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RESEARCH

Recruitment, survival and breeding success in a declining rifleman population

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Abstract: We used detailed life-history data collected over a six-year period from a colour-banded population of riflemen (*Acanthisitta chloris*) at Kowhai Bush, near Kaikōura, to estimate population vital rates and assess their likely contribution to a concurrent population decline. Both mean juvenile survival (18%) and mean adult survival (49%) were low in comparison with reports from other populations. In contrast, breeding success was high, with pairs producing c. 3 fledglings per season on average. High breeding success was likely associated with nestbox use. We then used survival and breeding success estimates to parameterise a population matrix model, and perturbation analysis of this model confirmed a projected negative trend, with reduced recruitment having the greatest absolute contribution to population decline. We discuss possible explanations for the comparatively low rates of recruitment and survival observed. Data from other populations of riflemen experiencing stable or positive population trajectories would be especially useful to better understand factors affecting vital rates, and to identify the thresholds that signal a rifleman population at risk of decline.

Keywords: *Acanthisitta chloris*, Acanthisittidae, Kaikōura, Kowhai Bush, nestbox, population matrix, regrowth, titipounamu, vital rate

Introduction

Bird conservation in New Zealand has generally focused on preventing the extinctions of its rarest species, sometimes with spectacular success. Nevertheless, many common birds have also declined in number in recent decades, probably due to the combined effects of habitat clearance and introduced mammalian predators (Elliott et al. 2010; Innes et al. 2010a). Although repeated counts at key sites have been important in identifying these declines (e.g. Elliott et al. 2010; Spurr & Ledgard 2016), detailed information on population dynamics is generally lacking due to a dearth of individual-based studies. Here we take advantage of a detailed six-year study of riflemen (tītipounamu, *Acanthisitta chloris*) to estimate vital demographic rates and their contribution to population decline.

The rifleman is the sole species in the genus *Acanthisitta* and one of only two remaining in the ancient endemic Acanthisittidae family. This highly distinct lineage represents the outgroup to all other passerine birds (Prum et al. 2015), and at least five of its species are thought to have become extinct since human colonisation of New Zealand (Holdaway 1989). South Island riflemen (*A. c. chloris*) are not currently considered at risk (Robertson et al. 2017), but have a fragmented distribution and are generally uncommon east of the Southern Alps (Robertson et al. 2007).

Kowhai Bush, near Kaikōura is often recommended as a reliable site to see riflemen (Heather & Robertson 2015),

and research here has contributed the bulk of knowledge of the species (Sherley 1985; Lill 1991; Hunt & McLean 1993; Preston et al. 2013). It has been similarly important to the study of life history in other common native passerines (Massaro et al. 2008; Starling-Windhof et al. 2011; Khwaja et al. 2019). Kowhai Bush also provides an interesting opportunity to investigate the effects of forest regrowth because grazing livestock, which were present in a part of the site up to 2010, have been excluded since then (see below). However, over the past decade the rifleman population at Kowhai Bush has declined to a critically low level, motivating the analyses we present here. By modelling key population demographic rates (survival and reproductive success), we identify those life history stages that contributed most to the population's decline as a first step towards determining the best course of action to aid population recovery.

Methods

Field site

Kowhai Bush is located 7 km inland from Kaikōura on the east coast of the South Island. Its area comprises a 240 ha block of alluvial forest dominated by kānuka (*Kunzea ericoides*), on the banks of the Kowhai River (Gill 1980). During this study, riflemen were restricted to approximately 30 ha within

the forest, in two sections. One, which we call the 'bush', is characterised by dry stony soil, with a canopy of kānuka and mānuka (*Leptospermum scoparium*); a subcanopy of native and introduced shrubs, especially broom (*Cytisus scoparius*), and a ground flora of mosses, ferns, lichens, grasses and hook sedges (Dobson 1979). The other, which we call the 'paddock', is a stand of kānuka and mānuka in a paddock that was grazed by domestic livestock until 2010. During this time the understorey was open, with occasional gorse (*Ulex europaeus*) and *Coprosma* shrubs, and short grass cover on the ground. Since 2010, livestock have been excluded from this paddock to promote forest regeneration, and the grass has grown long. The two sections are joined by a narrow stretch of forest, but riflemen are mostly absent from this stretch. Dispersal between the sections, which would otherwise require crossing c. 150 m of open farmland, is rare (3/39 natal dispersal events we recorded). Riflemen were thought to have been historically most abundant in these sections because of the availability of suitable nesting cavities (Gill 1980), and since the 1980s they have been furnished with nestboxes. Riflemen preferentially nest in these boxes, which provide protection from predators that significantly improves fledging success (Briskie et al. 2014). During the course of this study, riflemen were occasionally observed outside of the two study areas. However, these sightings were mostly in grazed bushland just outside the perimeter of the areas, suggesting that the population was mostly restricted to just this area of the Kowhai Bush.

