flight activity.

At no time in this study did *O. rhinoceros* adults feed prior to their first flight, although food was always available. This is analogous to the report that

host negative *D. pseudotsugae* became host positive after flight exercise (Atkins, 1966). Correlations between a beetle's emergent weight and weight at first flight and feeding (Figs 2 and 3, see also Fig. 4) show that the weight at feeding for a given size beetle is always less than the weight of that beetle at first flight, as would be expected if flight was a prerequisite of feeding. The feeding relationship shown in Fig. 3 is applicable throughout the several feeding cycles during the lifetime of adult beetles (Fig. 4). This extends the predictive power of the correlation and implies that the first flight data may also apply throughout the beetle's lifetime.

Adults whose weight decreased more than 5% below the percentage emergent weight that initiated feeding (which can be calculated from Fig. 3 or directly measured by taking daily weights) continued to lose weight until death occurred (Fig. 5). As expected adult longevity was variable, but an individual's proximity to death could be accurately monitored and predicted through the correlations in Figs 3 and 5. The weight loss is presumably symptomatic rather than causative of complex physiological and biochemical changes.

We have noted during weight studies with hundreds of beetles that they never regain their original emergent weight. Presumably, adults emerge with a full complement of energy reserves (5.9% of their emergent weight is lipid), taking them through their first flight to a host palm. In contrast, beetles that stopped feeding and died had depleted their lipid reserves to 0.17% of their emergent weight. There were no significant differences in lipid content between males and females at emergence or death; however, the same situation may not be true at points in between these two extremes. Why a beetle at a certain point in its lifespan ceases to feed is unknown and may reflect a combination of genetic and environmental factors (Clark and Rockstein, 1964) lumped into the catch-all term of senescence.

Figure 6, a–d is a family of lines defining several important physiological states of an individual beetle's adult life in terms of its emergent weight and its

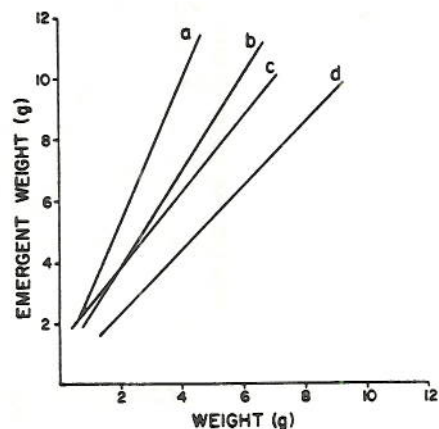


Fig. 6. The envelope of lines defining several events in the life cycle of adult rhinoceros beetles in terms of their adult emergent weight and their weight at the time of the behaviour in question. a = death, b = first feeding, c = first flight, d = pupal chamber egress.



weight at the behaviour of interest. As already mentioned, in the laboratory, the adult emergent weight can be measured both directly and indirectly (Vander Meer and McLean, 1975). The emergent weight of field-collected beetles from palms, breeding sites, or attractant traps (Maddison *et al.*, 1973; Vander Meer and McGovern, 1983) can be estimated from the strong correlation between emergent weight and the area of a beetle's elytra (Vander Meer and McLean, 1975). This information, coupled with Fig. 4, enables an investigator to determine if a beetle is (1) coming down from a palm after feeding (% emergent weight > 65), (2) going to a palm to feed (% emergent weight 55–65%), or (3) in its last bout with senescence (% emergent weight < 55%).

The family of lines in Fig. 6 is also interesting because it behaviourally defines the minimal possible size for *O. rhinoceros*. The lines for first flight and feeding cross at an adult emergent weight of about 3.8 g. Since we have established that the first flight must precede initial feeding, beetles with an adult emergent weight of < 3.8 g have little chance for survival. The requirement to replenish their energy reserves by feeding is arrived at before they take their first flight. If flight did occur they would already be in an energy deficit situation. Indeed, of the hundreds of beetles used in our studies the smallest had an emergent weight of 4.05 g.

