Metapopulation dynamics of the coxella weevil (*Hadramphus spinipennis*) on the Chatham Islands

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ABSTRACT

The endangered monophagous coxella weevil, *Hadramphus spinipennis,* is confined to Mangere and Rangatira (South-East) Islands, Chatham Island group, New Zealand. This study was carried out on Mangere Island, where a metapopulation of weevils inhabits eleven distinct patches of their host plant, *Aciphylla dieffenbachii*.

Local weevil population dynamics in one discrete patch of *A. dieffenbachii* were investigated using a capture-recapture method. Weevil numbers more than quadrupled during three consecutive summers, and survival and recruitment rates increased. Plant numbers halved over the same period. In the fourth summer the plant population died out and no weevils were found. Overexploitation by the weevils, particularly root feeding, was the probable cause of host plant death. In one local patch, over 90% of the weevils stayed within 0–6 m of where they were found during a 24-hour period. Weevils had a low tendency to leave a local patch.

An annual census was carried out for three successive years to assess weevil and host plant abundance for six patches. The weevil population in these six patches almost tripled over three consecutive summers while plant numbers increased by 11%. After a weevil density of more than 18 per plant was reached, three patches died out. Inter-patch migration only occurred after the death of a local population, when it was found that weevils had dispersed to neighbouring patches. Local weevil dynamics are unstable and persistence of the weevil metapopulation appears possible only in a spatially heterogeneous environment with asynchronously fluctuating local populations.

The two remnant island populations of *H. spinipennis* on Mangere Island and Rangatira Island showed significant differences in DNA band patterns obtained by PCR-RAPDs. No consistent differences were found between local populations on Mangere Island.

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1. Introduction

Islands often have a characteristic flora and fauna that frequently includes a high proportion of species that evolved on the islands and are not known to have ever occurred on the mainland (Watt 1986). Today, the distribution of a large proportion of New Zealand's species is restricted to islands, including over 40% of the insect species that have the highest or second highest priority for conservation (Molloy & Davis 1994). Insects play a profound role in ecosystem functioning (Wilson 1987), especially on isolated islands (Howarth & Ramsay 1991) In the past, however, they were almost totally neglected when the criteria for island reserves and restoration projects were set (Gibbs 1990, Howarth & Ramsay 1991). More recently, restoration programmes have included insects, but ecological knowledge of island invertebrates is still very poor (Howarth & Ramsay 1991), and even less information is available concerning interactions of endemic insect herbivores and their host plants. However, for appropriate restoration programmes, an understanding of habitat requirements and ecological interactions between different species is vital (Atkinson 1994, Clout & Saunders 1995).

This study investigated the interaction of a metapopulation (see below) of the endangered endemic monophagous coxella weevil, *Hadramphus spinipennis* Broun (Coleoptera; Curculionidae, Molytinae; Molytini), and its host plant, Dieffenbach's speargrass *Aciphylla dieffenbachii* (F. Muell.) Kirk (Apiaceae) on Mangere Island and on Rangatira (South-East) Island which are in the Chatham Island group.

1.1 METAPOPULATION DYNAMICS

A metapopulation is an assemblage of discrete local populations (also called subpopulations) within a larger area (Hanski & Gilpin 1997). Typically, local populations are confined to discrete habitat patches, which are separated by unsuitable habitat. Migration from one local population to another is possible, but is usually limited (Hanski & Simberloff 1997). Extinctions of local populations can occur and the persistence of a metapopulation depends on the dynamics of extinction and recolonisation of local habitat patches. As long as the rate of recolonisation exceeds or equals the extinction rate the metapopulation persists (Taylor 1990).

At a time when habitats are becoming increasingly fragmented, the metapopulation concept has become an important tool for conservation biologists (Hanski & Gilpin 1991, Harrison & Taylor 1997). In combination with studies of local population dynamics it provides a diagnostic approach to conservation. Factors that are vital for the persistence of a population can be identified and used as a foundation for conservation measures. For example: Is the number of individuals in a local population small and/or declining? Is the number of occupied patches within a metapopulation small and/or declining? How frequently does movement between local population occur? Does colonisation of new patches outweigh the rate of local extinction? For further information see Hanski & Gilpin (1997).

2. Background

Both *H. spinipennis* and *A. dieffenbachii* are endemic to the Chatham Islands (44° S., 176° 30′ W.), which are located 850 km east of the South Island of New Zealand. The distribution of the weevil is restricted to Mangere Island (113 ha) and Rangatira Island (218 ha) (Fig. 1), which are free of mammalian predators and are among the most biologically significant nature reserves of the Southern Hemisphere (Department of Conservation 1996). The Department of Conservation's current work on the islands is designed to rehabilitate their ecological communities.

The coxella weevil, *H. spinipennis*, belongs to a small genus of large, flightless weevils that is endemic to New Zealand. The weevil is listed as an endangered species with highest priority for conservation by the New Zealand Department of Conservation (Molloy & Davis 1994) and is classified as a vulnerable species by the IUCN (Groombridge 1993). The adult weevils are flightless and nocturnal and feed on the flowers and leaves of *A. dieffenbachii*. The larvae feed on the root parenchyma of the host plant. A literature review on *H. spinpennis* has been provided by Emberson et al. (1996). The genus *Aciphylla* is confined to New Zealand and Australia. *A. dieffenbachii* is restricted to the Chatham Islands and occurs on shallow soils and in treeless areas and is regarded as a 'vulnerable' plant in conservation terms (Molloy & Davis 1994). It is a dioecious perennial with leaf rosettes and has a taproot system.

Over the last decade, seven local extinctions of *A. dieffenbachii* patches have been observed on Mangere Island (Schöps et al. 1998; E.C. Young, pers. comm.). *H. spinipennis* was thought to be a causative factor in these local extinctions (Schöps et al. 1998). This led to concern that the *A. dieffenbachii* and, consequently, the *H. spinipennis* metapopulations on Mangere Island might not be viable in the long term. The general aims of this study are, therefore, to identify the factors that play an important role in the persistence of the *H. spinipennis* metapopulation on Mangere Island, to assess its vulnerability to extinction and to draw up a management plan for the species.

3. Objectives

- Determine the life cycle and phenology of the monophagous weevil and its host plant to provide a foundation for the subsequent work.
- Study the response of *H. spinipennis* to host and non-host plant odour.
- Identify patterns of genetic variation within and between local weevil populations and between two different islands so that releases on other islands can be planned.
- Examine local population dynamics in one population of *A. dieffenbachii* and *H. spinipennis* to ascertain if *H. spinipennis* causes local extinction of its host plant.

- Investigate weevil intra-patch movement to determine mobility and emigration of the weevils at varying food availability levels.
- Analyse population dynamics of the weevil and plant population in six selected patches.
- Assess inter-patch dispersal before and after the collapse of a local patch to determine the timing of dispersal.

Figure 1. Map of New Zealand and the Chatham Islands.

4. Description of the study sites

4.1 MANGERE ISLAND

This study was mostly conducted on Mangere Island (Fig. 2), where *A. dieffenbachii* and *H. spinipennis* are abundant. Mangere Island (113 ha) is 2.5 km west of Pitt Island (Fig. 1). Once covered in low native forest, the island is now dominated by non-native grassland and native shrubs as a result of 90% of the forest being burnt early this century to clear the island for farming. Sheep grazing suppressed the growth of most native vascular plant species (Ritchie 1970), but when livestock was taken off the island in 1968, plants such as *A. dieffenbachii* started to spread. 'Megaherbs' (e.g. *A. dieffenbachii* and *Myosotidium hortensia* Hook.) occur along the coastline on cliffs and in open grassland. *A. dieffenbachii* is patchily distributed over the whole island, often forming dense, almost monocultural stands (Fig. 2). Reforestation has occurred since 1974 (Butler & Merton 1992). A discrete, medium-sized patch of *A. dieffenbachii* (750 m^2) was chosen as a study site ('*A. dieffenbachii* patch 3', Fig. 2) and divided into 30 5-m × 5-m individually numbered quadrats (Fig. 3).

Apart from *A. dieffenbachii* the vegetation in the patch comprised the non-native species *Bromus catharticum* H.B.K., *B. mollis* L., *Carex trifida* Cav., *Cirsium* spp., *Holcus lanatus* L., *Lolium perenne* L., *Poa pratensis* L. and the native species *Disphyma papillatum* Chinnock, *Festuca coxii* Hack., *Hebe* spp., *Phormium* aff. *tenax* J.R. et G. Forst. and *Olearia traversii* (F. Muell.) Hook.

The island was visited six times between November 1993 and January 1997. Four trips took place in summer (25 November 1993–15 February 1994; 30 November–17 December 1994; 6–20 December 1995; 15–19 January 1997), one in autumn 1995 (22 March–3 April 1995) and one in early spring 1995 (12–20 September 1995).

4.2 RANGATIRA (SOUTH-EAST) ISLAND

Rangatira Island (Fig. 4) is mostly covered in remnant or regenerating native forest, and the plant and weevil populations are limited to a highly fragmented habitat, the coastal cliffs, bluffs and rocky shores (Given 1996). Rangatira Island was visited during the summers of 1993/94 and 1995/96. During the summer of 1995/96 the coastline and the open areas that were accessible were searched during the day for *A. dieffenbachii* and *H. spinipennis*. The locations of plant patches were mapped, the number of plants noted and the presence and absence of weevil damage in different patches was recorded (see letters A–D on Fig. 4). Plant group A can be found 50 m to the right of the track approximately 100–200 m after the track that connects the 'Trig' with the 'Clears' leads into the Clears. In 1995 it consisted of 17 plants (9 flowering females and 7 flowering males). Most plants were of medium large to large size (large plants were about 80 cm high and had a diameter of more than 1 m). All plants had

Figure 2. The distribution of *A. dieffenbachii* patches (numbers) and smaller groups of *A. dieffenbachii* (letters) on Mangere Island. The study site (number 3) is marked in black and points represent scattered plants. In *A. dieffenbachii* groups A, B and C, and at the edge of patches 2 and 5, marked weevils from a capture-recapture study (see text) that had dispersed from the study site were found in summer 1996/97.

