Received: 11 February 2021 | Revised: 13 September 2021 | Accepted: 22 September 2021

DOI: 10.1111/cobi.13843

Conservation Biology

CONTRIBUTED PAPER

Using experimental reintroductions to resolve the roles of habitat quality and metapopulation dynamics on patch occupancy in fragmented landscapes

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Article Impact Statement: Experimental reintroductions are essential for testing rapid inferences about effects of isolation and habitat quality on patch occupancy.

21–100

Abstract

Declines of species in fragmented landscapes can potentially be reversed either by restoring connectivity or restoring local habitat quality. Models fitted to snapshot occupancy data can be used to predict the effectiveness of these actions. However, such inferences can be misleading if the reliability of the habitat and landscape metrics used is unknown. The only way to unambiguously resolve the roles of habitat quality and metapopulation dynamics is to conduct experimental reintroductions to unoccupied patches so that habitat quality can be measured directly from data on vital rates. We, therefore, conducted a 15-year study that involved reintroducing a threatened New Zealand bird to unoccupied forest fragments to obtain reliable data on their habitat quality and reassess initial inferences made by modeling occupancy against habitat and landscape metrics. Although reproductive rates were similar among fragments, subtle differences in adult survival rates resulted in λ (finite rate of increase) estimations of <0.9 for 9 of the 12 fragments that were previously unoccupied. This was the case for only 1 of 14 naturally occupied fragments. This variation in λ largely explained the original occupancy pattern, reversing our original conclusion from occupancy modeling that this occupancy pattern was isolation driven and suggesting that it would be detrimental to increase connectivity without improving local habitat quality. These results illustrate that inferences from snapshot occupancy should be treated with caution and subjected to testing through experimental reintroductions in selected model systems.

KEYWORDS

connectivity, habitat fragmentation, habitat restoration, patch dynamics, population growth rate, reintroduction, species recovery, translocation

Uso de Reintroducciones Experimentales para Determinar las Funciones de la Calidad delHábitat y las Dinámicas Metapoblacionales en la Ocupación de Paisajes Fragmentados

Resumen: La declinación de las especies en paisajes fragmentados tiene el potencial de ser revertida mediante la restauración de la conectividad o de la calidad del hábitat. Se pueden utilizar los modelos ajustados a los datos de ocupación instantánea para predecir la efectividad de estas acciones. Sin embargo, estas inferencias pueden ser engañosas si se desconoce la confiabilidad de las medidas usadas para el hábitat y el paisaje. La única manera de determinar inequívocamente las funciones de la calidad del hábitat y de las dinámicas metapoblacionales es mediante la realización de reintroducciones experimentales en los fragmentos no ocupados, de tal manera que se puede medir directamente la calidad del hábitat a partir de los datos de las tasas vitales. Por lo tanto, realizamos un estudio de 15 años que involucró la reintroducción de un ave neozelandesa amenazada en fragmentos no ocupados de bosque para así obtener datos confiables de la calidad del hábitat y reevaluar las inferencias iniciales hechas por los modelos de ocupación en relación con las medidas de hábitat y paisaje. Aunque las tasas de reproducción fueron similares entre los fragmentos, algunas diferencias sutiles en las tasas de supervivencia de los adultos resultaron en estimaciones λ (una tasa finita de incremento) <0.9 en nueve de los doce fragmentos que no estaban ocupados previamente. Este fue el caso para uno solo de los 14 fragmentos ocupados naturalmente. Esta variación λ explicó en su mayoría el patrón original de ocupación, revirtiendo nuestra conclusión original obtenida del modelo de ocupación de que este patrón estuvo causado por el aislamiento y sugiriendo que sería perjudicial incrementar la conectividad sin mejorar la calidad del hábitat local. Estos resultados muestran que las inferencias a partir de la ocupación instantánea deberían abordarse con cautela y estar sujetas al análisis mediante reintroducciones experimentales en sistemas modelados selectos.

