

Colonisation dynamics during range expansion is poorly predicted by dispersal in the core range

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Decision date: 05-Feb-2019

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/ecog.04180].

Abstract

The potential ranges of many species are shifting due to changing ecological conditions. Where populations become patchy towards the range edge, the realised distribution emerges from colonisation-persistence dynamics. Therefore, a greater understanding of the drivers of these processes, and the spatial scales over which they operate, presents an opportunity to improve predictions of species range expansion under environmental change.

Species reintroductions offer an ideal opportunity to investigate the drivers and spatial scale of colonisation dynamics at the range edge. To this effect, we performed and monitored experimental translocations of water voles to quantify how colonisation and local persistence were influenced by habitat quality and occupancy. We used a novel statistical method to simultaneously consider effects across a range of spatial scales.

Densely occupied neighbourhoods were highly persistent and frequently colonised. Persistence was more likely in high quality habitat, whereas influence of habitat quality on colonisation was less clear.

Colonisation of suitable habitat in distant, sparsely occupied areas was much less frequent than expected from the well documented high dispersal ability of the species. Persistence of these distant populations was also low, which we attribute to the absence of a rescue effect in sparsely populated neighbourhoods.

Our results illustrate a mismatch between the spatial scales of colonisation dynamics in the core and edge of a species range, suggesting that recolonisation dynamics in established populations may be a poor predictor of colonisation dynamics at the range edge.

Such a mismatch leads to predictions of long lags between the emergence and colonisation of new habitat, with detrimental consequences for a species realised distribution, conservation status and contribution to ecosystem function. Conservation translocations that also reinforce existing populations at the range edge might stimulate the rescue effect and mitigate lags in expansion.

Keywords: Range dynamics, range shift, rescue effect, conspecific attraction, translocation, *Arvicola amphibius*

Introduction

A greater understanding of the population processes that underpin species range dynamics is vital for predicting how distributions will respond to rapidly changing environmental conditions (Urban et al. 2016), and the mismatches that already exist between the realised and potential distributions of some species (Talluto et al. 2017).

For populations occupying fragmented habitats, the persistence of the wider metapopulation is determined by the relative rates of colonisation and local extinction (Hanski 1998). When a large fraction of the habitat patches in the landscape is occupied, and produces emigrants, the abundance of dispersers increases the probability that vacant patches will be colonised, and that small populations will be “rescued” by immigration (Brown and Kodric-Brown 1977). At the scale of the patch, local densities and habitat quality also contribute to the probability of persistence (herein defined as $1 - \text{extinction probability}$) (Yamanaka et al. 2009). In such spatially structured populations, there is the potential for positive feedbacks to emerge between local population size and proportional occupancy at the “neighbourhood” scale (Hanski et al. 1995a), where a “neighbourhood” represents a group of patches that are within dispersal distance of each other. More generally, even species with near continuous distributions in the core of their range may become patchily distributed towards the range edge (Holt and Keitt 2000, Holt et al. 2005). This may result in differences in (re)colonisation dynamics, and the spatial scale over which dispersal mediates such dynamics in different parts of the range. While the location of the range edge may emerge from these metapopulation dynamics (Lennon et al. 1997), very little is known, even from the best studied species, about how local densities and/or regional occupancy might change from the core to the edge of the range (Devenish et al. 2017), and what the consequences are for both patch dynamics and rate of onward expansion.

A declining gradient in occupancy from the core to the edge of the range, due to lower density of available habitat patches and/or lower densities of individuals within those patches, is likely to result in a considerably smaller pool of dispersers being produced at the range edge relative to the core. It follows, from a relatively low prevalence of dispersers, that habitat patches distant from the core of the range have a lower chance of 1) being reached and selected for settlement, and of 2) being rescued from extinction by subsequent immigration. Founder populations at the range edge are therefore likely to be small, and as a result may face a higher risk of extinction due to demographic stochasticity (Liebhold and Bascombe 2003), and in some cases may even show reduced growth rates (an Allee effect: Stephens et al. 1999).

Furthermore, where emigration is positively density dependent, nascent populations may not produce emigrants that go on to successfully colonise further vacant patches until they become relatively crowded (Johnson et al. 2006, White et al. 2012). Where the frequency of (re)colonisation events – particularly of isolated patches – changes due to the size of the pool of dispersers, the abundance of dispersers has the potential to affect changes in the spatial scale at which colonisation-persistence dynamics operate from the core to the edge of the range.