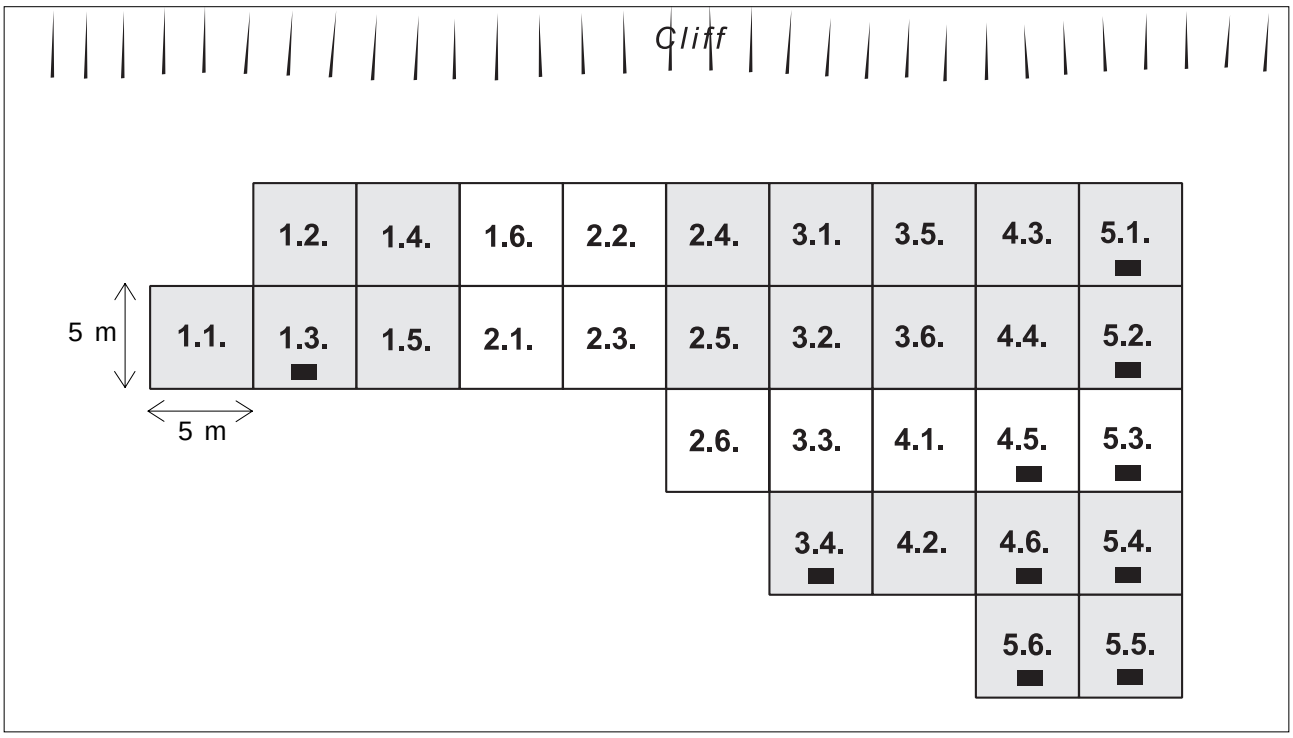

Figure 3. A schematic map of the Mangere Island study site showing a 5 m × 5 m gridline that was established for a capture-recapture study (see text). The sampling area is shaded and the quadrats marked with a black square did not contain any plants in spring 1995 and summer 1995/96.

moderate weevil feeding damage on the petioles, flowers and leaves. Six weevils were found in the leaf litter under the plants. Between 30 and 40 small- to medium-sized plants and about 30 seedlings are scattered along the coast from the clears to the South summit (plant group B). Only some of these plants showed distinct weevil feeding damage, but no *H. spinipennis* were found. In summer 1995/96 approximately 150 medium to large *Aciphylla* plants and numerous seedlings grew on a ledge below the North summit. Most of these plants showed weevil damage and in 1994 two weevils were found on the leaves of two plants. Plant group D is located on the plateau north of the North summit and contains eleven large plants, four of which were flowering in 1995. Unfortunately, a census of the weevil population on Rangatira Island was impossible, because most patches were inaccessible at night, when the weevils are active. However, the weevil and the *A. dieffenbachii* population on Rangatira Island appears to be much smaller than on Mangere Island.

5. Genetic differences between weevil populations

Weevils were collected from two different locations on Rangatira Island (from the Clears and from the patch below the North summit) and from patches 10, 12, 3 and 1 on Mangere Island. To minimise disturbance of local populations, weevils were only collected from populations with more than approximately

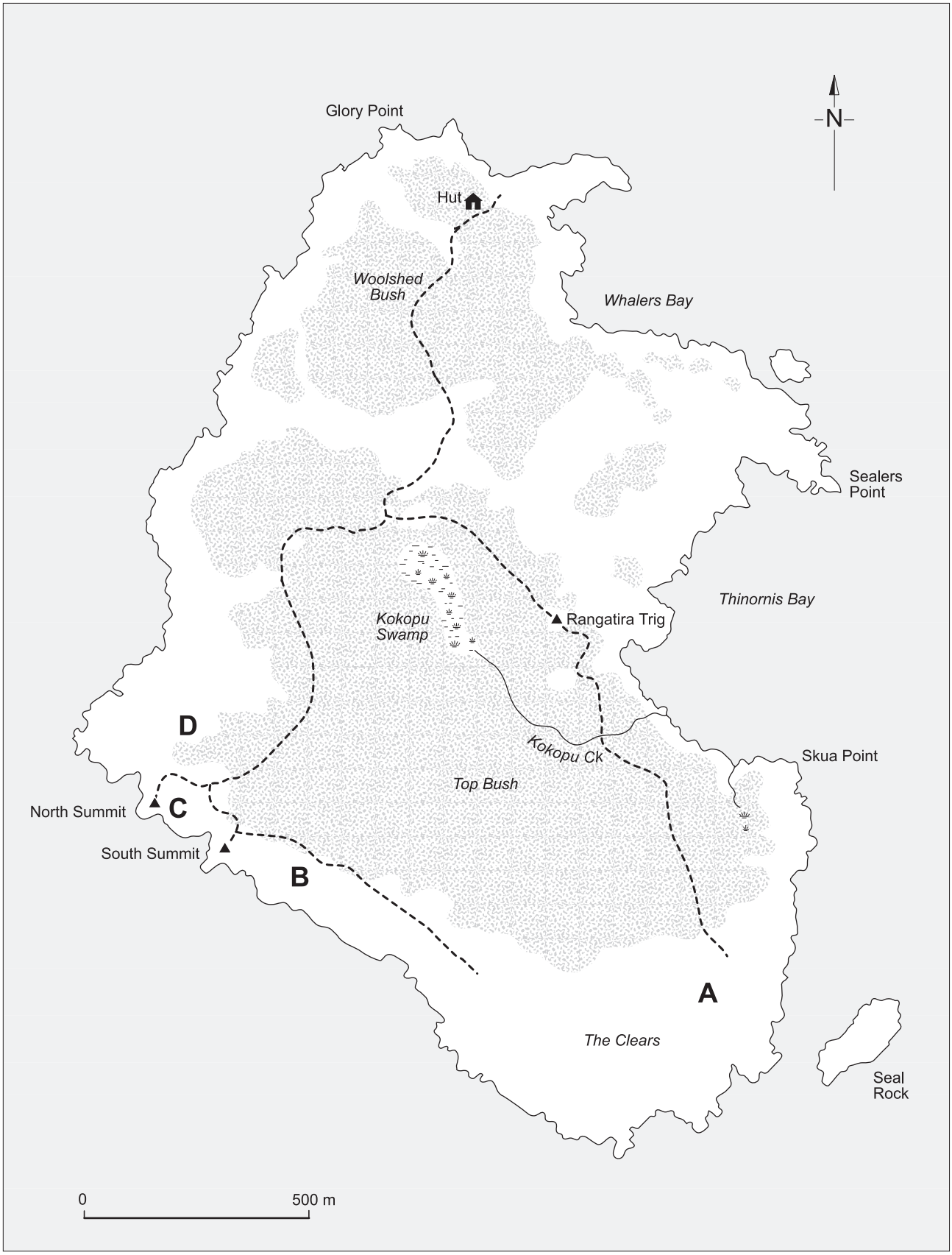

Figure 4. The distribution of *A. dieffenbachii* (letters) on Rangatira Island (for detailed information see text).

100 individuals. From Rangatira Island and from each patch from Mangere Island, 7 whole weevils were amplified, but for patch 12 only 4 individuals were available. The whole abdomen of a weevil was used for DNA extraction using a 'Prep-a-gene kit' (BioRad). Patterns of genetic variation were investigated using PCR-RAPDs. Universal primers A13 and C2 from OPERON primer kits A and C were used. Weevils from Rangatira Island and Mangere Island showed distinct differences in their band patterns. With primer C2, weevils from Rangatira Island showed two bands at 820 and 1220 bp, which did not occur in weevils from Mangere Island. Weevils from Rangatira Island had no band at 920 or 960 bp, while either or both bands were always present in individuals from Mangere Island. With primer A13, weevils from Rangitira lacked two bands at 540 and 620 bp, at least one of which was always present in weevils from Mangere Island. The levels of variation in band patterns within and between local populations on Mangere Island were similar and no consistent differences could be found between them. More specific genetic markers (e.g. allozymes or mirosatellites) would be needed in order to detect consistent genetic differences of subpopulations within the metapopulation on Mangere Island.

6. Life cycle, behaviour and phenology of weevil and host plant

The life history of *H. spinipennis* is strongly associated with its host plant. In a threatened or endangered herbivore-plant system the survival of both plant and herbivore depend on conservation programmes that preserve both mutualists (Samways 1994), which requires an understanding of their natural history and the herbivore-plant interactions. The life history of *H. spinipennis* is strongly associated with its host plant and it cannot reproduce without it. Larvae feed on the roots and adults on the foliage and flowers of *A. dieffenbachii*. This study therefore investigated the phenology of *H. spinipennis* and *A. dieffenbachii*, the life cycle of the weevil and its behaviour in relation to its host plant on Mangere Island.

