



Invertebrate food supply and reproductive success of two native forest passerines along an elevational gradient

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Abstract: Predation by mammals has been identified as the primary limiting factor of Aotearoa New Zealand native birds. Consequently, the ranges of many native forest bird species have contracted to cooler and higher elevation tracts of forest that support fewer introduced mammals. However, lower elevation forests are likely to be intrinsically more productive and able to sustain larger bird populations if control of mammalian pests removes predation as a primary limiting factor. We wanted to determine whether higher elevation forests provide less food for rat-sensitive, sedentary native insectivorous bird species, resulting in their reduced reproductive potential at higher elevations. In spring and summer 2020/21, we sampled invertebrate prey while simultaneously monitoring nest survival and number of fledglings produced by tītītipounamu / rifleman (*Acanthisitta chloris*) and miromiro / tomtit (*Petroica macrocephala*) across three elevational bands on Mount Pirongia, where mammal predators were suppressed. Tracking and camera indices together indicated that introduced mammals were at low relative abundance at all elevations, allowing us to investigate other habitat effects. Biomass of ground-dwelling invertebrates decreased with increasing elevation during the bird breeding season, but was similar across elevational bands later in the season. In contrast, biomass of flying or folivore invertebrates was independent of elevation and only showed clear seasonal trends. In both tītītipounamu and miromiro, nest survival rates marginally decreased with increasing available invertebrate prey, while the number of fledglings of successful nests marginally increased. There was no strong relationship between elevation and nest survival or number of fledglings. These results indicate no clear trend in the reproductive potential of tītītipounamu and miromiro with elevation but do suggest that food supply needs to be considered as an aspect of habitat quality that is related to reproductive success.

Keywords: *Acanthisitta chloris*, elevation, invertebrate abundance, *Petroica macrocephala*, productivity, rifleman, tomtit

Introduction

Population limitation is the outcome of several, often interacting, factors over multiple spatial scales that prevent a population from increasing or cause it to decline (Newton 1998). Determining the factors that limit populations is fundamental for conservation management of threatened species (Lindenmayer & Likens 2010).

In Aotearoa New Zealand, a higher proportion of vertebrate species are threatened with extinction than anywhere else in the world (Bradshaw et al. 2010). Forest cover has been reduced from 82% to 24% since human settlement (Ewers et al. 2006; McWethy et al. 2014) and remains a primary limiting factor constraining ranges of many native forest birds in some regions today (Innes et al. 2010). In forests, predation by introduced mammals is considered the primary limiting factor and has resulted in range contractions of the majority of forest bird species (Innes et al. 2010; Parlato et al. 2015).

In a number of New Zealand's predator-sensitive forest bird species, there is a clear pattern of range contraction into cooler forest tracts at higher elevations (Elliott et al. 2010; Walker et al. 2019a). This “thermal squeeze” is usually attributed primarily to predation because ship rats (*Rattus rattus*) and possums (*Trichosurus vulpecula*) are important bird predators, and their abundance decreases with increasing elevation (Forsyth et al. 2018; Walker et al. 2019b). Ship rats also sustain populations of stoats (*Mustela erminea*) that are themselves key predators of native forest birds (King & Veale 2021). All three invasive species are particularly damaging for native forest birds due to their arboreal behaviour and generalist diet that includes eggs, nestlings, and adult forest birds.

Food resources may also be a limiting factor for forest birds in New Zealand, especially at higher elevations, but are less studied (Innes et al. 2010). Finite rates of population change (λ) in birds are generally strongly related to fecundity, which is determined by clutch size, the number of breeding

attempts in a season, and the outcome of these attempts (Clark & Martin 2007). While predation directly affects the outcome of each attempt, the total number of eggs laid per season is primarily driven by food availability (Newton 1998; Zanette et al. 2006). Food availability is usually dependent on forest productivity (Moeed & Meads 1985; Seagle & Sturtevant 2005), and therefore on elevation. In forests overseas, bird breeding seasons are often shorter, fewer breeding attempts are carried out by individuals, and clutches are smaller in less productive forests at higher elevations (Boyle et al. 2016; Kitayama & Aiba 2002; Lundblad & Conway 2020) where food resources are often limited (Moeed & Meads 1985; Ferger et al. 2014; He et al. 2019). Invertebrate food resources can strongly influence population dynamics of forest birds (Jones et al. 2003) and smaller, more sedentary insectivorous birds that are unable to track locally abundant food resources may be especially sensitive to food availability gradients and changes (Wilson et al. 1988).

In New Zealand, patterns of food limitation in forest birds are likely to be obscured by predation and because omnivorous ship rats and possums are likely to compete for food resources such as invertebrates, flowers, seeds, and fruit with forest birds (O'Donnell & Dilks 1994; Sweetapple & Nugent 1998). However, if New Zealand's predation-sensitive birds are limited by food supply as well as predation, we would expect their population recoveries after the control of predators and omnivores to be faster in more productive, lower-elevation sites than in higher-elevation sites where food resources are intrinsically more limited. Demonstrating this pattern of limitation could inform conservation managers about where the control of introduced species would lead to the greatest bird population benefits.

In this study, we investigated whether populations of two small insectivorous bird species (tītīpounamu / rifleman *Acanthisitta chloris* and miromiro / tomtit *Petroica macrocephala*) within closed-canopy forest were less productive at high elevation than those at low elevation due to lower invertebrate food availability. We sampled invertebrate biomass over 18 plots across three elevational bands as a measure of prey availability for tītīpounamu and miromiro and simultaneously monitored these species' reproductive success across the elevational gradient. We were able to observe effects of elevation independent of the predation and omnivory effects of ship rats, possums and stoats, which were reduced to low densities at all elevations. We predicted that: (1) biomass of flying and ground-dwelling invertebrates would be lower at higher elevation throughout the year due to lower net primary productivity (Kitayama & Aiba 2002; Bellingham et al. 2013) and temperature (Kaspari et al. 2022) at higher elevation; and (2) fecundity of native forest birds would decline with increasing elevation due to lower numbers of fledglings produced per successful pair (Boyle et al. 2016) despite high levels of nest survival under low predation pressure (Innes et al. 2010).

Methods

Study species

We studied two forest bird species, tītīpounamu / rifleman (*Acanthisitta chloris*) and miromiro / tomtit (*Petroica macrocephala*). Tītīpounamu belong to the New Zealand endemic family Acanthisittidae, while miromiro are part of the Australo-Papuan family Petroicidae and endemic to

New Zealand at the species level. We chose these model species to investigate the effects of food availability on reproductive success along an elevational gradient, because (1) they have significantly declined since human colonisation of New Zealand (Parlato et al. 2015); (2) but they still coexist with mammalian predators in diverse podocarp-broadleaved forest and have the potential to benefit from large-scale pest mammal suppression; and (3) their current vulnerability and life-history traits differ, resulting in tītīpounamu having experienced larger declines in warmer forests or at lower elevation than miromiro (Elliott et al. 2010; Walker et al. 2019a, 2021). Both species are small, tītīpounamu 5–7 g and miromiro 10–13 g (Moeed & Fitzgerald 1982; O'Donnell & Dilks 1994; Peace 2010), and use vegetation from ground level to the upper understory while foraging either on the ground, by gleaning, or scanning for prey (O'Donnell & Dilks 1994; Peace 2010). Tītīpounamu forage most frequently (all orders > 50% occurrence in faeces) on weevils and other beetles (Coleoptera), wētā (Orthoptera), and spiders (Araneida); tītīpounamu nestlings are fed most frequently (all orders > 50% occurrence in faeces and casts) on beetles, moths (mostly adults, but also caterpillars, Lepidoptera), wētā, true bugs (Hemiptera), and spiders (Moeed & Fitzgerald 1982; Sherley 1985). Miromiro most frequently feed on beetles and weevils, moths and caterpillars, wētā, and spiders; miromiro nestlings were fed a similar diet that also included flies (Diptera), true bugs, wasps (Hymenoptera), and amphipods (Moeed & Fitzgerald 1982).

