Metapopulation dynamics of a flightless alpine insect *Hemideina maori* in a naturally fragmented habitat

P A U L T. L E I S N H A M and I A N G. J A M I E S O N   Ecology, Conservation and Biodiversity Research Group, Department of Zoology, University of Otago, Dunedin, New Zealand

Abstract. 1. Despite widespread acceptance of metapopulation theory, the effects that inter-patch dispersal and variability in patch size have on metapopulation dynamics in insects are two issues that require further study. In addition, previous studies of metapopulations have tended to focus on organisms with high dispersal capabilities such as some species of butterfly and bird.

2. Mountain stone weta *Hemideina maori* are a long-lived, flightless orthopteran that live on *island* rock outcrops or tors in the alpine region of southern New Zealand. A total of 480 adults and 789 juveniles was marked over three seasons on four large and 14 small tors to assess the effects of habitat fragmentation on the population dynamics of *H. maori*.

3. Only 12 adults (2.5% of marked adults and 4.0% of recaptured adults) and two juveniles (0.3% of marked juveniles and 0.7% of recaptured juveniles) dispersed between tors. The mean dispersal distance was 361 m (range = 36–672 m). Larger tors supported larger populations and had a higher number of emigrants and immigrants while smaller tors had proportionally higher emigration and immigration rates. Although adults on large and small tors had similar mean lifespans, five extinction events and three recolonisation events occurred during the study period, all on small tors.

4. *Hemideina maori* conform to many of the predictions of metapopulation theory even though they are flightless, show relatively low dispersal rates, and occur at low densities. Extinction and colonisation events are more common on small tors but may be relatively unimportant for the long-term survival of the metapopulation because they occur on the smallest habitat patches, which support the smallest proportion of the overall population.

Key words. Dispersal, habitat fragmentation, New Zealand, Stenopelmatidae, weta.

Introduction

Almost any spatially structured population is now considered a metapopulation, i.e. a collection of discrete local populations connected by dispersal, and metapopulation theory has been embraced widely by workers in insect population ecology and conservation (Harrison, 1991; Hanski & Simberloff, 1997; Hanski, 1998, 1999). Inter-patch dispersal rates and patch size variability are two critical features of all metapopulations that can determine

Correspondence: Ian G. Jamieson, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand. E-mail: ian.jamieson@stonebow.otago.ac.nz

local population turnover, extinctions, and colonisations. For example, natural habitat networks are likely to be composed of habitat fragments of different size, and the area of these habitat patches is likely to affect dispersal rates as well as the rate at which local populations go extinct and vacant patches are colonised (Harrison, 1991; Kindvall & Ahlén, 1992; Hanski *et al.*, 2000). Of the studies that have examined dispersal in a metapopulation context, most have focused on organisms with high dispersal capabilities such as butterflies and birds (Hanski, 1999). Fewer studies have been undertaken on species with low dispersal capabilities, but nevertheless living in highly fragmented habitat.

Weta is a Mäori name (no plural form) given to a group of nocturnal, flightless orthopterans endemic to New Zealand, with some species among the largest insects in the world

(Gibbs, 1998; Field, 2001a). Within the so-called true weta family Anostostomatidae (formerly Stenopelmatidae; Johns, 1997), the tree weta genus *Hemideina* comprises seven species (Morgan-Richards & Gibbs, 2001). Mountain stone weta *Hemideina maori* (Pictet & Saussure, 1891) are large (adults weigh up to 10 g) and live above the tree-line on a number of mountain ranges throughout New Zealand's South Island (Gibbs, 1998). In this alpine environment, weta tend to be long-lived; it is estimated that *Hemideina maori* take 2–3 years to go through a maximum of 10 instars, with adults living for a further one to three breeding seasons (P. T. Leisnham *et al.*, unpublished).

Hemideina maori shelters primarily under slabs of rock that have broken off isolated schist outcrops called *tors* (King *et al.*, 1996; Gwynne & Jamieson, 1998; Jamieson, 2002). Most tors, which vary in size, are separated by hundreds of metres of alpine meadow not inhabited by weta; therefore each tor potentially represents a discrete local population (Fig. 1). *Hemideina maori* appear to be particularly well suited to mark–recapture analysis because of their relatively high probability of recapture (60–70%), lack of apparent trapping or resighting bias, and because their refugia do not need to be destroyed or altered to survey a marked population (P. T. Leisnham *et al.*, unpublished). A preliminary mark–recapture study on two adjacent tors indicated that dispersal by adult *H. maori* was rare (one of 52 resighted weta; Jamieson *et al.*, 2000) but the extent of dispersal over a larger area is unknown. The objectives of the work reported here were to verify whether *H. maori* fit the criteria of a true metapopulation by determining the extent of dispersal between local populations and to examine the effect of patch size on immigration and emigration rates among four large and 14 small tors surveyed over three field seasons.