PALABRAS CLAVE
conectividad, dinámicas, de fragmentos, fragmentación, del hábitat, recuperación de especies, reintroducción, restauración del hábitat, reubicación, tasa de crecimiento poblacional

INTRODUCTION

Because habitat fragmentation is a major contributor to the global biodiversity crisis, attempts are being made worldwide to reduce its impacts (Fischer & Lindenmayer, 2007). Species may decline in fragmented landscapes due to deterioration of local habitat quality, where "habitat quality refers to the ability of the environment to provide conditions appropriate for individual and population persistence" (Hall et al., 1997). Deterioration in local habitat quality may be due to a wide range of factors, including changes in predation rates, interspecific competition, parasitism, and abiotic stresses, as well as resource availability (Chalfoun et al., 2002; Harrison & Bruna, 1999; Saunders et al., 1991). However, species may also decline due to isolation of fragments even if there is no change in local habitat quality. Such isolation-driven decline may occur through reduced colonization rates following chance extinctions (Levins, 1969) or through inbreeding depression caused by reduced gene flow (Frankham et al., 2019). Species declines in fragmented landscapes can, therefore, potentially be reversed by restoring local habitat quality in fragments, improving connectivity among fragments, or a combination of both.

The appropriate management actions can be guided by models fitted to occupancy data, but the models used will reflect the underlying paradigm for factors driving patch occupancy (Armstrong, 2005). Predictions can be made solely from within the metapopulation paradigm, for example, using the incidence function model, which allows extinction and recolonization rates to be modeled based on occupancy patterns in relation to patch size and isolation (Drechsler et al., 2003; ter Braak et al., 1998). This approach may be appropriate if a species' habitat can be defined by a simple metric, such as the presence of its host plant (Hanski et al., 1996). Predictions can also be made solely from within the habitat paradigm, typically by comparing multiple habitat metrics for occupied and unoccupied patches (e.g., Guisan & Zimmermann, 2000; Olden & Jackson, 2002). This approach may be appropriate if there is reason to believe that dispersal among habitat fragments is not a limiting factor. In most cases, it will be sensible to integrate these two approaches to allow the relative effects of metapopulation dynamics and local habitat quality to be evaluated. Armstrong (2005) found that 17 of the 43 analyses of occupancy data published in *Conservation Biology* from 1994 to 2003 involved elements of both paradigms.

The problem is that the resulting inferences are only valid if patch size, isolation, and habitat quality can all be measured accurately. Simple measures of isolation based on Euclidean distances may poorly reflect the true degree of isolation in relation to species' movement behavior, hence, considerable research may be needed to derive appropriate measures (Gobeil & Villard, 2002; Goodwin & Fahrig, 2002; Haynes & Cronin, 2006). Similarly, habitat metrics measured in conjunction with occupancy surveys may poorly reflect the true quality of the patches for the species concerned, especially if researchers take the shotgun approach of measuring many variables in the hope of finding useful predictors (Mortelliti et al., 2010). The only direct measure of habitat quality is the demographic performance of the species concerned (Hall et al., 1997), meaning that vital rates (reproduction and survival) must be estimated at individual sites (Breininger et al., 1995; Caughlin et al., 2019; Flesch, 2017). However, even with vital rate data, inferences about habitat quality need to be made carefully. In particular, several years of data may be required to make reliable inferences in the face of annual variation, and variation in rates among fragments may be confounded by movement, density-dependence, and variation in genotypes of the organisms under study (Armstrong, 2005).

The additional major problem is that because habitat quality can only be measured directly from vital rates, it cannot be measured directly at sites where a species is absent. Consequently, the relative roles of habitat quality and metapopulation dynamics on patch occupancy cannot be unambiguously resolved unless the species is reintroduced to empty patches or natural colonization occurs (Armstrong, 2005). Opportunities to monitor vital rates after natural colonization will be extremely rare if occupancy is truly isolation driven. Experimental reintroductions are, therefore, the acid test for inferences made from analysis of occupancy data (Hanski, 1999). However, there are few opportunities to conduct such experiments because they require sufficient release sites and monitoring to enable robust comparison of demographic performance between previously occupied and unoccupied patches; need to be conducted in systems where potential confounds can be reasonably accounted for; and will only be acceptable if there is low potential cost in terms of conservation or animal welfare.

We examined the long-term results of a unique opportunity to conduct such an experiment with a threatened forest bird, the toutouwai (*Petroica longipes*), in a fragmented landscape in the central North Island of New Zealand. We first collected data on occupancy over the landscape and assessed the degree to which occupancy was explained by habitat metrics or landscape metrics. This analysis suggested that the distribution of toutouwai was primarily isolation driven, with the cost-distance to the nearest continuous forest being the dominant predictor of occupancy (Armstrong & Richard, 2010a,b). We then established the species in 12 previously unoccupied fragments through reintroductions and compared their demographic performance to 14 naturally occupied fragments using finite rates of increase (λ) estimated from 15 years of survival and reproduction data. We then assessed the degree to which this direct measure of habitat quality supported or altered our initial conclusions based on habitat metrics.

