Observations on the Ecology and Behaviour of the Huhu Beetle, *Prionoplus reticularis* White. (Col. Ceramb.)

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Abstract

THE phenology and pattern of flight activity is recorded of the non-feeding nocturnal cerambycid *Prionoplus reticularis* White, based on data from emergence cages, light trapping and direct observation. The effect of some environmental factors on light trap captures is discussed. Display, combat, copulation and oviposition behaviour are described. Predators of *Prionoplus* in the Riverhead area are recorded.

INTRODUCTION

Prionoplus reticularis is a widespread and familiar member of the New Zealand coleopteran fauna. It occurs throughout the main islands but there appears to be no record of its occurrence on outlying islands. An endemic monotypic genus, it was before European settlement associated with podocarp and kauri forest, but with the introduction and subsequent wide planting of exotic conifers it has been quick to extend its range wherever the new hosts appeared (Edwards (1959), who omits the first record of *Prionoplus* adopting *Pinus radiata,* that of Walker (1904)). It is now a characteristic member of the exotic forest where dead wood greater than c 7–10 cm in diameter is to be found.

Despite its prominence, little has been written of the biology of the adult beetle. It is the purpose of this paper to record observations made during the flight seasons of 1953–4 and 1954–5 at the Riverhead State Forest, Auckland, where *Prionoplus* occurs in thinnings of *Pinus radiata.*

GENERAL

The adult beetle flies nocturnally throughout the warmer and drier part of the year, between late spring and early autumn. Its phototropism was first noted by Hudson (1892) thus: " It is greatly attracted by light and this propensity frequently draws it on summer evenings to invade ladies' drawing rooms when its sudden and noisy arrival is apt to cause needless consternation among the inmates." Neither male nor female feed: their adult life span in the field is about two weeks. The midgut which in late larvae is a large tube reaching a length of 8–10 cm, is reduced in the adult to a vestige of degenerate tissue linking fore- and mid-guts (Fig. 1). The fore-gut undergoes the converse transformation: the short tube of the larva extends to become a large air-filled sac extending into the abdomen, dilating as the initially massive fat body regresses, and in the female as eggs are laid. The hind gut remains relatively unchanged through metamorphosis but largely loses its heavy muscular layer in the adult. The cryptonephric malpighian tubules remain functional in the adult, retaining their role in water conservation. *Prionoplus* will take water in captivity but it is not known to what extent the beetle drinks in nature.

Gametogenesis is completed early in the pupal phase, and maturation of spermatozoa and ova is complete before eclosion. The gonads are indeed undergoing resorption throughout adult life (unpublished observations). The adult phase then is solely concerned with fertilization, distribution, host location and oviposition.

The sex *ratio of* beetles *that* emerged from enclosed logs (154 ♂♂ : 190 ♀♀) does not depart significantly from an expected 1 : 1 ratio.

PHENOLOGY

P. reticularis overwinters in the larval stage only. Final instar, non-feeding larvae may be found throughout the winter months. These dormant larvae resume activity about mid-August, when formation of the pupal chamber begins. It is