For active dispersers, use of information to inform individual decision-making during dispersal is a further potential influence on colonisation-persistence dynamics at the range edge. Dispersers may gather information on habitat quality and social context that influences emigration and settlement decisions (Clobert et al. 2009), and the use of social information when selecting for territories or mates is widespread across many taxa (Danchin et al. 2004). In the context of range expansion, the extent to which the presence of conspecifics modifies the decision by dispersers to settle in high or low-quality habitat could have far reaching consequences. A general attraction to the presence of all conspecifics can hinder a species' ability to rapidly track shifts in habitat quality (Stodola and Ward 2017), and attraction to large local populations can be detrimental to the establishment and persistence of new, smaller ones (Le Gouar et al. 2008). However, when dispersers search specifically for opposite sex conspecifics, it may be that fewer individuals remain unmated, and a larger proportion of the population contributes to metapopulation growth. At the range edge, where the pool of dispersers is smaller, delaying settlement until a potential mate is found may lead to iterated dispersal, and as such, the flexibility of such a mate-finding dispersal strategy may have important consequences for colonisation rate (Morgan 2019). Therefore, information gathered on habitat quality and social context, before and during dispersal, may influence local emigration and immigration rates, with consequences for the spatial scale over which dispersal mediates colonisation-persistence dynamics at the edge of the range.

Species translocations offer a unique opportunity to study important ecological processes, while simultaneously working towards conservation goals (Sarrazin and Barbault 1996) as several key processes operating in range expansion may also play out following translocations. Habitat availability and quality, population demographic rates, and post-release dispersal all influence the persistence of reintroduced populations (Armstrong and Seddon 2008), and habitat selection and conspecific attraction can also shape local growth rates (Mihoub et al. 2009, 2011). However, despite this, translocations have

rarely been used for exploring how the effects of key covariates, namely habitat quality and neighbourhood occupancy, influence colonisation-persistence dynamics across different spatial scales.

Here we use a reintroduced population of water voles in the north east of Scotland, which was monitored over three years post release using presence-absence surveys, to explore the dual influences of the presence of conspecifics and habitat quality on colonisation and local persistence. As little is known about how the spatial scale of colonisation-persistence dynamics at the range edge may compare to that in the core of the range, we apply a novel statistical tool that allows for the possibility that the strength of these effects varies depending on the spatial scale considered, while simultaneously exploring whether habitat selection is modified by the presence of conspecifics. Water voles are effective colonisers, with both sexes frequently dispersing away from the natal population (19 % of females & 33 % of males: Telfer et al. 2003, 44 % of females & 33 % of males: Aars et al. 2006). The dispersal kernel is well approximated by a negative exponential distribution (Telfer et al. 2003), and the average dispersal distance has been estimated at 2.1 km (Sutherland et al. 2014). Colonisation is driven by dispersing juveniles, and local persistence is a function of both local adult population size and juvenile immigration (Sutherland et al. 2012, 2014), and there is evidence of opposite-sex conspecific attraction during settlement (Fisher et al. 2009). Using this population reintroduced beyond the natural recolonisation front as a model system for scenarios that arise at the range edge by a potentially (re)colonising species, we predicted that 1) the probability of both colonisation and persistence would be higher when local habitat quality was higher; 2) the effect of presence of conspecifics on colonisation and persistence would be distance dependent; and 3) the spatial scale of this relationship would match closely with the already well-defined water vole dispersal kernel.

Methods

Species and study system

Water voles (*Arvicola amphibius*) are large microtine rodents that can reach a mass of around 300g, and populations in Britain tend to occupy the edges of waterways in a variety of habitats, from upland streams to agricultural ditches (Lambin et al. 2004). They exist as metapopulations, though the proportion of the waterway network that is suitable varies from 8 % in upland systems (Sutherland et al. 2014), to at least 40 % in the lowlands (Telfer et al. 2001). They are the UK's fastest declining mammal, with losses exceeding 95% of the population present in the 1950s (Strachan et al. 2000). This decline is largely due to invasion of the UK by the American mink (*Neovison vison*), which is a particularly effective predator of water voles (Woodroffe et al. 1990, Aars et al. 2001). In north east Scotland, a large scale, coordinated removal programme has been successfully implemented through community involvement and an adaptive management approach (Bryce et al. 2011). While the primary focus of the project was to preserve remnant, upland populations, the result has been to secure an area of 20,000 km² that has little to no evidence of breeding mink where suitable water vole habitat is in abundance, and where there were numerous reports of past presence of water voles (Bryce et al. 2011).

The Tarland burn in upper Deeside was selected for the reintroduction. Water voles were present in the catchment in 1989-1990, but absent by 1996-1998 (Strachan and Jefferies 1993, Strachan et al. 2000), and surveys of the catchment in spring 2015 also found no evidence of occupancy. This area constitutes lowland water vole habitat, with narrow water ways typically between 1 – 3 m wide separated by a mixture of arable fields and pasture that are mostly fenced. Herbaceous field margins dominate the riparian zone of the catchment, interspersed by scattered trees and some small forested sections, along with variable cover of rushes and grasses. The substrate of the waterways changes throughout the catchment, from silty to rocky, and bank penetrability, which impacts the ease of burrow construction by voles, is also variable.