Study area and methods

The study site was in the Rock and Pillar Range, located 60 km north-west of the city of Dunedin in the south-east of the South Island of New Zealand. The study site was located in the southern part of the range, about 1 km east of McPhee's Rock (1250 m a.s.l.) (45°28′S, 170°02′E). The vegetation at the study site consists mainly of cushion-herbfield and was described in detail by Bliss and Mark (1974).

In the context of weta habitat, tor size is defined by the amount of loose rocks under which weta can take refuge, rather than by the area of the tor itself. Tor size can vary from one or two loose rocks to more than 30 spread among four or five large rock columns. For the purposes of this study, *small* tors were defined as containing 1–12 loose rocks and a maximum of zero to six weta at any one survey; *large* tors were defined as containing 30–40 rocks and 15–40 weta. Four tors were classified as large and 14 as small. Although there were no tors within the study site with an intermediate number of rocks, the two patch sizes in this study represent opposite ends of a continuum of naturally occurring tor sizes (I. Jamieson, unpublished).

Ageing, sexing, and marking of weta

Weta were classified into different sex and age classes (i.e. adults versus juveniles) according to their external genitalia (see Gibbs, 1998; Stringer & Cary, 2001). Tors were surveyed once every 2 weeks on average (range = 1–4 weeks) during the spring–summer period (October–May) over three full field seasons (1997/98, 1998/99, 1999/2000) and early summer of a fourth season (2000/01). All liftable rocks that were considered suitable refuge sites for adult weta
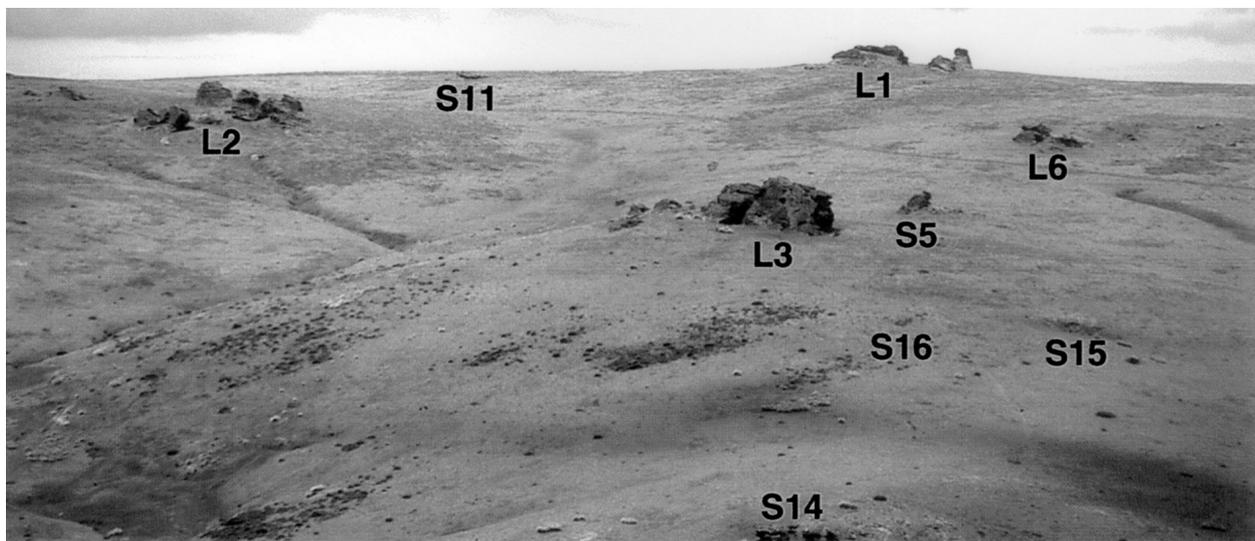

Fig. 1. Photo of the northern half of the study area showing the location of four large (L) and five small (S) tors. The distance between L3 and L1 is ≈ 500 m and between L3 and L2 is ≈ 300 m.

were numbered during initial surveys. During a survey, each numbered rock was lifted, any weta that were present were removed and placed in plastic containers, and the rock was placed back carefully in the same position. For each unmarked weta, the sex, age class, and location were recorded, and various morphological features were measured. Adults were marked using numbered waterproof tags super-glued to the pronotum using 10-s drying Selleys Supa Glue^{TM} (Selleys Chemical Co. Pty Ltd) (Jamieson *et al.*, 2000). Juveniles with large pronotums were also tagged, but smaller juveniles had water-based, non-toxic paint applied to a leg, with a leg-colour combination specific for each tor. After being measured and marked, weta were released under the edge of the rock from which they came and they were watched until they had moved freely back into their cavity.