Field methods

The rifleman breeding season at Kowhai Bush lasts from September until January. We collected the data presented here during a study of cooperative breeding in riflemen, for which we followed individually-marked birds during the six breeding seasons from 2008–2011 and 2012–2015 (see Preston et al. 2013; Khwaja et al. 2017). Riflemen were not intensively studied in the 2011/12 breeding season or the seasons beginning in 2015 or later. However, population estimates are available from surveys in the 2015/16 and 2017–20 breeding seasons; these were the number of occupied territories estimated by regular searches of the site and checks of nestboxes throughout the breeding season. We report them here, but as individual identities and detailed life-history data were not collected, they do not contribute to estimates of recruitment, survival or breeding success.

Riflemen at Kowhai Bush are socially and sexually monogamous, and pairs have not been observed to divorce between seasons (Preston 2012; Khwaja 2017). They make a maximum of two successful breeding attempts in a season (Sherley 1985). Males and females share both incubation, which lasts c. 18 days, and nestling provisioning, which lasts c. 24 days (Sherley 1994). Breeding pairs may also be aided in provisioning by adult helpers, observed at about a quarter of nests (Preston et al. 2013; Khwaja 2017). Adult helpers are associated with increased food delivery to offspring and enhanced recruitment (Preston et al. 2016). Second broods are often (65%) helped by juvenile birds fledged from first broods, but juveniles do not make a substantial contribution to care (Preston et al. 2016; Khwaja 2017).

Each rifleman in the population was banded with a unique combination of two colour bands on one leg and a Department of Conservation metal band (AP prefix: C-shaped band of 2.3 mm internal diameter × 5.5 mm height) on the other. Nestlings were banded at 15 days old, at which time they were also sexed based on size and plumage. Unbanded adults were caught and

banded using mist nets placed near to nests where they were observed breeding or helping. These captures were made when the nestlings were at least 10 days old, to avoid inducing nest abandonment in the earlier and more sensitive nesting period. We identified active nests before eggs hatched by checking all nestboxes on the site weekly, and then checked nests daily to monitor their progress, counting numbers of eggs and nestlings present. Nestlings were considered to have fledged if they were alive in the nest on the last observation before the nest fledged. This was considered the most accurate metric of breeding success: although follow-up observations of fledglings were made, individual fledglings can become cryptic and it was not practical to follow each to full independence. Nests in natural cavities were rare (Briskie et al. 2014) and were identified opportunistically by following pairs that were not using a nestbox.

Individuals were considered to have been recruited (for first-years) or survived (for other adults) from one breeding season to the next if they were recorded in a subsequent season; otherwise, they were considered to have died. Over the course of our study there were three occasions in which a bird was recorded that had been missed in a previous season. We consider this sufficiently rare to be confident in our estimates of survival and recruitment. Although we cannot rule out some birds emigrating from the study site, this is likely to have been minimal because we did not find birds during searches of the surrounding habitat, and most of the dispersal events we recorded were over distances less than 200 m. Sherley (1993) reached similar conclusions regarding low levels of emigration from this population in the 1980s.

Population model

We constructed a two-stage (juvenile and adult) deterministic matrix model from the parameters of recruitment, survival, and productivity, to project the rate of population decline from these data. For this we used only data from females as the reproductive sex. We therefore estimated the parameter S_1 (recruitment) as the survival probability for female fledglings, S_2 (survival) as the survival probability for female adults and F (fecundity) as the mean number of female fledglings produced per adult female per breeding season (adult females who failed to fledge any female young were included, with a value of zero; Fig. 1a). The number of adult females was equal to the number of pairs in each season: adult sex ratio was never female-biased and we did not observe any unpaired females. We calculated sensitivity and elasticity of recruitment, survival and fecundity using the *popbio R* package (Stubben & Milligan 2007), to assess their contribution to the decline. Sensitivity measures the absolute contribution of a vital rate to population growth. If all vital rates were increased by the same amount (e.g. 0.01), that with the highest sensitivity would cause the greatest increase in growth rate (λ). Elasticity measures the relative contribution of a vital rate to population growth. If all vital rates were increased by the same proportion of their current value (e.g. 1%), that with the highest elasticity would cause the greatest increase in growth rate.