Study site

Mount Pirongia (37°59' S, 175°05' E) is located in the north-western North Island and is of volcanic origin. It is administered as Pirongia Forest Park by the Department of Conservation (DOC), covers 13 600 ha and spans an elevation range of 90–959 m a.s.l. (Fig. 1). The vegetation changes from low elevation podocarp-broadleaved forest dominated by tawa (*Beilschmiedia tawa*) with emergent rimu (*Dacrydium cupressinum*) to upland forest comprised of kāmahī (*Weinmannia racemosa*), tāwari (*Ixerba brexioides*) and tāwheowheo (*Quintinia serrata*) (Burns & Smale 2002). Mammalian pests present on Mount Pirongia include feral goats (*Capra hircus*), pigs (*Sus scrofa*), red and fallow deer (*Cervus elaphus* and *Dama dama*), possums, cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), stoats, and rats. Feral goats are controlled annually by DOC (A. Styche, DOC Hamilton, pers. comm.). In addition, the majority of Mount Pirongia is subject to intermittent (c. every 6 years) sodium fluoroacetate (1080) aerial poisoning aimed at maintaining low possum densities to protect vegetation (Elliott & Kemp 2016), with recent treatments in 2014 and in September 2020. An area of 1135 ha on the eastern flanks does not receive aerial 1080 treatment, and here the Pirongia Te Aroaro o Kahu Restoration Society uses a network of over 1000 bait stations (spacing either 75 × 100 m or 100 × 100 m) filled with anti-coagulant poison twice a year between August and February to reduce rat and possum numbers, and 70 DOC 250 traps targeting stoats to aid nesting success of North Island kōkako (*Callaeas wilsoni*) and other forest bird species (Fig. 1).

We established a network of 36 temperature data loggers (Tinytag, Gemini Data Loggers UK Ltd, Chichester, UK) across three elevational bands (low = 200–300 m a.s.l., mid = 400–500 m a.s.l., high = 650–750 m a.s.l.) to measure seasonal temperature differences between elevational bands. Temperature data loggers were paired with tracking tunnel

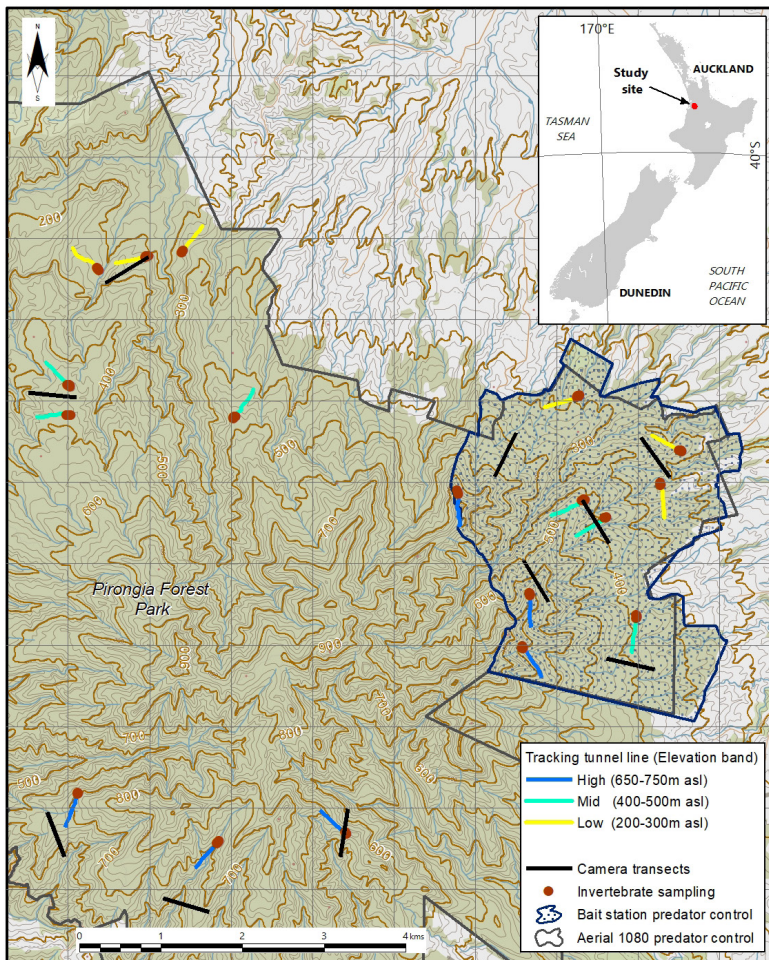


Figure 1. Map of study area showing Mount Pirongia. The blue dotted area shows where a bait station network is serviced with anticoagulant poison by the Pirongia Te Aroaro o Kahu Restoration Society from August to February each year, while the remaining forest area (dark grey outline) received aerial 1080 pest control in September 2020. Solid coloured lines show tracking tunnel and temperature logger locations stratified into elevation bands, black solid lines show camera transects (not stratified) and brown dots show invertebrate sampling locations.

transects (Fig. 1). We set up two data loggers per transect (12 per elevational band), with each data logger mounted on a stake at 1.3 m above ground level. Each data logger was programmed to record temperature every 30 minutes. We calculated mean monthly temperatures across elevational gradients, which are shown in the Supplementary Material (Appendix S1).

Mammal abundance

To account for residual mammals present at the study site after pest control, we measured indices of abundance focusing on the major nest predators and food competitors (i.e. ship rats, possums, and stoats). We used tracking tunnels to index ship rat (hereafter ‘rat’) abundance (Gillies & Williams 2013) following the standard procedure of 10 tunnels placed at 50 m spacing (‘line’) with 200 m minimum distance between lines. For all tunnels, Black Trakka Ink Cards (Gotcha Traps, Warkworth, New Zealand) were used baited with a pea-sized portion of peanut butter at each end for one fine night in October 2020, January 2021, and April 2021. Tunnels were established at least three months before monitoring to allow resident animals to become familiar with the tunnels. Six lines were set up in each elevational band (Fig. 1).

