

Habitat complexity and management intensity positively influence fledging success in the endangered hihi (*Notiomystis cincta*)

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Abstract: Age and structure of local vegetation (habitat complexity) are commonly assumed to be indicators of habitat quality for breeding birds, but for many species these relationships are poorly understood. The hihi (stitchbird *Notiomystis cincta*), an endangered New Zealand cavity-nesting passerine that only survives on mammalian predator-free islands or within fenced areas, has been the focus of intensive conservation management and research. Between 1992 and 2004 we examined the fledging success of 347 nests from four island populations. Habitat quality was improved at the two scrub/regenerating sites and one of the two mature/ climax sites through management using supplementary feeding, nest-box parasite control or both. At two sites (one mature, one regenerating) management was stopped during the study allowing us to measure fledging success with and without habitat quality improvement through management. At the population level, the number of chicks fledged per nest increased as management intensity increased and habitat quality increased. The positive effect of management was greatest for populations in lower quality habitats. To assess the relationship between fledging success and local habitat variables around the nesting site we used a height-frequency vegetation survey method sensitive to changes in vertical structural complexity at the two mature/climax sites. For 36 natural nests, a cross-validated regression-tree analysis ($R^2 = 0.69$) predicted that as habitat complexity increased, so did fledging success, which was generally higher for nests in trees with larger diameters (present in older forests). Because these habitats are free from nest predators, our results suggest that habitat age and complexity are proxies for habitat quality through effects on nestling food availability and/or nest-chamber characteristics. Our results support the current management approach of providing supplementary food to translocated hihi populations and suggest that supplementary food can be used to overcome resource deficiencies for this species in poorer quality habitats.

Keywords: breeding success; conservation management; food supplementation; nest predation; reintroduction; stitchbird; translocation

Introduction

Breeding habitat quality, defined as the local resources and conditions that influence reproduction by a given organism (Johnson 2007), is strongly linked to the sustainability of local populations (Newton 1998). Habitat quality may be largely influenced by the spatial configuration, productivity, and diversity of local vegetation, which are all measures of habitat complexity (Smith & Shugart 1987; Halaj et al. 2000). Thus, conservation managers often aim to improve local environmental conditions when addressing poor population growth of focal, at-risk species by manipulating characteristics associated with these factors, including (1) habitat restoration (e.g. revegetation; Komdeur & Pels 2005), (2) supplementary feeding (e.g. to compensate for lack of natural food plants; Edmunds et al. 2008), (3) providing shelter or nesting sites (e.g. nest boxes for sites with few mature trees; Castro et al. 2003), and (4) reducing predation risk (Moorhouse et al. 2003). Although adult survival is important in determining population growth (Newton 1998), conservation intervention may primarily target reproductive rates because these are often the vital parameters that are most easily measured and are responsive to short-term changes in environmental conditions (Stearns 1992; Morris & Doak 2002).

Food availability can be a major factor limiting reproductive success (Newton 1998); thus, food supplementation is a commonly used conservation tool worldwide when the goal is to increase reproductive output in focal populations (e.g. Treby et al. 2007; Schoech et al. 2008). However, supplementary feeding can be labour intensive, potentially limiting its applicability to recovery projects or easily accessible areas within a species' range. This suggests that in order to minimise constraints on population growth resulting from limited management resources, species translocations and reintroductions should aim to shift species into areas where the availability of natural food and breeding sites can satisfy the year-round demands of a growing population. Such an approach is one of the current goals of the recovery plan for the New Zealand hihi (stitchbird *Notiomystis cincta*; Taylor et al. 2005). However, for many species under conservation management it is unclear how best to assess habitats in terms of their quality to the focal species and to what degree supplementary food can compensate for reduced-quality habitats.

Until the widespread invasion of exotic mammalian predators in mainland New Zealand, the hihi was found throughout the forests of New Zealand's North Island (Buller 1888; Innes et al. 2010). However, by the late 1800s only a single relict population remained on Hauturu (Little Barrier Island), a

nature reserve off the north-east coast of the North Island (Taylor et al. 2005; Fig. 1). Since the 1980s, translocations to various predator-free locations have been attempted (Armstrong et al. 2002; Taylor et al. 2005; Bell et al. 2006). Until now these translocations have not resulted in self-sustaining hihi populations and have only been successful when supported by ongoing management involving year-round supplementary feeding and, where necessary, providing nesting boxes and nest parasite control (Armstrong & Ewen 2001; Armstrong et al. 2002, 2007; Castro et al. 2003; Taylor et al. 2005; Hihi Recovery Group pers. comm.). Evidence supporting the idea that the provisioning of supplementary food is important for improving population growth parameters for translocated hihi populations primarily comes from three sites: Mokoia Island, Kapiti Island and Tiritiri Matangi Island. Within-site comparisons for these islands show that the complete removal of supplementary food was associated with population declines and dramatic decreases in reproductive output of hihi (Armstrong & Ewen 2001; Castro et al. 2003; Taylor et al. 2005; Armstrong et al. 2007). In all cases, the re-establishment of supplementary feeding reversed population decline and increased reproductive output. The hihi population on Little Barrier Island (the source of all other hihi populations) continues to persist without any direct management. Consequently, it is assumed that the intact and diverse forest habitat present on the island provides significantly better feeding opportunities than those found at translocation sites (Taylor et al. 2005) and, potentially because of this, supports positive population growth through high survival and reproductive rates.

Despite the assumption that the old-growth forest on Little Barrier Island is a high-quality habitat for hihi and, thus, should guide the choice of future translocation sites (e.g. White 2008), there is currently little known about the demography of the hihi population (Rasch 1985; Toy unpubl. report 2010). In addition, the relationships between habitat complexity and productivity are generally unclear, especially in natural systems with no nest predation and limited adult predation (cf. Eggers et al. 2005).