Leech et al. (2007) and Withers et al. (2019) modelled rifleman populations in three stages rather than two. They considered first-year birds as a different stage to older adults, because only 75% of first-years made breeding attempts in a previous study (Sherley 1993). We did not follow this approach, for four reasons. First, all adult females one year and older were members of pairs attempting to breed during our study, so there was no difference in their tendency to make breeding

attempts (100% in each case). Second, we did not know the age of the breeding female in 42% of cases and preferred to specify a simpler model using more complete data. Third, we did not know the ages of any adult birds in the first year of our study; we used our model to project from this baseline (see Fig. 3) and wanted to do so with accurate information. Finally, we found no significant differences in survival or reproduction between first-year and older birds.

Following Leech et al. (2007) and Withers et al. (2019), we also did not consider the production of eggs, the survival of eggs to hatching and the survival of chicks to fledging as separate stages in the model, although it would be possible to do so. This was for two reasons. First, these data were only available for a subset of nests, and as above we felt it would be more accurate to specify a simpler model using more complete data. Second, such a model would imply that increasing egg production could drive population growth. We consider this biologically implausible in riflemen, because females only increased the number of eggs they laid beyond a maximum of nine if a clutch or brood failed.

This is a simplified model: it assumes 100% detection probability and does not account for parameter uncertainty. The former issue can mean growth rates are underestimated. However, despite its simplicity, the model mapped well to the population decline observed over the course of our study (see Fig. 3). Managers making rifleman population projections into the future are encouraged to use methods developed by Withers et al. (2019) to account for parameter uncertainty and imperfect detection.

Results

Recruitment

We documented the fate of 192 fledglings produced from 62 nests in breeding seasons when there was fieldwork the following season (2008/09, 2009/10, 2012/13 and 2013/14). Of these, 34 (18%) were observed as adults in the following season. The mean proportion of recruits per nest was 0.18 ± 0.03 SE. Table 1 shows recruitment by year in each part of the study site. Of 102 female fledglings, 17 survived to the following season (17%), and we used this parameter in our population model (Fig. 1).

Survival

We recorded the survival or death of adult birds 136 times, in breeding seasons when there was fieldwork the following season (see above); these data included 91 different individuals (51 males and 40 females). On 66 occasions (49%), the individual survived. Table 1 shows survival by year in each part of the study site. Of 66 records for adult females, 33 survived to the following season (50%), and we used this parameter in our population model (Fig. 1).

Breeding success

We documented the annual breeding success of rifleman pairs 89 times over six breeding seasons, including 69 distinct pairs composed of a total of 56 different males and 54 different females. Pairs failed to raise any broods to fledging 21 times
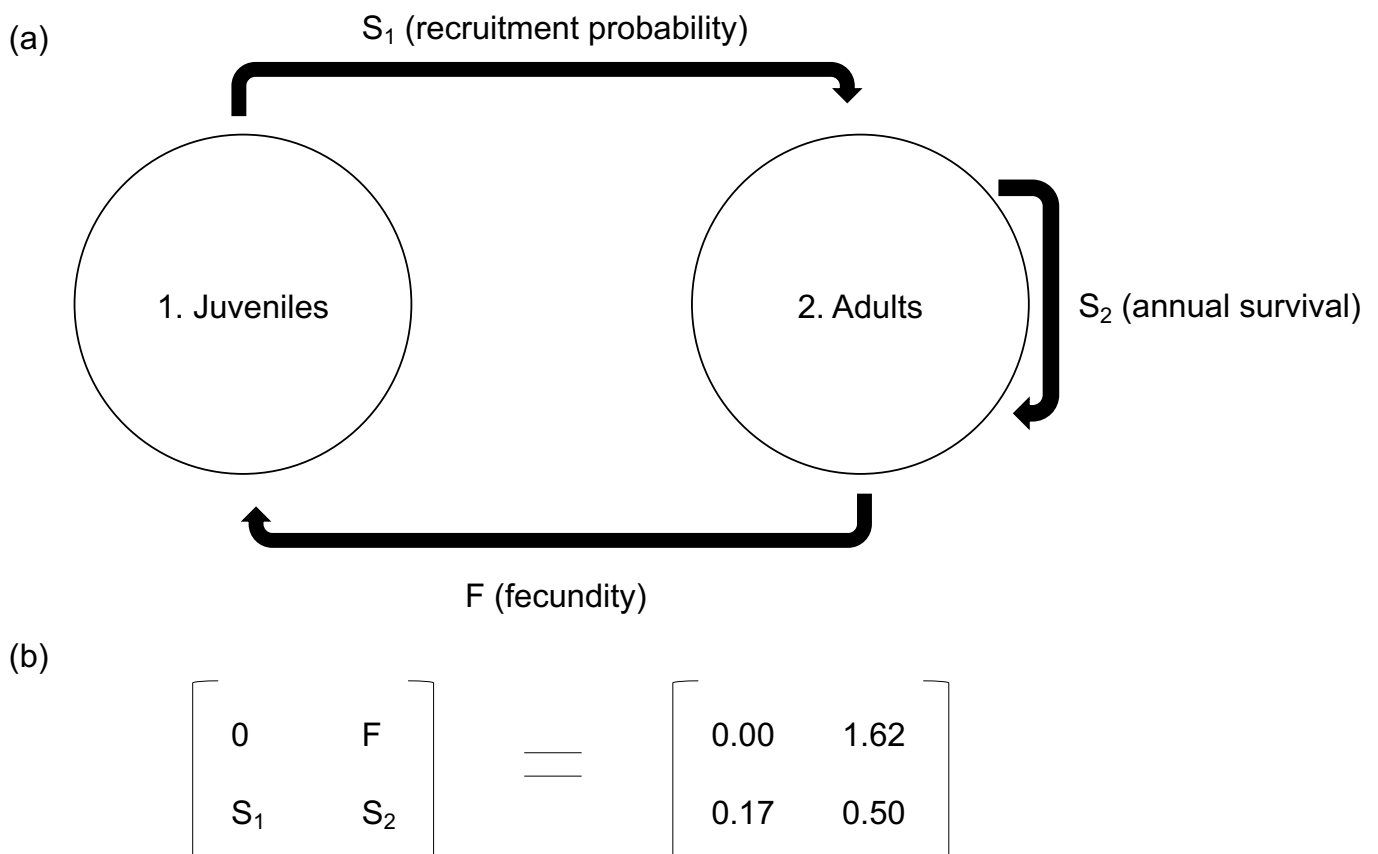