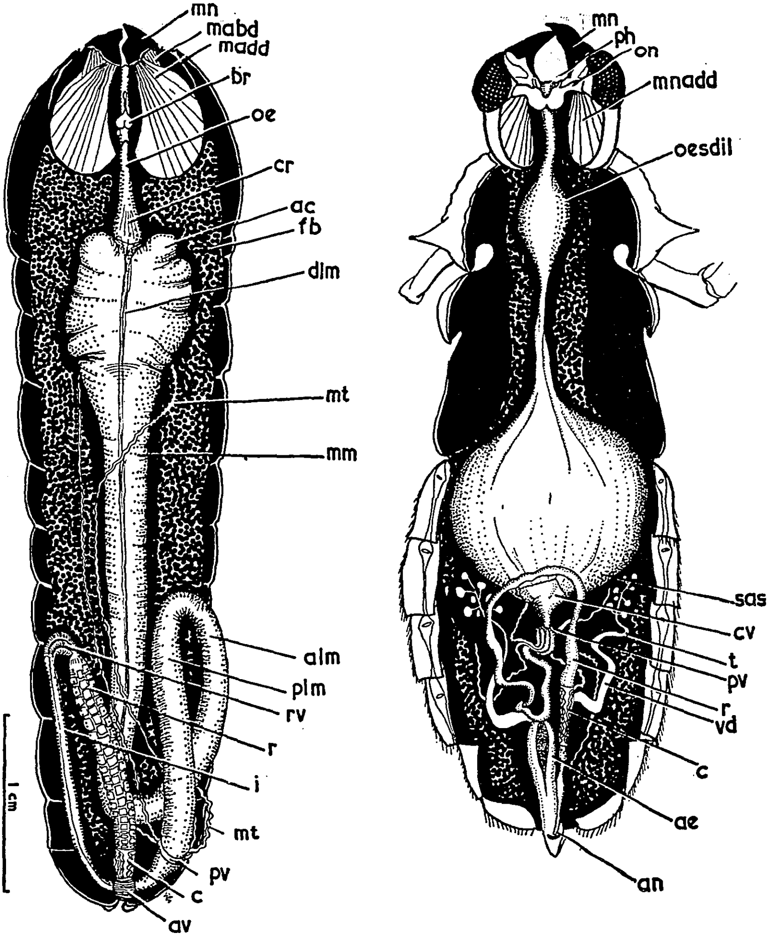

FIG. 1.—Gut of larval and adult *Prionoplus*. ac, anterior crypt; ae, aedeagus; alm, ascending limb of midgut; an, anus; av, anal valve; br, brain; c, cryptonephridial tubules; cr, crop; dlm, dorsal longitudinal muscle; fb, fat body; i, ileum; mabd, mandibular abductor muscle; madd, mandibular adductor; mm, mid mesenteron; mn, mandible; mt, malpighian tubule; oe, oesophagus; oed, oesophageal dilation; on optic nerve; ph, pharynx; plm, posterior limb *mesenteron; py, pyloric valve; r, rectum; rv, rectal valve;* sas, stomdeal air sac; t, base of testis; vd, vas deferens.

improbable that photoperiod could be responsible for breaking the apparent facultative diapause and it is suggested that a factor associated with the annual temperature rise may be involved in stimulating the formation of pupal chambers, for the initiation of these activities coincides with the onset of the spring rise (Fig. 2). First pupae may be found late in September and there is a rapid increase in their number as October advances. Adults begin to emerge in mid-November and

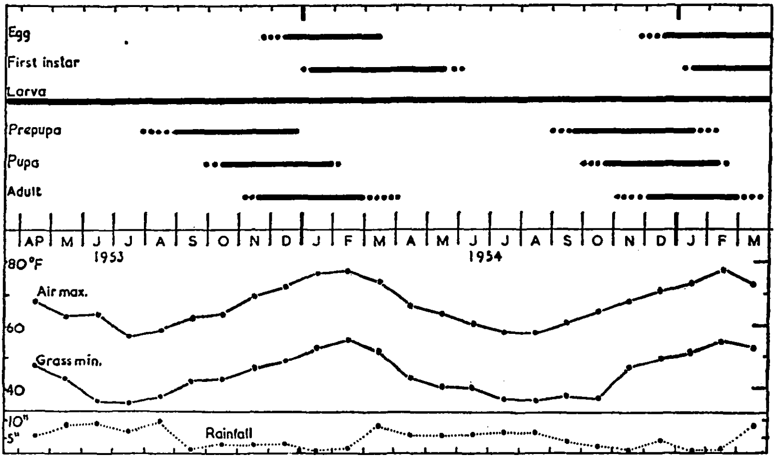

FIG. 2.—Annual distribution of the life cycle of *Prionoplus*, as found at Riverhead. Meteorological data from Riverhead Forest Headquarters. Temperature: monthly means, rainfall: monthly totals.

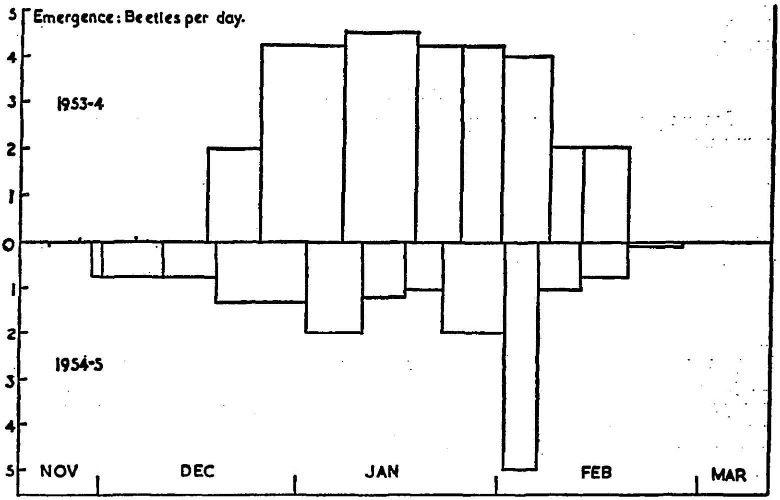

FIG. 3.—Emergence of *Prionoplus* from enclosed logs expressed as numbers of beetles emerging per day, during successive intervals between cage inspection.