METHODS

Species, landscape, and occupancy surveys

The toutouwai, or North Island robin, is a small (26–32 g) insectivorous forest passerine that has disappeared from >90% of its original range due to forest clearance and predation from exotic mammals. It has been reintroduced to >30 islands and mainland sanctuaries, where mammalian predators have been controlled or eradicated (Miskelly & Powlesland, 2013), but also persists in some unmanaged areas of the central North Island. They are highly territorial and sedentary, generally establishing a permanent territory within a few months after fledging (Higgins et al., 2001). They breed in monogamous pairs from September to February, producing up to three broods of two to three juveniles that undergo a dispersal phase if they survive to independence.

The study area (Figure 1) was a 15,000-ha landscape east of the township of Benneydale (175°220’ E, 38°320’ S). This landscape mostly consists of pasture used for livestock grazing, but it has 74 fragments of native podocarp-broadleaf forest ranging from 0.2 to 1600 ha. It is bordered to the east and south by exotic pine (*Pinus radiata*) plantations, which in turn border a 76,000-ha area of continuous native forest (Pureora Forest Park). The toutouwai for the experimental reintroductions were translocated from the pine plantations and were taken from blocks due for felling, so there was no potential conservation impact from the removals.

We conducted occupancy surveys in all 74 fragments in the first three breeding seasons (2002/2003–2004/2005) and found toutouwai in 33 of these fragments in at least one season. This surveying involved playing territorial calls at 150-m intervals, with this spacing designed to allow potential detection of any bird (Richard & Armstrong, 2010a). It was impossible to repeat this broad surveying more than once per season, partially because many of the fragments were difficult to access. However, given that survival surveys for marked birds (see below) indicated a 92% probability of an individual being detected in such surveying (Armstrong et al., 2014), there is likely to have been <1% probability of nondetection in any fragment with ≥2 individuals present. We simultaneously collected data on 11 habitat metrics (canopy height, secondary canopy height, mean tree diameter at breast height, tall tree density, small tree density, understory height, vine density, elevation, slope, distance to nearest stream, and distance to edge of fragment) and calculated four landscape metrics for each fragment (area, shape, cost-distance to the nearest continuous forest, and an index of functional patch connectivity [IFPC]).

The cost-distance to continuous forest (CDCF) and IFPC were both based on movement data for 53 juvenile toutouwai that were radio tracked over the first three breeding seasons (Richard & Armstrong, 2010b). These metrics were constructed by using a case–control design to quantify the resistance value of each pixel in the landscape based on its vegetation type and distance from nearest woody vegetation. The radio tracking showed that juvenile toutouwai moved readily between adjacent fragments but suggested that they could not cross the pasture gaps necessary to reach the most isolated fragments in the landscape (Figure 1). Later, radio tracking of 83 additional juveniles indicated that their probability of remaining in their natal fragments ranged from 0.17 to 0.53 depending on the cost-distance to the nearest neighbor (Armstrong et al., 2014).

Experimental reintroductions and monitoring of vital rates

In September 2002 (start of first breeding season), we initiated intensive monitoring of vital rates in 12 accessible fragments that had at least one toutouwai breeding pair. We added two additional occupied fragments over the next two breeding seasons, giving a total of 14 naturally occupied fragments that were monitored. These fragments ranged from 1.3 to 1600 ha. After the third breeding season, we selected 13 accessible fragments that had been unoccupied all three seasons and targeted these for experimental reintroductions and subsequent monitoring of vital rates. These unoccupied fragments ranged from 6.1 to 56.4 ha. Although the selection of fragments for intensive monitoring was constrained by ease of access via farm tracks, the fragments selected were well scattered over the landscape (Figure 1).