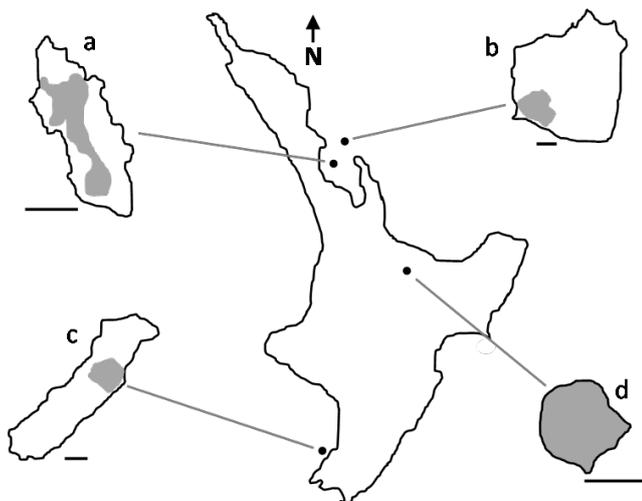


Figure 1. Location of the four island study sites relative to New Zealand's North Island (centre): (a) Tiritiri Matangi Island ($36^{\circ}36' S$, $175^{\circ}53' E$; 220 ha), (b) Little Barrier Island ($36^{\circ}12' S$, $175^{\circ}07' E$; 3083 ha), (c) Kapiti Island ($40^{\circ}50' S$, $175^{\circ}56' E$; 1965 ha) and (d) Mokoia Island on Lake Rotorua ($36^{\circ}06' S$, $175^{\circ}55' E$; 135 ha). The grey shading within each island represents the locations where hihi were monitored; the black bars beneath each island show their relative scale (1 km).

For the current study we used information on reproductive rates collected from the Little Barrier Island population (Makan 2006) and compared these with the translocated island populations for which we had comparable demographic data from past studies (i.e. Kapiti Island (Castro et al. 1994), Mokoia Island (Castro et al. 2003) and Tiritiri Matangi Island (Low et al. 2007); Fig. 1). These island populations are ideal for studying general questions regarding the effect of habitat complexity and quality on reproductive rates because (1) the islands are free from introduced mammalian predators and avian nest predators that could prey on hihi inside nest boxes and natural cavities and confound measures of productivity, (2) the islands differ dramatically in the age and structure of the dominant forest and the history of management intervention, and (3) the introduced populations have detailed long-term data on reproductive success from individually-marked birds. In addition, we collected information on a range of characteristics describing the structural complexity of vegetation around natural nest sites.

From these data, we examined the relationship between reproductive success (i.e. number of chicks fledged per nesting attempt) and probable indicators of habitat quality (i.e. management intensity and habitat maturity). Specifically, we hypothesised that (1) productivity should increase as management intensity increased (e.g. the addition of supplementary food) and (2) productivity should increase as local forest habitats mature and provide greater foraging and nesting opportunities (i.e. as habitat quality increases). Thus we expected that, in the absence of management, individuals on islands with mature forest (e.g. Little Barrier Island) should produce the highest number of fledged young per nesting attempt when compared with islands with younger forests (e.g. Mokoia Island). In addition, we expected within-island comparisons to show the productivity of birds would be higher in areas with local habitat variables associated with more mature habitat (e.g. greater structural complexity, larger tree size). From these correlations our aim was to gain a better understanding of the relative importance of factors determining habitat quality in this species and relate this to current management practices, providing advice for future management of this species and possibly other cavity-nesting species.

Methods

Study species

The hihi is a medium-sized (28–43 g), cavity-nesting, sedentary, endemic New Zealand passerine that breeds during the austral spring and summer (September to February; Higgins et al. 2001; Castro et al. 2003). Females lay up to five eggs per nesting attempt and pairs can successfully raise two broods per season (Higgins et al. 2001; Castro et al. 2003). Females incubate eggs for approximately 15 days, with chicks fledging 28–31 days after hatching (Higgins et al. 2001; Castro et al. 2003). Fledglings remain near their nest and continue to receive food from their parents for the first 7–14 days after leaving the nest (Higgins et al. 2001). Hihi feed on nectar, fruit and insects (Gravatt 1970; Angehr 1984 in Rasch et al. 1996; Rasch 1985; Castro et al. 1994; Castro & Robertson 1997; Higgins et al. 2001), with the proportion of insects in the diet reaching its peak during breeding (Rasch 1985; Castro et al. 1994). Both male and female hihi provision the young, with male contribution generally being lower than that provided by the female (Castro et al. 1994, 2003; Low et al. 2006, 2012).

Table 1. Summary habitat and management data for hihi (*Notiomystis cincta*) under different management scenarios on four islands in New Zealand used in this study to model the effects of management and habitat on fledgling success.

Island	Forest	Assumed habitat quality	Supplementary food	Parasite control	Nesting sites	Years	No. nests used
Little Barrier	Old	High	No	No	Natural	2004	23
Kapiti	Mature	Moderate	No	No	Natural	1992–1993	21
			Yes	No		2000–2004	54
Mokoia	Regenerating	Low	Yes	Yes	Boxes	1994–1998	50
			No	No		1999–2000	20
Tiritiri Matangi	Regenerating	Low	Yes	Yes	Boxes	1995–2004	179

Study areas

We compared hihi reproductive rates among four island populations off New Zealand's North Island with differing habitat characteristics and history of management (Fig. 1; Table 1; see also Low et al. 2012). Little Barrier Island is dominated by old-growth tall-forest habitat (>20 m high) with dense understorey; much of the island has remained undisturbed for >150 years (Hamilton 1961). The Little Barrier hihi population is not managed and the birds nest in natural tree cavities (Rasch 1985). For this study hihi nests were monitored in 750 ha in the south-western corner of the island (Fig. 1) that is dominated by mature rātā (*Metrosideros robusta*), tawa (*Beilschmiedia tawa*), kauri (*Agathis australis*), pōhutukawa (*Metrosideros excelsa*) and kānuka (*Kunzea ericoides*) forest (Hamilton 1961). The density of hihi in this part of the island ranges from 1.2 to 4.5 hihi per hectare (Toy unpubl. report 2010).

Kapiti Island retains approximately one-third of its area as tall forest that has not been logged since the early 1900s (>25 m high; Fuller 1985). Introduced mammals were eradicated by 1996 (Clout & Russell 2006). Our studies were conducted in a 185-ha area of forest on the central western section of the island where hihi were established by translocation (Fig. 1). The study area consisted of six forest types, as defined by Fuller (1985): kohekohe (*Dysoxylum spectabile*), kānuka, tawa/hinau (*Elaeocarpus dentatus*), five-finger (*Pseudopanax arboreus*), māhoe (*Melicactus ramiflorus*) and tawa/kāmahi (*Weinmannia racemosa*). Hihi were translocated to Kapiti Island on six occasions between 1983 and 1992 (Castro et al. 1994; Taylor et al. 2005) with the number of adult hihi declining to only one male and two females in 1990 (before the 1991 and 1992 translocations), and later to two males and nine females in 2000. Supplementary feeding (20% by volume sugar solution) was then instigated in the core breeding area; the population has since grown to >144 adults in 2007 (Gorman et al. unpubl. report 2008) with supplementary food freely available from 10 feeding stations during the breeding season. During the study, all adults were individually colour-ringed. Although some nest boxes have been provided on Kapiti Island, these are rarely used by the birds as the majority of hihi favour using natural tree cavities.

