The Biology and Ecology of Lepidiota vogeli, *a Brown Pasture Scarab (Family Melolonthidae) of the Highlands of New Guinea.*

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ABSTRACT.

The biology and ecology of Lepidiota vogeli *are discussed. Spring rains initiate beetle mating flights. Larvae feed on grass roots. The life cycle lasts one year. Population controlling factors are discussed as such, and in relation to the perennial cycle and to distribution.*

INTRODUCTION.

SPECTACULAR flights of a brown Scarab beetle, *Lepidiota vogeli* Brenske (Family: Melolonthidae), are common at dusk in the Eastern Highlands of New Guinea, following rains in the months of September and October. The larvae of this beetle feed on the roots of various grasses and the damage is so severe in some years that areas of grass are killed. Damage has been serious on airstrips, and has caused concern on golf courses and lawns. Cultivated crops have also been attacked. With the development of cattle-raising this beetle could become a more serious pest and of major economic importance in pastures. With this in view, a study was made of the biology, ecology and control of this insect.

Control will be dealt with in a second paper. Other species were encountered and are included in the discussion.

The work included both field and detailed laboratory studies and the results are to be of general interest as well as being of particular value to entomologists.

HISTORY.

Szent-Ivany (1958) discussed *L. vogeli* at Goroka in 1953, when the runway of the Goroka airfield was severely damaged by the larvae of this beetle. Simon-Thomas (1962) recorded a *Lepidiota* 'near *vogeli*' attacking the roots of *Hevea* rubber and *Cacao* trees in Dutch New Guinea (now West Irian), and also the attack by *L. stigma* F. on roots of Cacao, Coffee, Coconuts, Peanuts, Maize and Bananas.

About 25 species of the genus *Lepidiota* have been described from the Papuan region but little if any further information has been recorded.

DISTRIBUTION OF SPECIES.

The distribution of *Lepidiota vogeli* and some related species is discussed with remarks on the distribution of a few other Scarabs of the family *Dynastidae*, whose larvae are also found in the ground.

(*a*) *Lepidiota vogeli* has been collected at Goroka (elevation 5,100 ft.) in the Asaro Valley, at Henganofi and Moke to the south, and at Aiyura (5,400 ft.) and Kainantu to the south-east of Goroka. Mass spring flights occur in these areas and in the Arona Valley (4,500 ft.) which is further to the east. Both the larvae and the beetles are traditional items in the diet of the native peoples, and are considered a delicacy.

In the west *L. vogeli* has been collected in the Wahgi Valley at Kerowagi and Minj, but mass flights do not occur to a marked extent. Records in the British Museum (personal communication) are from Port Moresby, Ogwarra, Ishurava and the Upper Waria River. These localities are at elevations varying down to sea level. Insects

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regarded as *L. vogeli* were collected at Dagua (near Wewak) in December, 1953, and at Port Moresby in January, 1956, and February, 1964. Specimens in the collection of the Department of Agriculture, Stock and Fisheries at Port Moresby have been collected in that area in the summer season. The sparse summer flights of the beetle at these centres are in marked contrast to the mass spring flights of the Eastern Highlands.

(*b*) A smaller species of *Lepidiota* flies in the Baiyer Valley (4,500 ft.) to the north of Mount Hagen. The spring flight is similar in form to that of *L. vogeli.*

(*c*) A third species of *Lepidiota* is common at Akuna village (4,800 ft.) and flies about a month later than *L. vogeli.* It has not been collected at Aiyura which is only a few miles away to the west and separated by a ridge of 6,000 ft. and upwards in height. One specimen was collected at Bulolo at 2,000 ft. The distribution of this species is presumed to extend to the south and east of Akuna in areas of regrowth forest at elevations below 5,000 ft.

(*d*) Smaller undetermined species of *Papuana* (family Dynastidae), are common throughout the Highlands.

(*e*) A large *Papuana* species similar to *P. woodlarkiana* is common in the Highlands at Minj and areas further west. It is also present on the Papuan fall to the south-west at Chuave (3,800 ft.) where limited collecting has not yielded any *Lepidiota* species.

(*f*) Some adults of a genus close to *Lepidiota* have been taken at Akuna and one at Aiyura; and at Erave (3,800 ft.), Mendi (5,500 ft.), and in the Bomai area. These latter areas are all on the southern fall of the Highlands.

STAGES IN LIFE HISTORY.[1]

1. *The Adult.*

(*a*) *Lepidiota vogeli*, a typical melolonthid beetle, is an inch in length; the colour is brown with a grey tinge which results from white conical scales in shallow pits on the pronotum and elytra. Long, fine, light-grey hairs cover the under parts of the thorax. Beetles from the Wahgi and from areas at lower elevations are generally less than an inch in length—slightly smaller than the average in the Eastern Highlands.

(*b*) The Baiyer species is much smaller than *L. vogeli*—three-fourths of an inch long—and paler brown in colour. The pits on the elytra are very fine and the grey tinge is not marked.

(*c*) The Akuna species of *Lepidiota* is very slightly larger than *L. vogeli.* It is darker in colour, and the greyish tinge is less pronounced. Also, the under side of the abdomen may be darker. These two species are difficult to recognize from individual specimens but differences are apparent when specimens are placed side by side.

(*d*) The *Papuana* species include black beetles common at light at most times of the year but more commonly following a fall of rain. *P. angusta* Arrow is the largest. The smaller species are unnamed but sizes of mated pairs suggest that there are three. All the above species of *Papuana* have a relatively smooth and rounded pronotum.

(*e*) The common species of *Papuana* in the Western and Southern Highlands has processes and marked sculpturing on the pronotum and appears close to *P. woodlarkiana.*

(*f*) The last group comprises clear-brown beetles considered to be close to *Lepidiota.* The sides of the elytra are almost parallel, giving the beetles a more oblong appearance.

2. *The Egg.*

Eggs of *L. vogeli* are white, smooth without being shiny, and slightly elongated in shape. Eggs are initially 2.0 x 2.4 mm. but increase in size as they age, probably due to absorption of moisture. (*Plate* I)

3. *The Larval Stages* (*Instars*).