Figure 1. Schematic (a) and structure (b) of two-stage matrix model estimating the rate of population growth or decline for riflemen at Kowhai Bush. We used recruitment and survival probabilities of female fledglings and adults, respectively. Annual fecundity was the mean number of female fledglings produced per adult female per year.

Table 1. Recruitment of fledglings and survival rates for adult rifleman, from the 2008/09, 2009/10, 2012/13 and 2013/14 breeding seasons to each following season. The bush and paddock are the two main parts of Kowhai Bush in which riflemen occur. Totals are greater than the sum of bush and paddock for years when riflemen were recorded breeding outside these two areas. These birds are not included within either location but contribute to the total. In each case they bred just outside of the perimeter of the two sites, in bushland that remained grazed throughout the study. Three birds that moved between the paddock and bush are included in the proportions for the area they moved from, rather than where they were in the following year. Grazing livestock were excluded from the paddock from 2010, leading to regrowth of its understorey.

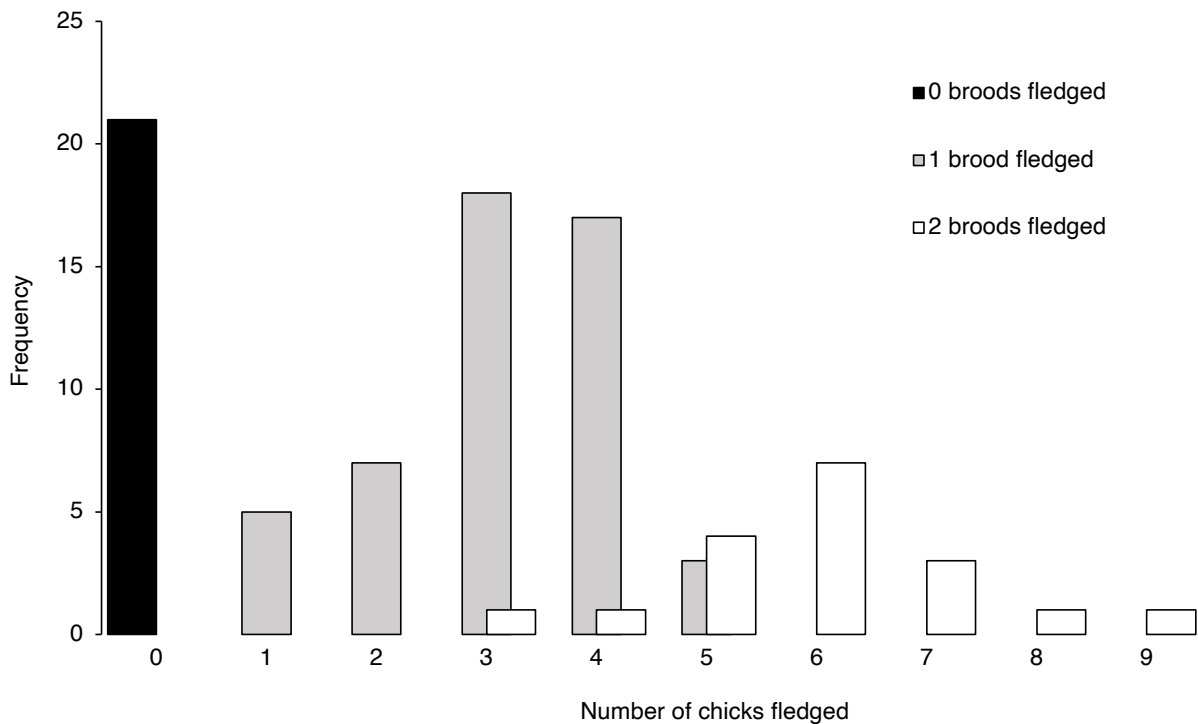|	2009	2010	2013	2014
Recruitment				
Bush	7/20 (35%)	3/17 (18%)	4/18 (22%)	5/21 (24%)
Paddock	9/47 (19%)	1/30 (3%)	3/17 (18%)	2/10 (20%)
Total	16/67 (24%)	4/47 (9%)	7/43 (16%)	7/35 (20%)
Survival				
Bush	8/16 (50%)	6/13 (46%)	11/15 (73%)	6/15 (40%)
Paddock	14/25 (56%)	11/25 (44%)	4/14 (29%)	3/5 (60%)
Total	22/41 (54%)	17/40 (43%)	17/33 (52%)	10/22 (45%)

Figure 2. Numbers of fledglings produced by rifleman pairs during a breeding season. Bars show the total number of times each number of fledglings was produced, divided into pairs that fledged no broods, one brood or two broods.

(24%), successfully raised one brood to fledging 50 times (56%), and successfully raised two broods to fledging 18 times (20%). Pairs produced a mean of 2.96 ± 0.24 SE fledglings per season, with a minimum of zero and maximum of nine (Fig. 2). Pairs produced a mean of 1.62 ± 0.15 SE female fledglings per year, and we used this parameter in our population model (Fig. 1).