All adults and any large juveniles that were thought to have reached the penultimate moult before adulthood (i.e. sub-adults) were tagged on large and small tors. All small juveniles that were found on small tors were also marked. Because of time constraints, however, only the juveniles within a designated area on large tors (representing about one-third of the tor) were marked. It should be noted that juveniles could only be marked temporarily until they moulted, when the tag or paint was lost along with the old cuticle. Therefore, they could not be tracked for any length of time with as much certainty as adults. Because tors were surveyed over relatively short time intervals (see above), however, it was assumed any marked juveniles that dispersed were likely to be detected.

Estimating population size and mean minimum lifespan

The Jolly–Seber stochastic method (Jolly, 1965) was first used to estimate the number of adult weta found on each tor during each survey, but it could only achieve reliable estimates of populations on large tors, as small tors had insufficient numbers of weta marked and re-caught. Therefore direct enumeration, also known as the *minimum number known alive* (Krebs, 1966), was also used. Direct enumeration indices are usually biased toward lower estimates, with the worst biases during periods of low recapture rates (Pollock *et al.*, 1990). To minimise this possibility, a total of four survey periods that had extremely low recapture rates were eliminated from the analysis (i.e. <0.02 compared with >0.40 for other periods; Leisnham, 2001). There is much empirical evidence that shows a strong positive relationship between enumerator estimates and known population sizes (e.g. $R^2 = 0.67$–0.87; Ruscoe *et al.*, 2001). Therefore, such estimates still allow the assessment of temporal and spatial trends of animal abundance, at least on a crude scale. Weta density on each tor was calculated by dividing the mean minimum number known alive estimate by the number of liftable rocks.

Survival rates of adult weta living on large and small tors were compared using the Cormack–Jolly–Seber model, but sample sizes for small tors were again too small. Therefore

the longevity estimates of adult weta were compared using the minimum lifespan method (Ehrlich & Gilbert, 1973). To calculate the minimum lifespan of adults, weta that were not recaptured were first eliminated from the data set. Then only those adults that were marked between mid-December 1998 (the fourth survey of the study) and April 1997 were included; it was assumed that this group of individuals had recently moulted to the final adult instar and would live out their natural lifetimes within the study period, until early summer 2000/01. Analysis of the parameters influencing overall recapture and survival probabilities of marked weta, using a reduced-parameter modelling approach in the program MARK, will be presented elsewhere (P. T. Leisnham *et al.*, unpublished).

Statistical analyses

Before analysis, data were transformed where necessary to meet the assumptions of parametric tests; non-parametric tests were used when transformation failed to normalise the data. Analysis of variance using a general linear modelling approach was used to test for variation in estimates of the minimum number known alive among years and months (nested within years); Bonferroni *post hoc* tests were used to identify significantly different means. An ANOVA was also used to test for differences in mean minimum lifespan between weta on large and small tors, with individual tors nested within each tor-size category. Linear regression was used to test for a relationship between tor size and mean abundance of weta. Data from tors within the same size class were pooled to generate larger expected values, and chi-squared tests were used to test for differences in immigration and emigration rates between large and small tors. Mann–Whitney *U*-tests were used to test for differences in inter-tor distance, dispersal distances, and number of emigrants/immigrants. Data analysis followed Zar (1996) and was carried out using the program Datadesk (1998). Means and standard errors are reported throughout; all tests were two-tailed, and significance was assigned at the 5% level.