The beetles are constantly bombarded with external stimuli with information about mating, oviposition, flight, food etc., but the best predictor of their physiological needs are changes in the physiological system itself. It appears that emergence from the pupal chamber, flight, feeding, and death are controlled by complex internal regulatory mechanisms that are expressed symptomatically as a distinct ratio between a beetle's adult emergent weight and its weight just prior to the behaviours studied. These correlations represent a measure of the beetle's physiological age rather than its temporal age. The specific causes of these events are not known. The predictive nature of the correlations presented here may be useful in attractant trap studies and ecological studies in general. It is reasonable to assume that similar correlations exist in other insects, especially Coleoptera.

*Acknowledgements*—I thank the University of the South Pacific and the Fiji Government's Coconut Pests and Diseases Board for financial and material assistance. We also thank Isaac Kahn, Sadaquat Ali, Anil Kumar Narayan, and John McLean for technical assistance.

## REFERENCES

- Atkins M. D. (1966) Laboratory studies on the behaviour of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. *Can. Ent.* **98**, 953–991.
- Adkins M. D. (1969) Lipid loss with flight in the Douglas-fir beetle. *Can. Ent.* **101**, 164–165.
- Bedford G. O. (1980) Biology, ecology, and control of palm rhinoceros beetles. *A. Rev. Ent.* **25**, 309–339.
- Bligh E. G. and Dyer W. J. (1959) A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* **37**, 911–917.
- Catley A. (1969) The coconut rhinoceros beetle *Oryctes rhinoceros* (L.). *PANS* **15**, 18–30.
- Cherian M. C. and Anantanarayanan K. P. (1939) Studies on the coconut palm beetle (*Oryctes rhinoceros* L.) in south India. *Indian J. Agric. Sci.*, IX, Part III, 541–559.
- Clark A. M. and Rockstein M. (1964) Ageing in insects. In *The Physiology of Insecta*, Vol. I. (Ed. by Rockstein M.), pp. 227–281. Academic Press, New York.
- Cumber R. A. (1957) Ecological studies of the rhinoceros beetle, *Oryctes rhinoceros* (L.). In *Western Samoa. S. Pac. Com. Tech. paper No. 107*, pp. 32.
- Garlovsky D. F. and Zelazny B. (1971) External morphology of *Oryctes rhinoceros*. *S. Pac. Com. Inform. Doc. No. 25*, pp. 25.
- Graham K. (1959) Release by flight exercise of a chemotropic response from a photopositive domination in a scolytid beetle. *Nature* **184**, 283–284.
- Gressitt J. L. (1953) The coconut rhinoceros beetle (*Oryctes rhinoceros*) with special reference to the Palau Islands. *Bernice P. Bishop Museum Bulletin* **212**, pp. 157.
- Maddison P. A., Beroza M. and McGovern T. P. (1973) Ethyl chrysanthemumate as an attractant for the coconut rhinoceros beetle. *J. econ. Ent.* **66**, 591–592.
- Pringle J. W. S. (1974) Locomotion: Flight. In *The Physiology of Insecta*, Vol. III. (Ed. by Rockstein M.), pp. 433–500. Academic Press, New York.
- Schipper C. M. (1976) Mass rearing the coconut rhinoceros beetle, *Oryctes rhinoceros* L. (Scarab, Dynastinae). *Z. Ang. Ent.* **81**, 21–25.
- Southwood R. T. E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.* **37**, 171–214.
- Vander Meer R. K. and McLean J. A. (1975) Indirect methods of determining the emergent weight of *Oryctes rhinoceros* (L.). *Ann. ent. Soc. Am.* **68**, 867–868.
- Vander Meer R. K., Ghatak U. R., Alam S. K. and Chakkraborti P. C. (1979) ( $\pm$ )-Des-N-morphinan: a unique bridged hydrocarbon attractant for the rhinoceros beetle, *Oryctes rhinoceros*; and the development of an olfactometer. *Envir. Ent.* **8**, 6–10.
- Vander Meer R. K. and McGovern T. P. (1983) Structure-activity correlations for derivatives of siglure: Attractants for *Oryctes rhinoceros* L. (Coleoptera: Scarabaeidae). *J. econ. Ent.* **76**, 723–727.
- Zelazny B. and Neville A. C. (1972) Endocuticle layer formation controlled by non-circadian clocks in beetles. *J. Insect Physiol.* **18**, 1967–1979.
- Zelazny B. (1975) Behaviour of young rhinoceros beetles, *Oryctes rhinoceros*. *Entomologia exp. appl.* **18**, 135–140.