The larvae of *L. vogeli* are typical 'White grubs' or 'Pasture grubs'. The general colour is creamy-white, with areas of the abdomen darker due to gut contents visible through the cuticle. The hard sclerotised areas of the head capsule are brown. The legs, along with two small shields behind the head and the line of spiracles (breathing holes) along each side of the body, are yellowish-brown.

The three pairs of legs near to the head are typical of larvae of the family.

There are three stages of larval development. The soft body expands at a relatively uniform rate in this type of larva but the hard (sclero-

[1] Where a species is not indicated the information refers to *L. vogeli.*

tised) parts grow in three 'steps'. The head, legs, dorsal shields and spiracles remain the same size until the larva sheds its old cuticle (skin). The new cuticle undergoes an increase in size before it hardens. The newly moulted larva has a relatively large head and long legs, and hairs are obvious. When ready to moult again, the body has become large in relation to these sclerotised parts.

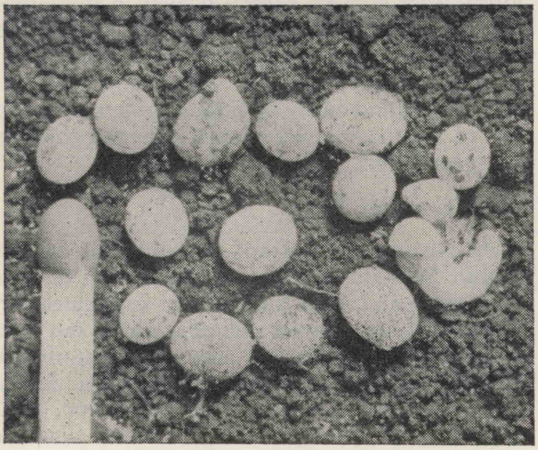

Plate I.—Eggs of ***Lepidiota vogeli.*** **The dark marks on the eggs are adhering fragments of soil. Size comparison—head of match. Size differences are correlated with age and probably are due to the absorption of moisture. Two eggs have hatched. (Photo. author)**

The average head capsule widths of *L. vogeli* larvae are—

First stage (from egg)			....	2.1 mm.
Second stage	....	....	....	3.7 mm.
Third stage	....	....	....	7.0 mm.

(range 6.8-7.4 mm.)

The fully grown larva reaches almost two inches in length. (*Plate* II)

Distinguishing Characters of Larvae of Various Beetles :—

Lepidiota larvae have a band of dark, inturned bristles on the bulbous area in front of the anus (venter). (*Figure* 1) The species from Baiyer has a shorter band which is broader in the central part than that of *L. vogeli* and so is rather elliptical in form. The head width measurements of the Baiyer species are also smaller.

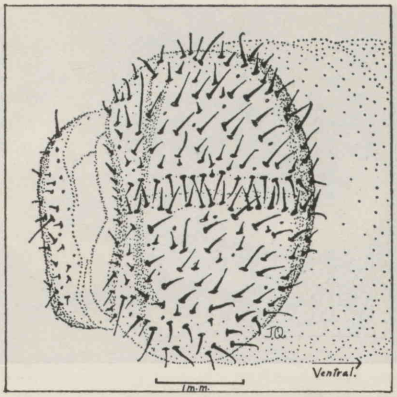

***Figure* 1.—Lower posterior view of last abdominal segment of a larva of *Lepidiota vogeli* showing bristle arrangement. The two central rows of inturned bristles are of diagnostic value in the identification of *Lepidiota* larvae. (Drawing : Jennifer Quinlan)**

Larvae presumed to be of *Papuana* species are sometimes common in the soil. They are more active than *L. vogeli.* The venter is covered with bristles arranged in a random manner. *Xylotrupes* (Elephant beetle) larvae are common in compost and sawdust heaps. They are usually so large as to be distinct but if small, may be grouped with *Papuana* larvae by the scattered bristles. (Rhinoceros beetles *Oryctes* spp. are *not* present in the Highlands.)

Another whitish larva resembling *Lepidiota* is commonly found in rotten sap wood. This is the larva of the large bronze-green Stag beetle *Lamprima adolphinae* Gestro. It is different from *Lepidiota* in a number of characters but the one most easily recognized is that of the outer margins of the mandibles being straight, and not curved as in *Lepidiota.*

4. *The Prepupa.*

Although not a separate instar this stage of *L. vogeli* is easily recognized. The larval skin becomes shrivelled and yellowish-brown, and the typical curled attitude becomes much less apparent. (*Plate* II) This general change in form is due to loss of moisture, excretion of the solid contents of the gut, and the development of the Fat-bodies.

5. *The Pupa.*

The pupa is pale-brown in colour, and about one and a quarter inches in length. It lies free in an earthen cell, there being no cocoon. Its

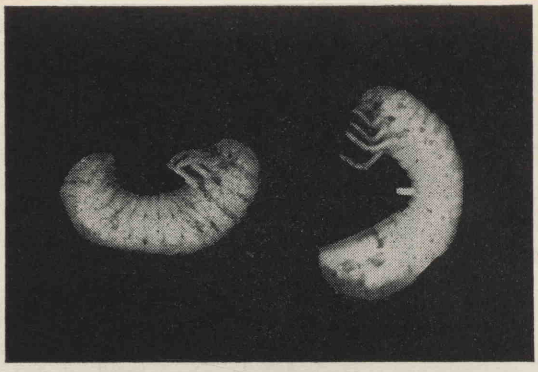

Plate II.—Fully grown larva of *L. vogeli* (right) carrying an attached egg of *Campsomeris formosa.* On the left is a prepupa. (Photo. author)

cuticle is shaped in the general form of the adult ; the developing head, legs and wings being easily discernible. (*Plate* III) With age, some parts begin to darken. The eyes are first followed by the legs and wings as development approaches the time when the pupal skin will be shed by the soft but fully developed adult.

HABITS AND ECOLOGY.

1. *The Adult.*

(*a*) *Habitat.*

Mass mating ' flights ' of *L. vogeli* are mostly restricted to areas where gardening, cultivation, or the establishment of new plants has interfered with the natural plant species. These areas include centres of settlement, old garden areas in various stages of early regrowth development, and banks of streams. Flights are also to be seen in the open grassland. Few beetles fly in the forest, except perhaps very close to the margin.