emergence rate increases through December, whence a fluctuating level persists until early February. Thereafter numbers decline rapidly to mid-March: only isolated individuals may then be found up to mid-May. The seasonal distribution of emergences of adult *Prionoplus* as indicated by records from enclosed logs over two successive seasons is seen in Fig. 3. The general pattern of distribution of phases of the life history is summarised together with relevant meteorological data in Fig. 2.

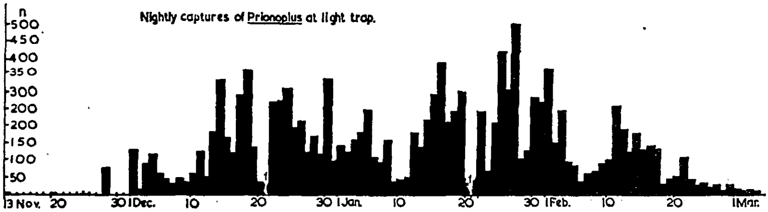

Fig. 4.—Distribution of nightly light trap capture through flying season 1954–55, at Riverhead. f: lamp failure during flight period.

Numbers

A total of 13,201 adults was captured at one Robinson-type, ultra-violet light trap on 93 nights out of a total of 110 periods of operation between 6 p.m. and 7 a.m. from December 1, 1954 to March 12, 1955. The distribution of catch throughout the flying season is seen in Fig. 4. While the sex ratio in *Prionoplus* is thought to be 1 : 1, only 2.9% (377) of the light trap capture were females. No correlation was found between the numbers of males and females caught per flying period.

The total number of beetles obtained from enclosed logs within the Riverhead forest was 227, of which 204 emerged during the first season of enclosure, and 123 in the second. A strong correlation was found between the average daily rate of emergence (Fig. 3) and the number of beetles caught at the light trap during corresponding intervals ($r = .774$, $t = 3.4$, $p < .01$).

Flight Activity

The unqualified use of trapping procedures based on tropic responses of an organism, to obtain indices of activity carry inherent disadvantages. Light traps, which depend on a little understood phototropic behaviour may yield results not in accord with a non-selective sampling method. For example, Williams *et al.* (1956), using section traps have shown that the well known lunar periodicity in captures of Lepidoptera at light traps is an artifact: moonlight is an antagonistic stimulus to light trap attraction. They conclude that "we are (therefore) still without evidence of an effect of moonlight on the activity or distribution of night flying insects".

Light trapping results with *P. reticularis* are of some interest, firstly because the nocturnal activity of Coleoptera has been little studied, and it has the merit that its large size and noisy flight allows a direct, albeit subjective assessment of activity. Flight activity as measured by numbers of animals flying will depend on two factors: the proportion of the population that is in an active phase, and the proportion of time the active animals spend in flight. The two are not distinguished in this paper, but they are thought to follow parallel trends.

Daily Activity Pattern

The daily activity pattern was examined during three periods of direct observation between 6 p.m. and 6 a.m., and separately by collecting light trap captures at ten minute intervals between 8 p.m. and 6 a.m. on ten nights spaced through the summer. The conclusions arrived at from direct observation parallel those results obtained by trapping.

P. reticularis is active by night. Daylight hours are spent hidden under debris or wedged deeply into furrows of bark on trunks, and when disturbed they can seldom be induced to fly, showing only ill co-ordinated display behaviour. The activity rhythm is to some degree innate, for individual beetles enclosed in light-tight metal containers showed by their periodic noisy movement that the cycle persisted for several days.

First flights are made shortly after dusk, that is between 8 and 8.45 p.m. at Riverhead. The onset of activity appears to be governed to some extent by sky light intensity, for it is delayed on lightly overcast evenings when the sky remains bright longer than on clear nights, and is also delayed when a full moon has risen before sundown on a clear night.