We used a generalised linear mixed model with a binomial error distribution and logistic link function to assess whether rat tracking indices differed between the three elevational bands. The response variable was the presence or absence of rat footprints in a tunnel. We compared models including

(1) season: spring (October), summer (January) and autumn (April), which also indicated time since the start of pest control; (2) the additive effects of season and elevation band; (3) an interactive effect of elevation band and season, i.e. seasonal differences depends on elevational band; and (4) a null model including only random effects, i.e. rat tracking is independent of season or elevation. In all models, we included tunnel nested within line as a random effect to account for non-independence between tunnels on a line and repeat-sampling of the same line.

We used camera traps to index stoats and possums (Smith & Weston 2017; Anton et al. 2018) on ten lines with four cameras placed at 200 m spacing with 500 m minimum distance between lines to ensure independence of lines (Fig. 1). Because of these spacing requirements, it was not possible to measure camera trap indices of possums and stoats in elevational bands, but only across the entire site where nests were monitored. Each camera (Bushnell Core DS) was baited with 150 g rabbit meat and two pieces of Connovation Erayz dried rabbit, wrapped in chicken wire and pegged to the ground 1–1.5 m in front of the camera to reduce bait removal. Each passive infrared activated camera operated continuously for a 21-day period and was set to record a burst of three photos when triggered followed by a 5 minute stand-down. Following Garvey et al. (2017), we considered records of a species independent at a camera site if observations were separated by > 30 minutes. Animals were identified to species-level, and we calculated the camera trap index (CTI) as the number of detections per

2000 camera hours (C. Gillies, Te Papa Atawhai Department of Conservation, Hamilton, pers. comm.). Camera surveys were carried out in December 2019 and immediately before the 1080 aerial poison operation in August 2020 (providing non-treatment comparisons) as well as in December 2020 and April 2021 after the 1080 operation.

Invertebrate biomass

We sampled invertebrate biomass as a measure of general prey availability to insectivores using six sets of five pitfall (PIT) and five flight-intercept traps (FIT) in each elevational band (Fig. 1). Due to logistical constraints, we did not attempt to sample all foraging microhabitat used by the insectivores (e.g. Johnson 2000), but treat invertebrate biomass as a general indicator of food availability. Each trap type was set up in a transect at 10 m spacing and a minimum of 200 m spacing between transects, resulting in 30 traps per type per elevational band. PITs targeted ground-dwelling invertebrates and consisted of a 100 mm deep plastic cup (105 mm diameter) and a cover positioned 10 cm above each trap to protect it from rain and debris; they were left sealed for > 1 month before sampling to reduce digging-in effects. FITs targeted flying or folivore invertebrates and consisted of two crossed clear acrylic panes (220 × 500 mm) positioned over a funnel set 3 m high in the primary feeding zone of birds (O'Donnell & Dilks 1994; Peace 2010). Each trap of each type contained 100 ml of 50% monopropylene glycol and was left open for 30 consecutive days. Samples were then removed and the traps sealed until the following sampling period. Sampling was undertaken in spring (September–October) and summer (December–January) during the bird breeding season and in the following autumn (April–May).

Contents of each trap were counted and sorted into two size classes to differentiate between items considered potential prey of birds compared to rats and possums: (1) bird and mammal prey: body length of invertebrates between 3 and 20 mm (Sherley 1985; A-KVS pers. obs.); (2) rat and possum prey only: body length > 20 mm. Any individuals < 3 mm in body size were discarded. We identified all individuals in each sample to order level. All samples were then dried for > 24 hours at 60°C and weighed to determine invertebrate biomass (in g).

We assessed whether invertebrate biomass differed between elevational bands using linear mixed models with a Gaussian error distribution. The response variable was invertebrate biomass, which was log-transformed to improve model fit. We compared four models for each trap type, including (1) only season (spring, summer, autumn), if invertebrate biomass changes seasonally with mean temperature fluctuations (Appendix S1) but not across the elevational gradient (Moeed & Meads 1984, 1985); (2) additive effects of elevation band and season, if invertebrate biomass differs between elevation bands and across seasons (Moeed & Meads 1984); (3) the interacting effects of season and elevation, if seasonal differences in biomass depends on elevation; and (4) a null model including only random effects, i.e. invertebrate biomass is independent of season or elevation. In all models, we included transect as a random effect to account for non-independence between traps on a transect and repeat-sampling of the same transect.

Nest survival

Nests of tītītipounamu and miromiro were located by intensively searching study areas and following individuals with nesting

material or food items to nest locations between 2 September 2020 and 1 February 2021. All elevational bands (focusing on areas with tracking tunnel and camera lines) were searched every 3–4 days for nesting pairs and to monitor outcomes of nests. Most nests were too high (> 10 m) to observe contents easily and without considerable disturbance to birds. Hence, nest status (incubation, brooding or failure) was determined by observing parental behaviour for at least 30 minutes. If the nest was found inactive on two consecutive visits and less time than the mean fledging time had passed, it was assumed to have failed. For tītītipounamu, mean incubation is 20 days and mean brood rearing 24 days (Sherley 1985); for miromiro, incubation is 16 days and brood rearing 18 days (Higgins & Peter 2002). Nests with unknown outcomes (e.g. impossible to determine hatching date and nest empty without family group nearby) were excluded from analyses. If a nest failed or chicks fledged between two consecutive visits, we assumed the outcome occurred mid-way through the interval of visits.

We modelled daily nest survival rates using the generalised linear modelling approach of Shaffer (2004). We fitted a logistic-exposure mixed model specifying a binomial error distribution and a logit link function accounting for the observation period (i.e. length of observation under which a nest is at risk of failing). Nest survival rates were modelled as a series of Bernoulli trials (0 = nest failed during observation interval; 1 = nest survived observation interval) until at least one chick fledged. In all models, we included species as a categorical covariate and nest as random effect to account for non-independence of repeated sampling. We initially considered time-specific effects on nest survival, i.e. nest age (categorical: incubation or brooding stage) and time of season (days since 1 August; scaled and centred) (Weiser 2021). A model without time-specific variables was top-ranked using Aikake's Information Criterion corrected for small sample size (AICc) (Appendix S2), and following the principle of parsimony we therefore did not include any time-specific variables in subsequent models.

Our primary interest was to understand variation in nest survival across the elevational gradient and potential relationships to available invertebrate prey. We therefore constructed a simple set of plausible candidate models:

- (1) Nest survival is independent of elevation and available invertebrate prey (null model).
- (2) Nest survival depends on elevational band (additive elevation), and effects of elevation may depend on species (interaction between elevation and species).
- (3) Nest survival depends on available invertebrate prey.
- (4) Nest survival depends on both elevation and prey availability (additive elevation and prey), and elevation may affect species differently (additive prey and interaction between elevation and species).