It is very probable that the mass flights of the insect, now regarded as a normal habit of this beetle, are a phenomenon associated with man's interference with its natural habitat in the Highlands. Some hundreds of years ago, before the present inhabitants became numerous and before gardened lands were of significant area, *L. vogeli* was most likely of little significance, being one of the many insect species dispersed through the grasslands.

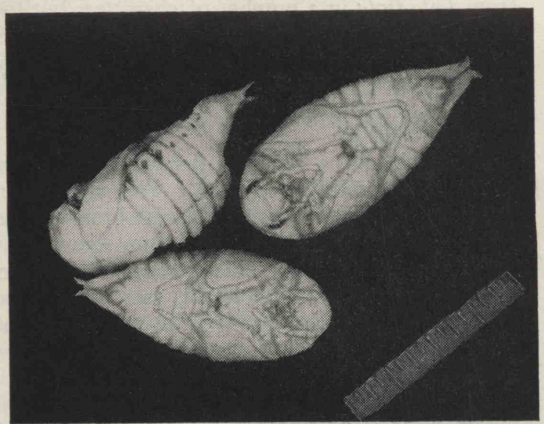

Plate III.—Pupae of *L. vogeli.* (The scale is 1 in. in length.) (Photo. author)

(*b*) *Season of Flight.*

At Aiyura, the first and largest flight follows within 28 hours of the first fall of rain of over 50 points and after the middle of September. Evidence from Goroka indicates that it can be a week or so earlier in that area ; temperatures are slightly higher. Rainfall records from Aiyura for the relevant periods of the years 1960, 1962 and 1963 are given in *Table* 1. These illustrate the relationship between rainfall and flights of beetles. (*Figure* 3)

In the year 1960, the first flight at Aiyura did not occur until the first day of October, although a storm at Kainantu some two weeks earlier resulted in a mass flight in that area, only six miles from Aiyura. Falls of rain of 100 points and 50 points in early September of 1962 and 1963, respectively, did not result in general flights.

The first general flight of the year has been found to be followed by flights on following evenings. Numbers fall off abruptly if no further rain falls, but remain fairly high for three or four evenings if wet conditions continue. Marked flights can be expected until late October, particularly if falls of rain remain low for intervals of ten days or so. In 1962 there were flights at this time and one sparse final flight on 21st November, but this was unusually late.

Falls of rain earlier in the season occasionally bring a response from a few beetles, e.g., a small flight on the 22nd August, 1962, following 70 points of rain.

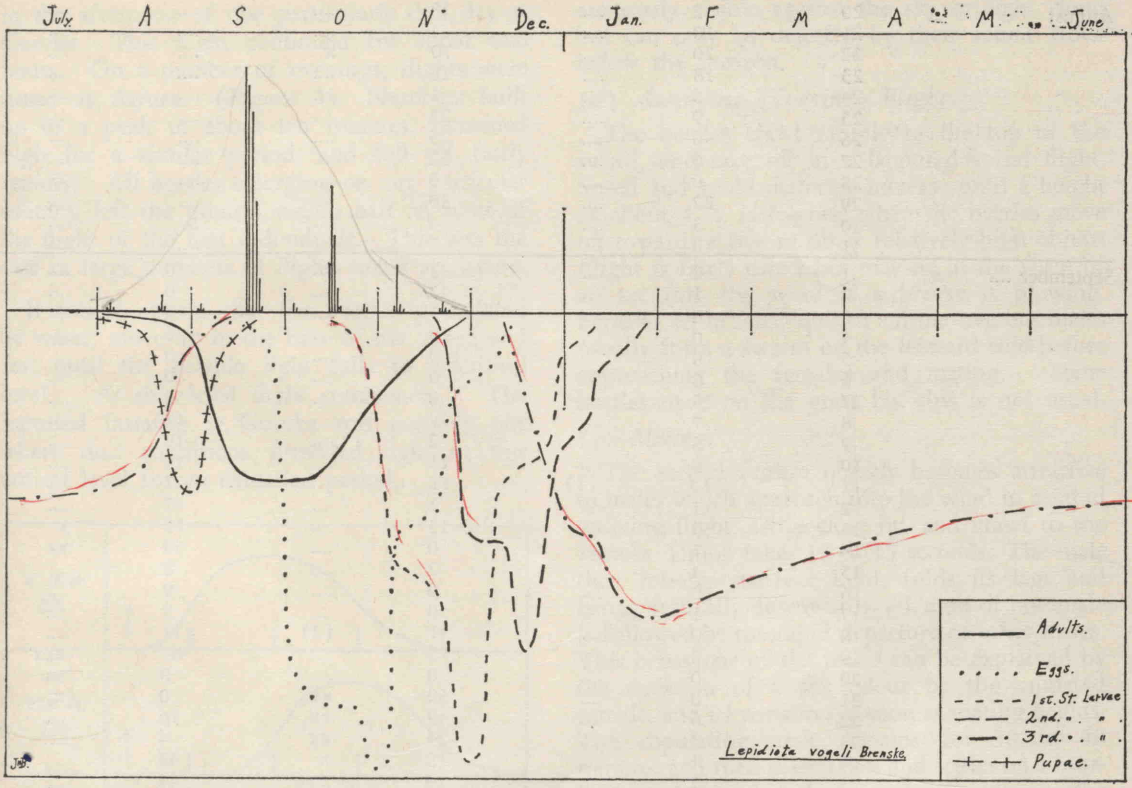

Figure 3.—Relative distribution of the various stages of *Lepidiota vogeli* over a year. The vertical lines represent flights of beetles, and the curves relate to the below-ground stages. Of note are—(*a*) Reduction in numbers from the first to the second stage larvae. (*b*) The long life of the third stage larvae. (*c*) The second rise in egg numbers due to a flight of beetles a month after the first flight.

Under laboratory conditions where 7 lb. tins of soil were used, each with a clump of grass growing in it, emergence took place as early as June. Routine watering tended to be irregular, and the soil in the pots was inspected at intervals to check on development. Of the factors which were abnormal, perhaps the most important was the laboratory temperature. This was up to 15 degrees Fahrenheit above the day screen temperature, and about five degrees higher at night. Soil temperatures in the field are relatively uniform. Thus, larvae in pots were subjected to a greater fluctuation in temperatures at levels well above those of the soil.