Reintroduction

In order to establish a metapopulation, water voles were released at six different locations spread over the 63 km² area within previously documented dispersal distance of one another (Telfer et al. 2003, Sutherland et al. 2014) (locations a-f, Fig. 1). The release cohort consisted of 25 voles sourced from a thriving upland population 25 km away from the release site, and 66 captive-bred voles descended from another Scottish population. The total number of voles released at each site was as follows: a = 33, b =

10, c = 14, d = 6, e = 78 and f = 31; and full details of the release protocol are in supplementary material Appendix 1.

Dispersal away from the release site is an important cause of reintroduction failure (Le Gouar et al. 2011, Hardouin and Robert 2014). As such, four release pens (1 m² enclosed pen containing half a bale of straw), each containing a single overwintered female vole, were placed at the ends of release sites in the expectation this would favour settlements of released voles. These voles remained in place for eight weeks, at which point they were released. They were fed with apples and carrots and given fresh water every two days.

Data collection

The water way network (72.8 km) was split in 200m sections, which reflects the approximate home range length of water voles in similar habitat (~50 m for females & ~200 m for males, Telfer et al. 2001), though this is typically smaller than the grain of habitat fragmentation in this catchment. An independent study in nearby lowland habitat with similar agricultural land use took measurements of environmental variables at the midpoint of sections, and used a logistic regression to identify predictors of occupancy (Telfer et al. 2001). The key variables were waterway width and substrate, bank penetrability, total vegetation cover, tree cover, and cover by *Juncus* species and *Filipendula ulmaria*, and we used parameter estimates from this study to derive a habitat quality score for all sections. Details on collection of habitat variables and calculation of quality score are in supplementary material Appendix 2 (table S3). Based on this score, probability of occupancy (termed habitat quality hereafter) in the catchment, while variable, was generally predicted to be high (mean = 0.80, 1st quartile = 0.75, 3rd quartile = 1.00), and as such, all sections were deemed suitable for at least temporary occupancy.

To assess the establishment and spread of the reintroduced population, repeated surveys for faecal droppings, which we used to confirm current occupancy, were carried out following release. Sections were classified as 1) newly colonised, if they contained faecal droppings and had not been occupied before or during a previous survey; 2) persistent, if droppings were detected across consecutive surveys; 3) abandoned, if droppings were no longer detected; and 4) uncolonised.

A total of 364 200 m sections (72.8 km total waterway) were surveyed multiple times during the whole study (average surveys per section = 5.03, standard error (SE) = 0.14). We defined five survey “seasons”: 1) June-July 2015, 2) August-October 2015, 3) March-July 2016, 4) August-October 2016, 5) May 2017, and there was some variation in the number of sections surveyed during each season (table 1).

In order to visualise spatio-temporal changes in occupancy, we derived the cumulative number of occupied sections per season, grouped by waterway (waterways displayed in Fig. 1).

When detection probability for a species of interest is < 1 , repeated surveys within a period of “closure” (i.e. no sections are abandoned or colonised between survey events) allow this probability to be estimated without bias (MacKenzie et al. 2002). Due to the large and rapidly expanding length of waterways potentially occupied, our survey design did not always include repeated surveys within any a priori selected closure period. Moreover, the true length of this closure period is unknown for a recently reintroduced population. Therefore, we calculated an approximation of detection probability under three assumptions of closure period length (10, 20 and 30 days) as $(N - f) / N$, where N is the total visits to sections with > 1 survey and ≥ 1 detection within the assumed period of closure, and f is the number of negative detections in those sections. Detection probability per survey and section was high across all three assumptions of closure, though decreased for longer periods (10 days = 0.80, SE = 0.03, $N = 168$; 20 days = 0.76, SE = 0.03, $N = 214$; 30 days = 0.72, SE = 0.3, $N = 226$), implying closure was temporary. Due to this high detection probability, rather than adopting a probabilistic approach, sections were assigned a status based on any positive detections within the assumed period of closure, and we carried out separate analyses under the three different assumptions of closure period.

Analysis

To evaluate the drivers of colonisation and local persistence probabilities at different spatial scales, we fit binary logistic regression models using habitat quality and presence of conspecifics at a range of distances from the focal section.

To evaluate the distance dependent effect of neighbourhood occupancy, we calculated the proportion of occupied sections in concentric rings around the focal section, using only neighbouring sections surveyed within the assumed period of closure. For example, if assuming closure over 10 days, only sections surveyed up to 10 days before or after the survey of the focal section were included. Concentric rings were at 250 m intervals up to 2500 m, though we set the first interval at 270 m to ensure that every section had at least one neighbour at the smallest interval. This yielded 10 predictors of colonisation and local persistence. The mean proportion of neighbouring sections that were surveyed was highest for closer concentric rings (270 m = 0.93, SE = 0.01; 2500 m = 0.56, SE = 0.06), and longer periods of closure (10 days = 0.62, SE = 0.05; 30 days = 0.78, SE = 0.03; see Supplementary material Appendix 3 figure S3 for more detail).