Modelling population decline

We constructed a simple two-stage population matrix with parameters derived from our data: recruitment probability of female fledglings (S_1) 0.17, survival probability of female adults (S_2) 0.50 and mean number of female fledglings produced per adult female per breeding season (F) 1.62 (Fig. 1b). This model predicts a population growth rate (λ) of 0.83, or a decline of 17% per year (Fig. 3), described by the dominant eigenvalue of the matrix.

The results of sensitivity analysis showed recruitment to have the greatest sensitivity and survival to have the greatest elasticity (Table 2). In other words, an increase in female recruitment from 17% to 18% would have approximately double the effect on λ as an increase in female survival from 50% to 51% (this is interpreted from their sensitivity values). Nevertheless, because adult survival probability is currently much higher than recruitment probability, a proportional increase in adult survival leads to a greater effect on λ than the same proportional increase in recruitment. As such, adult survival is estimated to have higher elasticity than recruitment
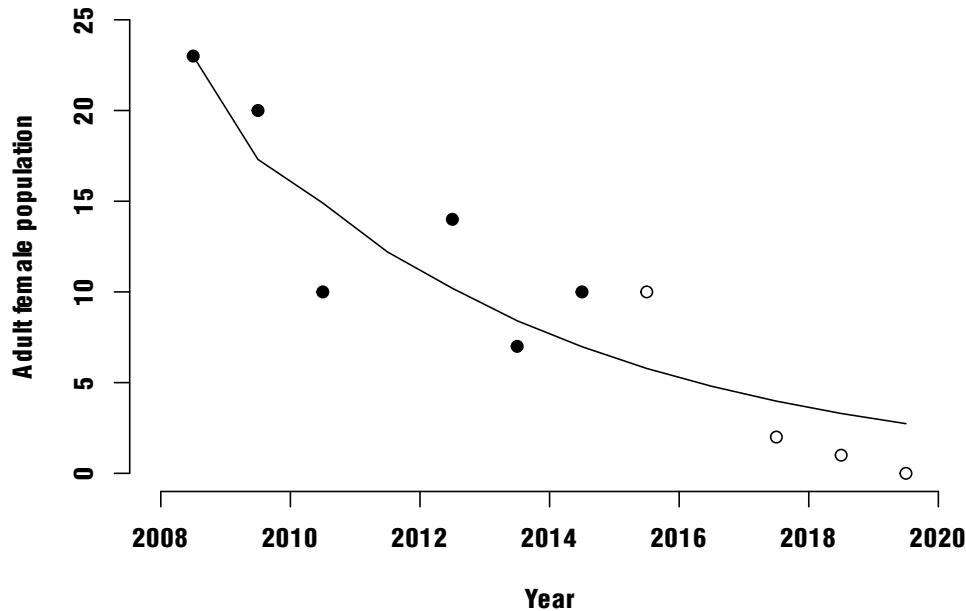
Figure 3. Rifleman population at Kowhai Bush since 2008. Filled points show numbers of female riflemen in the 2008/09, 2009/10, 2010/11, 2012/13, 2013/14 and 2014/15 breeding seasons (birds were marked with colour bands to confirm identity, so individuals in the population were counted accurately). This was equal to the number of breeding pairs as all adult females recorded were paired. The line shows the projected population from a two-stage matrix model fitted using recruitment, survival and fecundity data collected from female birds during these seasons. Open points show numbers of pairs observed in the 2015/16, 2017/18, 2018/19 and 2019/20 breeding seasons; detailed life history data were not collected during these seasons, and so they did not contribute to estimates of population parameters, but confirm the population continued to decline as predicted by the model.