We translocated a total of 190 toutouwai to the 13 fragments over five successive postbreeding periods (late March to early June in 2005–2009), resulting in a total of 55 settlers (present in September) in 12 previously unoccupied fragments (see Armstrong et al., 2013 for methods). Due to subsequent natural colonization (≥13 birds) and recruitment from juveniles produced, we were able to monitor survival of 115 color-banded

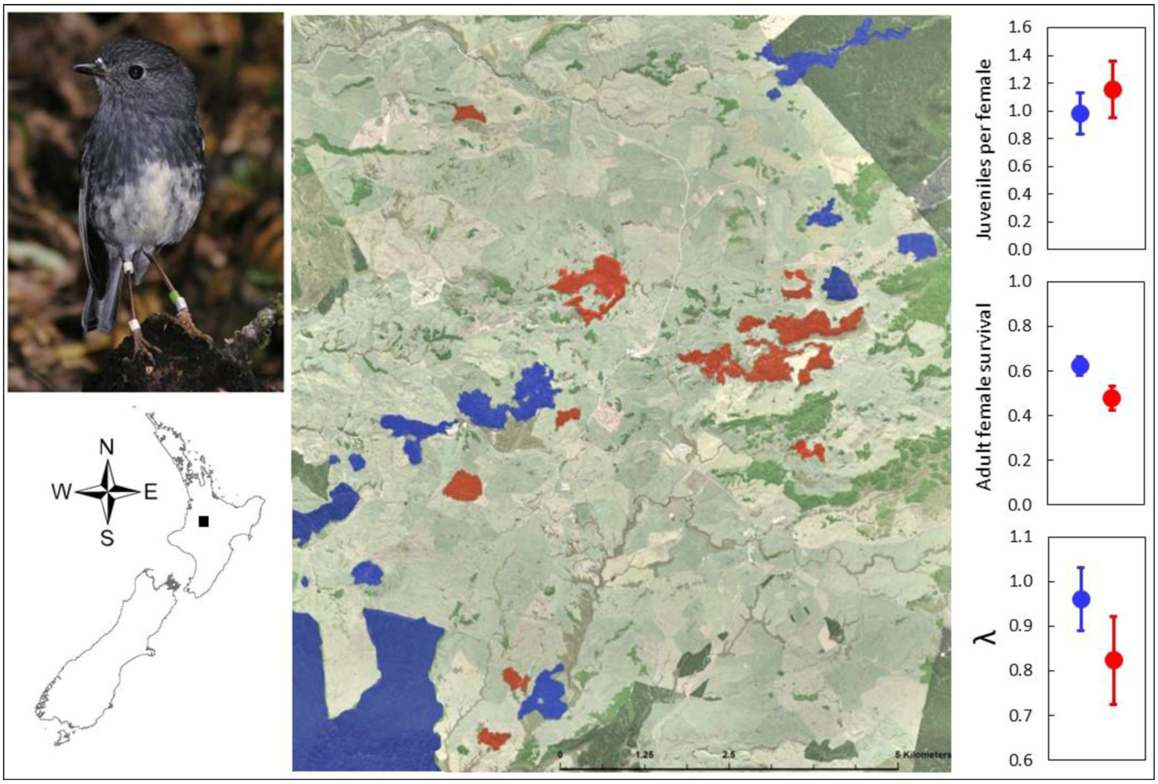

FIGURE 1 Landscape where toutouwai (inset) were reintroduced to 12 unoccupied forest fragments from 2005 to 2007, and their subsequent survival and reproduction in these fragments (red) compared with that of toutouwai in 14 naturally occupied fragments (blue). The estimated reproduction rates, annual adult female survival probabilities, and finite rates of increase (λ) are averages for the two types of fragments derived from a Bayesian hierarchical model fitted to the data (vertical bars, SE). These fragments consist of native broadleaf-podocarp forest, which is also found in the other forested (deep green) areas except for the exotic *Pinus radiata* plantations in the upper-right and lower-right corners. The matrix is pasture used for livestock grazing. Toutouwai photo by Rebecca Boulton

adults in these fragments and obtained 100 reproduction observations (number of independent juveniles produced by a female over a breeding season) for 82 individual females. For naturally occupied fragments, we monitored survival of 267 color-banded adults and obtained 251 reproduction observations for 211 individual females.

We monitored adult survival through triannual surveys (September, January, and May) conducted for 15 years (2002–2017) and monitored numbers of juveniles produced by individual breeding pairs for nine breeding seasons (2002/2003–2010/2011) (see Armstrong et al., 2014 for monitoring methods). The monitoring was unbalanced to some extent because the previously unoccupied fragments were added after the first 3 years, and due to logistic constraints, monitoring needed to be discontinued in two naturally occupied fragments after 3 years and a further two fragments after 6 years. We, therefore, included temporal random effects in our models (see below) to avoid differences in rates among fragments being confounded with variation in environmental conditions over time (e.g., due to variations in food abundance, predator cycles, or weather). We assumed this temporal variation acted in parallel among the fragments because this is a reasonable assumption given the small scale of the landscape. All data are in Appendix S1.