In the field the general mating flights show relations, firstly to the time of the year, and secondly to rainfall. From observation it seems highly likely that development is controlled by a cumulative factor of soil temperature, and further, that once the beetle has shed the pupal skin and hardened it becomes responsive to a factor related to rainfall. The response, to dig upwards to the base of the sward or close to the surface of the soil, could be to flooding of the pupal chamber. The soils are generally well drained and this could explain the response to individual falls of rain of over 50 points.

(*c*) *Time of Diurnal Emergence.*

Emergence from the ground is fairly closely related to waning light intensity. On dull evenings emergence is earlier than when conditions are brighter, as when there is a bright glow from light cloud in the west. Szent-Ivany (personal communication) reported an isolated case where the adults were to be seen as early as four o'clock

Table 1.—Rainfall registration in points and flight-level of *L. voglei* at Aiyura in three seasons. Flight ratings indicate *generally* the numbers of beetles as 10's (x), 100's (xx), or 1,000's (xxx).

Year.		1960.		1962.		1963.	
Month.	Date.	Rainfall.	Flight.	Rainfall.	Flight.	Rainfall.	Flight.
August	20	2	....	18	....	....	....
	21	10	....	1	....	....	....
	22	20	....	70	x	....	....
	23	18	....	16	....	....	....
	24	5	....	1	....	....	....
	25	9	....	22	....	....	....
	26	6	....	25	....	....	....
	27	6	....	22	....	....	....
	28	0	....	3	....	....	....
	29	22	....	30	....	....	....
	30	3	....	4	....	....	....
	31	0	....	7	....	....	....
September	1	0	....	23	....	0	....
	2	1	....	42	....	0	....
	3	0	....	3	....	4	....
	4	0	....	90	....	26	....
	5	8	....	100	....	0	....
	6	0	....	0	....	0	....
	7	23	....	8	....	50	....
	8	7	....	9	....	11	....
	9	8	....	2	....	10	....
	10	8	....	11	....	19	....
	11	10	(1)	11	....	21	....
	12	11	....	1	....	47	....
	13	35	....	13	....	16	x
	14	1	....	0	....	54	xx
	15	4	....	2	....	8	....
	16	10	....	6	....	9	....
	17	1	....	0	....	9	....
	18	0	....	1	(2)	11	....
	19	0	....	2	....	67	xxx
	20	0	....	0	....	8	xx
	21	0	....	60	xxx	0	x
	22	6	....	49	xx	16	....
	23	3	....	24	xx	4	....
	24	1	....	9	x	44	....
	25	2	....	13	....	64	....
	26	0	....	1	....	46	....
	27	1	....	32	....	0	....
	28	2	....	95	x	4	....
	29	1	....	23	....	33	....
	30	0	....	69	xx	25	....
October	1	56	xxx	113	xx	....	....
	2	120	xx	2	x	....	....
	3	14	xx	9	....	....	....
	4	0	x	23	....	....	....
	5	17	....	0	....	....	....
	6	3	....	6	....	....	....
	7	140	....	0	....	....	....
	8	37	....	5	....	....	....
	9	2	....	12	....	....	....
	10	0	....	2	....	....	....
	11	2	....	0	....	....	....
	12	23	....	15	....	....	....
	13	39	....	43	x	....	....
	14	56	....	13	x	....	....
	15	55	....	14	x	....	....
	16	23	....	28	x	....	....
	17	25	....	39	x	....	....
	18	10	....	37	....	....	....
	19	7	....	1	....	....	....
	20	4	....	3	....	....	....
	21	46	....	21	....	....	....
	22	0	....	5	....	....	....
	23	106	....	2	....	....	....
	24	42	....	1	....	....	....
	25	35	....	50	(3)	....	....

(1) A heavy storm at about this time in the Kainantu area resulted in a flight in that area, but rain at Aiyura was insufficient to initiate a marked flight.

(2) Beetles were dug up from the ground in a sample area.

(3) Small flights continued in early November and the last one was an isolated instance on the 21st of that month.

Note: Flights resulting from rain after 9 a.m. (time of measurement of rainfall) are recorded for the in the afternoon of one particularly dull day at Goroka. This flight continued for about two hours. On a number of evenings, flights were timed at Aiyura. (*Figure* 2) Numbers built up to a peak in about ten minutes, remained high for a similar period, and fell off fairly rapidly. All beetles emerging on any particular evening left the ground within half an hour of the flight of the first individuals. This was the case in large numbers of flights noted at Aiyura.

It would appear that the beetles, stimulated by water, move up to the base of the sward and rest until the outside light falls to a critical level. At this level flight commences. The reported instance at Goroka was possibly one where dull conditions provided light at this critical level for an extended period.

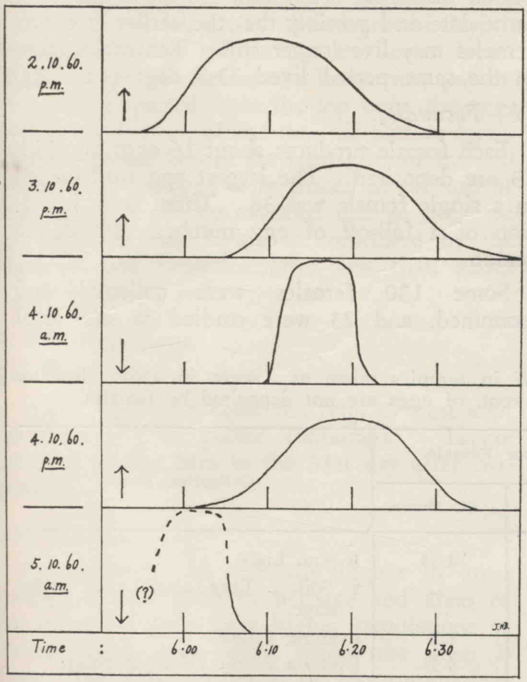

Figure 2.—Graphs of relative numbers of ***Lepidiota vogeli*** in relation to time, flying at Aiyura. The direction of flight, whether from or to the ground, is indicated by the arrows, and the time of day is indicated along with the date.