In order to account for the effect of bird species and remaining mammal abundance (see earlier Mammal Abundance section), we included species and rat tracking index as covariates in all of our models. Inclusion of camera trap indices as well as rat tracking indices resulted in variance inflation factors > 3 due to multicollinearity (Zuur et al. 2010) between these measures of mammal abundance. Camera trap indices were therefore not included in the model set. Our intention was not to examine the magnitude of the effect of bird species or rat tracking indices but to control for their possible effects. Each nesting attempt was assigned a measure of invertebrate biomass (flying/folivore and ground-dwelling invertebrates combined for body size between 3 and 20 mm

as potential prey size, log-transformed) and rat tracking index (scaled and centred) closest to the time of nesting (October or January) and nest location. Nest was again included as a random effect to account for repeated sampling. We defined nest survival as the probability of a nest surviving from clutch completion to fledging. Hence,

$$\text{Nest survival} = \text{Daily nest survival rate}^t \quad (1)$$

with t being 44 days for tītītipounamu and 34 days for miromiro.

Number of fledglings per successful nest

We checked each nest for up to 4 days around the expected date of fledging, and for successful nests we counted the number of young where possible by observing fledglings being fed by parents close to the nest location. We modelled reproductive output as the number of fledglings produced per successful nest using generalised linear mixed models with a Conway-Maxwell-Poisson error distribution to account for under-dispersion (Brooks et al. 2019). We again compared a simple set of candidate models, which each included species as a factor:

- (1) Number of fledglings is independent of elevational band and available invertebrate prey (null model).
- (2) Number of fledglings depends on elevational band (additive elevation), and effects of elevation may depend on species (interaction between species and elevation).
- (3) Number of fledglings depends on available invertebrate prey.
- (4) Number of fledglings depends on both elevation and prey availability (additive elevation and prey), and elevation may affect species differently (additive prey and interaction between elevation and species).

All analyses were done using R v.4.1.0. (R Core Team 2021) and the packages lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) for mixed models. For all models,

assumptions were checked by plotting residuals versus fitted values and versus each covariate included in models, and checked for over-/underdispersion using the package DAHRMA (Hartig 2021). We used AICc to compare competing models and calculated 95% credible intervals (CIs) of estimates using the function sim (1000 simulations) in the package arm (Gelman & Su 2020).

Results

Residual mammal abundance

Rat tracking indices were generally low on Mount Pirongia throughout the bird breeding season in spring (mean percentage of tracking tunnels with rat footprints \pm SE; Aerial 1080: $2.0 \pm 2.0\%$ and bait station: $17.0 \pm 4.0\%$) and summer (Aerial 1080: $1.0 \pm 1\%$ and bait station: $3.0 \pm 2.0\%$) after pest control. Across the elevational gradient, rat tracking was highest in spring at mid elevation during the bird breeding season, was low in summer across elevational bands, and increased in autumn the most at low altitudes (Fig. 2). The best model (AICc weight = 0.82) describing variation in residual relative abundance of rats included an interaction between season (also the time since onset of pest control) and elevation (Appendix S3, S4).

Mean possum CTI across Mount Pirongia during the bird breeding season in December 2020 ranged between 0.60–0.66 encounters per 2000 camera hours (Fig. 3). In comparison, mean possum CTI was 15.01 encounters per 2000 camera hours immediately before aerial 1080 poisoning in August 2020 (Fig. 3) and 5.79 encounters per 2000 camera hours in the previous bird breeding season (December 2019) (Appendix S5).

Mean stoat CTI in December 2020 ranged between 0.26–0.60 encounters per 2000 camera hours (Fig. 3). Again, this represented a reduction in stoat CTI compared with immediately

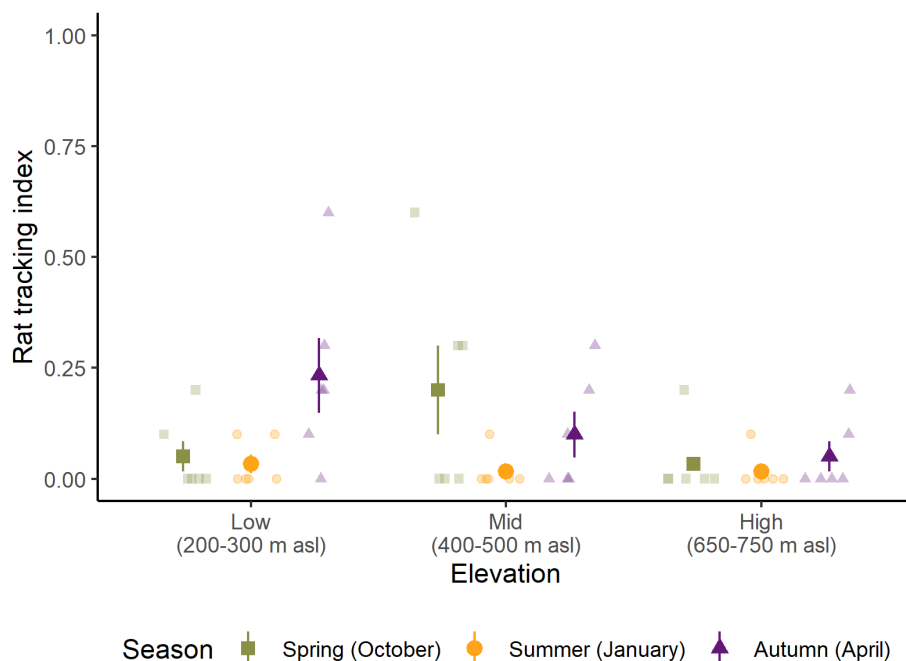


Figure 2. Rat tracking index (percentage of ink tracking tunnels per line with rat footprints) in spring (October 2020), summer (January 2021), and autumn (April 2021) after pest mammal suppression by aerial 1080 or bait station poisoning across three elevation bands on Mount Pirongia, New Zealand. Large symbols show mean rat tracking rates \pm SE in each altitude band (6 lines per band). Small symbols show tracking rates on individual lines.