6.1 PHENOLOGY OF *A. dieffenbachii*

Each time Mangere Island was visited, the phenology and the reproductive status of *A. dieffenbachii* were recorded in an attempt to relate the phenology and behaviour of *H. spinipennis* to developmental stages of its host plant. *A. dieffenbachii* could easily be sexed when close to anthesis and when fruiting. An inflorescence of *A. dieffenbachii* comprises flowers borne in compound umbels (i.e. a 'flower head' on a central stem) (Oliver 1956). When senescing, male flowers and, eventually, the whole inflorescence wilt and collapse, while female inflorescences dry and often remain intact until the next

spring. For the study site (750 m²) (Fig. 3) the number of plants and their sex were recorded each summer. Inflorescences per plant were counted, their phenological stages recorded and the ratio of flowering to non-flowering plants was determined.

Flowering in both sexes began at the end of October. Males flowered from October to late January, with a peak in November–December. The female flowering period was comparatively short but had a similar peak. By mid December, most female plants had developed green fruits that ripened and released seeds in late January to early February. As with other *Aciphylla* spp. (Lloyd 1973, Lloyd & Webb 1977, Webb 1979, Given & Williams 1984) a strong male bias in the sex ratio of flowering plants was recorded (Table 1). Ninety percent of the plants (excluding seedlings and small plants that had only a single leaf rosette) flowered in December 1993 and December 1994, whereas only 79% flowered in December 1995.

6.2 MORPHOLOGICAL DIFFERENCES BETWEEN *H. spinipennis* SEXES

At the beginning of this study no information on how to sex *H. spinipennis* was available. To sex weevils in the field, copulating pairs were separated and the individuals were examined by eye for morphological differences. Consistent differences in the morphology of the last sternite were found. In males the end of the last sternite is emarginate and is framed by two small tufts of bristles, with females this sternite is rounded (Fig. 5). In old males these bristles can be worn off, but the emargination is still easily distinguishable from the rounded tip of the last sternite in females.

To find out whether there was a size difference between the two sexes the length from the head (excluding the rostrum) to the tip of the abdomen was measured with callipers in December 1993 (n = 146), December 1994 (n = 341), March (n = 404), September (n = 201) and December 1995 (n = 590). Female weevils (x = 21.34 mm ± 1.25 S.D.) were significantly larger than males (x = 19.61 mm ± 1.23 S.D.) ($F = 662.07$; 1 d.f., $P < 0.001$).

TABLE 1. THE NUMBER OF MALE AND FEMALE PLANTS IN THE STUDY SITE AND THE MEAN NUMBER OF INFLORESCENCES PER PLANT ± S.D. IN THREE CONSECUTIVE SUMMERS.

	FEMALES		MALES		TOTAL
YEAR	FLOWERING PLANTS	MEAN NO. OF FLOWERHEADS/PLANT	FLOWERING PLANTS	MEAN NO. OF FLOWERHEADS/PLANT	FLOWERING & NON-FLOWERING
1993	169	-*	212	-*	430
1994	154	1.8 ± 1.57	209	2.4 ± 1.64	406
1995	71	1.6 ± 1.09	99	1.7 ± 1.41	216

* In 1993 flowerheads per plant were not counted.

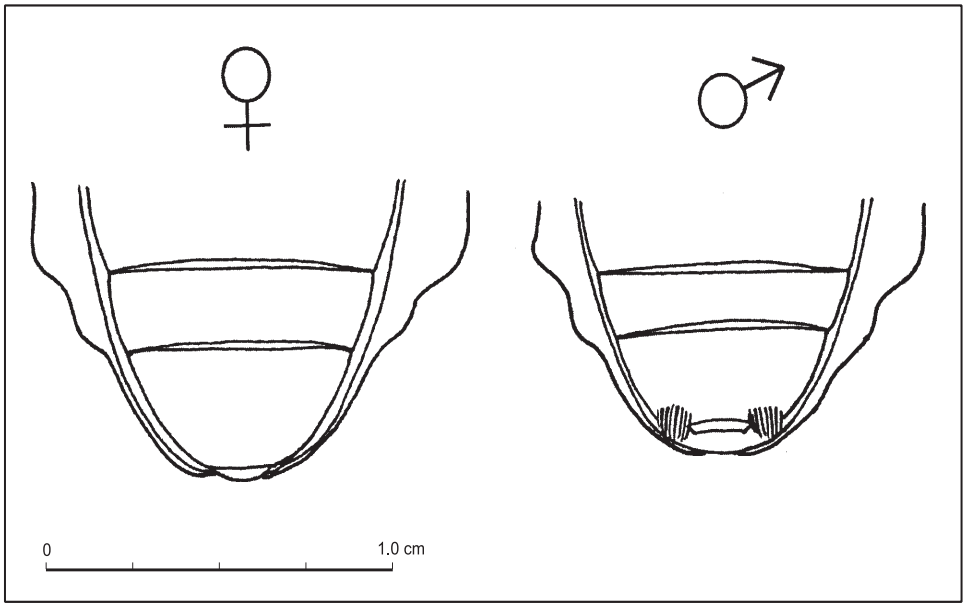

Figure 5. *H. spinnipennis*, last sternite of abdomen (ventral).

6.3 NUMBER OF LARVAL INSTARS

Larvae collected in the field were used to ascertain the number of larval instars of *H. spinipennis* by measuring their head capsule width. First instars were difficult to detect in the field and therefore 50 laboratory-hatched neonates were measured (for details on the measurement procedure see (Schöps et al. 1999). It is most likely that *H. spinipennis* has five larval instars, because when goodness of fit tests using the programme MIX 3.1 (MacDonald & Green 1995) were applied to test the data against models with three, four or five peaks, the five-peak model fitted best (χ^2 = 28.8, 20 d.f., P = 0.0911).

6.4 FIELD OBSERVATIONS OF *H. spinipennis*

Every time Mangere Island was visited, general observations on the weevils' life cycle, behaviour and phenology were made. The presence of adults and where they fed, mated and oviposited were recorded. Information on presence or absence of the subterranean larvae and pupae of *H. spinipennis* was obtained by excavating *A. dieffenbachii* plants. Each year 20 plants were randomly chosen from different *A. dieffenbachii* patches. Each plant and the surrounding soil was removed from the ground at a radius of ca. 200 mm from its centre and a depth of ca. 50–60 cm and searched for pupae and larvae. The vegetation and root ball were put into a 400 × 600 mm white plastic tray. Larvae and pupae were stored in either 90% ethanol or PEA fixative (Walker & Crosby 1988).

In the field, copulation and oviposition were observed in September, December, January, February and March, resulting in overlapping of the larval cohorts (Table 2). Before, during and after copulation the males often rode on the back of the female and nibbled off the small hairs on her elytra leaving a bare patch.

TABLE 2. NUMBER OF DIFFERENT JUVENILE STAGES OF *H. spinnipennis* COLLECTED ON MANGERE ISLAND.

	SEPTEMBER 1995	DECEMBER 1995	MARCH 1995	JANUARY 1997	MARCH 1997
2nd larval instar	0	14	6	3	2
3rd larval instar	0	1	9	4	4
4th larval instar	0	1	11	2	4
L5/pre-pupa	10	9	21	7	3
pupa	10	present	–	present	–

Female *H. spinipennis* oviposited in soil under, or close to, their host plants. Eggs were laid singly. If the soil was dry and hard, eggs were deposited in small cracks. In soft ground females burrowed their abdomen into the soil, using their hind legs and the tip of their abdomen to create a hollow. An egg was deposited in each hole and then covered with soil. Often eggs were glued to a small lump of soil or litter. Eggs were ovoid, cream colored and 2.12 (± 0.03 S.D.) by 2.95 (± 0.23 S.D.) mm in diameter (n = 10). Larvae were apodous and scarabaeiform with a cream-coloured body and a sclerotised head capsule (see May 1993).

After hatching, neonate larvae burrowed to the roots of *A. dieffenbachii* plants and started feeding on the root parenchyma. Often a tunnel was eaten into the root crown of *A. dieffenbachii*, but most larvae fed at the cortical region of the large taproots. Larvae were found as deep as 500 mm below ground level. The suggestion that larvae also feed on petioles and leaves (Emberson et al. 1996) is incorrect; all larvae extracted from the petioles and leaves by Emberson et al. (1996) and during this study belonged to the small eugnomine weevil, *Stephanorhynchus purus* Pascoe (B. May, pers. comm. 1995). The *H. spinipennis* larvae observed entered a pre-pupal stage, in which they changed to a dark yellow and became inactive. Pre-pupae formed normal exarate pupae with pupation taking place close to the host plant in earthen chambers excavated by the larvae up to 600 mm below the soil surface.

First instar larvae were very small and easy to overlook, so only the presence or absence of first instar larvae was recorded. Numerous pharate weevils were observed on the host plants in September and many pupal chambers containing fully developed weevils were also found. The capture-recapture study revealed that adult weevils lived for from several months up to almost four years (Schöps 1998). They spent days and cold nights sheltering in the leaf litter zone or in the vegetation close to their host plants. On warm nights, activity increased at dusk, when the weevils started climbing up their host plants. Weevil activity was positively correlated with temperature ($r^2 = 0.70$, $F = 25.18$, 1 d.f., $P < 0.001$), although it may also have been influenced by humidity. Activity increased in late spring, and peak weevil numbers occurred on warm and humid summer nights (K. Schöps, unpublished information).

6.5 LABORATORY STUDIES ON THE LIFE CYCLE AND PHENOLOGY OF *H. spinipennis*

In February 1994 a captive weevil population of 30 male and 30 female weevils was established in an insectary at Lincoln University. Weevils were kept in mesh cages lined with soil and bark chips at ambient temperature and fed with *A. dieffenbachii* leaves. In winter the weevils fed little and spent most of the time buried amongst the bark chips, although on warm days they emerged and fed. In September, when the temperatures rose, the weevils began to feed more frequently and started ovipositing. In the insectary, copulation was observed from September until April. The first oviposition occurred on 1 September and the last egg was layed on 23 April. In October–November first-instar larvae hatched after 15–20 days.