Mokoia Island, in Lake Rotorua, was cleared for cultivation and since 1950 has been allowed to regenerate naturally (Andrews 1992). Thus the island is primarily covered by low-canopy (<10 m), intermediate-successional native forest with canopy species such as māhoe, māpou (*Myrsine australis*), and cabbage tree (*Cordyline australis*), with an absence of nesting tree cavities (Perrott & Armstrong 2000). Hihi were translocated to the island in 1994 and provided with intensive management: (1) nest boxes; the number and distribution of

boxes were regulated to ensure hihi were not cavity limited; (2) nestling parasite control against the blood-sucking mite *Ornithonyssus bursa*; nest mites were effectively controlled by replacing infected nest boxes with clean ones during the nestling stage (Taylor & Castro unpubl. report 2000); and (3) ad libitum food supplementation using a nutritionally-balanced artificial nectar diet (Wombaroo honeyeater diet replacement formula; protein = 40 g L⁻¹, fat = 20 g L⁻¹, carbohydrates = 22 g L⁻¹, minerals and vitamins) from three communal food stations and several within-territory food stations around the island (Castro et al. 2003). All birds on the island were individually colour-ringed. From their introduction until 1998, the number of breeding females ranged from 7 to 15 and the total number of adult birds on the island never exceeded 33 (Castro et al. 2004). In 1998, food supplementation was stopped, which was followed by a dramatic population decline primarily because of poor reproduction and recruitment (Castro et al. 2003; Armstrong et al. 2007). Hihi were removed from the island in 2002.

Until 1971 Tiritiri Matangi Island was intensively grazed, with all but 6% of the forest cleared for pasture. Since then over 300 000 trees have been planted and approximately 80% of the island is covered with early-successional native coastal forest (canopy height generally <10 m) with an absence of nesting tree cavities and little understorey (Rimmer 2004). Pōhutukawa (*Metrosideros excelsa*) was the main tree initially replanted followed by taraire (*Beilschmiedia tarairi*), kohekohe, and pūriri (*Vitex lucens*) (Rimmer 2004). In 1995 and 1996, hihi were introduced with ongoing intensive management: (1) nest boxes – the number and location of boxes being modified each year to ensure all birds had access to breeding cavities; (2) nest parasite control using nest-box replacement or miticides (fipronil) when parasites were first detected; and (3) year-round ad libitum supplementary food as a 20% by volume sugar solution from six communal feeding stations. The individually-colour-ringed hihi population on Tiritiri Matangi has grown from six breeding females in 1996 to 1987 breeding females in 2010. Until 2004, the period covered by this study, there was no evidence of population regulation through density dependence (Low & Pärt 2009).

Data collection

Nesting success measures

We used fledgling success (i.e. the number of fledglings produced per nesting attempt; range 0–5) from first-clutch nests as the comparable measure of reproductive output between populations. We used this parameter for comparison because (1) differences in between-nest fledgling rates were overwhelmingly driven by differences in nestling survival

rather than clutch size (Castro & Low unpubl.), and that these differences were likely related to local habitat factors such as microclimate in the nest cavity (Low & Pärt 2009) and local food availability (Castro et al. 2003; Armstrong et al. 2007; Low et al. 2012), (2) fledging rates were accurately known for all populations, whereas recruitment was only known for two of the four populations (i.e. Mokoia and Tiritiri Matangi), and (3) early nest failure would be unlikely to bias our estimates of fledging rates because (a) for the Mokoia and Tiritiri Matangi populations we had complete knowledge of the population (Castro et al. 2003; Low & Pärt 2009) and (b) for Kapiti and Little Barrier, pairs were followed from nest building until fledging/nest failure. There is no nest predation in these populations and almost all nest failures occur after egg hatching because of nestling mortality mainly due to temperature-related factors (Low & Pärt 2009) or disease (Rippon et al. 2010, 2011). For sites without nest boxes, observations of provisioning behaviour by adults or eggshells under the cavity entrance provided evidence of the hatching date. Each nest was visited daily beginning several days prior to the predicted time of fledging to ensure all fledglings were located and counted soon after leaving the nest.

For the Little Barrier Island population, data were collected in late 2004 from 23 nests (Makan 2006). For the Kapiti Island population, data were collected during two periods: from 1992 and 1993 ($n = 21$; Castro 1995) when the population was receiving no supplementary food and from 2000 to 2004 ($n = 54$; DOC unpublished reports: Knegtman et al. 2001; Newell & Moorcroft 2002; Barr & Moorcroft 2003; Howard & Moorcroft 2004; Gorman & Moorcroft 2005) when the population was being food supplemented. For Mokoia Island ($n = 70$; 1994–2000) and Tiritiri Matangi Island ($n = 179$; 1997–2004), fledging rates were known exactly because all nests were in nest boxes and these were monitored daily during the breeding seasons (Castro et al. 2003; Low et al. 2006).

Habitat measurements

We used different habitat classifications depending on whether we were looking at general or local patterns in the analysis. Because we were interested in the relationship between chick fledging and habitat complexity as a measure of habitat quality, we used a simple proxy for habitat complexity in the general analyses, i.e. habitat age. To specifically look at the relationship between habitat complexity around the nest site and the number of hihi fledged in the absence of supplementary feeding, we recorded habitat information at the natural nest sites on Little Barrier Island ($n = 23$) and Kapiti Island ($n = 13$). We used the height-frequency vegetation survey method developed by Scott (1965; see also Dickinson et al. 1992; Tanentzap et al. 2009). The method records changes in vertical vegetation diversity and structural complexity and has been shown to provide a representative sample of both structural and floristic features of the local habitat (Dickinson et al. 1992).

We established five 80-m transects radiating from each nest. The direction of each transect was generated randomly with at least 10 degrees difference between transects. At 4-m intervals along each transect the height-frequency of all plant species was recorded by noting the presence of any foliage that intersected an imaginary vertical cylinder (20-cm diameter) that was projected from the forest floor to the canopy (see Scott 1965). Plant species were recorded as being present or absent in height categories along each vertical sampling point (2-m tiers with the lowest tier including an additional 30-cm ground cover category; i.e. 0–0.3 m, 0.3–2 m, 2–4 m, 4–6 m,

and so on). A 2-m pole was used to measure foliage height accurately up to 4 m; beyond that, all heights were estimated from ground level.