Results

Seasonal abundance and dispersal

A total of 1269 weta (480 adults and 789 juveniles; 1006 tagged and 263 painted) was marked on the study tors over three full field seasons; 602 weta were recaptured on at least one occasion. The study site was for the most part geographically isolated from other large tors. Tors close to the southern and western boundary of the study site (Fig. 2) were isolated from tors along the adjacent ridge (500 m away) by a large grassland valley that had no tors. The closest tor to the eastern boundary of the study site was 50 m away and the closest tor on the northern boundary was 300 m away. Both of these latter tors were surveyed
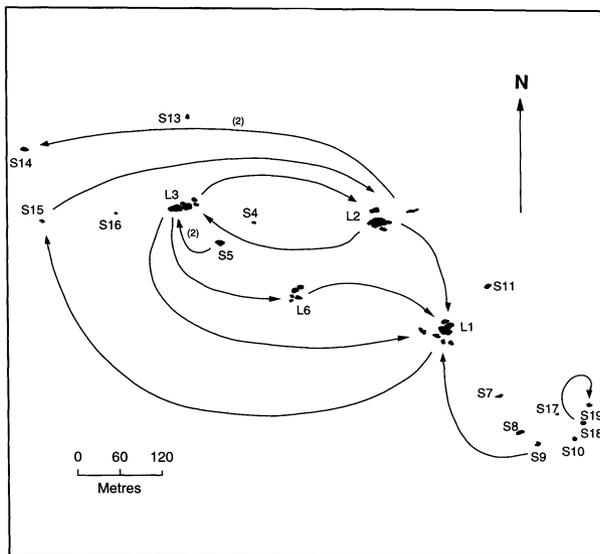
Fig. 2. A map of the study site showing the location of all large (L) and small (S) tors. Arrows indicate dispersal events between tors that occurred over three field seasons between November 1997 and April 2000. Numbers in parentheses indicate the number of times that a dispersal event involving two particular tors took place.

estimates of adult weta did not vary significantly by year (nested ANOVA, $F_{2,51} = 0.04$, $P = $ NS) or month ($F_{2,51} = 0.21$, $P = 0.06$). The only significant drop in the number of adults occurred on Tor L3 between February and March 1998 (interaction effect, $F_{2,51} = 3.20$, $P < 0.05$, Bonferroni *post hoc* test $P < 0.05$), which may have been due to predation by a possum (see Discussion). The mean number of adult weta on a tor was related positively to tor size (i.e. the number of rocks) ($R^2 = 0.89$, $F_{1,16} = 12.9$, $P < 0.01$), indicating that larger tors support larger numbers of weta.

Fourteen tagged individuals, 12 adults (2.5% of marked adults, 4.0% of recaptured adults) and two juveniles (0.3% of marked juveniles, 0.7% of recaptured juveniles) dispersed between the study tors on one occasion each (Fig. 2). A significantly higher proportion of adults dispersed than juveniles ($\chi^2 = 5.95$, d.f. = 1, $P < 0.05$). For the adults, dispersal did not vary by sex ($\chi^2 = 0.46$, d.f. = 1, $P = $ NS), with seven males (3.0% of marked males, 5.0% of recaptured males) and five females (3.2% of marked females, 5.2% of recaptured females) each dispersing on one occasion. The average dispersal distance was 361 ± 54 m (range = 36–672 m), with no significant difference in dispersal distance between adult males (368 ± 64 m) and females (433 ± 104 m) (Mann–Whitney *U*-test, $U_{5,7} = 13$, $P = $ NS). The two juveniles dispersed relatively short distances (36 and 230 m). Only three out of the 12 dispersing adults were resighted.

Effects of tor size on emigration and immigration

Not surprisingly, large tors with larger numbers of weta produced more adult emigrants on average (2.0 ± 0.71) than

twice in 1998/99 and again in 1999/2000 but no marked weta were found. Therefore, the recapture and dispersal data reported below are considered to be reasonably accurate.

A summary of the number of adults on each of the 18 tors is presented in Table 1. The minimum number known alive

Table 1. Adult population parameters for four large (L) and 14 small (S) tors. Population estimates per survey are based on the mean minimum number known alive (MNKA). Tors were surveyed between 14 and 29 times and are listed in order of largest to smallest estimate of the minimum number known alive.

Tor	Number of rocks†	Mean MNKA $\pm$ SE per survey (range)	Density (mean MNKA/rock)	Total number of marked adults resighted at least once
L2	38	27.6 $\pm$ 1.4 (11–41)	0.7	97
L1	37	25.7 $\pm$ 0.8 (20–35)	0.7	77
L3	37	20.4 $\pm$ 3.0 (3–38)	0.6	66
L6	30	8.5 $\pm$ 0.8 (2–15)	0.3	31
S14	11	3.2 $\pm$ 0.4 (0–6)	0.3	9
S11	9	2.1 $\pm$ 0.4 (0–3)	0.2	3
S8	4	1.9 $\pm$ 0.2 (0–3)	0.5	6
S5	6	1.0 $\pm$ 0.2 (0–4)	0.2	4
S15	9	0.7 $\pm$ 0.8 (0–2)	0.08	3
S9	11	0.6 $\pm$ 0.2 (0–3)	0.05	2
S19	3	0.3 $\pm$ 0.2 (0–2)	0.1	1
S17	3	0.1 $\pm$ 0.1 (0–1)	0.03	1
S4	4	0.1 $\pm$ 0.1 (0–1)	0.03	0
S18	3	0.1 $\pm$ 0.1 (0–1)	0.03	0
S7	9	0.0	0.0	0
S10	6	0.0	0.0	0
S13	5	0.0	0.0	0
S16	5	0.0	0.0	0