Females oviposited into cracks in the soil. Eggs were collected and reared through to neonate first instar larvae. In October 1995 five laboratory-reared first instar larvae were transferred onto each of 22 potted one-year-old *Aciphylla* plants kept in a shade house in the nursery at Lincoln University. A small brush was used to place the larvae carefully onto the soil next to the root crown. Every 21 days the plants were taken out of their pots and the roots and the soil were searched for larvae and pupae. In order to identify the larval instars, the head capsule width of the larvae were measured. Then the plants were re-potted, and the larvae and pupae were returned to the original plants (each larva was inserted in a separate hole next to the root crown). To minimise disturbance of larvae, they were inspected at 28-day intervals from July 1995 until the end of the experiment in November 1996. The inspection started out with seven plants. At every inspection, we added one 'new' plant to the sample that had been treated similarly to the others, but had not been inspected before. This enabled us to assess if larvae on previously inspected and 'new' plants developed at the same rate and consequently if our information on developmental times was reliable. Movement of larvae under the microscope meant that it was only possible to distinguish between small (head capsule diameter: < 2.5 mm), medium (2.5–3.65 mm) and large larvae or pre-pupae (> 3.65 mm). Larvae on previously inspected and 'new' plants developed at similar rates. Since head capsule measurements were taken at either three- or four-week intervals, only the maximum time a larva took to enter the next developmental stage could be estimated.

The development time from first instar larva to pupa was about nine months (Table 3). However, most pupae died during pupation. It is possible that handling at this vulnerable developmental stage and the exposure to sunlight caused the deaths. Only three weevils hatched in the insectary in March 1997. In these three cases the development from the last instar larva to the adult weevil took less than 30 days; so *H. spinipennis* can complete its life cycle in six to ten months.

TABLE 3. DURATION OF DEVELOPMENT FROM NEONATE LARVA TO MEDIUM-SIZED LARVA, TO LARGE LARVA OR PRE-PUPA AND TO PUPA AT LINCOLN (FOR DETAILS SEE TEXT).

	MEDIUM LARVA n = 14	LARGE LARVA OR PRE-PUPA n = 9	PUPA n = 11
Shortest development time	42 days	84 days	147 days
Maximum development time ± S.D.	72 days ± 16	152 days ± 44	271 days ± 93

6.6 SUGGESTED LIFE HISTORY OF *H. spinipennis*

Overwintered adult weevils resumed feeding in early spring, while overwintered larvae, pre-pupae and pupae eclosed. At this time copulation and egg laying began. Mating and oviposition in the field occured from September to April–May. Eggs laid early in the season developed into adult weevils that summer. Evidence from captive rearing and the capture-recapture study (Schöps 1998) strongly suggested that the adults emerged after mid February. Eggs laid late in the season developed into large larvae, pre-pupae and pupae during autumn and winter, but did not emerge as adults until the following spring. This is a possible explanation for why no pupae were found in late March (Table 2). Larvae destined to hatch in the same summer had already completed eclosion and the remaining larvae or pre-pupae were overwintering. However, the development of the new generation of larvae in the field was probably slower than during the experiment in the insectary. It is possible, therefore, that the youngest overwintered larvae did not pupate until December– January. This could mean that new generation weevils did not hatch until the following spring and, therefore, that *H. spinipennis* had only one generation per year.

6.7 BEHAVIOUR OF *H. spinipennis* IN RELATION TO ITS HOST PLANT

Weevil behaviour was observed in detail on four nights in September and December 1995. In September, when the plants were not flowering, 162 plants and in December 1995, 35 female and 41 male flowering plants were examined. The plants were subdivided into foliage, petioles and flowers. The volume of flowering male plants was estimated to be approximately 50% foliage, 20% petioles and 30% flowers. Female flowers were smaller and less common. Female plants were estimated to be approximately 55% foliage, 25% petioles and 20% flowers. These percentages were used in statistical tests to calculate the expected numbers of weevils for different parts of the plants if a random distribution was assumed. Four major types of weevil behaviour were identified: feeding, walking, pre-copulatory activity, and copulation. The weevil's sex was recorded, as well as the part of the plant on which it was

found. The number of weevils per male and female flower head was also assessed for 169 female and 241 male plants in December 1994. To assess if weevil distribution on its host plant was aggregated or random, the number of individual weevils and weevil groups (individuals that aggregated in the same location on a plant were recorded for 100 plants on 12–13 March 1995.

Similar numbers of male and female weevils occurred on either sex of *A. dieffenbachii*. Overall, weevils occurred more frequently on flowering plants of both sexes than on non-flowering plants, with the majority being found on male plants and, more specifically, on male flower heads. In September and in December 1995, 55% and 41% respectively of all weevils observed were mating, whereas in March 1995 mating was infrequent. Weevils preferred to mate on male plants and mated more frequently on flowers and petioles than on foliage of either plant.

The most common type of feeding damage consisted of oval notches that weevils chewed in the petioles, usually associated with an outer leaf near the ground. Adult weevils also fed on leaflets, from the tip or by chewing notches in the edges, and on anthers. Often only the outer tips of female flowers and fruit were eaten (see also Emberson et al. 1996). More weevils fed on male than on female plants and they occurred more often on petioles and flowers than on foliage. The mean weevil group size was 2.26 ± 2.51 S.D. and their distribution on the host plants was aggregated (χ^2 = 618.79, z = 20.24; variance mean ratio: 2.78).

6.8 *Pseudopanax chathamicum*, A POSSIBLE HOST PLANT

Weevils were repeatedly found on *Pseudopanax chathamicum* in the Kokopu swamp area on Rangatira Island (Fig. 4) (Schöps et al. 1999), where no *A. dieffenbachii* plants grew near by. Therefore the potential of *P. chathamicum* as a host plant for *H. spinipennis* was also assessed. The host plant preference tests were conducted in the laboratory, with weevils being randomly allocated to six groups of four and placed in individual containers. Each group was offered two *A. dieffenbachii* and two *P. chathamicum* leaves in 'choice feeding tests'. The feeding damage of each leaf was recorded after 48 hours and 96 hours. After 48 hours, only three of twelve *P. chathamicum* leaves showed feeding signs, while ten out of twelve *A. dieffenbachii* leaves had been fed on. After 96 hours, the weevils had fed lightly on seven of the twelve *P. chathamicum* leaves, while all twelve *A. dieffenbachii* leaves had considerable feeding damage. Significantly more of each *Aciphylla* than *Pseudopanax* leaf material was consumed (48 h: 11 d.f., paired t = –3.09, P = 0.0103; 96 h: 11 d.f., paired t = –5.71, P < 0.001). It is likely that adult weevils can survive for a while on *Pseudopanax* leaves, but given their strong preference for *Aciphylla* it seems very unlikely that *P. chathamicum* is a host plant of *H. spinipennis*.

7. Host-finding ability of weevils

H. spinipennis is strongly dependent on its host plant and recognising and locating a host plant patch must be fundamental for survival in its fragmented habitat. The host-finding ability of *H. spinipennis* was studied in two ways. First, a release experiment was carried out in summer 1994 to investigate the weevils' host-finding ability (Schöps et al. 1998).

Weevils were released 100 m away from the nearest host plants. Within ten weeks of release at least 68% of the released weevils, a much higher proportion than would be expected from random movement (23%), dispersed to host plants (Schöps et al. 1998). The weevils are nocturnal and visual cues as the main stimulus for orientation and location of food sources, as in some other insects (e.g. Wyatt et al. 1993, Bernays & Chapman 1994), are unlikely. Secondly, wind tunnel experiments were carried out to test the hypothesis that *H. spinipennis* is able to respond to *A. dieffenbachii* by using host plant specific volatiles.

Thirty weevils were collected from Mangere Island in December 1994 and were transferred to an insectary at Lincoln University and kept under natural daylength and ambient temperatures. As the response to host plant odour may be affected by the herbivore's hunger (Wallin & Ekbom 1994, Zhang & McEvoy 1995), the weevils were starved for 48 hours before the experiments were begun.

Experiments were conducted in a wind tunnel at 20–25°C and 50–60% r.h. and an airflow of approximately 0.1 m/s. The wind tunnel was positioned in a dark-room and the only light source used during the tests was infra red. The experimental platform was placed at half the height of the tunnel and consisted of a sheet of transparent acrylic lined with paper. It was illuminated from below by a fibre optic cold light source covered by a diffuser and a red light filter. A high-resolution video camera was mounted pointing vertically downward and weevil behaviour was recorded (for further information on the wind tunnel and experimental setup see Schöps 1998).

The movements of weevils were investigated by using host plant (*A. dieffenbachii*), non-host plant (*Lolium perenne* L.) or control (no plant) odours. The plant material was crushed up separately with a food blender and mortar and placed in petri dishes. The sequence in which the 24 individual weevils used in the experiment were to encounter the different treatments was assigned by a Latin Square Design. The petri dishes with plant material were placed upwind on the experimental platform and 1 m away from the 'experimental arena'. The arena consisted of a 28-cm diameter circle in the middle of the paper which was placed in the centre of the experimental platform and replaced after each experiment. A weevil was placed in the centre of the circle and was covered with a black film container. Weevils were left for two to five minutes to settle and assume a random heading direction before the film container was removed. Each treatment was video-recorded for each weevil from when the film container was removed until the weevil left the experimental arena. If a weevil did not move within 30 minutes, it was replaced. Weevils encountered only one treatment per day. For digitisation and

analysis of the video images the method described by Varley et al. (1994) was used. The programme BUGSY digitised the images (one co-ordinate/s) and recorded the x, y coordinates, while a FORTRAN programme analysed the coordinates and computed the parameters of the weevils' track in the arena (for further information on the data analysis see Schöps 1998).

In insects, most olfactory receptors are located on their antennae (Visser 1986). When the plastic container that covered the weevil was removed at the start of each experiment, most weevils started waving their antennae with the head held up. They turned around on the spot and when they encountered a host plant odour plume from upwind their turning angle often decreased until they eventually paused and then started walking upwind. Significantly more weevils walked upwind in all three treatments (*A. dieffenbachii*: $c^2 = 38.8$; 1 d.f.; $P < 0.001$; *L. perenne*: $c^2 = 4.55$; 1 d.f.; $P < 0.05$; Control: $c^2 = 4.16$; 1 d.f.; $P < 0.05$) In the *A. dieffenbachii* treatment, however, highly significantly more weevils walked up-wind and consequently towards the host plant odour source. The distances weevils moved until they left the arena (Table 4) were significantly different for the three treatments ($c^2 = 7.219$; 2 d.f.; $P < 0.05$). The tests were not significant, however, when the *L. perenne* treatment was compared with the control.