From these data we generated the following habitat variables for each nest: (1) the number of plant species detected in the survey (range 26–54; see Appendix 1 for a full list of species recorded); (2) a Shannon–Weiner diversity index from the summed values from transects at each site (2.39–3.47); (3) a complexity score from the summed height-frequency values at each site (i.e. the sum of all plant species in all height categories for the five transects; range 395–623; see Appendix 1 for species-level mean height-frequency values); (4) a complexity score from the summed height-frequency values of nectar-producing species at each site (i.e. the sum of nectar-producing plant species in all height categories for the five transects; range 144–387); (5) island identity; (6) local topography (ridge, face, gully); (7) diameter at breast height (dbh) of the nest tree (36–230 cm); (8) altitude above sea level (18–320 m); (9) aspect of the slope (N, S, E, W).

Analysis

Effect of habitat age and management on fledging success

We used generalised linear mixed models (GLMM; package ‘lme4’ (Bates et al. 2012) in R; R Development Core Team 2012) to predict the influence of habitat and management factors on fledging success. Habitat was defined as a two-level categorical variable (‘mature older forest’ – Little Barrier and Kapiti; vs ‘regenerating young forest’ – Mokoia and Tiri) for the analysis. Because specific management factors were sometimes confounded by site (e.g. nutritionally balanced supplementary formula was only used on Mokoia, nest box management was not used on Kapiti), we created a simple two-level management variable (yes or no) related to the provisioning of supplementary food. The structuring of the variables in this way ensured we could reliably estimate the direction of the habitat age and management effects and their interaction. The simple addition of nest boxes to an island was not considered management because of evidence that hihi on Kapiti and Little Barrier are not limited by nest cavity availability and continue to use natural cavities when nest boxes are available (Rasch 1985; Castro et al. 1994); hihi on Mokoia and Tiritiri Matangi were not nest-site limited as management ensured that there were an excess of nest boxes relative to the number of females on each island (Taylor & Castro unpubl. report 2000). Habitat is confounded with supplementary feeding for some populations (e.g. we have no data for the effect of management on the Little Barrier population), and thus may still be influenced by some unaccounted-for site effects in the habitat × management interaction analysis (above).

Thus we carried out an additional set of analyses to consider finer-scaled levels of management intensity or habitat age where we partly controlled for confounding effects. For this we used data from the three islands that utilised hihi breeding management (Table 1; $n = 324$ nests) and created a ‘management’ variable with four categories of increasing management intensity and related these to number of chicks fledged: (1) no management or only providing nest boxes, (2) supplementary sugar water, (3) supplementary sugar + nest box parasite management, (4) sugar + nest box management + protein. Similarly, we created a three-level habitat age variable for sites of varying age where we had information on numbers of fledglings during periods of no management (i.e. young = Mokoia, mature = Kapiti, old = Little Barrier Islands; $n = 64$ nests).

We fitted models using a Poisson distribution with a log-link to constrain estimates above zero (estimated multiplicative overdispersion 0.96 ± 0.06). All models included random-effects terms (identity of the female parent, year, and island) to account for potential between-year non-independence for birds that had more than one monitored nest and possible within-island effects. We created a balanced candidate model set through combinations of the two parameters (habitat and management) and their interaction term. Models were compared and ranked using the Akaike Information Criterion corrected for sample size (AIC_c). Parameter estimates for model predictions were derived from model averaging based on AIC_c model weights (Burnham & Anderson 2002). Confidence intervals for predictions are Bayesian 95% credible intervals generated using a Gibbs-sampler (JAGS; Plummer 2003) called from R (R Development Core Team 2012).

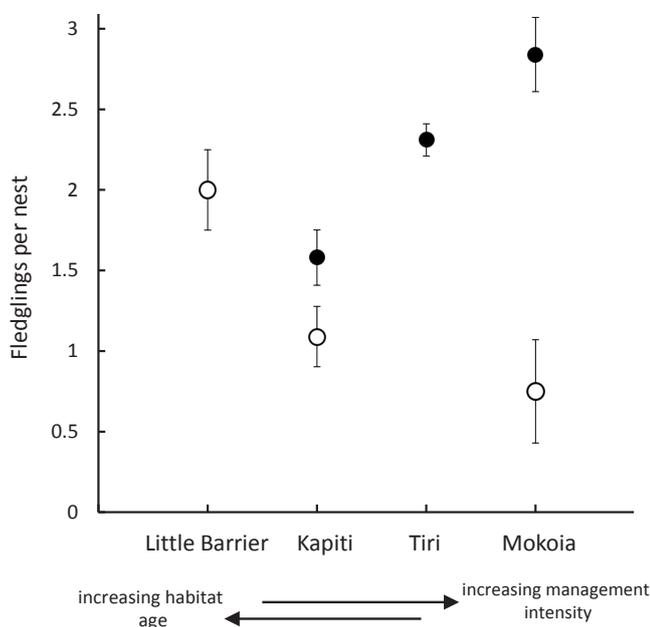


Figure 2. The number of chicks fledged (mean \pm SE) from first-clutch nests at the different island sites. Closed circles show number of fledglings during periods of management; management intensity increases from left to right from sugar water (Kapiti Island), to sugar + parasite control (Tiritiri Matangi Island), to commercial nutritionally balanced artificial nectar + parasite control (Mokoia). Open circles show number of fledglings during periods of no management; habitat age increases from right to left; regenerating = Tiritiri Matangi Island and Mokoia Island, mature = Kapiti Island, climax = Little Barrier Island.

Effect of local habitat complexity on fledging success

Regression trees are a non-parametric recursive partitioning procedure, constructed by continuously dividing data into mutually exclusive groups by comparing every possible binary split in every independent variable and choosing the division that minimises heterogeneity of the dependent variable in the resulting two groups (De'ath & Fabricius 2000; Low et al. 2006). This process is then repeated on the next grouping level; thus, the output resembles a tree-diagram with a single node at the top containing the entire dataset, with each branch a decision-rule based on the values of an independent variable leading to a subset of the data. To determine the optimal tree size, i.e. the number of data divisions, we first grew the tree to its maximum size and then pruned it back to the size that best predicted excluded data. This leave-one-out cross-validation procedure involved excluding one observation, reconstructing the model and then predicting the response of the excluded observation. This was repeated for the entire dataset, with a correlation coefficient derived from comparing predictions to observations for each tree size. Regression trees were analysed and cross-validated using macros written in the MatLab[®] programming language.