†These were rocks large enough for adults and large juveniles to shelter under.

Table 2. The number of weta that were resident on, emigrating from, and immigrating to large and small tors in the study area.

Tor size		Number of residents	Number of emigrants	Number of immigrants	Emigration rate	Immigration rate
Large	Adults	263	8	9	0.0295	0.0331
	Juveniles	258	1	1	0.0039	0.0039
	Sub-total	521	9	10	0.0170	0.0188
Small	Adults	25	4	3	0.1212	0.0938
	Juveniles	42	1	1	0.0233	0.0233
	Sub-total	67	5	4	0.0658	0.5333
	Total	588	14	14	0.0231	0.0231

small tors (0.5 ± 0.27) (excluding six small tors where there were no recaptured adults) (Mann–Whitney U-test, $U_{4,8} = 37.5$, $P < 0.05$). The same was true for the number of immigrants (large tors: 2.3 ± 0.85, small tors: 0.2 ± 0.15; $U_{4,14} = 57.5$, $P < 0.01$), presumably because the four large tors provided a larger target area for a dispersing weta than the 14 small tors. The four large tors were close to the mid-point of the study site (Fig. 2), so it was possible that the higher number of immigrants to large tors was due to their central location rather than their size *per se*. Of the nine adult weta that immigrated to large tors, however, five actually bypassed the closest large tor and settled further away. Overall, only three of the 14 weta that dispersed (including the two juveniles) moved to the closest neighbouring tor.

The mean minimum lifespan of adult weta on large tors (209 ± 21 days) and small tors (185 ± 50 days) did not differ significantly (nested ANOVA, $F_{1,56} = 43.14$, $P = $ NS). Although large tors had larger absolute numbers of emigrants and immigrants (see above), small tors had a significantly higher emigration and immigration rate than large tors (emigration rate: $\chi^2 = 5.81$, $P < 0.05$; immigration rate: $\chi^2 = 5.33$, $P < 0.05$; Table 2).

All but one of the 18 tors were occupied during the course of the study. The one unoccupied tor (S13) was on the northern boundary of the study area (Fig. 2) and had a small stream running between it and Tor L3; both of these factors may have made it more isolated and contributed to the lack of colonisation. Tors S14 and S15 were also found along the same boundary of the study area as S13 but were not separated from L3 by a stream. An extinction event was also recorded on Tor S4, where no weta were sighted for nearly 2 months at the end of the study. A further three tors (S10, S15, S16) had no weta sighted on them for 1 month to 1 year before being recolonised. In two of these cases (S10 and S16), the tors were recolonised by unmarked juvenile weta. In the remaining case, Tor S15 was recolonised by an adult female weta marked on Tor L1. The mean distance to the closest large tor did not differ significantly among the five small tors that experienced extinction events (138 ± 28 m) and the nine that did not (156 ± 22 m) ($U_{5,9} = 35.0$, $P = $ NS). Therefore, except for Tor S13 (see above), the degree of isolation did not seem to influence the small numbers of extinctions and recolonisation events.

Discussion

Most insects disperse to new habitat during the adult stage when their wings develop (Gullan & Cranston, 2000). Despite being flightless, *H. maori* appear to follow this trend because a significantly higher proportion of adults than juveniles dispersed between tors. Although juveniles lose their mark when they moult, it was presumed that the relatively frequent rate at which tors were surveyed increased the likelihood of detecting dispersing juveniles. It is not clear how weta find their way between tors. Although weta are sensitive to vibrations, touch, and possibly air-borne chemicals, they are unlikely to be able to see objects at long distances (Field, 2001b). In only three of the 14 cases of dispersal did weta move to the closest neighbouring tor, suggesting that dispersal direction patterns might be random.