Figure 2 is drawn from progressive observations during a number of flight periods. During the later stages of the evening flights the beetles are easily visible against the sky or light cloud but can only be detected by their sound when below the horizon.

(*d*) *Ascending* (*Evening*) *Flight.*

The beetles crawl rapidly to the top of the sward, and take off in a laboured spiral flight. Speed and spiral diameter increase until a height of about 4 ft. is reached when the beetles move off towards a tree or other relatively high object. Flight is fairly direct but may be in the form of an arc into the wind if a breeze is blowing. Females settle fairly quickly on the tree but males usually form a swarm on the leeward side before approaching the females and mating. Some beetles mate on the grass but this is not usual.

(*e*) *Mating.*

The settled female quickly becomes attractive to males which approach into the wind in a rapid weaving flight, settle close by, and crawl to the female. Union takes 10 to 15 seconds. The male then releases its foot hold, folds its legs and hangs vertically downwards. Union of one male is followed by the rapid departure of other males. This behaviour of the males can be explained by the emission of a sex odour by the unmated female, and its cessation as soon as mating begins. The copulating male remains for 30 to 40 minutes and then disengages and settles on a near-by twig, remaining there until morning. At the time the males are settling back onto the twigs a few beetles may be taken at light and it is assumed that some beetles fall off the trees and fly.

(*f*) *Descending* (*Morning*) *Flight.*

All beetles move back to the ground in the early morning. This is particularly dramatic, again probably stimulated by a level of light intensity. The whole movement takes less than 20 minutes and the majority move in a five to ten minute period. Two observations are recorded in *Figure* 2.

Many beetles descend directly and enter the ground close to the tree on which they have rested overnight. There is also a general dispersal movement, probably mainly females. They fly to within a few feet of the ground and then move off for varying distances up to several hundred yards. The final stage of flight is close to the sward ; the beetles then land and burrow immediately.

(*g*) *Number of Flights of Individual Adults.*

Evidence available indicates that most individuals fly only once but this is difficult to prove. Samples of females collected from flights a few days apart commenced egg laying uniformly after the elapse of a fixed period from the date of collection. If some females had flown previously this uniformity would not be expected, some females commencing to lay earlier than the rest.

The habit of the adult is fairly consistent. Flight ceases with the onset of darkness. However, beetles can be taken at light an hour or so later, or coincident with a heavy fall of rain. At the former time the males are settling on the trees after mating, as mentioned above. Such numbers have been relatively small when large numbers of beetles have been present on trees in close proximity to a light.

On one occasion 300 beetles from a morning flight were marked and released. They were not present in following flights and there was one doubtful record of a single individual seen dead on the ground some three weeks later, and at a distance of about 10 chains from the point of liberation.

(*h*) *Feeding.*

Some hundreds of adults have been dissected to check on sex and egg numbers. In all cases the gut was empty. Damage to trees has not been observed. Emerging beetles have large 'fat-bodies' and it is concluded that they do not need to feed, all feeding taking place in the larval stage and sufficient reserves being stored to mature the eggs.

(*i*) *Sex Ratio.*

Small samples have not varied significantly from a 1 : 1 sex ratio. (*Table* 2)

(*j*) *Longevity.*

From data available it can be stated that males and females have a similar longevity of about 30 days.

Five females collected on the 22nd September, 1962, died after 38.5 days (s.e. 5.5) and 16 females collected on the 27th September, 1962, died in 26.1 days (s.e. 2.7). This suggests that females emerging on different days during a period following heavy rain die off at about the same date and possibly that the earlier emerging females may live longer still. Ten males taken in the same period lived 33.3 days (s.e. 3.2).

(*k*) *Fecundity.*

Each female produces about 16 eggs of which 13 are deposited. The largest egg load carried in a single female was 38. There is an indication of a fall-off of egg numbers late in the season.

Some 130 females were collected and examined, and 23 were studied in individual

Table 2.—**Counts of males and females of** ***Lepidiota vogeli*** **in samples taken at Aiyura in 1962. Females were dissected and eggs counted. About 20 per cent. of eggs are not deposited by females.**

Date.	Sample.		Eggs per Female.		Collection Data.
	Males.	Females.	Mean.	St. Error.	
21.8.1962	5	5	12.5	4.25	8 p.m. Light.
18.9.1962	3	17	....	....	x Soil. Eggs small ; Fat bodies large.
22.9.1962	32	29	15.8	1.2	Evening Flight.
22.9.1962	....	5	19.8	4.5	Evening Flight (Held in pots).
24.9.1962	29	30	15.0	1.3	Evening Flight.
27.9.1962	....	16	10.4	1.6	Evening Flight.
1.10.1962	14	4	9.5	4.5	Morning Flight.
18.10.1962	1	6	17.8	7.0	8 p.m. Light.
22.10.1962	10	17	....	....	U.V. Light (Eggs not examined).
3.11.1962	2	6	8.1	2.7	Evening Flight.
4.11.1962	15	15	7.0	1.8	Morning Flight.
21.11.1962	4	6	....	....	Evening Flight.

pots of soil. Results are given in *Table* 2. Five females taken on the 22nd September, 1962, carried 19.8 eggs (s.e. 4.5) per female, of which 90 per cent. were deposited. Sixteen females of 27th September, 1962, carried a mean of 10.4 eggs (s.e. 1.6) of which 80 per cent. were deposited.

(*l*) *Time of Egg Deposition.*

Females in pots in the laboratory deposited 60 per cent. of all eggs on the 8th to the 10th day after mating, and a further 35 per cent. in the next eight days. Of the 23 females observed only one deposited eggs after the 32nd day.

(*m*) *Egg laying.*

Eggs are deposited singly about three-quarters of an inch apart in cells about one-third of an inch in diameter in a wandering column of compressed soil. Eggs are found at depths of 4 to 7 in. In the laboratory the depth of laying was controlled by compacting the lower layers of soil in the pot before the beetle was put in. In a pot compacted from the top only, the eggs were at the bottom of the tin. If bottom layers were compacted before the remainder of the soil was put in, the eggs were placed at the top of this layer. It can be assumed that in the field the depth of egg laying is controlled by the depth of any impacted layer less than about 8 in. deep in the soil.