Results

Effect of management and habitat age on fledging success

The number of chicks successfully fledged per nest from first broods was positively related to management and habitat age (Fig. 2; Table 2). There was overwhelming support ($AIC_c w_i = 0.99$) for management and habitat effects largely being traded off against each other; i.e. older habitats had little benefit from management, while younger sites showed large effects of management – mean (95% credible interval) for model estimates: mature forest = 1.47 (1.17–1.82) fledglings per nest; mature forest + management = 1.57 (1.29–1.88); immature forest = 0.73 (0.42–1.15); immature forest + management = 2.39 (2.22–2.58).

For the finer-scaled analyses that separately considered management or habitat age, both factors were related to an increased number of chicks fledged (Fig. 2). There was overwhelming support for increasing management intensity resulting in increasing numbers of offspring fledged (GLMM with management categories vs model without: $AIC_c = 529.9$ vs 571.5 respectively; estimates for mean number of chicks fledged per nest (\pm SE) for each management category (numbered 1–4 to indicate increasing intensity): 1 = 0.96 ± 0.13 ; 2 = 1.65 ± 0.28 ; 3 = 2.4 ± 0.36 ; 4 = 3.09 ± 0.53). Similarly, looking at the number of hihi fledged from sites with no management,

Table 2. AIC_c -ranked candidate model set showing the relative importance of habitat and management factors influencing hihi (*Notiomystis cincta*) fledging success (habitat = mature/old vs regenerating/young; management = yes vs no). Additive effects are shown as +, interactions as \times , and the number of estimated parameters as k . Models fitted the number of fledglings as a Poisson distribution and included nest site and year as random factors. ΔAIC_c shows the AIC_c relative to the best model ($\Delta AIC_c = 0$); AIC_c weights (w_i) show the relative strength of support for each model.

Models of fledging success	k	AIC_c	ΔAIC_c	w_i
Habitat + management + habitat \times management	6	564.2	0	0.99
Management	4	572.9	8.75	0.01
Habitat + management	5	574.9	10.8	0
Habitat	4	587.7	23.5	0
Intercept only	3	592.1	27.9	0

increasing habitat age had strong support in explaining fledgling output (GLMM with habitat categories vs model without: AIC = 111.3 vs 116.4 respectively; Fig. 2).

Effect of local habitat on fledging success

Local habitat complexity (i.e. the summed height-frequency values from transects around nest sites; Fig. 3) and nest-tree diameter were useful predictors of hihi fledging success from natural nests without food supplementation (Fig. 4). The optimised regression-tree explained 69% of the variation in fledging success (cross-validated, $R^2 = 0.69$) predicting that as habitat complexity increased, so did fledging success. Within the habitat-complexity categories used, fledging success was generally higher for nests in trees with larger diameters (Fig. 4). We obtained a similar pattern when the regression-tree analysis was rerun using separate complexity scores for different height categories (< 0.3 m, 0.3–6 m, 6–12 m, 12–26 m, > 26 m), rather than a single summed complexity score. Subcanopy complexity score for the initial division (0.92 fledglings for complexity <150 vs 2.17 fledglings for complexity >150), and ground cover complexity score (1.0 fledglings for complexity < 38 vs 2.35 for complexity >38) and tree diameter (0.38 fledglings for dbh < 120 cm vs 1.8 fledglings for dbh > 120 cm) for the subsequent division, were useful predictors of fledging success (cross-validated $R^2 = 0.49$).

Discussion

We found a positive association between habitat complexity and fledging success, with nests in older and more structurally diverse habitats fledging more chicks. Similar habitat associations have been found in other studies (e.g. Conner et al. 1986; Braden et al. 1997; Eggers et al. 2008). Our study,

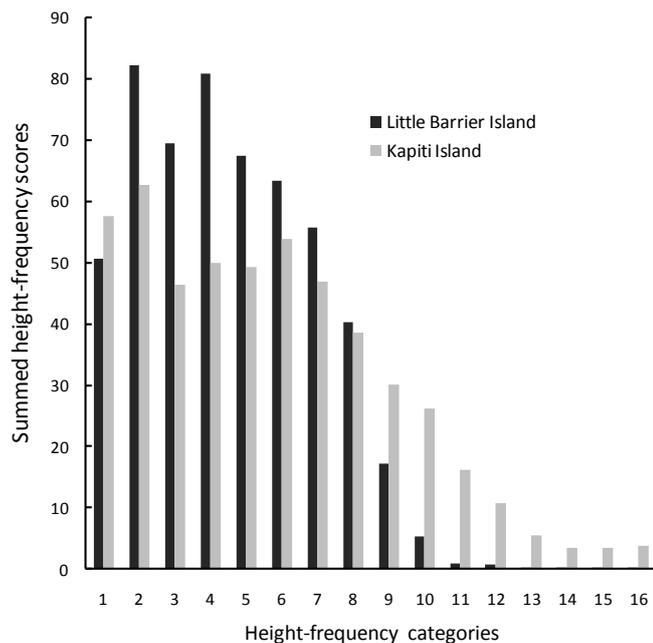


Figure 3. Summed habitat-complexity scores around natural nests on Little Barrier Island and Kapiti Island for different height categories. Height-frequency category 1 = 0–0.3 m above ground level; category 2 = 0.3–2 m; subsequent categories are 2-m-high consecutive tiers (i.e. 2–4 m, 4–6 m, etc.).

however, is free from the confounding effects of nest predation (Angehr 1984 unpubl.; Low 2004; Innes et al. 2010) allowing us to quantify the association between habitat and habitat-associated resources, such as the potential food available to birds (e.g. via a higher diversity of food-producing trees or invertebrates).

The islands with younger forests and presumed lower habitat quality (i.e. Mokoia and Tiritiri Matangi) received more intense management compared with the more mature habitat of Kapiti Island. Thus, the relatively higher effect of management on the poor-quality islands is likely to result from this confound. Indeed, the raw data and secondary analyses show clear patterns in the number of chicks fledged as (1) the intensity of management increased from nest parasite control to the addition of simple and nutritionally-balanced supplementary foods and (2) the vegetation structure changed from regenerating bush (Mokoia and Tiritiri Matangi) to mature forest (Kapiti) to complex old forest (Little Barrier) (Fig. 2). We found strong support for sugar and protein supplementation helping to ameliorate deficiencies due to poor habitat quality (i.e. regenerating forest; Table 2). Indeed, nests in the poorer-quality habitats that received the most intensive management (i.e. parasite control, supplemented sugar and protein) had higher fledging rates than unmanaged nests in the higher-quality habitat of Little Barrier Island (Fig. 2).