To evaluate the effect of habitat quality on colonisation and persistence, we used the habitat quality scores of waterway sections to derive four different covariates: 1) The quality score of the focal section; 2) the average quality score within a radius of 500 m; 3) the average score within a radius of 750 m; and 4) a distance dependent effect of habitat quality that included the quality score of the focal section, then the average quality score in concentric rings, 250 m wide, around the focal section up to 2250 m away. Again, this yielded 10 predictors for the distant dependent effect.

To test whether the effect of habitat quality is modified by presence of conspecifics, we evaluated the interaction between mean proportion occupancy within a fixed radius of the focal section and habitat covariates 1-3 described above. One thousand m was chosen for this radius as our results revealed that the distance dependent effect of neighbourhood occupancy exceeded 1000 m for both colonisation and local persistence (see Results below).

The use of multiple correlated predictors can induce collinearity issues, and we therefore applied the varying coefficient regression method of Sims et al. (2007) in a spatial (rather than temporal) context (Cornulier in prep). To constrain and stabilise parameter estimates, the varying coefficient regression method uses a generalised additive model (GAM) to fit a smooth curve through the effect sizes at each distance, multiplied by the vector of values of the covariate in each concentric ring. This allowed us to learn about the shape of the decay of the effect of conspecifics and habitat quality with distance from a focal section, without the need to make unwarranted a-priori assumptions. The method is flexible enough to allow for non-linear patterns of decay, and the resultant shape reflects the spatial scale, or neighbourhood size, over which covariates of interest drive the processes of colonisation and persistence in the population.

GAMMs (Generalised Additive Mixed Models), in the R package `gamm4` (R Core Team 2017, Wood and Scheipl 2017), with binomial error structure and logit link function were fitted by maximum likelihood (Laplace Approximation). Models included binary response variables representing colonisation (focal section was colonised or not) or persistence (focal section remained occupied or did not), with random effect of section ID and of the month-year combinations (e.g. June-2016). Distance dependent effects were fitted using thin-plate splines with the default number of knots (Wood 2003).

We selected the best models from the candidate set using AICc, the corrected Akaike Information Criterion for small sample size (Burnham and Anderson 2002). For the best models, we further scrutinised model predictions by testing two further methods of accounting for heterogeneity in

the variance: 1) we fit a thin-plate spline (Wood 2003) on eastings and northings to account for spatial autocorrelation at the scale of the study site (up to 9 km for colonisation and 7 km for persistence), and 2) we fit a continuous, autoregressive (CAR1) correlation structure that included date of survey grouped by section ID to account for any temporal autocorrelation (models fit in R package mgcv; Wood 2011).

Results

In the first week following phase 1 of the release, 3 km of waterway was colonised, and a further 3.2 km was colonised in the first week following phase 2 (waterways 1-2 and 5-7, Fig. 1). By the end of the first survey period (a month and a half following the initial release), 3.8 km of waterway remained occupied. The population expanded into the waterways adjacent to release site e (Fig. 1), colonising 1.2 km of waterway in the 1st year, and a further 1.2 km in the 2nd year (waterways 3, 4 and 8, Fig. 1). Only two local populations were colonised > 1 km from the core population (waterways 5 and 9 Fig. 1), and neither persisted to the next survey season. A “core” area had emerged by the 2nd year, wherein between 2.2 – 4.8 km of water way was occupied per survey seasons (waterways 2, 4 and 8, Fig. 1).

Colonisation

Water voles were more likely to colonise vacant sections when conspecifics were present in surrounding waterways (table 2). Occupancy in adjacent sections, 270 m away, was the strongest predictor of colonisation, and the magnitude of the effect decreased linearly with distance to around 1500 – 2000 m (Fig. 2 a). When compared to a section in an empty neighbourhood, the probability of a vacant section being colonised was over 5 times higher given 100 % occupancy at 270 m, and 20 times higher if there was also 100 % occupancy at 500 m (Fig. 3 a). A decreasing effect size with distance was found for all models across all three assumptions of closure period (result not shown).

We found some evidence that voles were more likely to colonise sections with high habitat quality scores, particularly when conspecifics were present in the surrounding waterways, up to 1000 m away (table 3). However, there was equal support for a model containing no habitat variables when closure was assumed to be 10 days (table 2). For different assumptions of closure, the suite of models within $\Delta AICc < 2$ of the best model was different, and therefore there was some uncertainty as to whether the quality score of the focal section, or the mean quality score of all sections within a 750 m radius best predicted colonisation, and only weak evidence for an interaction between either of these habitat

measures and proportion occupancy within a 1000 m radius (table 2). We found no evidence for a distance dependent effect of habitat quality (table 2).