(Table 2). As fecundity is measured on a different scale to survival and recruitment, it can only be compared meaningfully in elasticity, which shows perturbations as a proportion of current fecundity would have similar effects to perturbations of the same proportion in recruitment (but less than perturbations of the same proportion in survival).

The effect on λ of varying each parameter, while holding the others constant, is demonstrated in Fig. 4. This shows that the population would be expected to grow ($\lambda > 1$) if recruitment probability increased above 0.31, survival probability increased above 0.73, or females produced more than 3 female fledglings per year on average.

Discussion

In this study we documented juvenile recruitment, adult survival, and breeding success in the rifleman population at Kowhai Bush and estimated the contributions of each to an observed and concurrent population decline. Recruitment was particularly low at 18%, and this had the greatest absolute contribution to decline (sensitivity). Adult survival, at 49%, had the greatest relative contribution to decline (elasticity). Breeding pairs produced on average close to three fledglings per year. Population decline continued despite forest regeneration in one of our study sites; in fact, the years with the lowest recruitment and survival in the formerly grazed paddock occurred after livestock were excluded (Table 1).

Table 2. Estimates of recruitment and survival probabilities for female riflemen, and fecundity (mean number of female offspring produced per year), with their sensitivity and elasticity calculated from a two-stage matrix model.

Parameter	Estimate	Sensitivity	Elasticity
Recruitment	0.17	1.40	0.28
Survival	0.50	0.72	0.43
Fecundity	1.62	0.14	0.28

The data we present are perhaps most notable for the low proportion of fledgling riflemen recruiting into the breeding population, and the strong influence this appears to have on population dynamics. We estimated recruitment (= juvenile survival) at just 18%. Previous studies of riflemen have estimated much higher proportions from 31% (Withers et al. 2019) to 60% (Leech et al. 2007). As Fig. 4 shows, these proportions would have contributed to a stable or growing rather than declining population in our study, if combined with the survival and fecundity we observed. The higher value of 32% reported by Sherley (1985) is especially relevant as it was measured in the same population we studied. The reasons for the decline in juvenile survival between the two periods is not known.