Modeling

Our aim was to assess whether our inferences about factors driving occupancy of fragments (Richard & Armstrong, 2010a) were changed when we replaced the initial metrics of local habitat quality with direct measures of habitat quality obtained from vital rates. We, therefore, conducted two separate logistic regression exercises in which initial occupancy of the 26 fragments selected for intensive monitoring was regressed against the initial habitat and landscape metrics for the fragments and regressed against fragment-specific λ values in combination with any landscape metrics retained in the first analysis.

The first analysis followed the backward stepwise variable selection used by Richard and Armstrong (2010a), but with occupancy of fragments as the response variable rather than occupancy of individual survey sites within fragments. Richard and Armstrong (2010a) assessed the predictive value of all 15 habitat and landscape variables for explaining occupancy of 400 individual sites. They removed variables sequentially based on Akaike's information criterion (AIC); assessed the fit of selected models based on correct classification rate, area under the curve of the receiver operating characteristic plot, and the Cohen's kappa; and checked for spatial autocorrelation in the models with semivariograms of the residuals. Building on this earlier research, our full model included the five variables found to be potentially useful predictors of occupancy by Armstrong and Richard (2010a). However, because our analysis was at the fragment level, the habitat metrics were average scores for each fragment rather than scores for individual sites and there was no fragment random effect because there was only one observation per fragment. The full model took the form:

$$logit\ (p_i) = \alpha + \beta_{CanH} * CanH_i + \beta_{SmallTreeD} * SmallTreeD_i + \beta_{USH} * US\,H_i + \beta_{IFPC} * IFPC_i + \beta_{CDCF} * CDCF_i, \quad (1)$$

where p_i is the initial occupancy of fragment i (1 if occupied, 0 otherwise), α is the intercept, CanH is canopy height, SmallTreeD is small tree density, USH is understory height, CDCF is cost-distance to continuous forest, IFPC is index of functional patch connectivity, and β parameters are the effects of the variables. Following Richard and Armstrong (2010a), IFPC and CDCF values were subjected to log and square-root transformations, respectively, all variables were standardized, and variables were removed based on AIC. We repeated this procedure with both the glm function in R (binomial family) and with our own code (Appendix S2) written in OpenBUGS 3.2.3 (Spiegelhalter et al., 2014) with uninformative priors used for all parameters. Our rationale was to allow direct comparison with the second analysis, which was done in OpenBUGS to allow the derivation of λ values to be integrated with the occupancy modeling (see below), while also allowing direct comparison with Richard and Armstrong's (2010a) analysis conducted in R.

We derived the λ values for the 26 fragments by fitting a Bayesian hierarchical model to the survival and reproduction data. The OpenBUGS code is in Appendix S4, and a full explanation of the modeling approach is in Armstrong et al. (2014). Fragments were treated as random effects, allowing fragment-specific estimates to be obtained for vital rates. Fragment-specific finite rates of increase were derived as:

$$\lambda_i = s_{a,i} + 0.5 * f_i * s_{j,i}, \quad (2)$$

where $s_{a,i}$ is annual survival probability of adult females, f_i is the mean number of juveniles produced per female per year, and $s_{j,i}$ is juvenile survival probability, which was taken to be the probability of a juvenile surviving the first month of independence (estimated from radio-tracking data) multiplied by the probability of an adult female surviving from February to September (Armstrong et al., 2014). These λ values are designed to measure local habitat quality, so they deliberately exclude immigration and emigration. The model incorporated random temporal variation in survival (4-month intervals), detection (surveys) and reproduction (years), random variation in reproduction among individual females, and fixed effects of sex and season on survival. Because some fragments were subject to experimental rat control from 2008 to 2014 (Armstrong et al., 2014), the models included further effects to exclude increases in survival and reproduction in years when rats were suppressed. The results reported here are, therefore, representative of the landscape in its unmanaged state (i.e., with no rat control). Because monitoring of reintroduced birds began in September, 3–6 months after translocation, survival rates for these birds are unlikely to have been confounded by the postrelease elevation in mortality that can occur within the first 3 months after toutouwai translocations (Armstrong et al., 2017).