For the individual beetle, the behaviour leading to flight is as follows. On emergence from the daylight refuge it walks, seemingly at random. If it is in a trunk or branch it falls to the ground and continues intermittent bouts of walking, which gradually increase in vigour. After a varying period, the characteristic and constant behaviour preparatory to flying occurs. The body is raised on fore and mid legs, the antennae are raised from the ground, the elytra are raised to an angle of 30°, and the wings are unfolded. A pause of a half to one second follows before wing movements begin. They are at first of small amplitude and evidently function in the "warming-up" of the flight muscle (Rüschkamp 1927, Krogh and Zeuthen, 1941). Sufficient lift is seldom generated at the first attempts to become fully airborne and the beetle may travel only a few feet, or fail to leave the ground and overturn. Short, weak flights follow and these become successively stronger until between 15 and 30 minutes after emerging for the evening controlled flights of several minutes duration occur. As more beetles reach the full flight phase the level of flight activity of the population rises. It increases until a maximum, fluctuating level is reached about 10.30–11 p.m. and this continues until about 1–2 a.m. Thereafter activity declines and ceases between 4 and 5 a.m.

It will be seen from Fig. 5 that the general pattern of capture described is that of the male beetles. The majority of females arrived at the trap in the early part of the activity period and their catch is at a minimum during the peak of the male activity. Direct observation indicates that this truly reflects a sexual difference in activity pattern: females emerge from their daylight refuges early in the acitvity period and remain relatively sedentary, as may be expected when a male-assembling mechanism is operating. This difference in activity pattern also accounts for the small percentage of females caught at the light trap.

The marked lunar periodicity in light trap captures is evident in Fig. 6. Its relationship to normal flight activity is less certain than in the case of the daily activity rhythm; direct observation suggested that flight activity within the forest did parallel the monthly trapping cycle, but assessment was necessarily more subjective than with the nightly pattern. Plate 61, fig. 1, shows an instance in which a full moon rose under calm, clear conditions. A marked, but transient increase in activity occurred, followed by a decrease, until the moon was obscured by cloud. This may be regarded as a disturbance stimulus along with others discussed below.

Temperature

No correlation was found between the size of light trap catch and either daily air maxima or minima, as recorded at the Forest Headquarters c 200 yards from the trapping station.

Rainfall

Following Williams (1940) a comparison of 24-hour periods with and without rain in terms of increase or decrease of capture between successive nights is presented in the following table:

	Catch Increase	Catch Decrease	
Days with rain	14	13	27
Days without rain	32	25	57
	46	38	84

The slight predominance of catch increase on nights without rain lacks significance (Chi square = .064). On the other hand it was observed during the night on which a light N.W. wind with low cloud brought brief showers of fine rain through the forest, that flight activity was briefly stimulated when the shower began. As with light intensity it appears that a short term fluctuation can cause transient flight activity.

Wind

It was similarly recorded that the arrival of light winds on a previously calm night stimulated a brief burst of activity, often reflected in a sharp peak in trap enclosures (Plate 61, fig. 1).

Observations on Behaviour of the Adult Beetle

1. *Emergence from the Log*

Between 12 and 36 hours after eclosion the beetle starts work on the emergence gallery. The larval passage to the pupal chamber is seldom utilized; instead a new passage lying usually in a radial plane, but seldom perpendicular to the axis of the log is started from the roof of the pupal chamber. A powdery frass is produced, none of which is ingested. The emergence hole is ovoid with cleanly incised borders, and axes of 2–3 cm x 1–1.5 cm. On reaching the surface, the beetle moves to the underside of the log, or to a deep crevice. Here hardening and pigmentation is completed, and quantities of pultaceous urate material are excreted. Laboratory bred animals did not attempt to fly until at least two days after emergence.

2. *Reproductive Behaviour*

(a) Assembly of males: The possession of a male-attracting mechanism by female *P. reticularis* was detected as a result of predation by hedgehogs in the vicinity of enclosed logs (see Predators, below). Heads and thoraces, recognisable as males only by the antennae, were found in numbers on and about cages when females had emerged from the enclosed logs. When no females were present, no dismembered males were found. The attracting stimulus appears to be olfactory, as newly killed females were attractive both when visible and when covered by muslin.

(b) Display: If molested by one of its kind, irrespective of sex, or by an observer, a characteristic display behaviour is evoked. Contact with the antennae, mouthparts, legs, thorax or elytra, in that order of sensitivity brings a response, though its intensity depends on the current state of excitation of the beetle. The head is thrust forward and the mandibles are opened to their full extent. The antennae are flailed and the head raised and lowered. Any object touching the mandibles is instantly seized on and strongly held. Further excitation brings the beetle to a higher straight-limbed stance, which is unstable and usually causes the animal to overturn.