Management intensity and fledging success

All reintroduced hihi populations are currently supplemented with sugar water to some extent and, in some cases, nestling ectoparasite control (Castro et al. 2003; Bell et al. 2006; Armstrong et al. 2007; Low et al. 2007). Our results support the use of this management to enhance local habitat quality and increase the number of fledglings produced per nest. Also, results suggest that these factors (i.e. ectoparasite control, sugar supplementation, protein supplementation) are additive with respect to the number of chicks that successfully fledge. It is likely that food supplementation has the highest relative benefit of the management factors examined, with support for this coming not only from our results, but also from the history of hihi management during the past three decades:

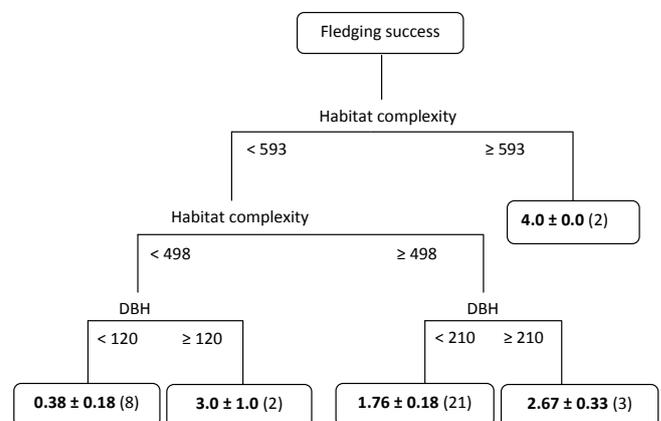


Figure 4. Regression tree output showing the relationship between the number of hihi (*Notiomystis cincta*) chicks fledged from natural nests ($n = 36$; terminal nodes show prediction means \pm SE (n)) and general habitat complexity (i.e. summed height-frequency values for all height categories) and nest tree diameter at breast height in centimetres (dbh).

(1) on Mokoia Island, population growth estimates were largely linked to the effect of supplementary food on nestling survival (Armstrong & Perrott 2000; Armstrong et al. 2007); and female productivity was increased at the laying, fledging and recruitment stages by food supplementation (Castro et al. 2003); (2) on Kapiti Island in the years before supplementary food being widely available, fledging success was low and the population generally declined following each translocation. This trend was reversed when sugar water was accessible to all birds and permanently maintained, with the population rapidly expanding during this time (Gorman et al. unpubl. report 2008); (3) on Tiritiri Matangi Island, an experimental test of supplementary feeding showed that it increased both condition and survival of adult birds (Armstrong & Ewen 2001); and (4) the failed hihi translocations in the 1980s (i.e. Hen and Cuvier Islands; Higgins et al. 2001) were to islands without any management intervention. This positive effect of supplementary feeding on the reproductive output of hihi appears to be mediated through higher parental feeding rates (Low et al. 2012) and possibly higher female survival (Castro et al. 2003).

Little Barrier Island, where hihi have persisted since at least the 1800s, is the only location where hihi are currently found to sustain population size without management. Despite this, the rate of fledging production was lower compared with populations from relatively poor quality habitats with food supplementation and parasite control (Fig. 2). This suggests that the reproductive output of managed populations is unusually high and driven by freely available food resources and, to some extent, lower parasite loads. Thus, even when hihi are introduced into areas with the potential for them to be self-sustaining without management (e.g. complex forest habitats like Little Barrier Island), it is likely that fledging rates in these populations could be increased if necessary with additional management.

Forest age, habitat complexity and fledging success

In the general analysis it was clear that fledging rates were not only influenced by management factors, but also a habitat classification related to forest age (i.e. immature regenerating forest vs mature old forest; Fig. 2), which was broadly related to forest structural complexity and diversity. Our results suggest that under conditions of food supplementation these habitat effects would become redundant with respect to reproductive success. This association between habitat age and hihi productivity was further strengthened by the analysis of natural nesting sites, and the relationship between their local habitat variables and fledging success. Of the nine variables we considered, only local habitat complexity (as measured by summed height-frequency scores of vegetation) and the nest tree diameter at breast height were good predictors of fledging success – both factors are correlated with habitat age.

The final regression-tree analysis, where we divided the height-frequency complexity scores into five categories, suggests that it is vegetation structure and probably diversity in the lower to mid-sections of the forest (i.e. <12 m high) that are most important for hihi. Although this is based on only 36 nests, this result is supported by two other pieces of information. First, we know that competition between hihi, bellbirds (*Anthornis melanura*) and tūī (*Prosthemadera novaeseelandiae*) leads to species-specific partitioning of vertical space in the forest, with hihi mainly utilising resources in the lower to mid-sections (Rasch & Craig 1988; Wilson 1997). Because invertebrates account for a large proportion of nestling diets (Castro et al.

1994; Newton 1998), and vegetation structural complexity is positively correlated with invertebrate abundance (e.g. Conner et al. 1986; Huhta et al. 1998; Halaj et al. 2000), it stands to reason that vegetation complexity in these forest layers would have positive benefits for hihi fledging success. Second, the habitat age analysis showed that in the absence of management, natural nests on Little Barrier Island had higher fledging rates than nests on Kapiti Island (Fig. 2). This was not related to a generally greater level of vegetation complexity (as measured by summed height-frequency) on Little Barrier Island, but rather to a much greater level of vegetation complexity in the lower to mid-sections of the forest on Little Barrier Island as compared with Kapiti Island (Fig. 3).

The diameter (dbh) of the nesting tree was also positively correlated with hihi fledging success. Because there are no cavity predators in this system, the effect of tree size on fledging success could be related to the stability of the microclimate within the nest cavity (Sedgeley 2001; Wiebe 2001); this has been observed in other cavity-nesting species (e.g. tree swallows *Tachycineta bicolor*, Dawson et al. 2005; acorn woodpeckers *Melanerpes formicivorus*, Hooge et al. 1999). For hihi, sudden fluctuations in temperature within the nest cavity are known to be lethal for nestlings; in poorly insulated nest boxes these high ambient temperatures are associated with nestling mortality (Low & Pärt 2009). Alternatively, dbh could be related to the maturity of the local vegetation and thus be an index for foraging opportunities around the nest site, and this deserves further study.