It can be therefore concluded that weevil movement towards *A. dieffenbachii* was more directed than towards *L. perenne* or the control and that weevils were obviously able to recognise and distinguish between host plant and non host plant odour.

TABLE 4. AVERAGE TOTAL DISTANCE (± STANDARD ERROR) MOVED BY *H. spinnipennis* EXPOSED TO *A. dieffenbachii* VOLATILES (n = 26), *L. perenne* VOLATILES (n = 23) AND A CONTROL (NO PLANT) (n = 24) IN A WIND TUNNEL.

	AVERAGE TOTAL DISTANCE ± S.E. (mm)
A. dieffenbachii	247.82 ± 46.17
L. perenne	328.58 ± 36.65
Control	271.24 ± 36.65

8. Population dynamics of the weevil and its host plant

Over the last decade, seven local extinctions of *A. dieffenbachii* patches have been observed on Mangere Island (Schöps et al. 1998, Appendix 2; E.C. Young, pers. comm.). *H. spinipennis* was thought to be a causative factor in these extinctions (Schöps et al. 1998). This led to concern that the *A. dieffenbachii* and, consequently, the *H. spinipennis* metapopulations on Mangere Island might not be viable in the long term. However, predictions about persistence and effective conservation measures can be made only when the population

dynamics of the endangered species are understood (Atkinson 1989, Caughley 1994, Hanski & Gilpin 1997). The first aim was to determine whether *H. spinipennis* caused the death of local host plant populations. Therefore the population dynamics of *A. dieffenbachii* and *H. spinipennis* were examined in detail for one distinct host plant patch. The second aim was to assess the metapopulation structure and dynamics of *H. spinipennis* to make predictions about its persistence, by studying the population dynamics of the weevil and its host plant in six patches. Weevil and plant abundance as well as local extinction and colonisation of other patches were also investigated. It was also assessed, whether there was a critical weevil density above which a plant patch became extinct and how long it took for plant patches to regenerate after a local extinction. Finally, whether or not plant and weevil population dynamics were locally and/or spatially correlated was investigated.

8.1 LOCAL POPULATION DYNAMICS

The *A. dieffenbachii* population in the study site was monitored every summer. The location of each *A. dieffenbachii* plant and the approximate area it covered was recorded on a detailed map. Plant sex and the number of inflorescences per plant were also recorded, as were the phenological stages and the ratio of flowering to non-flowering plants.

The study of the local population dynamics of *H. spinipennis* focused on adult beetles, using a capture-recapture study to estimate their abundance, recruitment and survival. A total of 12 888 captures comprising 9310 different weevils during 18 sampling occasions were made. Adult weevils were marked individually by gluing coloured plastic bee tags with individual numbers on their prothoraces (glue: 'Zap-a-Gap', Pacer Technology, Great Britain; bee discs: Opalitplättchen, Striewski Bienenbedarf, Jevenstedt, Germany). As a contingency for the discs being lost during the study, a combination of enamel paint coloration and positions on the elytra was also used to mark each weevil uniquely. Only 13 marks were lost. Marking did not seem to affect the survival and longevity of the weevils because, in captivity, no marked or unmarked weevils died within six months after marking. On each nocturnal sampling occasion, the foliage and flowers of all *A. dieffenbachii* in the study site were searched for weevils. The plant surface was scanned first, then the leaves were parted and lower regions of the plant as well as the ground under it were searched. Weevils from different quadrats (Fig. 3) were marked (or recorded, if they were recaptured). The location (quadrat number) was noted each time a weevil was captured or recaptured and each was released into the centre of the quadrat from which it was captured. In summer 1993/94 all quadrats (Fig. 3) in the study site were sampled systematically on five sampling occasions. Due to time constraints and high weevil numbers, only 10 quadrats out of 30 were sampled randomly on five sampling occasions in summer 1994/95. In autumn 1995, spring 1995 and summer 1995/96 always the same 21 quadrats (Fig. 3) were sampled on four, five and four sampling occasions, respectively.

This capture-recapture study was designed according to Pollock's 'robust design' (Pollock 1982), which uses closed models to obtain robust population size estimates for each visit to the island and open models for estimating

survival rates between different visits. The programme CAPTURE (Otis et al. 1978) was used to estimate population sizes for each visit to the island and the programme JOLLY (Pollock et al.1990) to estimate survival and birth rates between different visits and for the population size estimate for 1994/95 (for more details see Schöps 1998). The time between different visits was 298, 98, 165 and 81 days and the time between sampling occasions during one visit varied between one and seven days. Time between visits was sufficiently long to allow for death, birth, immigration and emigration to occur and the time between different sampling occasions during one visit was sufficiently short to assume that recruitment and loss were negligible and that the population was closed. The assumption that the population was closed between 'secondary periods' was assessed by estimating survival rates between 'secondary periods' using JOLLY (Pollock et al. 1990). If survival rates are 1.0, or close to it, it may be assumed that weevils did not die or emigrate between sampling occasions and that the population was closed. During most visits, the estimated average survival rates between sampling occasions were close to 1.0 and the weevil population in the study site was therefore considered closed. However, in spring 1995 the average survival rate was 0.90, recapture rates were low, and new generation weevils emerged and joined the population. At this time, the population was not closed and population size was therefore estimated using Jolly-Seber's open population model.

8.1.1 Population, recruitment and survival estimates between 'primary periods'

The number of weevils in the study site more than quadrupled over the three summers of this study (Fig. 6). In spring 1995 the capture-recapture trial was carried out after winter mortality had occurred and before the majority of the new generation weevils had emerged. The population was, therefore, smaller than that in autumn 1995. With the new generation of weevils entering the population between spring 1995 and summer 1995/96, the total population increased. In January 1997, no weevils were found in the study site and all the host plants had disappeared.

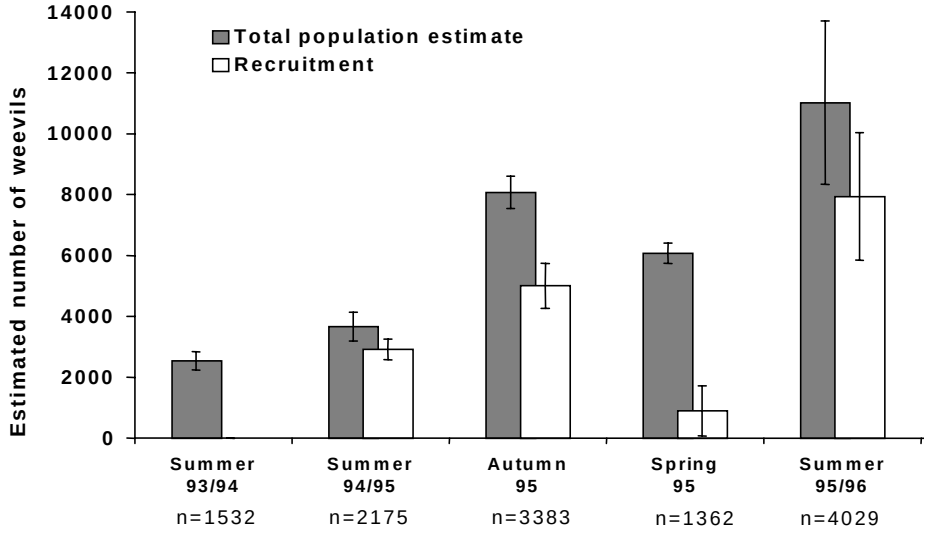

Figure 6. Population and recruitment estimates between 'primary periods' for the *H. spinnipennis* population in the Mangere Island study site using program for recruitment (Pollock et al. 1990) (with 95% confidence intervals) and CAPTURE (White et al. 1982) for population estimates (with 95% confidence intervals).

From summer 1993/94 until summer 1995/96, no interaction between the weevil population in the study site and those in other patches was detected (see below). It was therefore concluded that emigration and immigration from and to the study site were negligible and that recruitment occurred mainly through birth, while loss was caused primarily by death. Recruitment was measured between early spring and autumn (Fig. 6). By summer 1994/95, most recruitment of the new generation males had already taken place and hardly any new males entered the population until autumn 1995. Fewer females than males hatched between summer 1993/94 and summer 1994/95. In autumn 1995, between 1624 and 2856 females entered the population (Appendix 1). Each female produced, on average, 3.84 adult offspring between summer 1993/94 and summer 1994/95 and 4.01 between summer 1994/95 and summer 1995/96. Most female weevils died between autumn and spring, whereas most male weevils died between spring and summer (Appendix 1). Only 20% of females survived from the first summer to the second, but 40% of females present in summer 1994/95 survived until summer 1995/96. Male survival rates were 39% from the first to the second summer and 48.9 % form the second to the third. Since overall survival rates increased dramatically over the three summers and recruitment either ceased or increased, it may be concluded that the weevil population was still growing between summer 1994/95 and summer 1995/96.

8.1.2 The life expectancy of an adult weevil

Females marked in summer 1993/94 were likely to survive for a maximum of two years four months, while males marked at the same time lived up to three years nine months. However, most of these weevils did not survive until the next summer (Fig. 7).