2. ***The Egg Stage.***

(*a*) *Duration.*

Eighty eggs from about ten females were kept on moist soil in plastic containers. Larvae emerged on the 28th to the 31st day after oviposition.

(*b*) *Distribution.*

Egg numbers are generally higher in areas covered by low grass or herbage and areas of cut or grazed grass have higher populations of larvae initially than areas where the grass is long. The grass species is of less importance. Areas of grass seem to be preferred to weeds or other plants. Development of larval populations in cultivated areas (Peanuts and Strawberries) has been noted but may have resulted from eggs deposited before the crops were planted. High populations also develop in certain areas of *Themeda* and other grassland species where the cover is tall.

3. ***The Larval Stage.***

(*a*) *Seasonal Occurrence.*

Larvae can be found six weeks after the first flights of females. The greatest density is reached in November, when most of the eggs have hatched and larval mortality is still low. These are predominantly first stage larvae, the second stage making their appearance in December. The first and second stages are relatively short and by January, the majority of larvae are large and in the third stage. These remain for about six months before becoming comatose as prepupae. (*Figure* 3 and *Plate* II)

(*b*) *Distribution.*

This is determined by the effect of the dominant plant of the area being super-imposed on the distribution pattern of the eggs. Few larvae from eggs deposited in areas of Kikuyu grass survive beyond the first stage and practically none beyond the second.

In areas of suitable food species the distribution is patchy in any one year. At Goroka in 1960, an area in front of the Department of Agriculture, Stock and Fisheries Office was very severely attacked. In the following year, the population was very low in this area while a lawn some 200 yd. distant carried a heavy population of larvae. Reasons for this type of distribution are not known but a heavy attack in one year results in death of grass, weed development, or young grass with relatively sparse roots. These types of cover are incapable of carrying a heavy population of larvae, but other factors are thought to be involved.

(*c*) *Feeding.*

The larva is mainly a grass root feeder although roots of other types of plants can be attacked. Young larvae are found at depths of 4 to 7 in. and apparently feed at random in this stratum. High populations of second or early third stage larvae are usually found closer to the surface. It is thought that depletion of the supply of roots at lower levels is followed by a progressive upward movement. Large third stage larvae may be found in the top 2 in. of soil by the end of January, if populations are high. Since the supply of roots is related to the age of the sward and the plant species, these two factors determine the amount of food available, and so the depth of feeding in the later stage.

(*d*) *Host Plants.*

Attack has been noted on a number of species of grasses at Aiyura and Goroka. 'Thurston Grass', Blue Couch *Digitaria didactyla*, and Carpet Grass *Axonopus compressus*, are all severely attacked. Blue Couch can withstand heavier populations than the other two. Heavy populations have not been found in Common Couch *Cynodon dactylon*. Kikuyu Grass *Pennisetum clandestinum* is notably unsatisfactory as a host plant. The Strawberry is readily attacked, as is the Peanut, but this may result in part from residual populations in the soil prior to planting.

Kangaroo Grass *Themeda australis*, is a satisfactory host and is probably the natural food plant.

(*e*) *Effect on the Host Plant.*

Since the population varies through the season the January population has been taken as a useful measure. The effect on the grass depends very much on the age and vigour of the stand of grass. A vigorous, well developed sward of Blue Couch requires at least four larvae to the square foot to cause death. Three larvae per square foot will kill out Thurston Grass and Carpet Grass. The effect on Kangaroo Grass, being tussocky in growth, is difficult to estimate. In one case a stool about a foot across had ten larvae under it. Nearly all the roots had been cut off but there was a vigorous development of new roots from the crown and this particular stool survived.

Larvae may be present in such numbers that the grass runners are destroyed, but if feeding does not reach within about half an inch of the surface of the soil, new roots are produced and the grass will survive. It is quite common for the roots to be cut to such an extent that the grass forms a loose carpet over the churned up soil beneath. Such areas will survive (if not disturbed) except in the occasional years when rains fail in late summer, or conditions in May and June are particularly dry and sunny. Under such circumstances runners dry out in patches. When rain falls in the following spring weeds commonly take over.

(*f*) *Movement.*

Larval population counts were made at Goroka in January, 1961, in an area where patches of grass had been killed. In the bare areas up to ten larvae per square foot were present. On the margins of the green areas up to 16 were present. Averages of 6 and 7.5 respectively for these areas were not significantly different due to gross variation, but it can be safely assumed that an area with 16 larvae to the square foot could not have been supporting this population for a long period of time. It seems that they had moved into the area. It is concluded that there is some outward movement from heavily infested areas. This would result from random burrowing of hungry larvae, some individuals reaching the green margin in the process. Samples in green areas a few yards from their margins averaged only one per square foot, which was significantly lower than the above populations.

4. *The Prepupa and Pupa.*

Fully fed larvae move downwards in May and June, and excavate cells at depths of 5 to 9 in. The depth is less where the subsoil is hard or stony. The prepupal period lasts a few weeks, when the last larval skin is shed to reveal the pupa. The pupal stage is relatively short, also lasting less than four weeks.

The adult is ready to leave the cell in about two weeks after shedding the pupal skin but the time of movement from the ground depends on outside conditions. All data on these final stages are based on field observations.

NATURAL CONTROL (MORTALITY) FACTORS.

1. *Survival of Adults.*

Adults have been found dead in the pupal cell. Some have been affected with the Green Muscardine Fungus, *Metarrhizium anisopliae* while others have died for unknown reasons.

Adults are eaten by man, being collected in large numbers at the time of the main flights. This has been described by Brass (1964).

A large species of spider takes a toll, the beetles being entangled in the webs on the taller trees.

2. *Survival of Eggs.*

Fungal attack was noted in the laboratory when eggs were crowded in covered containers of damp soil. All clean eggs hatched and it is considered that field emergence of larvae would be close to 100 per cent. No predators are known.

3. *Survival of Larvae.*

(*a*) *Host Plants.*

The importance of food plants has been discussed previously. The species of plant available has a marked effect on the survival of young larvae. The stage of development of the sward may regulate the nutritional level of larvae.

(*b*) *Parasites.*

Two larval parasites are known ; one is a *Scoliid* Wasp and the other an unidentified mite.