In the second analysis, we integrated the two blocks of OpenBUGS code so that the initial occupancy of the 26 fragments was predicted by their λ_i values rather than the original habitat metrics (Appendix S5). That is, the λ_i values derived through Equation (2) were substituted into Equation (1) along with any landscape metrics retained following the stepwise variable selection in the first analysis. The integration of the OpenBUGS code meant that uncertainty in the λ_i values was propagated into the occupancy analysis through the Markov chain Monte Carlo fitting. As for the first analysis, we standardized the variables to allow direct comparison of effect sizes.

RESULTS

The first analysis suggested that initial toutouwai occupancy of the 26 fragments was best explained by one landscape metric (CDCF) and one habitat metric (understory height) (Table 1) because the backward selection resulted in the other three variables being removed (Appendix S3). Under this model, occupancy was predominantly explained by connectivity, with occupancy probability clearly declining as the cost-distance from continuous forest increased (Table 1). Understory height had a tentative positive effect on occupancy, but the effect size was approximately half that of CDCF and the 95% credible interval for the effect included 0. The stepwise variable selection gave similar results when models were fitted in R or OpenBUGS (Appendix S3), and the result was similar to Richard and Armstrong's (2010a) analysis, which showed CDCF to be the dominant predictor of occupancy for 400 individual survey sites among all 74 fragments in the landscape.

The analysis of vital rates, however, revealed differences in habitat quality that were not apparent from the habitat metrics. The average reproduction rate in the 12 fragments where toutouwai were reintroduced was similar to that in the naturally occupied fragments (Figure 1), and there was no indication of variation among fragments at all. However, adult female survival was highly variable among fragments and tended to be lower at the previously unoccupied fragments (Figure 1 & Appendix S6). Consequently, λ_i was estimated to be <0.9 for 9 of the 12 fragments that were previously unoccupied, whereas this was the case for only 1 of 14 naturally occupied fragments (Figure 2 & Appendix S6). In addition, there was a negative correlation between λ and CDCF (Figure 2), meaning that the apparent effect of CDCF on occupancy was at least partially explained by differences in λ.

Therefore, when we used λ_i rather than understory height as the measure of habitat quality in the second occupancy analysis, λ became the dominant predictor of the initial occupancy pattern, with an effect size much larger than that of either variable in the first analysis (Table 1, Figure 2, & Appendix S7). This analysis suggested that CDCF had a secondary effect on the

TABLE 1 Models that best explained initial occupancy of 26 forest fragments by toutouwai when probability of occupancy was modeled based on two landscape metrics[a] and three habitat metrics[b] and when habitat metrics were replaced by fragment-specific finite rates of increase (λ) derived from a Bayesian hierarchical model fitted to survival and reproduction data collected from toutouwai in the fragments[c]

Analysis	Parameter	Mean	SE	2.5%	Median	97.5%
Occupancy modeled based on habitat and landscape metrics	α	0.35	0.51	−0.62	0.33	1.39
	β_{CDCF}	−1.94	0.80	−3.73	−1.86	−0.59
	β_{USH}	1.00	0.64	−0.12	0.97	2.38
Habitat metrics replaced by fragment-specific finite rates of increase (λ)	α	−0.43	2.15	−5.29	−0.31	4.58
	β_{CDCF}	−5.12	4.05	−15.04	−4.49	1.03
	β_{λ}	13.23	6.05	2.86	12.62	25.74

Note: All variables standardized to allow effect sizes to be compared, and all parameters had uninformative priors.

[a] Cost-distance to continuous forest (CDCF) and index of functional patch connectivity (IFPC).

[b] Canopy height (CanH), understory height (USH), and average small tree density (SmallTreeD).

[c] Models fitted using logistic regression: α, intercept; β_{CDCF}, effect of cost-distance to continuous forest; β_{USH}, effect of understory height; and β_{λ}, effect of finite rate of increase (λ).