One possible explanation for lower juvenile recruitment in our study is an increase in predation risk. The effect of
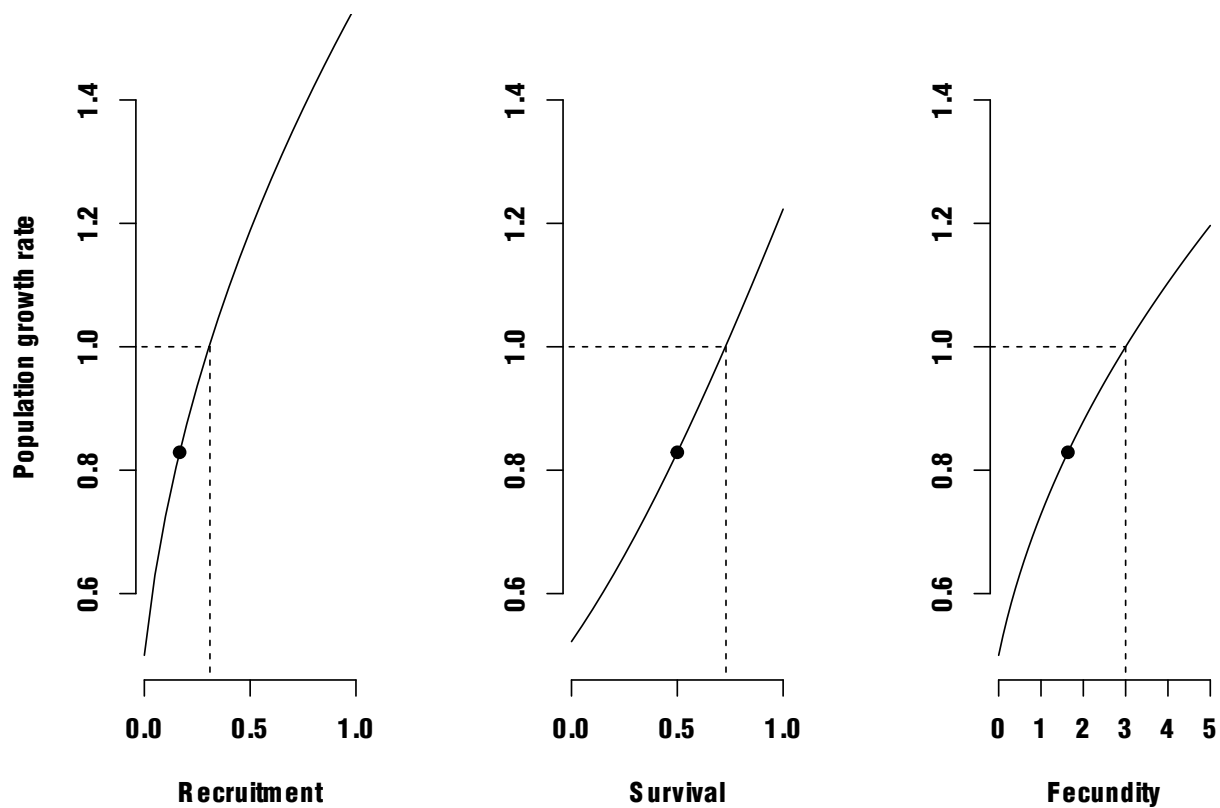
Figure 4. The effect of varying probability of recruitment, probability of survival and fecundity (production of female fledglings) on rifleman population growth rate (λ), when the other two variables are set to their current values. Points show the current value of each parameter and the current λ of 0.83, calculated from a two-stage matrix model. Dashed lines illustrate values of x required for population stability if the other two variables remain as they are. Five is shown as the maximum fecundity: riflemen produce up to nine fledglings per season, and the fledging sex ratio is 53% female (Khwaja et al. 2018), giving a maximum mean number of female fledglings per year of $9 \times 0.53 = 4.77$.

introduced predators on recruitment is indicated by Leech et al. (2007), who studied the dynamics of a reintroduced rifleman population on predator-free Ulva Island after translocation. Although there is some uncertainty around their estimate of 60%, as it is based on an estimate that pairs produced three fledglings each rather than direct observation and over only a single year, it is almost certain that recruitment was higher than observed in our study (even if all pairs had produced nine fledglings rather than the estimated three, recruitment in that study would still at 20% have been higher than that we observed). Further, adult survival on Ulva Island was 86%, also much higher than the 50% we observed at Kowhai Bush. There are a number of possible explanations for these differences. One is the absence of mammalian predators on Ulva, in contrast to Kowhai Bush where we recorded ship rat (*Rattus rattus*), house mouse (*Mus musculus*), brushtail possum (*Trichosurus vulpecula*), stoat (*Mustela erminea*), ferret (*M. furo*), and feral cat (*Felis catus*) during our study period. This difference between the sites suggests predation may limit rifleman survival and recruitment (Innes et al. 2010a).

Apart from predation risk, there are also likely to be differences in habitat quality and food availability between the sites that could explain changes in recruitment. For example, increased intra- and interspecific competition could limit survival and recruitment, but we consider this unlikely at Kowhai Bush because (1) the site has previously supported higher densities of riflemen (Sherley 1985), and (2) other insectivores such as grey warblers (riroriro, *Gerygone igata*),

fantails (pīwakawaka, *Rhipidura fuliginosa*), and brown creepers (pīpipi, *Mohoua novaeseelandiae*) occur only at low density in the paddock, where survival and recruitment have been especially low and the rifleman population has been historically high. Finally, the forest on Ulva Island is less disturbed and more diverse and thus may simply have provided unusually good conditions for riflemen, at least in the one year in which it was recorded.