Persistence

Water voles were more likely to persist when conspecifics were present in surrounding waterways (table 2). Again, occupancy of adjacent habitat, 270 m away, was the strongest predictor of persistence, and the magnitude of the effect decreased linearly with distance to around 1250 – 2000 m away (Fig. 2 b). When compared to a section in an empty neighbourhood, the probability of a vacant section remaining occupied was 3 times higher given 100 % occupancy at 270 m, and 5 times higher if there was also 100 % occupancy at 500 m (Fig. 3 b).

Voles were more likely to persist in clusters of waterway sections with high quality scores, and we found evidence for a positive effect of mean habitat score over a 500 m radius across all three closure assumptions (table 3). It is worth noting that the second best model ($2 < \Delta AICc < 4$ across all three closure assumptions) which included an interaction between mean habitat score over a 500 m radius and mean occupancy in a 1000 m radius resulted in greater uncertainty regarding the distance dependent effect of presence of conspecifics in surrounding waterways (Supplementary material Appendix 4 Fig. S3). Again, no evidence for a distance dependent effect of habitat quality was found.

For both colonisation and persistence, results of the best models were consistent after accounting for potential spatial autocorrelation in patterns of occupancy status (colonised vs uncolonised, persistent vs abandoned) at the scale of the study site, as well as temporal autocorrelation in the occupancy status of focal sections (results not shown).

Discussion

Our study provides new insight in to the drivers and spatial scale of colonisation-persistence dynamics at the range edge. Our estimates of the largest distances over which conspecifics contribute to these dynamics (Ca. 1250 – 2000 m away, Fig. 2) were below the average, and much below observed extreme dispersal distances previously observed in core areas of this extensively studied species (Telfer et al. 2003, Sutherland et al. 2014). High neighbourhood occupancy resulted in highly persistent local populations, and waterway sections adjacent to these populations had a high probability of being colonised. Persistence was more likely in high quality habitat, whereas the influence of habitat quality on colonisation was less clear. Together these findings hint at a fundamental contrast in the effectiveness of

dispersal in mediating patch recolonisation in extant metapopulation networks, versus the colonisation of empty networks.

High dispersal ability is expected to result in rapid range expansion through the colonisation of distant habitat spaces (Kot et al. 1996). In this reintroduced population, only two long distance colonisation events (> 1 km) were detected, which is at odds with two independent, yet highly consistent estimates of dispersal and colonisation potential for this species. Telfer et al. (2003) – in a landscape with very similar level of fragmentation of habitat – found that up to 33 % of juveniles emigrate, and that the dispersal kernel fits a negative exponential distribution, with a mean of 1.8 km, and maximum dispersal distances exceeding 5 km. Sutherland et al. (2014) used a stochastic patch occupancy model – a fundamentally different methodology to Telfer et al. (2003) – to infer a remarkably similar average dispersal distance of 2.1 km. While Sutherland et al. (2014) carried out their study in an upland setting characterised by smaller, more distant discrete patches, there is no suggestion that the average dispersal distance of 2.1 km emerged as a consequence of interpatch distances (the mean and range of distances between patches and their nearest neighbour were 0.53 km and 0.09 – 1.86 km respectively). Here we estimated a linear decay of the influence of conspecifics on colonisation and persistence, with negligible effects at shorter distances (around 1800 m) than both of these previous estimates of the average water vole dispersal distance. The varying coefficient regression method we used is flexible enough to show a range of patterns in spatial decay of influence, though detecting more complex, and biologically realistic patterns, such as a negative exponential, may require larger sample sizes or covariate data over greater distances. Despite this, our findings are indicative of a mismatch between the spatial scales of colonisation dynamics in this reintroduced population compared to more established metapopulations.

Small rodents have been found to have a high capacity for colonising vacant habitat networks through use of enclosure experiments (Glorvigen et al. 2013). Crucially, in Glorvigen et al. (2013), vacant patches were never more than 150 m away from the source populations, which were introduced to both ends of the vacant network. As such, the experimental setup used by Glorvigen et al. (2013) was more akin to the recolonisation of a recently abandoned (empty for a couple of generations) part of the current range than colonisation of a hitherto vacant (or empty for 10s – 100s of generations) part of the potential range. Connectivity in established metapopulations can be maintained by long distance dispersal even when both the rate of effective dispersal and local densities are very low (in an upland water vole metapopulation an estimated 1.5 % of dispersers are effective dispersers, and the expected density of

adult females is < 2 per km of suitable waterway, Sutherland et al 2014), and as such we suggest that the lack of expansion in to distant habitat spaces we find here represents a fundamental mismatch between recolonisation dynamics in the core, and colonisation dynamics at the edge of the range. As such, a good understanding of dispersal behaviour in the core may not lead to accurate predictions regarding colonisation dynamics at the edge.