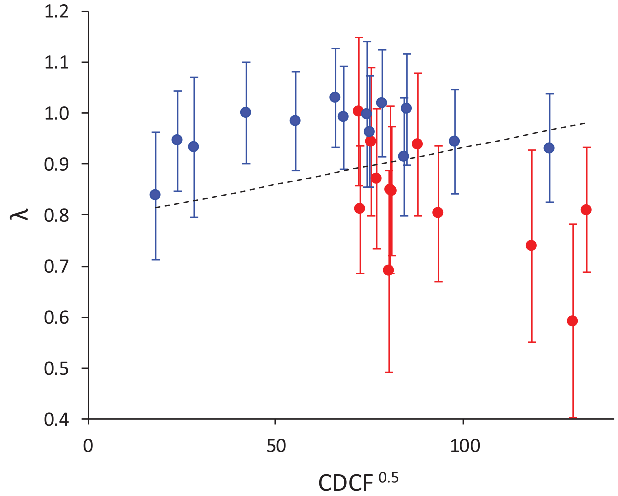

FIGURE 2 Comparison of naturally occupied fragments (blue) and previously unoccupied fragments (red) in relation to cost distances to continuous forest (CDCF) and finite rates of increase (λ) estimated from survival and reproduction data for toutouwai in these fragments (vertical bars, SE; dashed line, combinations of λ and CDCF estimated to give a 0.5 occupancy probability based on the model shown in the lower portion of Table 1)

occupancy pattern; for example, the occupied fragment with the lowest λ_i estimate was the one closest to continuous forest (Figure 2). However, the estimated effect size of CDCF was much smaller than that of λ (Table 1 & Figure 2), and its 95% credible intervals overlapped 0 (Table 1).

DISCUSSION

Our study illustrates how perceptions about factors driving patch occupancy can change with improved data, as was also illustrated by Flesch (2017). When habitat quality was assessed based on simple habitat metrics, our analysis suggested that occupancy of forest fragments by toutouwai was mainly driven by isolation, similar to our previous conclusion based on occupancy of individual survey sites within fragments throughout the landscape (Richard & Armstrong, 2010a). However, experimental reintroductions to unoccupied fragments accompanied by long-term collection of vital rate data revealed that the original occupancy pattern was primarily explained by variation in habitat quality. Long-term data on patch dynamics have reinforced this conclusion—toutouwai disappeared from 8 of the 12 reintroduction fragments within 1−9 years but subsequently recolonized them (all 26 fragments were occupied in our final survey in September 2017). In combination with the immediate natural arrivals following reintroductions (see "Methods"), these observations suggest that isolation was not actually a major barrier to occupancy. However, our analysis suggests that isolation did have a secondary effect on occupancy, as is to be expected given that marginal habitats are likely to be occupied if they can be easily colonized (Pulliam, 1988).

The potential misperceptions from rapid inferences will depend on the nature of the data. The importance of isolation may be underestimated if poor measures of connectivity are used (Goodwin & Fahrig, 2002), so many years of data may also be needed to accurately assess effects of connectivity on biodiversity (Damschen et al., 2019). However, habitat quality is notoriously difficult to quantify, so its role in landscape dynamics is often poorly understood (Mortelliti et al., 2010; Morrison et al., 2020). In our study system, this problem was exacerbated due to local habitat quality being negatively correlated with isolation, meaning the apparent effect of isolation was exaggerated due to this confound. We do not expect such correlation to occur in most systems. Consequently, we do not expect an isolation metric, such as CDCF (cost distance to continuous forest), to ever be a useful predictor of local habitat quality. We also do not expect occupancy analysis based on rapidly collected metrics to normally give the type of misleading results found in our system. However, it is important to be aware that isolation will not always be independent of local habitat quality.

Inferences about habitat quality based on vital rates can also be misleading, especially if key components are missed.

Reproduction rates are convenient measures of habitat quality because they can be measured fairly rapidly (Flesch, 2017), and evidence of good reproduction following experimental reintroductions has previously been cited as evidence that declines were isolation driven (Cooper & Walters, 2002). However, we found that interfragment variation in habitat quality was not reflected in reproduction rates, but instead in adult female survival, which is often a key driver of population growth (Caswell, 2001). Consistent with our results, the brown tree creeper (*Climacteris picumnus*) subpopulations established by Cooper and Walters (2002) later disappeared, and longer-term monitoring suggested the decline of the species from the wider landscape was due to habitat degradation rather than patch isolation (Armstrong & Ford, 2015).

Although we believe the fragment-specific finite rate of increase (λ) we derived were the best possible measures of local habitat quality, it is important to be wary of further potential confounds in the use of such measures (Armstrong, 2005). We do not expect adult female survival, the key driver of λ, to have been confounded by movement in our study system because adult females are extremely sedentary and any emigrants had a high probability of being detected. We do not expect adult survival to have been affected by genetic structuring or inbreeding depression, partly because adult survival appears to be insensitive to inbreeding in the species (Armstrong et al., 2021). We do not expect adult survival to have been density dependent because it appears to be density insensitive in toutouwai (Armstrong et al., 2021) and all fragments were at low density. We also do not expect postrelease effects to have operated beyond the 3–6 months elapsed between translocations and initial data collection. We cannot completely exclude such confounds, and they need to be considered in any inferences about habitat quality from vital rates. Nevertheless, monitoring of vital rates following reintroductions provides the clearest information about habitat quality of previously unoccupied sites.