Do *H. maori* living on tors represent a metapopulation? The relatively low dispersal rate between tors and the low frequency of colonisation events recorded in this study suggest that weta on rock tors act like semi-isolated *island* populations, agreeing with conclusions of a preliminary study by Jamieson *et al.* (2000); however *H. maori* live in sufficiently high numbers on large tors, and a few adults disperse relatively long distances (for a flightless insect), that the observed dispersal rate can generate enough migrants to potentially colonise or recolonise uninhabited tors. Thus, weta in the Rock and Pillar Range fit the requirements of a metapopulation: a network of discrete local populations on habitat fragments that are connected by dispersal (Hanski, 1999). Very similar metapopulation dynamics have been described in a relatively sedentary species of butterfly *Plebejus argus* (Lewis *et al.*, 1997).

The dispersal rate of *H. maori* was low; only 12 of the 300 recaptured adult weta (4%) emigrated to a neighbouring tor. A model has recently been developed and applied to a metapopulation of the butterfly *Melitaea diamina*, which has a relatively high dispersal rate (8.3%, $n = 372$), to estimate mortality rates during migration and scale migration rates with habitat patch area and isolation (Hanski *et al.*, 2000). It remains to be seen whether such a model can usefully be applied to a metapopulation with a much lower emigration rate (Davidson *et al.*, in prep.). Nevertheless, metapopulations with low dispersal rates can still have

enough gene flow to result in limited genetic differentiation (e.g. Lewis *et al.*, 1997). Indeed, an earlier molecular genetics study of *H. maori* found little genetic structure across a large area of the Rock and Pillar Range (King, 1997).

Rock tors can vary considerably in size. The number of weta on a tor is correlated positively with tor size (i.e. number of rocks), therefore larger tors support larger populations of weta. Assuming that weta are unable to see or detect distant tors and the fact that many dispersers settled beyond the nearest adjacent large tor, dispersal direction might be random and/or the arrival at a particular tor might be the result of chance. Although large tors generated more emigrants in total, proportionally more weta emigrated from small tors, presumably because small tors or habitat patches have higher perimeter to area ratios than large tors/habitat patches (Kareiva, 1985). This effect of patch size on the dispersal dynamics of *H. maori* is seen commonly in many metapopulations (reviewed by Harrison, 1991), and is what would be expected if *H. maori* were responding to habitat geometry (Kareiva, 1985). The higher emigration rate found on small tors/habitat patches is likely to be a factor contributing to their higher frequency of extinctions compared with large habitat patches (Kindvall, 1999).

Although adults on large and small tors had similar mean lifespans, the four extinction events that were observed all occurred on small tors, suggesting that they are more prone to extinction. Although much longer studies are required to estimate extinction rates properly, the results are consistent with the hypothesis that local extinctions should be related inversely to patch size, due to increased demographic stochasticity and higher emigration rates (Harrison, 1991; Hanski, 1999; Kindvall, 1999), and also support patterns found in studies of other insects (e.g. bush crickets; Kindvall & Ahlén, 1992). Little support was found for a relationship between distance from nearest large tor (i.e. degree of isolation) and probability of extinction (see Hanski, 1999), perhaps because most tors on the study area were similar distances apart. Small peripheral tors further from the main study area do exist and presumably these would be less likely to be recolonised if their populations went extinct. Although extinction events may be more common on small tors, their overall impact on the regional dynamics of *H. maori* might be minimal because small tors hold a relatively small proportion of the overall population compared with large tors; however even the very largest population in the study had a relatively small number of weta and would still have a significant risk of extinction.

The one significant drop in the estimated number of adult weta on one of the large tors (L3) in 1998 might have been due to predation by a brush-tail possum *Trichosurus vulpecula* that had established a den on the tor. Possums, which were introduced from Australia, are known to eat weta occasionally (Gibbs, 1998), but occur in low densities in alpine areas including the Rock and Pillar Range (B. McKinley, pers. comm.). Theory predicts that a metapopulation should have a much lower probability of extinction than one large population with equivalent overall numbers of weta because the risk of a localised catastrophe (such as the arrival of a large transient predator like a possum) would be portioned among individual isolated tors (Harrison, 1991; Hanski, 1999).

In summary, *H. maori* living in naturally fragmented habitat patches conform to many of the predictions of metapopulation theory even though they are flightless, show relatively low dispersal rates, and occur in low densities. Extinction and colonisation events are more common on small tors yet may be relatively unimportant for the long-term survival of the metapopulation because they are confined to the smallest habitat patches, which support the smallest proportion of the overall population.

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