(c) Combat: High intensity display between individuals may lead to combat. Preliminary grappling with the fore legs leads to a tight clutching of the partners, one individual usually being thrown onto its back (Plate 61, fig. 2). The mandibles seize on to any object coming within their compass—it may be one of their own appendages—and sections of antennae, palpi, and tarsi are frequently lost. Old males taken in the field are often found to be badly mutilated and scored as a

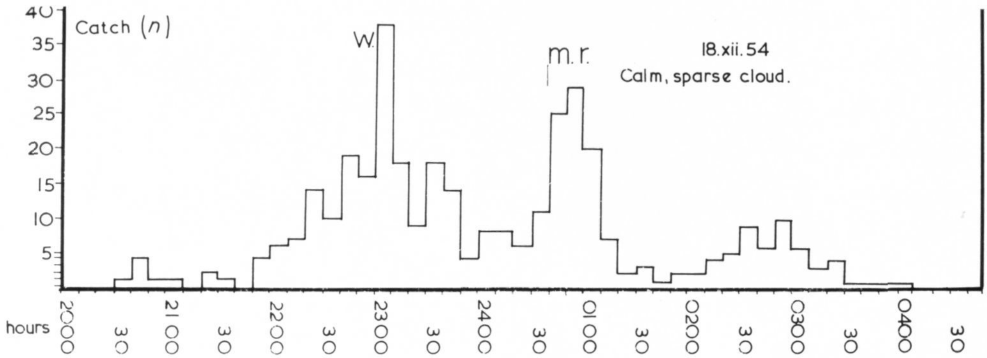

FIG. 1.—Distribution of catch in successive ten-minute periods during night of 18–19. xii. 54. mr: moonrise, w: wind burst.

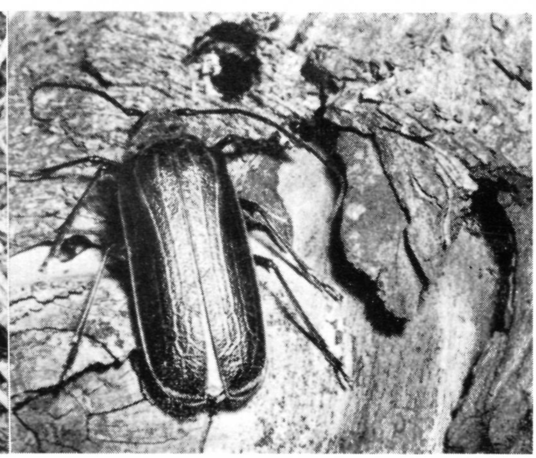

FIG. 2.—Combat between two male *Prionoplus*.

FIG. 3.—Female locating oviposition site.

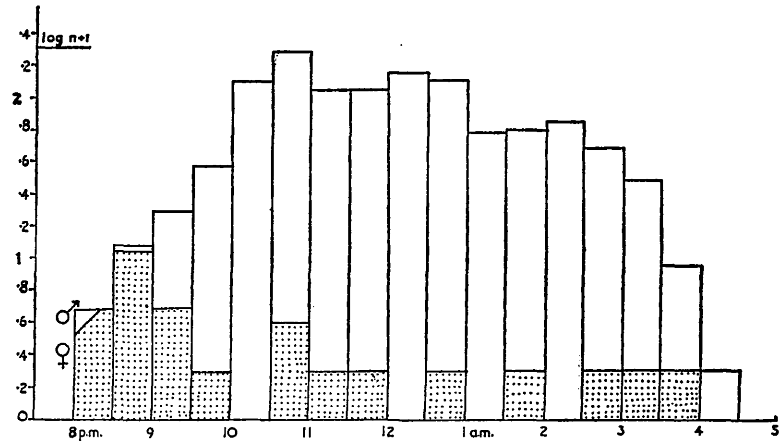

FIG. 5.—Distribution of trap capture through night. Totals for ten nights expressed as log n + 1. Female catch (stippled) superimposed on male catch.