Despite our results being generally consistent with expectations, we recommend some caution when interpreting the among-population comparisons in this study. First, the Little Barrier Island data are limited to a subsample of the population during a single year, while other studies sampled entire populations across multiple years. Thus, the variation in reproductive parameters as a result of environmental stochasticity in the Little Barrier Island population still needs to be investigated. Second, the number of chicks successfully fledged from first-clutch nests may not necessarily be a comparable measure of reproductive output between populations. Hihi commonly double brood, which has statistically significant effects on individual reproductive output (Castro et al. 2004; Low et al. 2007). However, the probability of double brooding within populations may be related to factors not accounted for in our study. Similarly, recruitment rates may differ between populations (i.e. proportion recruited per individual fledged), further distorting the relationship between fledging rates and population growth. Third, population viability is not only related to reproductive output, but also to juvenile and adult survival probabilities. For example, because of low rates of adult survival, the Mokoia Island population was marginally viable despite having fledging rates higher than those measured for Little Barrier Island (Armstrong et al. 2007). Finally, the degree to which inbreeding depression might affect reproductive output in these bottlenecked populations (Castro et al. 2004; Low & Pärt 2009; Brekke et al. 2011) may be population specific.

Management implications

Regardless of the method used to measure habitat quality as a function of local vegetation characteristics (e.g. permanent plots, Wardle & Guest 1977; percentage cover, Allen 1992; point-sampling, Halliwell et al. 1995), it is necessary that

these measurements explain a large proportion of the variation in reproduction/survival of the focal species. Because hihi glean insects and take fruits and nectar from a wide variety of forest plants (Castro & Robertson 1997; Higgins et al. 2001), we used a height-frequency sampling method that is sensitive to changes in vertical structural complexity and has been shown to provide a representative sample of both structural and floristic features of the local habitat (Scott 1965; Dickinson et al. 1992; Tanentzap et al. 2009). In our study these measures were highly correlated with fledgling production, suggesting that this method may be a useful tool for the quantitative assessment of future translocation sites. Therefore, we recommend this method be further trialled at previous and current translocation sites to gauge its accuracy in predicting hihi habitat quality over a wide range of habitats.

The structural complexity of subcanopy vegetation and degree of food supplementation are important determinants of reproductive output in hihi populations, and to a large extent appear to be interchangeable (i.e. good habitat without supplementary food \approx poor habitat with supplementary food). This means that when identifying future translocation sites both habitat quality and potential for management can be used to grade the suitability of the site. The importance of this is that the value of sites need not be judged only in terms of, for example, their vegetation quality, but should equally consider the feasibility of supplementary feeding. In New Zealand, where habitat degradation is widespread and sites with habitat structure similar to that on Little Barrier Island are extremely rare, managers have the potential to use supplementary feeding as a simple replacement for habitat complexity when choosing sites for translocation. Also, as local habitats mature, the need for this management will become less critical (however, restoration of habitat complexity may take several decades). It may be tempting to view the need for ongoing management as some sort of ecological failure to be avoided; rather, we suggest that management, in this case the provisioning of supplementary food stations, is a relatively simple way to immediately overcome habitat inadequacies and ecosystem function for certain species under specific conditions.

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Appendix 1. Summed height-frequency values (mean, standard deviation and range) for plant species around natural hihi (*Notiomystis cincta*) nest sites on Little Barrier Island ($n = 23$) and Kapiti Island ($n = 13$). Blank rows indicate the species was not encountered. Plant names follow the Allan Herbarium (2000–2013).

Species	Little Barrier Island			Kapiti Island		
	Mean	SD	Range	Mean	SD	Range
<i>Adiantum</i> spp.	0.1	0.4	0–2			
<i>Agathis australis</i>	10.3	14.9	0–50			
<i>Alseuosmia macrophylla</i>	12.1	8.6	2–34			
<i>Aristotelia serrata</i>	0.2	0.5	0–2	0.4	1.3	0–4
<i>Asplenium bulbiferum</i>	3.7	3.8	0–14	14.8	8.3	2–27
<i>Asplenium flaccidum</i>	0.2	0.5	0–2			
<i>Asplenium oblongifolium</i>	1.8	1.6	0–5	4.1	5.2	0–14
<i>Asplenium polyodon</i>	0.2	0.5	0–2	0.3	0.7	0–2
<i>Astelia</i> spp.	1.3	1.3	0–4	0.5	1.0	0–3
<i>Astelia trinervia</i>	4.4	6.5	0–21			
<i>Beilschmiedia tarairi</i>	68.5	52.2	1–158			
<i>Beilschmiedia tawa</i>	17.7	12.5	0–37	105.9	52.2	17–161
<i>Blechnum discolor</i>	4.1	5.3	0–18	2.4	1.5	0–4
<i>Blechnum filiforme</i>	1.5	2.1	0–7	19.4	8.9	4–32
<i>Blechnum fluviatile</i>	2.5	5.4	0–22			
<i>Blechnum fraseri</i>	0.1	0.6	0–3			
<i>Blechnum novae-zelandiae</i>	1.7	3.2	0–11			
<i>Brachyglottis kirkii</i>	0.7	1.4	0–5			
<i>Brachyglottis repanda</i>	1.0	1.6	0–7	0.2	0.6	0–2
<i>Carex</i> spp.	1.1	1.8	0–5	0.6	0.8	0–2
<i>Carpodetus serratus</i>				0.2	0.6	0–2
<i>Collospermum hastatum</i>	7.7	3.9	2–17	1.4	1.9	0–6
<i>Coprosma arborea</i>	35.0	36.0	0–124			
<i>Coprosma areolata</i>				1.1	3.5	0–11
<i>Coprosma crassifolia</i>	0.7	1.8	0–8			
<i>Coprosma foetidissima</i>				0.2	0.6	0–2
<i>Coprosma grandifolia</i>	2.1	2.2	0–7	8.5	6.1	2–20
<i>Coprosma lucida</i>	0.9	1.4	0–6	1.0	1.2	0–3
<i>Coprosma rhamnoides</i>	0.3	0.6	0–2	0.6	1.1	0–3
<i>Coprosma robusta</i>	1.0	1.6	0–6	0.9	1.4	0–4
<i>Coriaria arborea</i>	0.1	0.5	0–2			
<i>Corokia buddleioides</i>	0.2	0.8	0–4			
<i>Corynocarpus laevigatus</i>	3.1	4.8	0–17	3.5	4.4	0–12
<i>Cyathea dealbata</i>	49.5	19.3	10–93	11.3	12.3	0–37