Distribution of species across landscapes will generally be determined by a mixture of habitat and metapopulation factors (Thomas, 1994; Hanski, 1999; Fischer & Lindenmayer, 2007). However, the relative importance of these factors will vary among systems, and perceptions about this relative importance will determine management actions (i.e., belief that habitat quality is the key limiting factor will lead to local restoration initiatives, whereas belief in isolation limitation will lead to attempts to improve connectivity through corridors and stepping stones [Beier & Noss, 1998] or strategic translocations [Lubow, 1996; Marsh & Trentham, 2000]). Incorrect perceptions could have disastrous consequences.

In particular, it is critical to avoid translocating endangered species to unsuitable locations on the belief that their absence is due to chance local extinctions and inability to recolonize (IUCN, 2013). Consequently, reintroduction practitioners usually follow the habitat paradigm in that unoccupied patches are assumed to have unsuitable conditions for the species unless there is reason to believe that habitat quality has been restored, either through human intervention or natural regeneration (Armstrong & Ford, 2015). Within this paradigm, there are well-developed methodologies for deciding the suitability of potential reintroduction cites and adaptively managing reintroduced populations (Ewen et al., 2012).

In addition, while improving connectivity is essential for ecological restoration (Hilty et al., 2020), it is important to be aware that this may negatively affect some species in some systems. It is well known that many species have been saved from extinction by isolation, particularly isolation from invasive predators on offshore islands (Jones et al., 2016). Where there is unrecognized variation in quality among habitat fragments, improvements in connectivity could result in detrimental source-sink dynamics (i.e., reduce metapopulation size by facilitating the movement of animals from good habitats to unsuitable sites) (Pulliam, 1988). Indeed, even before we used reintroductions to obtain direct data on habitat quality of previously unoccupied fragments, simulations from an individual-based model suggested that any increases in connectivity would have detrimental effects on the toutouwai metapopulation due to the variation among fragments (Richard, 2007).

It is, therefore, important to take advantage of opportunities to validate models used to infer the roles of habitat quality and metapopulation dynamics on species distributions. Although it is inevitable that such models will continue to be parameterized based on rapidly collected metrics or expert judgment (Davies et al., 2018), a small proportion of cases may lend themselves to validation through experimental reintroductions. In our case, such reintroductions were possible because we could source the animals from pine plantations, so no potential conservation cost was incurred. These reintroductions were valuable in showing that unoccupied fragments could not be repopulated just by increasing connectivity and led to further research showing that such repopulation was possible if local habitat quality was improved through predator control (Armstrong et al., 2014; Armstrong, 2017). In our case, the vital rate data showed that our original habitat metrics were unrelated to true habitat quality, and, in fact, more data-intensive indices of predator activity and food abundance were also found to be ineffective predictors (Armstrong et al., 2014). However, in other systems, the results could validate that some simple metrics are, indeed, good predictors of habitat quality. Regardless, it is important for sound conservation to be able to assess the reliability of predictions being used to decide management actions.

ACKNOWLEDGMENTS

We thank R. Peacocke, the late T. Ballentyne, I. Valler, M. Thompson, R. Walker, L. Crown, and the Tiroa E & Te Hape B Trusts for access to the landscape, K. Morgan, R. Johnston, B. Kreigenhofer, C. Getzlaff, and many volunteers for help with fieldwork, and B. Wintle and D. Breininger for comments on the manuscript. Our research was funded by Marsden Grants MAU003, MAU0404, and MAU0707 and approved by the New Zealand Department of Conservation and the Massey University Animal Ethics Committee.

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SUPPORTING INFORMATION

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How to cite this article: Armstrong, D. P., Boulton, R. L., McArthur, N., Govella, S., Gorman, N., Pike, R., & Richard, Y. (2022). Using experimental reintroductions to resolve the roles of habitat quality and metapopulation dynamics on patch occupancy in fragmented landscapes. *Conservation Biology*, *36,* e13843. https://doi.org/10.1111/cobi.13843