8.1.3 Changes in plant numbers and sizes

The number of adult plants (flowering female and male plants, and non-flowering medium and large plants) and the total area covered by *A. dieffenbachii* decreased continuously from summer 1993/94 to summer

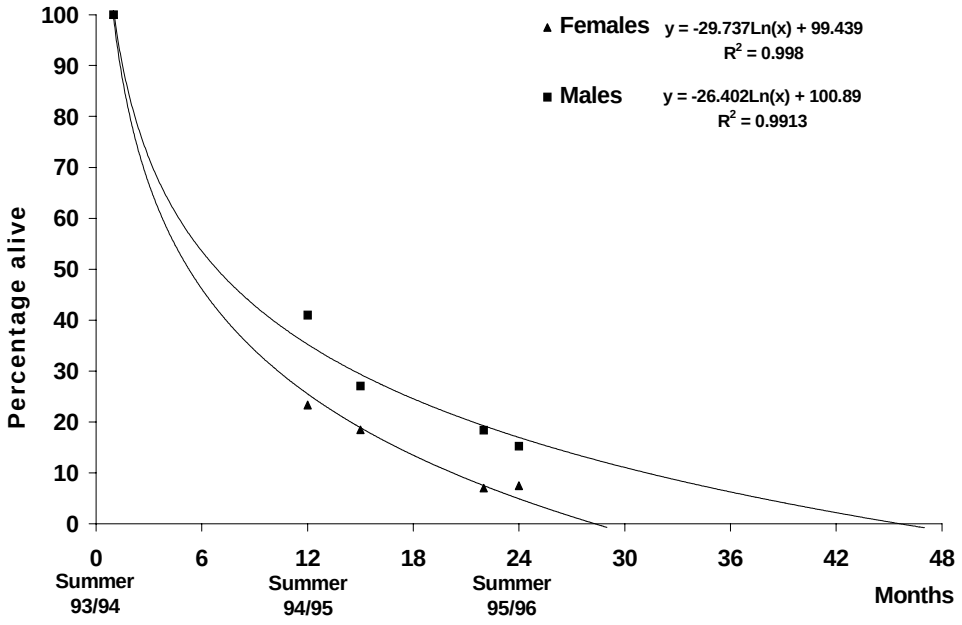

Figure 7. Survival of male and female weevils that were marked in summer 1993/94. Population estimates for the 'primary periods' were obtained from CAPTURE (White et al. 1982).

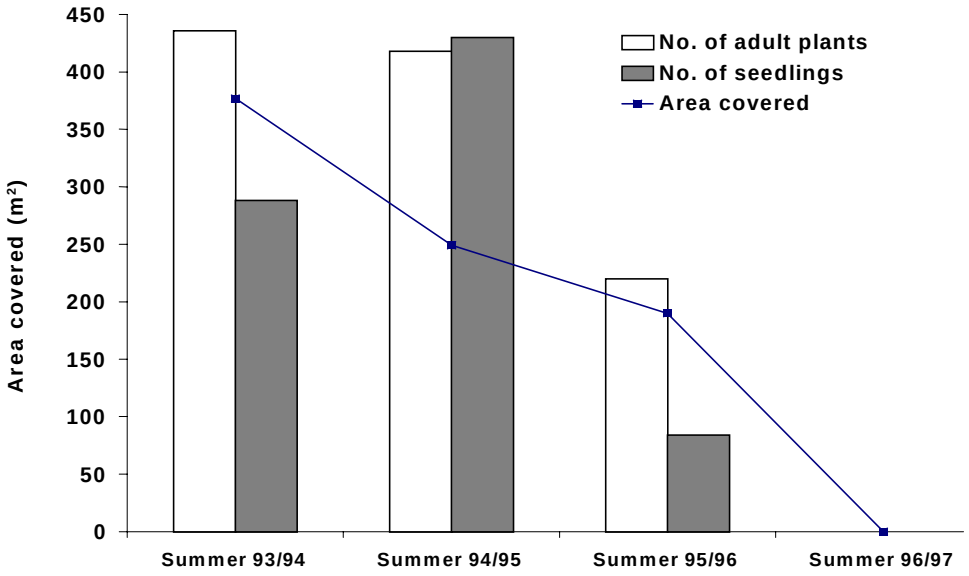

Figure 8. Number of adult *A. dieffenbachii* and seedlings and the total area they covered in the Mangere Island study site.

1996/97 (Fig. 8). Male plants were always more numerous than female plants and covered a larger part of the study site (Table 5). The rate of decline in number and area covered, however, was similar for both sexes. The area female and male plants covered declined by 44 % and 41 % respectively during the first year and by 33 % and 37 % the next year (Table 5).

The number of non-flowering adult plants and the area they covered was consistent over the three years (ranges: 43–46 plants; 9 m²–12 m²). Most very large plants died between 1993/94 and 1994/95. More seedlings were recorded in summer 1994/95 than in the previous summer (Fig. 8). In the third summer, however, the number of seedlings had dropped dramatically. Before summer 1995/96, weevils were hardly ever observed on seedlings, but that year they were found on every plant in the study site, including seedlings.

8.1.4 Relationship between weevil and plant numbers

Weevil numbers quadrupled from summer 1993/94 to summer 1994/95. The area covered by *A. dieffenbachii*, however, decreased linearly ($y = -66.12x + 278.6$, $R^2 = 0.96$, $P < 0.05$; Fig. 9), halving in the same period. Weevil densities increased from 12 weevils/m² *A. dieffenbachii* in summer 1993/94 to 37 in summer 1994/95 and 105 in summer 1995/96. Plant numbers appeared to be negatively

TABLE 5. NUMBER OF FLOWERING *A. Dieffenbachii* AND THE AREA THEY COVERED IN THE MANGERE ISLAND STUDY SITE.

	SUMMER 1993/94	SUMMER 1994/95	SUMMER 1995/96
Number of female plants	169	154	71
Area covered (m²)	79.4	44.6	30.1
Number of male plants	212	209	99
Area covered (m²)	102.4	60.2	37.8

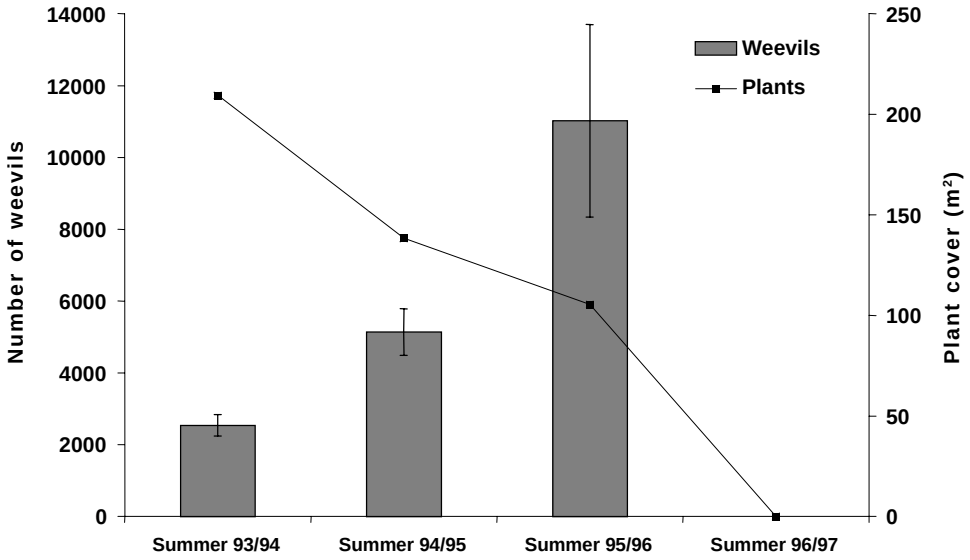

Figure 9. Estimated numbers of *H. spinnipennis* and the area covered by *A. dieffenbachii* plants in the Mangere Island study site. Weevil population estimates and 95% confidence limits were calculated with CAPTURE (White et al. 1982).

correlated with weevil numbers, although this was not significant. By summer 1996/97 the plant and the weevil population in the study site had collapsed and no plants or weevils were found. *H. spinipennis* can obviously cause the extinction of local host plant populations by over-exploitation of the local food source.

8.2 Metapopulation dynamics

In summer, each *A. dieffenbachii* patch was traversed repeatedly and scanned with binoculars (10 × 8). The number of medium and large plants (> 1 rosette) was recorded, as was the ratio of flowering to non-flowering plants. The positions of all patches were plotted on a map (Fig. 2). For smaller *A. dieffenbachii* patches, the plants were counted, while for large patches the mean of repeated estimates was used. For each patch, the abundance of seedlings and small plants (1 rosette), relative to the number of larger *A. dieffenbachii*, was recorded as rare, abundant or very abundant. Six patches (2, 3, 4, 10, 11, 12), which were accessible at night and which had similar size distributions of *A. dieffenbachii*, were selected to estimate their plant and weevil populations sizes (Fig. 2). These patches incorporated a large proportion of the *A. dieffenbachii* and *H. spinipennis* populations. The proportion of each patch covered by *A. dieffenbachii* was assessed as a rough estimate. Since each summer, 80–90% of the plants in all six patches flowered, it was decided to measure weevil density as the number of weevils per flowering plant, rather than weevils per square metre of *A. dieffenbachii*.

To estimate the number of weevils, 10% of the flowering male and female *A. dieffenbachii* in each patch were randomly sampled for *H. spinipennis*, as it was assumed that they would be representative of each patch. Weevil numbers for the six selected *A. dieffenbachii* patches were sampled each year on one night in mid December. The population estimate that was obtained with CAPTURE for the study site was used to estimate the proportion of weevils found on 10% of the flowering plants in the study site on a particular night. The weevil population estimates for other patches were extrapolated from these values.

The numbers of plants and weevils in the six selected *A. dieffenbachii* patches increased continuously over the three summers (Fig. 10). Although three patches became extinct in the third year (Fig. 11), the total number of weevils increased by 180%, while plant numbers increased by eleven percent (Fig. 10). The weevil density in all *A. dieffenbachii* patches increased. If a weevil density of 18 per plant was exceeded, the plant and weevil population died out (Fig. 11). Below that density, no decline in weevil numbers was observed. When weevil densities in an *A. dieffenbachii* patch were high, large numbers of plants became yellow and wilted. Roots were often heavily damaged by the larvae. In some cases, the roots were completely missing and only the wilted leaf rosettes were left. Feeding by adult weevils did not have a visible impact on plant appearance and survival until weevil numbers were very high, after which some plants became so heavily damaged that only a small piece of stem remained with up to 55 weevils aggregating on it. After a plant patch had died, no sign of it remained the following summer.