<i>Cyathea medullaris</i>	1.2	2.2	0–8	2.7	3.0	0–9
<i>Cyathea smithii</i>				0.6	1.3	0–4
<i>Dianella nigra</i>	0.4	0.9	0–3			
<i>Dicksonia fibrosa</i>				0.1	0.3	0–1
<i>Dysoxylum spectabile</i>	45.8	32.8	4–101	46.9	59.7	2–161
<i>Earina</i> spp.	0.1	0.5	0–2			
<i>Elaeocarpus dentatus</i>	0.1	0.5	0–2	21.5	19.3	1–60
<i>Entelea arborescens</i>	0.4	1.2	0–4			
<i>Freycinetia banksii</i>	0.6	0.9	0–3	3.6	4.5	0–13
<i>Fuchsia excorticata</i>	0.2	0.5	0–2			
<i>Gahnia</i> spp.	3.1	4.9	0–19	0.7	2.2	0–7
<i>Geniostoma rupestre</i>	10	6.1	0–23	10.4	14.6	0–41
<i>Griselinia lucida</i>	0.2	0.5	0–2	0.4	0.7	0–2
<i>Hebe stricta</i>	0.6	1.2	0–4			
<i>Hedycarya arborea</i>	1.0	1.3	0–3	26.6	16.6	0–46
<i>Hymenophyllum</i> spp.	5.6	3.9	1–16	6.2	5.2	1–18
<i>Knightia excelsa</i>	9.4	7.9	1–34	17.4	8.2	3–28
<i>Kunzea ericoides</i>	24.2	22.2	0–78	6.8	16.8	0–54
<i>Lastreopsis glabella</i>				2.6	4.1	0–12
<i>Laurelia novae-zelandiae</i>				16.7	20.7	0–59
<i>Leptocophylla juniperina</i>	1.5	2.8	0–10			
<i>Leptopteris hymenophylloides</i>				3.4	4.6	0–14
<i>Leptospermum scoparium</i>	1.3	3.4	0–14			
<i>Leucopogon fasciculatus</i>	0.9	1.9	0–8			
<i>Litsea calicaris</i>	0.1	0.5	0–2			
<i>Lycopodium</i> spp.	0.3	0.8	0–3			
<i>Lygodium articulatum</i>	3.5	3.2	0–12			
<i>Macropiper excelsum</i>	0.3	0.5	0–2	6.4	7.3	0–25
<i>Meliccytus ramiflorus</i>	10.4	5.8	3–23	21.0	12.9	9–45
<i>Metrosideros</i> spp.	14.2	12.2	1–45	12.9	7.0	5–22
<i>Metrosideros excelsa</i>	12.6	15.8	0–49			
<i>Metrosideros robusta</i>	19.7	21.5	0–71	24.1	27.7	0–86
<i>Microsorium pustulatum</i>	2.1	1.3	0–5	1.4	1.6	0–4
<i>Microsorium scandens</i>	0.7	1.1	0–3	4.6	5.0	0–12
<i>Mida salicifolia</i>	0.5	1.3	0–6			
<i>Myrsine australis</i>	17.6	15.1	0–56	11.3	20.1	0–67
<i>Myrsine salicina</i>	1.1	1.6	0–5	2.2	3.8	0–12
<i>Nestegis cunninghamii</i>	6.2	7.8	0–31	0.3	0.9	0–3
<i>Nestegis lanceolata</i>	2.0	3.7	0–17			
<i>Nothofagus truncata</i>	9.4	16.9	0–62			
<i>Olearia furfuracea</i>	3.5	7.7	0–32			
<i>Olearia rani</i>	5.6	5.7	0–19	8.4	7.2	0–20
<i>Parsonsia heterophylla</i>				0.2	0.6	0–2
<i>Pennantia corymbosa</i>				0.8	1.0	0–3
<i>Phebalium nudum</i>	0.1	0.3	0–1			
<i>Phyllocladus trichomanoides</i>	2.4	6.8	0–32			
<i>Pittosporum cornifolium</i>	0	0.2	0–1			
<i>Pittosporum crassifolium</i>	0.1	0.4	0–2			
<i>Pittosporum eugenioides</i>				1.4	2.4	0–7
<i>Pittosporum tenuifolium</i>	0.7	1.0	0–4	0.8	1.9	0–6
<i>Pittosporum umbellatum</i>	9.2	10.8	0–35			
<i>Pneumatopteris pennigera</i>	0.4	0.8	0–3	0.7	0.8	0–2
<i>Prumnopitys ferruginea</i>	0.6	1.4	0–5	1.3	2.8	0–9
<i>Pseudopanax arboreus</i>	5.7	4.8	0–15	10.2	11.5	0–29
<i>Pseudopanax crassifolius</i>				5.3	8.3	0–22
<i>Pseudopanax discolor</i>	1.5	2.5	0–8			
<i>Pseudowintera axillaris</i>				8.2	11.0	0–33
<i>Pseudowintera colorata</i>				0.2	0.6	0–2
<i>Pteridium esculentum</i>	0.1	0.5	0–2			
<i>Pyrrhosia eleagnifolia</i>	0.1	0.5	0–4	0.1	0.3	0–1
<i>Raukaua simplex</i>				0.2	0.4	0–1
<i>Rhabdothamnus solandri</i>	0.4	1.5	0–7			
<i>Rhopalostylis sapida</i>	35.9	30.7	1–105	6.0	8.8	0–23
<i>Ripogonum scandens</i>	8.4	6.3	0–24	13.9	6.7	1–23
<i>Rubus cissoides</i>	0.2	0.5	0–2	0.7	0.9	0–2
<i>Schefflera digitata</i>	1.1	1.5	0–6	2.2	3.3	0–10
<i>Tmesipteris lanceolata</i>	0	0.2	0–1			
<i>Toronia toru</i>	0.3	1.2	0–4			
<i>Trichomanes reniforme</i>	0.6	1.7	0–7			
<i>Uncinia uncinata</i>	0	0.2	0–1			
<i>Vitex lucens</i>	7.3	8.5	0–30			
<i>Weinmannia racemosa</i>				13.5	23.1	0–62
<i>Weinmannia silvicola</i>	4.2	3.9	0–13			