I. *Campsomeris formosa* Guer. Family : *Scoliidae* : Szent-Ivany (1958) recorded two species of *Campsomeris* wasps believed to be parasitic on *Lepidiota vogeli.* An early Departmental report describes *C. formosa* but not *C. tasmaniensis* Sauss. attacking larvae caged with these two species of wasps.

(The *Campsomeris* genus of wasps belongs to the Family *Scoliidae*, the Hairy Flower Wasps. They are bright yellow and black in colour and the above species are larger than a honey bee. They commonly feed on nectar in *Eucalyptus* and *Poincettia* flowers on warm sunny days. The males are less robust and have long antennae. They may be seen on flowers or numbers may be seen flying back and forth a few inches above lawns. The two species are very similar. The related *Scolia* species are black, but of very similar form and habits and are parasitic in larvae of at least one *Dynastid* Beetle of the genus *Papuana.*)

On one occasion, at Aiyura in August, parasitised larvae and one parasitised pupa of *L. vogeli* were dug up along with a female wasp. This female *C. formosa* parasitised further larvae in the laboratory. The wasp eggs hatched but the larvae did not survive. The egg was placed ventrally on the larvae, and was dorsal on the pupa observed. (*Plate* II) The wasp stung the host and paralysed it prior to laying the egg.

Collections of *C. formosa* have been made at Baiyer River, Minj, Kerowagi, Goroka, Kainantu, Aiyura and Akuna, in the months of August to October, and January to April. Collections were limited but suggest two generations per year. The first, in March, coincides with the occurrence of well developed third stage beetle larvae. The September (second) generation emerges when only small numbers of late host larvae and pupae are present. This would limit the numbers of wasps, and hence the overall effectiveness of the parasite. In general *C. formosa* cannot be regarded as a very satisfactory parasite in the Highlands areas.

One female of *C. tasmaniensis* was taken at Aiyura in September, and Szent-Ivany and R. S. Carne have collected this species at Goroka in October.

II. *Mites* :Examination of larvae encountered in plots at Goroka in early January, 1961, revealed heavy populations of a mite of pale-amber colour, and large enough to be seen with the naked eye.

Counts ranged from 4 to 260 per larva on 43 larvae. The distribution of the mites is in a marked pattern. When few are present they are concentrated on the basal segments of the second and third legs. With larger numbers they may be seen on the first leg, lower down the second and third legs, and in the body folds. With very high populations they are also present in numbers in body folds, on the mouth parts, and around the spiracles.

Mites were more numerous where larvae were plentiful. Twelve large larvae from an area with about four per square foot had 152 mites (s.e. 18) per larva. Fourteen larvae from where the density was about two per square foot had 77 (s.e. 12.5) per larva. Five larvae from an area of grass not showing damage with 1.1/square foot had 38 mites (s.e. 32) per larva. Another area averaged 105 mites per larva. There was a trend in ' mites per larva ' related to the density of larvae. On the larvae examined there was an increase of about 40 mites per larva for each additional larva per square foot.

This trend in mite population may be related with mites breeding on varying larval populations in the previous year ; or with movement of mites from larvae dying-off in a high population of larvae, and concentrating on the remaining larvae.

Mites from larvae which died in pots in the laboratory moved actively through the soil and evidently attached themselves to live larvae. Free mites are few in the soil, particularly in the vicinity of live larvae.

Twenty-five larvae were graded according to mite load and placed in pots with established grass and examined two months (March), and six months later. At the first examination most larvae were active but were yellowish in colour, suggestive of approaching the prepupal stage. This development was abnormally early and may have been due to laboratory temperatures. Some beetles emerged before the second examination. In July, some dead beetles were present along with decomposed pupae and empty skins of dead larvae. Larvae infested with over 200 mites did not develop. There was an indication that large larvae with less than 80 mites had a greater chance of full development than those with more than about 80.

Effects on small larvae have not been investigated but in areas of heavy infestation the loss of hosts by death or emergence results in a high population of free mites. When larvae hatched from eggs deposited by the emerged beetles they would become infested. Such infestation has been observed in the field. Populations would also increase on late-emerging insects, tending to reduce their numbers.

(*c*) *Predators*.

Larvae are destroyed by man, pigs, bandicoots, birds of prey and fowls.

I. At Aiyura areas of grassland are dug up in April and May, by the women who collect the larvae for food.

II. 'Rooting' by pigs is common in re-growth and grassland areas in the general vicinity of villages and hamlets. In some years the animals concentrate on particular tracts of grassland. At Henganofi, in 1961, an area of several acres on the side of the top of a ridge about 600 ft. high was denuded in this way. Only the few scattered hard shrubs remained. A much smaller area on a ridge near the Tairora Creek on the Aiyura-Kainantu road was similarly damaged by pigs in the following year. Pigs find larvae in their usual rooting in grassland and it is thought that some areas were particularly attractive because of the presence of high populations of larvae. The activity of pigs results in uneven ground which holds surface water and contributes to the landslide development common in the Kainantu area ; the characteristic conchoidal form of these slips influencing the topography of the grassland areas.

III. Bandicoot foraging holes are occasionally seen in grub-infested areas where they apparently feed on some larvae.

IV. A Fork Tailed Kite *Milvus migrans*, shot down at Aiyura, contained 11 large *L. vogeli* larvae. This large brown hawk, common in the Highlands at certain times of the year, follows fires and frequents areas of cultivated land. On the occasion at Aiyura there had been no ploughing within eight miles of the collection site and the source of the larvae is not known.

V. Fowls readily scratch out larvae in severely damaged lawns, removing any grass remnants in the process.

(*d*) *Diseases*.

1. The Green Muscardine Fungus, *Metarrhizum anisopliae*, has been identified from the *Lepidiota* at Baiyer River and has been seen on large larvae at Aiyura. Incidence appears to be low. The fungus appears as a white felted mass over the insect and when spores are produced they are white, turning to a dark olive green in a few days. The spores are clumped and come away in loose irregular masses.

2. When dug from the soil, larvae may appear normal but turn bluish-black in a few hours. This has been regarded as due to physical injury or the effects of the sun. Up to 20 per cent. of larvae have been affected. However, work on the Rhinoceros beetle *Oryctes Rhinoceros L.* sp. suggests that this could be due to a virus disease.