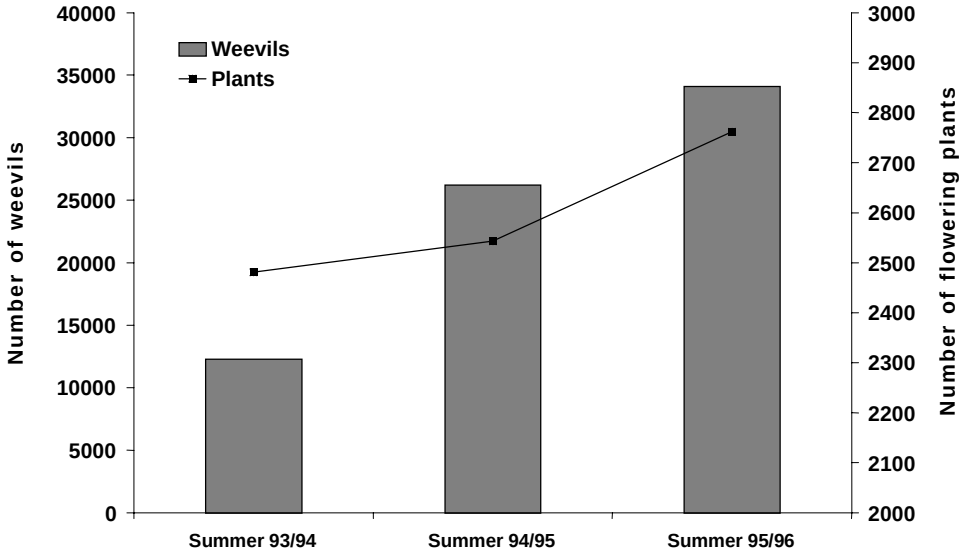

Figure 10. Totaled numbers of *H. spinnipennis* and of flowering *A. dieffenbachii* plants for six selected patches on Mangere Island.

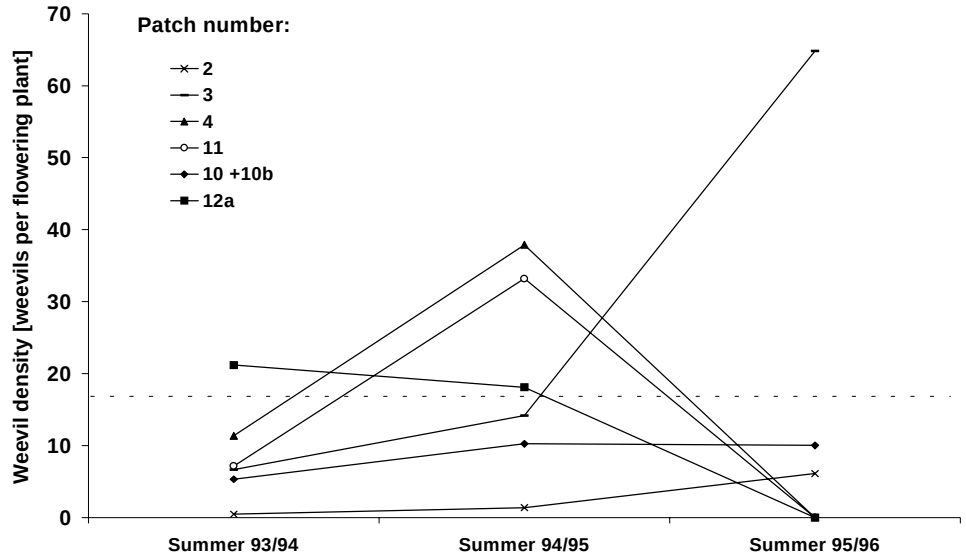

Figure 11. Weevil densities for six selected patches on Mangere Island. Weevil densities were obtained by dividing the weevil numbers by the number of flowering plants. Populations with a density that exceeded 18 weevils per flowering plant (dashed line) became extinct.

Regeneration of patches that became extinct during the study had not been observed by December 1997 (E.C. Young, pers. comm. 1997). Patches 6 and 10c established between summer 1994/95 and summer 1995/96 and contained only small plants and seedlings. Patch 10c was close to patch 10 and was 'connected' to it by scattered plants, while patch 6 was distinct. Patch 10c already contained weevils, but no weevil damage was initially observed in patch 6. E.C. Young (pers. comm.) recorded that patch 5 contained at least 430 adult plants in summer 1988/89 and by summer 1990/91 it was extinct. Nineteen young plants were found in summer 1991/92 (E.C. Young, pers. comm.) and, from then on, plant numbers slowly increased. In summer 1993/94, most plants in the area were seedlings and only 140 flowered. A year later, most seedlings had matured; around 1000 plants were flowering and the size distribution of *A. dieffenbachii* was similar to that of long-established patches (e.g. 3, 2 and 10). Weevil numbers in patch 5 increased from 55 to 541 between summer 1993/94 and summer 1994/95. In summer 1995/96, 1200 plants were flowering in patch 5 and the weevil population had increased to 1645.

8.2.1 Do local extinctions depend on patch size and patch isolation?

Mann-Whitney U-tests were performed to test whether local extinctions were dependent on the size of a patch and its isolation from other patches. Local patch size was defined as the number of flowering plants per patch. Isolation was the distance from the edge of one patch to the edge of the next closest patch. Patches that became extinct were significantly smaller in the year before extinction ($U = 12$, 1 d.f., $P = 0.032$), but were not more isolated ($U = 5.5$, 1 d.f., $P = 0.86$) than patches that persisted.

8.3 INTRA-PATCH MOVEMENT AND DISPERSAL

Only a small proportion of native herbivorous insects become temporarily so abundant that they inflict serious damage upon their hosts (Caughley & Lawton 1981). Native herbivores rarely cause the death of a large part of the host plant population, and extinctions that have been reported are not, as far as is known, part of a metapopulation system. The metapopulation of *H. spinipennis* on Mangere Island, however, regularly depletes its local food source and completely destroys host plant patches. In a metapopulation context, dispersal is defined as 'movement between spatially separated populations' (Harrison 1991, Hanski & Gilpin 1997) and can stabilise the metapopulation dynamics (den Boer 1968, Harrison & Taylor 1997), particularly if local extinctions are common (Holyoak & Lawler 1996). Dispersal of *H. spinipennis*, however, has never been observed in the field, although there is anecdotal evidence (E.C. Young, pers. comm.) that adult weevils might have colonised the easternmost part of Mangere Island between 1990 and 1991. Since *H. spinipennis* frequently causes local extinctions of host plant patches, knowledge of the weevil's ability to reach new patches and the timing of dispersal is necessary to understand its metapopulation dynamics and, consequently, for the adequate protection of the species.

8.3.1 Intra-patch movement

Information on intra-patch movement of *H. spinipennis* was obtained from the capture-recapture study described above, using only data from autumn 1995, spring 1995 and summer 1995/96. The elongate shape of the study site determined the directions and distances weevils could move within the *A. dieffenbachii* patch. It also introduced a bias, because some distances and directions were sampled more often than others (Fig. 3). If a weevil was captured in quadrat 2.4., for example, it could move only into five adjacent quadrats (or directions) in order to stay in the study site (instead of eight theoretically possible directions). The weevil could also be picked up only in certain quadrats at certain distances, because some quadrats (e.g. quadrat 2.2. and quadrat 2.3.) were not sampled. To compensate for unequal sampling effort at different distances and directions, the frequencies were corrected before statistical tests were carried out (for more detail see Schöps 1998).

To determine the distances individual weevils moved on a daily basis, only movement data from three-day intervals of the same capture-recapture sampling regime (autumn 1995 (n = 780), spring 1995 (n = 73) and summer 1995/96 (n = 285)) were used to avoid a bias in the analysis and for comparison between different years and seasons. To simplify the calculation of distances moved it was assumed that weevil movement between quadrats occurred in a straight line from the centre of one quadrat to the centre of the other. Weevils that remained in their original quadrat were assumed not to have moved.

Weevils of both sexes moved at similar rates, and no difference in movement rates was detected between different seasons (P = 0.421; P = 0.381). Most weevils moved no more than 6 m in a day and, consequently, either stayed in the same quadrat, or moved to a neighbouring one (Fig. 12), fewer than 10% moving > 6 m per day. Survival rates close to 1.0 (see above) between different capture-recapture occasions during one visit to the island, also indicated that weevils tended not to leave the study area.

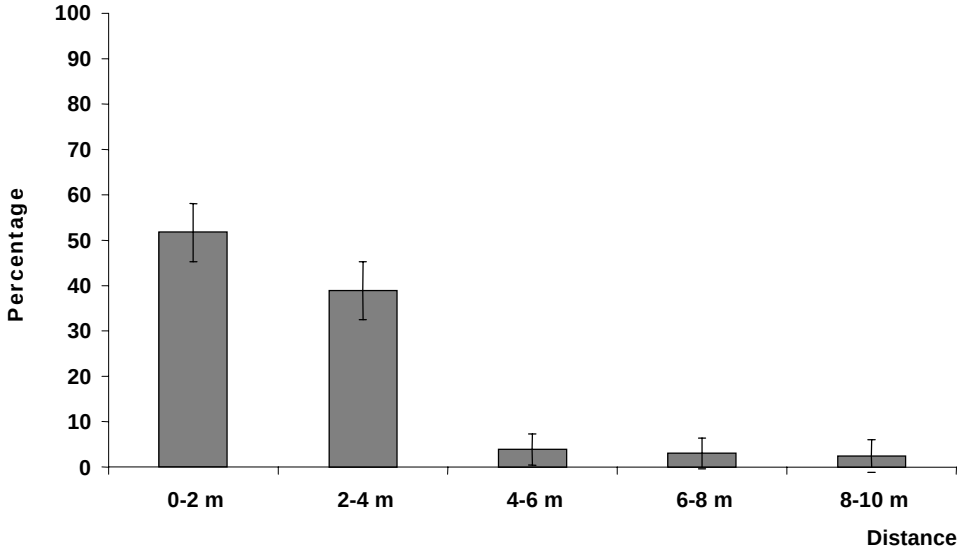

Figure 12. Distances individual weevils moved within a patch in the Mangere Island study site on a daily basis (± S.E.) in autumn, and spring 1995 and summer 1995/96.

8.3.2 Dispersal

Inter-patch movement from the study site to the nearest *A. dieffenbachii* plants and to neighbouring *A. dieffenbachii* patches (Fig. 2) was monitored on each visit to the island. At least 10% of the plants in each *A. dieffenbachii* patch were searched thoroughly for marked weevils. All individual plants between the study site and neighbouring *A. dieffenbachii* patches were also searched. If a marked weevil was found, its number and location was recorded.