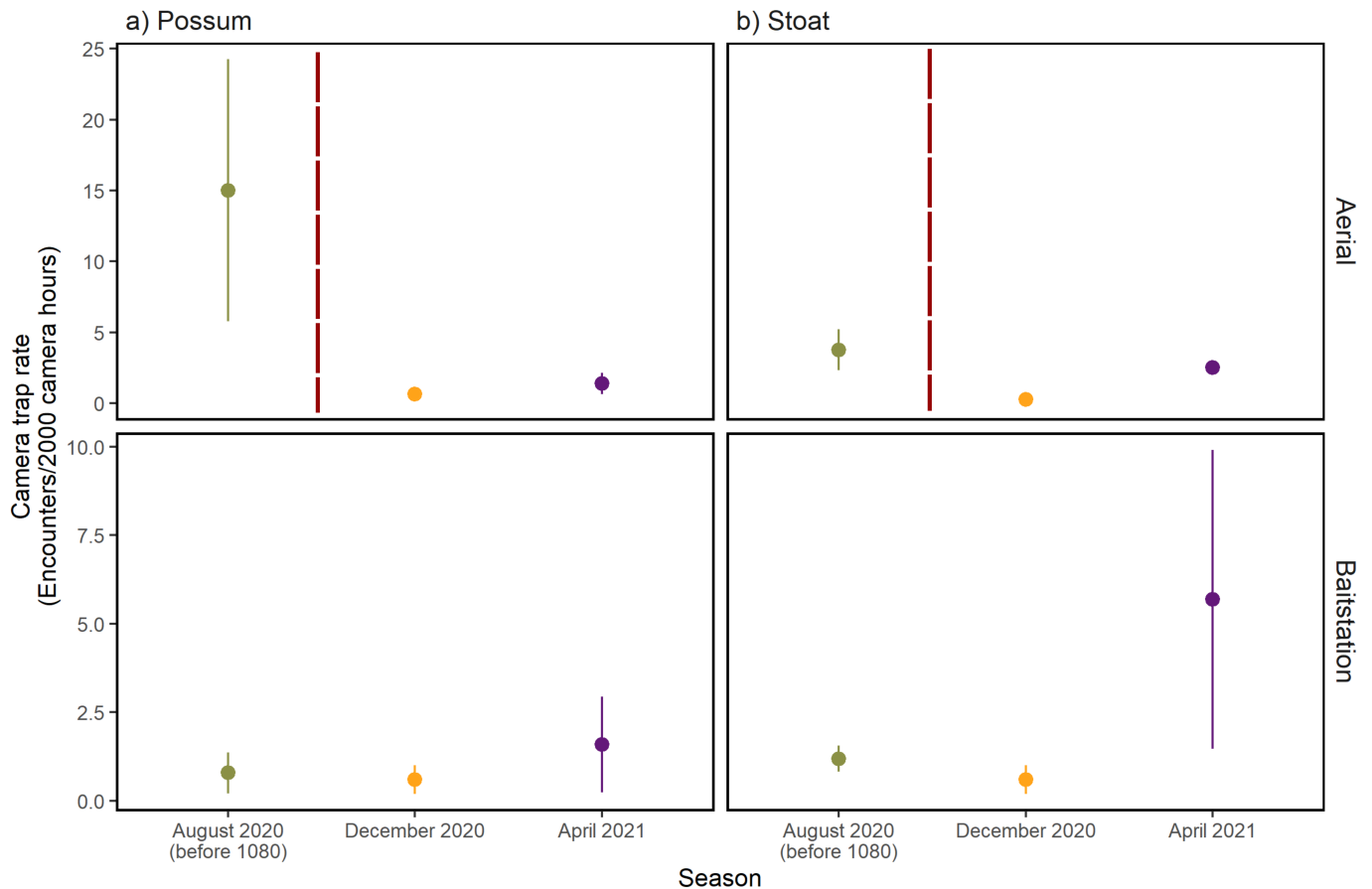


Figure 3. Camera trap rates (mean encounters \pm SE across camera transects per 2000 camera hours) of (a) possums (*Trichosurus vulpecula*) and (b) stoats (*Mustela erminea*) immediately before the aerial poisoning with 1080 (August) and afterwards, within the south-eastern Pirongia Te Aroaro o Kahu Restoration Society predator control area using bait stations with anticoagulant poison and trapping targeting stoats. The red dotted line indicates the timing of the aerial poisoning with 1080 outside of the bait station area (Fig. 1).

before the aerial 1080 operation in August (mean CTI 1.19–3.77 encounters per 2000 camera hours, Fig. 3) and the previous (2019) bird breeding season (8.85–13.72 encounters per 2000 camera hours, Appendix S5) before aerial 1080 and trapping inside the bait station network commenced.

Invertebrate biomass

We detected 26 orders of invertebrates from a total of 8317 individuals caught during the bird breeding season and 11 858 individuals caught across all three seasons. Coleoptera, Diptera, and Lepidoptera made up over 80% of flying or folivore invertebrates sampled, while Coleoptera, Amphipoda, Hymenoptera, and Collembola made up over 68% of all ground-dwelling invertebrates sampled during the bird nesting season (Appendices S6, S7 for percentage of biomass of the ten most common orders sampled over all seasons). These orders have also been most commonly detected in the diet of tītīpounamu and miromiro (Moed & Fitzgerald 1982; Peace 2010).

Across all seasons, biomass contribution of each size class was similar for ground-dwelling invertebrates (3–20 mm in body length mean: 0.195 ± 0.032 (SE) vs. > 20 mm in body length: 0.203 ± 0.030), but smaller flying or folivore invertebrates contributed less than half to overall biomass of this group (3–20 mm in body length: 0.065 ± 0.013 vs. > 20 mm in body length: 0.147 ± 0.072). This difference in contribution of size classes was mostly due to larger individuals being

trapped during summer in flight-intercept traps (Appendix S8). Coleoptera were sampled generally the most frequent across elevations and seasons, with the percentage of biomass of Collembola, Hymenoptera, Diptera, Amphipoda and Lepidoptera sampled changing within elevation bands depending on season (Appendix S9).

The best model describing differences in flying or folivore invertebrate biomass included season alone (AICc weight = 0.86; Appendix S10): flying or folivore invertebrate biomass was similar in spring and autumn but doubled in summer (Fig. 4, Appendix S11). In comparison, the best model describing differences in ground-dwelling invertebrate biomass included an interaction between elevation and season (AICc weight = 0.53; Appendix S12). Seasonal differences in ground-dwelling invertebrate biomass were smallest at low elevation and largest at high elevation, primarily due to very low biomass at high elevation in spring (Fig. 4, Appendix S13). However, the model including season or additive effects of season and elevation also received some support, with the former resulting in an increase of 1.36 AICc units (AICc weight = 0.27) and the latter in an increase of 2.01 AICc units (AICc weight = 0.20) compared to the top (interactive) model (Appendix S12, S14, S15).

Nest survival

We monitored the fate of 55 tītīpounamu and 33 miromiro nests across the elevational gradient (Appendix S16). For