Our results are consistent with the suggestion that voles may have been attracted to conspecifics when colonising vacant habitat sections, as the effect of adjacent conspecifics (270 m away) was four times higher than the effect of those in more distant waterway sections (1750 m away) (Fig. 2 a). Furthermore, close proximity of conspecifics also conferred higher persistence, and the effect of conspecifics in adjacent waterway sections (270 m away) was 2.5 times stronger than of those at 1500 m away (Fig. 2 b). Therefore, conspecific attraction is likely to have had positive consequences for local population growth and persistence, and may lead to positive feedbacks between local population size and proportion occupancy at the neighbourhood scale (Hanski et al. 1995a), as larger local populations attract ever more immigrants. At the range edge, such feedbacks may provide a mechanism by which local populations become sufficiently crowded such that they produce enough emigrants to colonise hitherto vacant habitat patches, driving range expansion forwards (Johnson et al. 2006). Where the utilisation of information about conspecifics influences both emigration and immigration (Bowler and Benton 2005, Le Galliard et al. 2012), both local scale densities and regional occupancy will influence dispersal decisions. We therefore might resolve the apparent mismatch between recolonisation dynamics in the core, and colonisation dynamics at the edge, as increased patchiness towards the range edge (Holt and Keitt 2000) results in lower regional occupancy.

In spite of compelling evidence that the rescue effect contributes to local population persistence in a well-established metapopulation of the same species (Sutherland et al. 2012), we found that no populations arising from long distance colonisation events (>1 km) persisted from one season to the next. This suggests that immigration by long distance dispersers was insufficient for rescuing local populations. For both Glanville fritillary (*Melitaea cinxia*) and water vole metapopulations, the rescue effect is important for persistence at both the local and metapopulation scale (Hanski et al. 1995b, Sutherland et al. 2012). Though in both these classical metapopulation model species, the role of the rescue effect at the range edge is largely unknown. Here we provide some evidence of a weak or absent rescue effect at the range edge, where immigration by long distance dispersal is not sufficient for saving local populations

from extinction. We suggest that for onward expansion, local populations at the range edge must contribute sufficient dispersers to act as both founders and joiners of hitherto vacant habitat patches. The length of the resultant lag (which we suggest would be in the order of multiple of generations) before more distant parts of the potential range are reached, will depend on both emigration rate, and whether local growth rates are lower in small founder populations (an Allee effect: Stephens et al. 1999).

We found good evidence that voles were more likely to persist in areas of high habitat quality (table 3) even though some sections with low habitat quality score were colonised. Interestingly, the role of habitat quality in driving colonisation was less clear, and we believe this demonstrates the different processes that underlie colonisation and persistence. While colonisation is driven by settlement of dispersing individuals, persistence arises from both immigration (the rescue effect), and survival and reproduction of residents (Hanski et al. 1995a, b, Sutherland et al. 2012). These results suggest that while selection for the very best quality habitat is secondary to conspecific attraction during colonisation, local persistence is more likely in high habitat quality areas; maybe reflecting higher food resource availability influencing survival, fecundity, or site fidelity. The use of an independent measure of habitat quality, developed in a geographically distinct lowland population of water voles (Telfer et al. 2001), allowed us to measure habitat quality independently of any settlement decisions made by voles in the reintroduced population, helping to disentangle habitat selection from quality.

The length of any lag between new habitats becoming available and being colonised is likely driven by a complex interaction between individual decisions, habitat configuration and how population growth rate and persistence depend on local density and larger-scale occupancy. Through the use of a targeted species translocation, we demonstrate how proximity to conspecifics played an important role in both colonisation and subsequent persistence of vacant habitat patches. We suggest that the utilisation of information about conspecifics to inform dispersal decisions can lead to very different emergent colonisation dynamics at the range edge compared to the core. Conspecific attraction could produce a positive feedback, as persistent local populations attract ever more immigrants, while small nascent populations decline to extinction; the resultant Allee effects leading to lengthy lags before onward range expansion. This has important consequences for conservation of species that are undergoing range shifts in response to destruction of old and/or creation of new habitat. While invasive control programs have recognised the importance of control efforts at the expanding edge, as well as the established range (Walter et al. 2015), translocation programs that combine reintroductions beyond the range edge with

reinforcements behind the range edge may be able to harness those positive feedbacks, stimulating the rescue effect and mitigating lags in onward range expansion.

Declarations

Acknowledgements

We would like to thank the MacRobert Trust and all farmers of the estate for their support, and for granting access to their land. Particular thanks to Julio Dominguez, as well as Deon Roos, Emma Bryce, Emma Sheehy, Rupert Houghton and Jennyfer Lecroart for help with data collection.

Funding

The research leading to these results received funding from the Aberdeen Western Peripheral Route/Balmedie to Tippetty project.