(*e*) *Cannibalism*.

This occurs if larvae are confined in containers or small pots. Only two larvae consistently survived if more were placed in a breeding pot. This corresponded to eight larvae per square foot, and suggests that populations will reduce automatically to a maximum of about eight larvae per square foot in the field. Averages over an area would be below this level and field populations with a mean of more than six large larvae per square foot are not usual or to be expected.

(*f*) *Starvation*.

High populations have been observed early in the year in areas where the food supply has been eaten out. The larvae are probably reduced by cannibalism and movement. Remaining larvae may pupate and produce underfed beetles which deposit reduced numbers of eggs.

4. *Climate.*

The climate of the New Guinea Highlands is mild. In summer, cloud and rain are normal and hot dry weather is not unusual. In winter, day temperatures are relatively high. Night temperatures do not reach freezing point in areas where *L. vogeli* is common.

The only marked effect of weather is on the timing of the first spring flights.

General effects of climatic conditions on populations have not been observed.

POPULATION CHANGES.

1. *Annual Cycle.*

(*a*) *Changes.*

The relative abundance of the various stages is illustrated in *Figure* 3 and has been discussed previously in the sections dealing with each stage. The change in numbers may be made clearer by considering the development of a population from eight females. One hundred and four eggs will be produced. One hundred larvae are to be expected and 25 of these will survive to become prepupae. A further five insects die in the prepupal and pupal stages, leaving 20 to develop into beetles capable of mating. Of these, four are lost and in the final 16 half are males and half are females. The original number—eight females—remains and the population is stable.

(*b*) *Determining Factors.*

In the field this balance occurs but rarely. Abundance changes as a result of the varying effects of the mortality agents previously listed. Observations indicate that the most important of these operate against the larval stages.

The total area of suitable food plants determines initially the number of first-stage larvae surviving. In areas where larval density is high the quality (age and vigour) of the food plant sward becomes important, and both cannibalism and starvation may become operative.

Predators are more active when numbers of the insect are high, both against larvae and adults, and disease incidence may rise. Mites are the most obvious of the parasites and, although their effect on large larvae is limited, they may be responsible for the death of small larvae. The soil of areas carrying an abundance of grass-grubs would be provided with such a mite population in the following season.

2. *Perennial Cycle.*

(*a*) *Changes.*

Reliable information is not available on flights before 1949. Beetles were reported in that year and were probably from the last of a series of flights over a few years. There was a peak in 1952, 1953 and 1954, when the Goroka Airfield was seriously damaged. In 1960, 1961 and 1962, beetles were again very abundant. These records suggest a cycle of about seven years. If this is a fact a build up can again be anticipated about 1966, with a peak in the years following. →1973→1980.

Peaks are spread over three or four years. This results from a patchy distribution of larvae. Areas of a few square chains may carry peak populations in one year, while adjacent areas may be affected one, or two years later. In many parts of an area larvae may be present for the whole period without the development of acute affects on the grass.

(*b*) *Determining Factors.*

Where the sward is severely damaged weeds tend to take over and larvae in the following year are few due to reduced egg deposition or larval mortality. In areas of chronic infestation development of mite populations may be the operative factor.

In each case the factors leading to the increase of mortality are governed by the levels of the populations in previous years. There can be no new development of high insect numbers until these factors are eliminated—grass replaces weeds, and mites (or other agents) are rendered inactive by the absence of the host.

3. *Populations in Lowland Areas.*

(*a*) *Incidence.*

Mass flights have been neither observed nor reported. Beetles have been collected from late December, to early February.

The populations of the lowlands may be 'normal', and the mass flights of the Highlands an 'abnormal' development, the food supply of the area being the basic cause.

(*b*) *Possible Factors.*

Of the agents active in the Highlands the *Campsomeris* wasps offer the best possibility of explaining the occurrence in the lowlands. Adaptation to conditions at lower altitudes could result in the apparent ineffectiveness of these parasites in the Highlands.

Alternatively, two ecological forms or even sub-species of *L. vogeli* may be present.

(Received January, 1965)

ACKNOWLEDGEMENTS.

Assistance was received from members of the staff at the Highlands Agricultural Experiment Station, Aiyura, and officers of the D.A.S.F. staff at Goroka and Baiyer River. Dr. A. R. Brimblecombe, Miss K. Barnard, Mr. N. Heather and Mr. W. Yarrow of the Entomology Branch, Department of Primary Industries, Brisbane, and Dr. T. E. Woodward of the University of Queensland, have made most valuable comments on the earlier draft of this paper. The author is most grateful for this help, and also to Mrs. Jennifer Quinlan, of Aiyura, for the drawing of *Figure* 1.

IDENTIFICATION.

Campsomeris tasmaniensis, C. formosa, and *Scolia* spp. were identified by scientists of the Commonwealth Institute of Entomology and the British Museum (London).

Lepidiota vogeli, *Lepidiota* sp. (Baiyer River), *Papuana angusta*, *Papuana* spp., *Lamprima adolphinae*, and *Xylotrupes* sp. were identified by Dr. E. B. Britton of the British Museum (Natural History) now of Division of Entomology, C.S.I.R.O., Canberra, and Mr. R. W. Pope of the Commonwealth Institute of Entomology, now of the Department of Entomology, British Museum (Natural History), London. The author gratefully acknowledges the efforts and interest of these specialists.

REFERENCES.

BRASS, L. J. (1964). Results of the Archbold Expeditions. Number 86. Summary of the Sixth Archbold Expedition to New Guinea (1959). *Bull. Amer. Mus. nat. Hist.* 127, article four : 145-216.

SIMON THOMAS, R. T. (1962). Checklist of pests on some crops in West Irian. *Bull. Dept. Economic Affairs : Agricultural Series,* 1962. Number 1 : 1-126, figures 1-73. (In Dutch.)

SZENT-IVANY, J. J. H. (1958). Insects of cultivated plants in the Central Highlands of New Guinea. *Proc. tenth internat. Congr. Entom. Volume* 3, *Agricultural Entomology, General Papers* : 427-437 : Montreal, Canada, 1956 (1958).