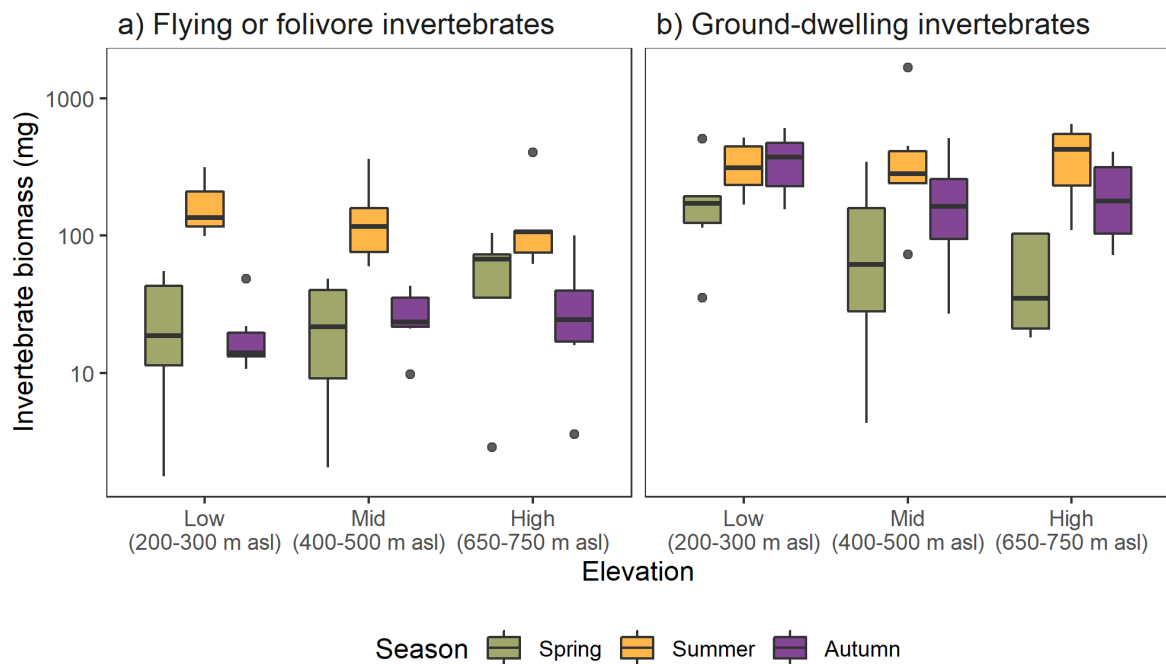


Figure 4. Box-and-whisker plots of biomass of (a) flying or folivore invertebrates and (b) ground-dwelling invertebrates captured in flight-intercept traps and pitfall traps, respectively, opened for one month during the forest bird breeding season in spring (September–October) and summer (December–January) and after the bird breeding season in autumn (April–May) in three elevational bands on Mount Pirongia, New Zealand. Boxes indicate the 25th and 75th percentiles and the horizontal line indicates the median. The whiskers cover data points no more than 1.5 times the interquartile range from the box, with points being outside of that range. Note the y-axis is on a log-scale.

fititipounamu, the mean start date of incubation was 29 October (± 22.6 days SE) and the mean hatching date was 19 November (± 19.5 days SE). For miromiro, the mean start dates of incubation and hatching were 30 October (± 25.1 days SE) and 16 November (± 24 days SE), respectively. The last fititipounamu and miromiro chicks hatched on 11 and 4 January, respectively (Appendix S17). Overall, 10 fititipounamu (18%) and 11 miromiro (33%) nests failed. Nest survival across all elevation bands was 0.62 (95% CI: 0.41–0.78) for fititipounamu and 0.43 (95% CI: 0.02–0.83) for miromiro.

Under the best model, daily survival of nests was a function of species and rat tracking index only (null model; AICc weight = 0.53). Adding invertebrate biomass to the model resulted in an increase of 1.87 AICc units (AICc weight = 0.21), while adding elevation in an increase of 2.32 AICc units (AICc weight = 0.17; Appendix S18). These latter two models suggested a decreasing trend of nest survival with increased availability of invertebrate prey and increasing elevation, respectively (Fig. 5a, 5b; Appendices S19, S20), although 95% CI of each effect were relatively wide and overlapped zero.

Number of fledglings across elevational bands

We could confidently identify the number of fledglings for a total of 34 fititipounamu and 21 miromiro successful nests (Appendix S21). A mean of 3.15 (± 0.14 SE) fititipounamu and 3.24 (± 0.17 SE) miromiro chicks fledged from successful nests. Again, in the best model, the number of fledglings only depended on species (AICc weight = 0.55; Appendix S22). Adding invertebrate biomass to the model resulted in an increase of 1.13 AICc units (AICc weight = 0.31; Appendix S22). In comparison, adding elevation resulted in an increase of 3.79 AICc units compared to the best model (AICc weight = 0.08; Appendix S22). In contrast to nest survival, these models

suggested an increasing trend in the number of fledglings with increased availability of prey, and fewer fledglings at high elevations (Fig. 5c, 5d, Appendices S23, S24). Nevertheless, the 95% CIs of each effect were wide and overlapped zero.

Discussion

Our study provides weak support for the hypothesis that high elevation habitats provide less invertebrate prey and that the reproductive potential of two endemic insectivorous bird species (fititipounamu and miromiro) depends on available prey. However, elevation was not a major driver of bird productivity. Tracking and camera indices together indicated that rats, possums and stoats were suppressed across our study site on Mount Pirongia enabling us to test the effects of other factors related to elevation on reproductive success of fititipounamu and miromiro. In our models of biomass of ground-dwelling invertebrates, there was strongest support for those including elevation as a factor: availability of ground-dwelling prey was lower at high elevation during the key nesting period of our insectivorous birds in spring, but not during other seasons. However, effects of season, but not elevation, were supported in models of biomass of flying or folivore invertebrates. In our models of nest survival and number of fledglings per successful attempt by fititipounamu and miromiro, those that included effects of invertebrate prey received some support, with effect sizes that were small and variable.

Relationship between nest survival, number of fledglings, invertebrate prey and elevation