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Figure Legends

Fig. 1. Left panel summary: A map of the study site showing the entire waterway network and release locations. Right panel summary: Plots showing the changing number of 200 m sections that were occupied through time for the whole study site (Total), and for individual waterways (numbered plots with coloured lines). Left panel detail: The waterway network is represented by grey or coloured lines (coloured lines show waterways that were occupied at some point during the entire study period). Coloured waterways are numbered, and these numbers correspond to plots in the right-hand panel. Release locations are denoted by letters a – e: Release phase 1 = a – c (bold italics), where a total of 49 voles were released; release phase 2 = d – f, where a total of 100 voles were released (see Supplementary material Appendix 1 for further details). Shape outlines represent three different spatial scales: dashed line is the whole study site; dotted lines are sub catchments; and solid lines are release sites. Shape fill colours represent the density of over wintered female voles released per km of water way at each of the three spatial scales (see table S1 for more detail). Only voles released during phase 1 and 2 contribute to the density calculations. Right panel detail: Plots show the number of 200 m sections that were occupied at the end of each survey season: 1 = July 2015, 2 = October 2015, 3 = July 2016, 4 = October 2016, and 5 = May 2017. Vertical, dotted lines on these plots separate different years. Diamonds denote the number of sections that were initially colonised following the release.

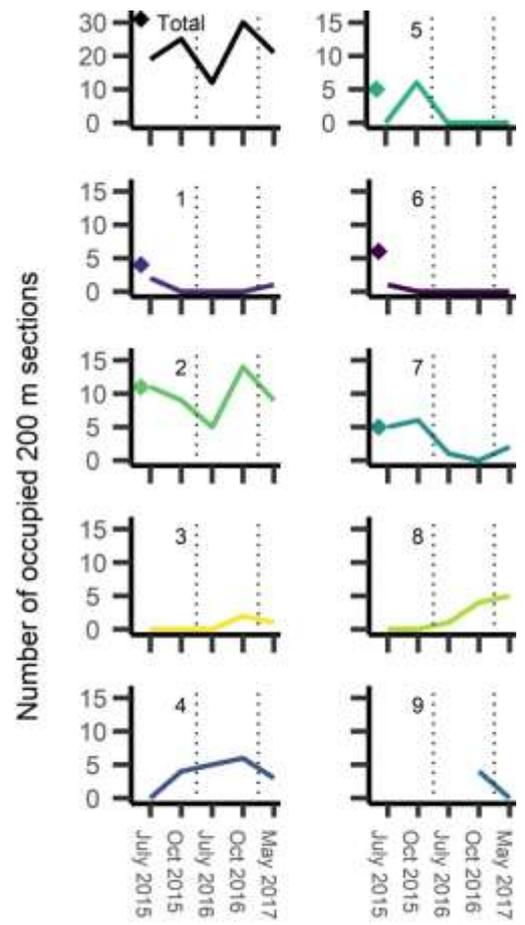
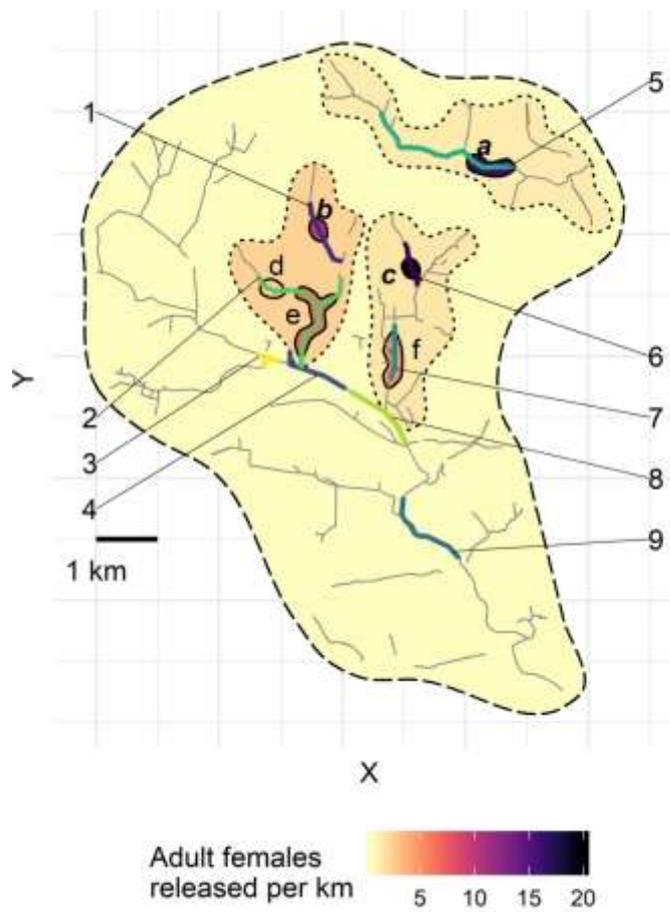


Fig. 2. The distance dependant effect size of proportion neighbourhood occupancy on a) probability of colonisation, and b) local persistence, for the top ranked model when closure (i.e. no change in true occupancy state) is assumed over a 10 day period. The shaded area shows the standard error around the estimate of the effect size.