Comparison with Sherley (1985) is interesting because he also studied the rifleman population at Kowhai Bush. He studied birds in both bush and paddock, but we focus on his paddock results here because "some individuals in the main study area [bush] went unrecorded", meaning estimates of survival and recruitment there are inaccurate (Sherley 1985). In 1982/83, recruitment in the paddock was estimated at 32% (52/161 juveniles), significantly greater than the recruitment we recorded in the same area in 2009–2014 (15/104 juveniles, 14%; $\chi^2 = 9.76$, df = 1, P = 0.002). Survival of newly-banded adults in the paddock was 63% (24/38 adults of unknown age), again greater than survival in the paddock during our study (32/69, 46%) although not significantly ($\chi^2 = 2.13$, df = 1, P = 0.144). These results suggest that the recent decline in the population of riflemen at Kowhai Bush, compared to that observed during the 1980s, is primarily associated with reduced recruitment, complementing our sensitivity calculations that suggest recruitment has the strongest absolute contribution to population decline.

There are a few possible explanations for why recruitment

levels we observed (and to a lesser degree survival) are much lower than in the 1980s. Differences in climate or predation pressure between the study periods could have played a role. Competition is an unlikely cause here, as reduced survival and recruitment has coincided with reduced population density. The changing habitat in the paddock during our study period due to the cessation of grazing is a clear difference that may have had an effect. Although we cannot demonstrate causation, it is noteworthy that this intervention, which aimed to improve conditions for native species, has been associated with reduced recruitment. At the least, we can say with confidence that it has had no noticeable positive effect on riflemen. Riflemen, especially juveniles, foraged on the ground regularly while the paddock was grazed and were observed to get caught in longer grass after grazing was ceased (SAJP, pers. obs.). Long grass has also been associated with higher densities of predatory ship rats in a study in the Waikato (Innes et al. 2010b). Although monitoring and control of predatory mammals at the site has been carried out by Environment Canterbury since 2015 (J Jack, Environment Canterbury, pers. comm.), there are no comparable data from the 1980s and so it is not possible to determine whether predator densities during our study period are likely to have been higher. It is notable that the rifleman population has continued to decline even during this predator control, in contrast with an apparent recovery in the population of South Island robins (*Petroica australis*) in the more closed canopy areas of the forest (JVB, unpubl. data).

In contrast to survival and recruitment, breeding success during our study was not lower than in previous studies of riflemen. On Ulva, first-year breeding females were estimated to produce 0.68 female offspring per year, and older adult females were estimated to produce 1.24, including those that died between conception and fledging (Leech et al. 2007). In our study, all pooled adult females produced an average exceeding this, of 1.64 female fledglings per year. Although our perturbation analysis shows positive growth could be achieved if females fledged over 3 female offspring per year on average, this comparison suggests such an increase in breeding success would be biologically unrealistic, in contrast to increases in survival and especially recruitment. Instead, it appears that rifleman breeding success is already relatively high at Kowhai Bush. This is due in large part to their use of nestboxes, which by excluding predators increase the probability of nest success from 0.16 to 0.80 (Briskie et al. 2014). Without this boost to productivity, riflemen would likely have disappeared from the site some time ago.

The rate of decline modelled for this population (λ of 0.83) exactly matches that estimated by Withers et al. (2019) for a translocated population in the North Island. Both being small populations, stressors limiting vital rates may have been exacerbated by inbreeding depression, which can act especially strongly on juvenile survival (Heber et al. 2013).

In summary, despite the high breeding success associated with nestbox use, our observations at Kowhai Bush document a population decline, which has been influenced primarily by low juvenile survival and recruitment. The data we present provide valuable information on vital demographic rates in riflemen, in this case for a nestbox population in regenerating forest habitat without predator control. Comparison with data from areas with different conditions will improve our understanding of the factors driving variation in rifleman population dynamics. As the rifleman population has now all but disappeared in Kowhai Bush, recovery may only be possible through an assisted reintroduction. However, determining the cause of low recruitment is critical to prevent any reintroduced population from facing the same fate.

Data and code availability

The data and code used in this manuscript are not publicly accessible, but will be shared upon reasonable email request to the corresponding author.

Author contributions

NK and SP conceptualised the project, devised the methods, completed the investigation and analysis along with JB. Data curation was undertaken by NK and SP. NK wrote the original draft and all authors contributed to reviews and editing.

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