Neither nest survival nor the number of fledglings of

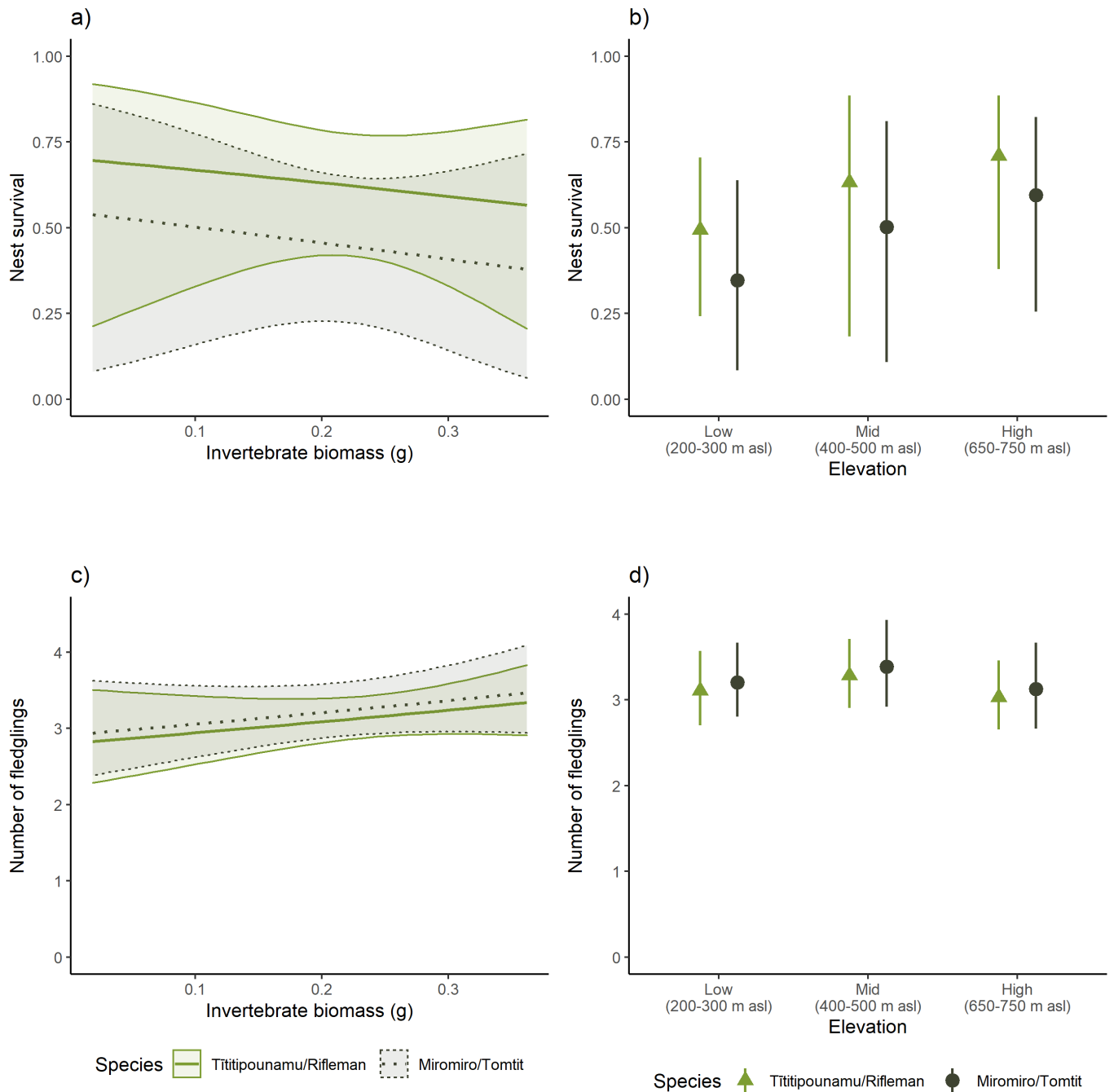


Figure 5. Reproductive success of tītīpounamu and miromiro on Mount Pirongia, New Zealand across elevational bands and in relation to invertebrate prey. Probabilities (\pm 95% CI) of nests surviving time from egg laying to fledging for tītīpounamu (44 days) and miromiro (34 days) in relation to (a) invertebrate prey available and (b) across three elevational bands. Rat tracking was kept at the mean (0.08). Estimated mean number of fledglings per successful nest (\pm 95% CI) of tītīpounamu and miromiro pairs in relation to (c) invertebrate prey available and (d) across three elevational bands.

tītīpounamu and miromiro were strongly influenced by elevation in our study. This result contrasts with consistently larger effects of elevation on measures of reproductive success of birds reported internationally (Boyle et al. 2016). Our different finding may be partly explained by the comparatively small elevation range available in our study (c. 500 m with continuous forest cover) compared with those overseas (c. 1000 m; Boyle et al. 2016). Larger elevational ranges span not only wider primary productivity gradients but also wider temperature ranges. Boyle et al. (2016) suggested that primary

productivity and food availability alone are not able to fully explain intraspecific variation in fecundity of birds along elevational gradients, and that direct effects of temperature (increased physiological cost or direct mortality) need to be considered. On Mount Pirongia, changes in vegetation composition across the elevational gradient are evident (Clayton-Greene & Wilson 1985) and our data showed less ground-dwelling invertebrate prey at high elevations in spring. However, the temperature difference of about 3°C between elevational bands throughout seasons (Appendix S1) is unlikely

to be large enough to significantly increase physiological costs of basal metabolism of forest birds (Jetz et al. 2008).

Tītītipounamu primarily glean (i.e. take food from the surface of a substrate) as a foraging strategy while miromiro scan (i.e. use a vantage point to look for prey) (O'Donnell & Dilks 1994). Our invertebrate sampling was representative of the main prey of both species (Moeed & Fitzgerald 1982) and designed to capture general prey availability across the elevational gradient. However, the invertebrate sampling was not necessarily representative of invertebrate availability and detectability as perceived by the birds themselves using their specific foraging strategies. For example, miromiro are more commonly observed foraging on the ground compared to tītītipounamu (O'Donnell & Dilks 1994; Peace 2010), and hence the samples of ground-dwelling invertebrates may be less relevant as a measure of food availability to tītītipounamu compared to sampling bark of different tree species (Murphy & Kelly 2003) or trunk-intercept traps (Moeed & Meads 1983). Nevertheless, the trend in reproductive potential (Fig. 5, Appendices S18, S22) was similar for both insectivores and consistent with expectations of fewer available food resources leading to fewer fledglings produced per successful attempt. However, it is surprising that nest survival marginally decreased with increasing invertebrate availability. One potential explanation may be that inexperienced birds that are likely to experience higher nest failure, are likely to nest at higher rates when invertebrate availability is higher. As the populations in this study were not fully marked, the ages of monitored pairs were unknown and further study is required.

To our knowledge, the only other New Zealand study of the role of invertebrate food abundance on forest bird fecundity is that of Boulton et al. (2008). They showed that nest survival of insectivorous toutouwai/North Island robin (*Petroica longipes*) was positively correlated with invertebrate biomass in different-sized forest fragments in the central North Island, but found no relationship between invertebrate biomass and the number of fledglings produced per successful pair.

Our results may have been influenced by factors other than invertebrate food which vary with elevation on Mount Pirongia, but we are confident that mammal predators and omnivores had little effect (Appendices S19, S20). The majority of New Zealand forest bird nesting attempts fail in the absence of predator control (e.g. Innes et al. 2010; Remeš et al. 2012), but only a small proportion of our monitored nests failed under the levels of predator suppression achieved. Unmanaged ship rat tracking rates in North Island podocarp-broadleaved forests are typically 60–100% (e.g. Innes et al. 1999) but on Mount Pirongia mean residual ship rat tracking indices were below 1% across areas treated with aerial 1080 in September 2020, and mostly below 17% in areas subject to rat ground poisoning (although one line at mid elevation had 60% tracking in October 2020). Detection rates of stoats and possums on cameras were also considerably lower than in the previous bird breeding season, and immediately before the aerial 1080 poisoning operation.

Relationship between invertebrate biomass, season, and elevation

Generally, invertebrate abundance declines with increasing elevation, and temperature has been shown to be a strong predictor of invertebrate abundance or activity (Moeed & Meads 1985; Röder et al. 2017; Vergara Parra 2018). A unimodal relationship between invertebrate biomass and temperature has been shown to exist on a continental scale within forests

(Kaspari et al. 2022). On Mount Pirongia, invertebrate biomass increased between spring and summer as mean monthly temperature increased by around 7°C, consistent with the seasonal trend expected given the life cycles of invertebrates and the seasonal increase in mean temperature (Moeed & Meads 1984; Moeed & Meads 1985).

Biomass of ground-dwelling invertebrates sampled on Mount Pirongia decreased with elevation in spring, but not in summer. A possible explanation for the seasonal dependence of the elevational trend may be that first emergence of ground-dwelling invertebrates across the elevational gradient starts later in spring at high elevation (Appendix S1), but once a temperature threshold is met, activity (and therefore sampled biomass) of invertebrates is not further increased with increasing temperatures in summer. Interestingly, we found no relationship between flying or folivore invertebrate biomass and elevation within any season. Flying or folivore invertebrates may be more strongly affected by precipitation than ground-dwelling invertebrates (Totland 1994). Precipitation at Mount Pirongia is likely to have affected all elevational bands together, perhaps overwhelming or masking any underlying elevational trend in the abundance of flying or folivore invertebrates within the continuous forest cover. Alternatively, the mobility of folivore or flying invertebrates may have also diminished differences between elevational bands over our sampling interval of 30 days.