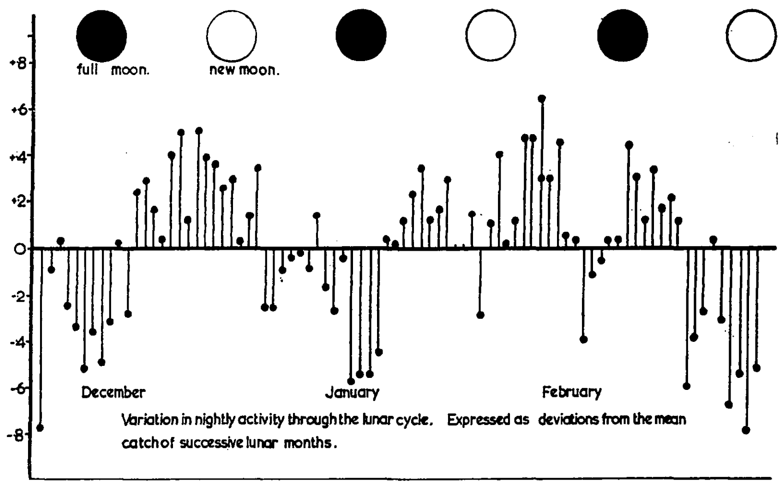

FIG. 6.—Lunar periodicity in light trap captures of *Prionoplus*.

result of these encounters. A bout may last as long as 30 to 40 seconds, after which the opponents leave the site, usually taking to the wing.

(d) Copulation: Mating activity usually occurs between 10 p.m. and 1 a.m. A male approaches the female and may precede an attempt by light nibbling at the female's head and thorax. Several attempts to mount may be countered by the female's moving away a short distance. In a successful mounting the male approaches the female from behind and to one side, grips the thorax with fore and mid hind legs, and the hind femora with his hind tarsi. An apparently inactive period follows, interrupted by occasional tittilation of the female's dorsal surface with the male's mandibles and maxillary palpi, accompanied by the twitching of the antennae of both partners. This alternating rest and activity continues for up to 15 minutes before the female extends and retracts the ovipositor. Shortly after the male flexes the pygidium to the ventral surface of the slightly everted ovipositor. During evagination of the elongate flagellum, the antennae of both partners continually twitch. The flagellum reaches the base of the spermatheca at full evagination. Coitus may last up to 12 minutes but successful fertilization can occur within 12 to 15 seconds. It is not known whether one mating is sufficient to fertilize all eggs, but females with few eggs remaining may be found in copula.

(*e*) *Oviposition*: The lateral oviducts of newly emerged females are distended with closely packed ova which occupy the greater part of the abdomen. Ovulation is completed early in the pupal phase. Females captured in the field immediately after mating did not oviposit on the same night, but usually did so after one to three nights.

Butovisch's (1935) classification of Cerambycid oviposition would describe *Prionoplus* as " By means of ovipositor only, in cracks or under scales of bark, and crevices in wood." The female moves over the stump or log, seemingly at random with the antennae in a characteristic transverse position with the distal quarter turned down on to the substratum. The distal part of the ovipositor is extended, the subterminal lobes making contact with the surface. During this period of site selection the abdomen and antennae continually twitch. When the antennae move into a crevice (Plate 61, fig. 3) the female turns about and inserts the extending ovipositor. Accompanied by convulsive contraction of the abdomen, and antennal twitching, one egg at a time passes through the ovipositor. The eggs are deposited as an irregular single layer. Egg counts made on the oviducts of 20 newly emerged females gave extremes of 240 and 398, with a mean of 330.

Predators

Of its native predators, only the morepork *Ninox novaezelandiae* Gmel. was seen to take adult *Prionoplus* from branches at night. Two introduced animals take adult *Prionoplus* at Riverhead. The white backed magpie (*Gymnorhyna hypoleuca* Gould) enters the forest margin to take *Prionoplus* at dawn when their activity periods overlap. The hedgehog (*Erinaceus europaeus* Linn.) is the major predator in the Riverhead forest. At three well separated localities hedgehogs took numbers of males attracted to enclosed females. They were observed nipping the fat-laden abdomen from the more sclerotized parts. Fragments collected at the three sites throughout the emergence season indicated that at least 416 males were taken. The gut contents of hedgehogs killed in the neighbourhood of emergence cages were composed almost entirely of fat body and recognisable parts of male *Prionoplus* together with fragments of *Hemideina thoracica* and *Melampsalta cingulata*. Away from emergence cages, *Prionoplus* ova predominated in the gut contents. In a study of the Little Owl *Athene noctua* in the Dunedin district, Marples (1942) recorded 12 *Prionoplus* imagines among the gut contents of 242 birds.

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