Until summer 1996/97, no marked weevils were found on any of the *A. dieffenbachii* nearest the study site or in the neighbouring *A. dieffenbachii* patches. Weevils did not even disperse to patch 4, which was separated by only 40 m of grassland and scree from the study site. When the island was visited in summer 1996/97, however, not a single plant was alive in the study site and no weevils were found (see above). All *A. dieffenbachii* nearest the study site and all neighbouring *A. dieffenbachii* patches (Fig. 2) were then searched for marked weevils over four consecutive nights (15–18 January 1997). Estimates of the marked weevil populations were obtained for plant group A (six plants) and for plant group B (25 plants) using CAPTURE (White et al. 1982). However, in some cases the sample size was too small to estimate the population sizes for males and females separately (Table 6). There was no significant difference in the number of male and female weevils that had dispersed from the study site to new host plants ($P > 0.5$, 1d.f., $\chi^2 = 0.342$).

Marked weevils which had dispersed from the extinct study site and were recaptured in summer 1996/97 had travelled minimum distances of 200 m to 360 m to plant groups A and B (Table 6) and at least 500 m and 600 m to patches 2 or 5.

TABLE 6. MINIMUM DISTANCES WEEVILS DISPERSED FROM THE MANGERE ISLAND STUDY SITE TO PLANT GROUPS, TOTAL NUMBER OF WEEVILS RECAPTURED IN DIFFERENT PLANT GROUPS AND THE PERCENTAGES SEEN IN THE STUDY SITE OVER TIME.

SEX	PLANT GROUP	MINIMUM DISTANCE DISPERSED (m)	TOTAL NUMBER OF WEEVILS (n)
Female male	A	320	13 27
Female male	B	200	89 105
Female male	C	480	20 11

9. Conclusions

H. spinipennis can cause the extinction of local host plant populations by over-exploitation of the local food source. The weevils primarily selected large plants for oviposition because they were the first plants to either decrease in size or disappear from the study site. This strategy is likely to maximise the reproductive success of individual weevils, because large plants have an extensive root system, which will supply the larvae with enough food for the six to 13 months it needs to develop into an adult. However, eventually food must become scarce for larvae and weevils and plants of all sizes were consumed by the adults, used for oviposition and then fed on by the larvae.

The collapse of local plant and weevil populations appeared to be a common event. Four local extinctions were observed over the three years of this study, and a high proportion of the weevil population was affected. Local populations underwent oscillations and crashes, yet the whole *A. dieffenbachii-H. spinipennis* system persisted as a metapopulation. This study was too short to allow conclusions as to whether the rate with which the weevils colonised new patches exceeded, equalled or was lower than extinction rates and at what rate new patches established. Further, it was impossible to monitor the whole *H. spinipennis-A. dieffenbachii* metapopulation because many patches were inaccessible. Therefore, it could not be ascertained whether the *A. dieffenbachii-H. spinipennis* metapopulation on Mangere Island was at an equilibrium of extinction and recolonisation. However, the fact that three out of the six monitored populations died during the three years of this study makes it questionable that the metapopulation on the grassland was at equilibrium.

Particularly in a metapopulation, where the consumer causes frequent local extinction of its food resource, asynchrony in local population dynamics is one of the main requirements for the stability of the system (Crowley 1981, Reeve 1988, Taylor 1988, 1990). In the *A. dieffenbachii-H. spinipennis* metapopulation, asynchrony of local dynamics can only be maintained if the weevils are able to disperse far enough to reach new patches after the extinction of a host plant patch. However, at the same time disperal rates also have to be low enough not to synchronise the metapopulation. If local populations became synchronised they would eventually behave like one large single population in which the weevils would deplete the plant population and eventually die out. In the *A. dieffenbachii-H. spinipennis* system the weevils showed little tendency to disperse in the presence of host plants. After a local host plant population was depleted, however, they were very capable of long-distance dispersal. None of the host plant patches on Mangere Island were further apart than 600 m and most patches were separated by only a few hundred metres, well within the range that *H. spinipennis* is able to cover by dispersal. Consequently, weevils have the potential to reach new patches after the collapse of a local patch. However, my data is insufficient to state whether the dispersal rate of the weevils on the grassland is low enough to maintain the asynchrony of local weevil population dynamics.

The larger and the more spatially heterogeneous a system is, the less likely it is that factors causing extinction will affect all patches simultaneously (Fahrig & Paloheimo 1988, Hanski 1991) and that local dynamics will get synchronised (Holyoak & Lawler 1996, Taylor 1980, 1988). Before most of the forest on Mangere Island was burned (Given 1996) the plant and weevil populations were restricted to a very fragmented habitat—the cliffs and bluffs along the coastline. Today, the plants are numerous and occur throughout the grassland, as well as on cliffs and on bluffs. Host location by *H. spinipennis* is likely to be more successful and, consequently, dispersal rates are probably much higher than in the original habitat.

Even if we suppose that the *A. dieffenbachii-H. spinipennis* metapopulation on the grassland might die out, because large number of successfully dispersing weevils will synchronise the system, the weevils and host plants in the original habitat, the cliffs, bluffs and crevices, would most probably remain. This habitat is highly fragmented and plant and weevil populations are likely to have persisted and coexisted there for many thousands of years. The fragmentation of the original habitat will have maintained asynchrony of local population dynamics in the past and there is no reason why it should not do the same in the future. Continuing reforestation of the island would eventually have the same effect, as it would isolate the local populations on the grassland, increase habitat fragmentation and enhance the stability of the metapopulation. I conclude that the *A. dieffenbachii-H. spinipennis* metapopulation can only persist in a fragmented habitat where local dynamics will not get synchronised. Under the current management, with continuing afforestation and increasing fragmentation of the plant and weevil habitat, the survival of the *A. dieffenbachii* and *H. spinipennis* metapopulation appears likely. The biggest threat to the metapopulation on the grassland would be an increase of the connectivity between different patches by, for example, corridors of *A. dieffenbachii* plants. This would most probably synchronise the dynamics of the local populations on the grassland.

10. Suggested management plan

There are only two viable *H. spinipennis* populations left, which is very little considering that the population on Rangatira Island seems to be small and there is always the possibility that natural catastrophes or diseases may occur. To secure the long-term survival of *H. spinipennis* I recommend that it should be ensured that there is at least a third viable population. In 1997 Mike Bell found *H. spinipennis* on Little Mangere. I suggest that the size and viability of this population should be assessed. *A. dieffenbachii* also occurs on other islands in the Chatham Island group and these islands should also be surveyed for *Hadramphus* (e.g. the Murumurus). If no other viable populations are found, the establishment of a third *Aciphylla-Hadramphus* population on a predator-free island in the Chatham Island group should be considered. The DNA analysis showed distinct genetic differences between the weevil populations on Mangere Island and Rangatira Island and care should be taken not to inter-mix

these two populations. However, if a population is to be established on another island, consideration could be given to using weevils from both populations in order to increase the genetic variability of the founder population and the probability that it will establish successfully. A suitable network of *A. dieffenbachii* patches should be found or established, preferably in a highly fragmented habitat, and weevils should only be released in half of the habitat patches. The aim of the releases should be to establish local weevil populations with different densities that will form a metapopulation with asynchronously fluctuating local populations. The weevil densities I observed during this study should be used as a guideline to work out the size of local releases.

Captive breeding of the weevils is possible and does not seem to be difficult. Although most of the pupae died during my laboratory experiment, six adult weevils hatched from plants on which I had overlooked some eggs. These plants were not part of the experiment and were not taken out of their pots and checked for larvae. Weevils can be reared on potted *A. dieffenbachii* plants at ambient temperature (but frost-free) and in winter they should be supplied with leaf litter for shelter from low temperatures. *A. dieffenbachii* can easily be reared in pots from seeds in a sand and turf mixture, but they can also be obtained from the DOC nursery at Motukarara. However, I do not think that it would be necessary to keep a captive breeding population of *H. spinipennis*. Instead I propose that the weevil populations on Mangere and Rangatira Island should be monitored every two to three years. The location and size of local *A. dieffenbachii* populations should be estimated. To follow the long-term demographic trends of the weevil populations, all accessible patches should be visited in mid to late summer for a weevil census. In each patch ten percent of the adult plants (with more than one leaf rosette) should be searched for weevils during two or three warm nights. Only if a substantial drop in weevil abundance between years is recorded should weevils be collected for captive breeding.

My conclusion that the survival of the *A. dieffenbachii-H. spinipennis* metapopulation is likely without further interference or management measures is too speculative to be useful for the immediate management of the two species. However, it would be important to fully understand the dynamics of the two species in their original habitat, since the ultimate conservation goal is to maintain viable populations that do not require continuous management. A better understanding of the *A. dieffenbachii-H. spinipennis* system in the original habitat might also be helpful for the management of the closely-related weevil *Hadramphus stilbocarpae*, and its host plant, *Anisotome layalli*, which also appear to form a metapopulation in a similar type of habiat in Fiordland (B.W. Thomas & K. Schöps, unpublished information). Therefore it would be very useful to monitor accessible cliff populations of *A. dieffenbachii* and *H. spinipennis* on Mangere and/or Rangatira Island for several years.

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Appendix 1

Survival and recruitment estimates (± standard error) between primary periods for the *Hadramphus spinipennis* population in the main study site using programme JOLLY (Pollock et al. 1990).

		SUMMER 1993/94– SUMMER 1994/95	SUMMER 1994/95– AUTUMN 1995	AUTUMN 1995– SPRING 1995	SPRING 1995– SUMMER 1996/97
Female	Survival rate	0.203 ± 0.012	0.901 ± 0.042	0.601 ± 0.038	0.731 ± 0.079
	Survivors	229 ± 26	1962 ± 180.8	2525 ± 315.4	2136 ± 231.6
	Recruitment	1947 ± 485	2240 ± 616	396 ± 517.9	3117 ± 2249.5
Male	Survival rate	0.392 ± 0.015	0.906 ± 0.028	0.7557 ± 0.038	0.7145 ± 0.067
	Survivors	409 ± 29.3	2647 ± 82	2560 ± 252.3	2352 ± 217.6
	Recruitment	2512 ± 445	740 ± 441.4	733 ± 407.7	3394 ± 1662.1