Study limitations

There are several limitations to this study due to the difficulty of monitoring animals that occur at low densities (Fitzgerald & Innes 2021), tend to be secretive, or occupy challenging terrain. Fecundity is the product of clutch size, the number of breeding attempts, and outcome, and we were only able to assess outcomes in our study. Clutch size could not be measured due to the height of nests of both species and often fragile substrate used by tītītipounamu. Moreover, although breeding seasons may be shorter at high elevation (Lundblad & Conway 2020), we could not assess the number of breeding attempts of pairs because individuals were not marked (we could not mist-net pairs across the entire study site, and territories overlapped). If there are more successful breeding attempts at lower elevations, the total number of fledglings produced per female within a season may be greater, even although nest survival and number of fledglings per attempt may be similar across elevations.

In short-lived species, fecundity is expected to have the greater influence on population dynamics, but limitation at a local scale could also occur due to limited recruitment of juveniles (e.g. Drummond et al. 2019). We were unable to monitor survival of juveniles and adults with robust mark-resight methods in this study because we lacked mist-netting opportunities in suitable conditions (leading to low capture rates) and because tall or dense vegetation reduced resight probabilities.

In addition, measuring food availability for insectivorous birds that use a range of feeding strata, foraging activities, and forage on a wide range of invertebrate prey is challenging. Future studies may benefit from using a wider range of methods (e.g. sweep netting or sticky traps) as well to ensure different subsets of the invertebrate community are sampled (e.g. Kent et al. 2019) and potentially assessing the realised diet of each species at a site using molecular tools (e.g. Shutt et al. 2020).

Conclusions

This is the first study in New Zealand to address differences in the reproductive potential of forest birds along an elevational gradient. Endemic forest bird ranges are expected to contract further into New Zealand's colder, higher elevation forests as climate warming progresses (Walker et al. 2019a), and measuring vital rates is the key to both understanding habitat quality and using population models to assess population vulnerability (Hall et al. 1997; Armstrong et al. 2021). We found that biomass of both ground-dwelling and flying invertebrate prey of tītīpounamu and miromiro showed seasonal increases across elevations and fewer ground-dwelling invertebrate prey were available in spring (October 2020) but not in summer (January 2021) at high elevations on Mount Pirongia. However, nest survival and number of fledglings produced by tītīpounamu and miromiro was not strongly related to elevation or prey availability. The restoration of New Zealand's threatened forest bird communities requires a commitment to research into the significance of non-predation aspects of habitat quality on bird populations.

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Data and code availability

All data from this article are openly available through Datastore URL: datastore.landcareresearch.co.nz/dataset/bird-productivity-along-elevation-gradients. There is no publicly available code associated with this article.

Author contributions

All authors conceptualised the idea for the study. AS and NF collected data. AS carried out data analyses and led the writing of the manuscript. All authors provided editorial input.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Mean monthly temperature across three elevational bands on Mount Pirongia, New Zealand.

Appendix S2. Comparison of models for time-specific factors affecting nest survival of miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*).

Appendix S3. Comparison of models affecting rat tracking indices after predator control through poisoning across three elevational bands on Mount Pirongia,

Appendix S4. Parameter estimates for the best generalised linear mixed model (Appendix S3) of the rat tracking indices after predator control on Mount Pirongia across three elevational bands.

Appendix S5. Mean camera trap rate (Encounters/2000 camera hours ± SE) in December 2019–January 2020 on Mount

Pirongia based on six camera transects in the no predator control and four camera transects in the bait station area.

Appendix S6. Overview of the contribution to overall biomass by the ten most common orders sampled with flying intercept-traps opened for one month in spring (September–October), summer (December–January) and autumn (April–May) across three elevational bands on Mount Pirongia, New Zealand.

Appendix S7. Overview of the contribution to overall biomass by the ten most common orders sampled with pitfall traps opened for one month in spring (September–October), summer (December–January) and autumn (April–May) across three elevational bands on Mount Pirongia, New Zealand.

Appendix S8. Overview of relative contribution of flying/folivore and ground-dwelling invertebrate body size class to mean biomass sampled with flying-intercept and pitfall traps, respectively, opened for one month in spring (September–October), summer (December–January) and autumn (April–May) across elevational bands on Mount Pirongia, New Zealand.

Appendix S9. Overview of relative abundance of invertebrates sampled in pitfall or flying-intercept traps opened for one month in spring (September–October), summer (December–January) and autumn (April–May) across a) low, b) mid, and c) high elevational bands on Mount Pirongia, New Zealand.

Appendix S10. Comparison of models affecting biomass of flying or folivore invertebrates (log-transformed) during the forest bird nesting season across three elevational bands on Mount Pirongia, New Zealand.

Appendix S11. Parameter estimates for the best linear mixed model (Appendix S10) of flying or folivore invertebrate biomass during spring, summer, and autumn across three elevational bands on Mount Pirongia.

Appendix S12. Comparison of models affecting biomass of invertebrates (log-transformed) caught in pitfall traps during the forest bird nesting season across three elevational bands on Mount Pirongia, New Zealand.

Appendix S13. Parameter estimates for the best linear mixed model (Appendix S12) of ground-dwelling invertebrate biomass during spring, summer, and autumn across three elevational bands on Mount Pirongia.

Appendix S14. Parameter estimates for the second best linear mixed model (Appendix S12) of ground-dwelling invertebrate biomass during spring, summer, and autumn across three elevational bands on Mount Pirongia.

Appendix S15. Parameter estimates for the third best linear mixed model (Appendix S12) of ground-dwelling invertebrate biomass during spring, summer, and autumn across three elevational bands on Mount Pirongia.

Appendix S16. Overview of number of nests monitored across species and elevational bands.

Appendix S17. Observed hatching dates of tītītipounamu/rifleman (green) and miromiro/tomtit (black) nests throughout the breeding season 2020/21.

Appendix S18. Comparison of logistic-exposure mixed models of daily nest survival of miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*) across an elevational gradient.

Appendix S19. Parameter estimates for the second best linear mixed model (Appendix S18) of nest survival of miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*) across an elevational gradient on Mount Pirongia.

Appendix S20. Parameter estimates for the third best linear mixed model (Appendix S18) of nest survival of miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*) across an elevational gradient on Mount Pirongia.

Appendix S21. Overview of the number of nests where the number of fledglings could be determined across species and elevational bands.

Appendix S22. Comparison of generalised linear mixed models with Conway-Maxwell-Poisson error of habitat-specific factors affecting the number of fledglings of miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu/rifleman (*Acanthisitta chloris*) of successful nests.

Appendix S23. Parameter estimates for the second best linear mixed model (Appendix S22) of number of fledglings produced by miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*) across an elevational gradient on Mount Pirongia. Biomass was log-transformed.

Appendix S24. Parameter estimates for the third best linear mixed model (Appendix S22) of number of fledglings produced by miromiro/tomtit (*Petroica macrocephala*) and tītītipounamu /rifleman (*Acanthisitta chloris*) across an elevational gradient on Mount Pirongia.

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