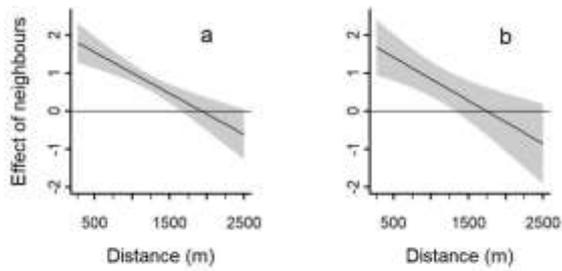


Fig. 3. Probability of a) colonisation, and b) local persistence, based on the proportion of occupied sections at 500 m away, for two levels of proportion occupancy at 270 m away, including 95 % confidence intervals around model predictions. Closure (i.e. no change in true occupancy state) is assumed over a 10 day period.

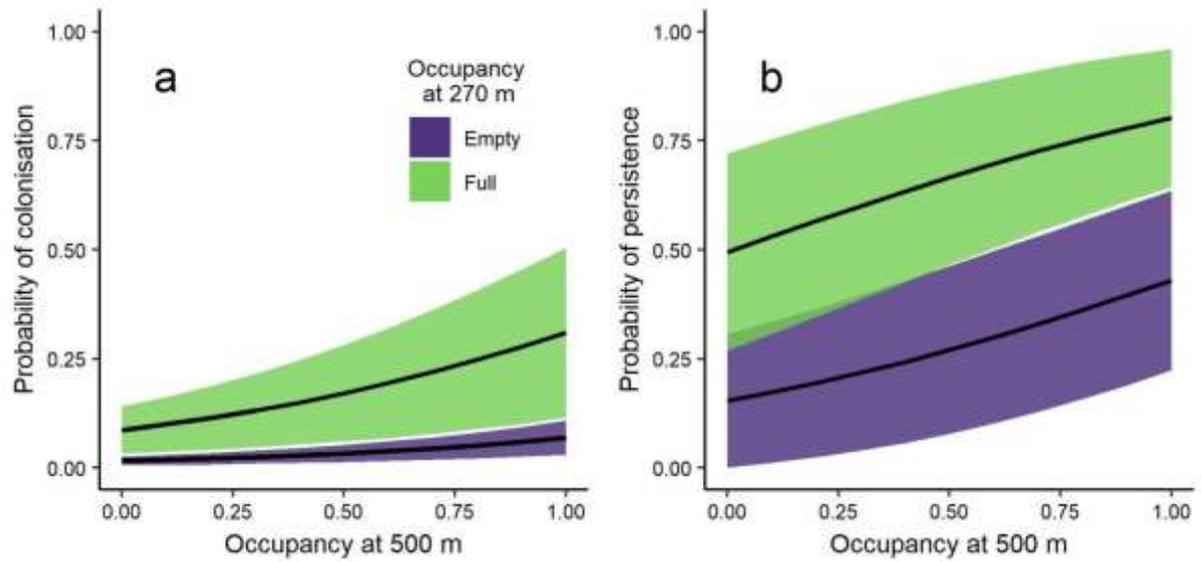


Table Legends

Table 1. The amount of water way surveyed during each survey season shown as both number of 200 m sections and km of water way. Total effort refers to the total number of sections surveyed (or km of water way surveyed) within that survey season. Number of visits to sections refers to the number of sections that were surveyed once, twice, three times or four times within that survey season.

Survey season	Survey effort				Total effort			
	No. 200 m sections visited	km	No. visits to sections				200 m sections	km
			1	2	3	4		
June - July 2015	126	25.2	13	39	30	44	357	71.4
Aug - Oct 2015	178	35.6	116	62			240	48
March - July 2016	104	20.8	72	19	13		149	29.8
Aug - Oct 2016	340	68	1	310		29	737	147.4
May 2017	364	72.8	364				364	72.8

Table 2. Model selection for colonisation and persistence, where $s(\text{OCC})$ = distance dependent effect of proportion occupancy, $s(\text{Q})$ = distance dependent effect of habitat quality score, QSEC = habitat quality of focal section, Q500 = average habitat quality of all patches within a 500 m radius, Q750 = average habitat quality of patches within 750 m, OCC1000 = mean proportion occupancy within a 1000 m radius. Models including OCC1000 include the habitat main effect, and an interaction ($:$) between the habitat covariate and OCC1000. The closure period refers to the length of time over which we assumed that the occupancy status of a cell did not change. K = number of parameters, ΔAICc = difference in AICc from best model, W_t = AICc weight. Where $\Delta\text{AICc} < 2$, ΔAICc and W_t are shown in bold.

	Model	Parameters	Closure period						
			10 days			20 days		30 days	
			K	ΔAICc	W_t	ΔAICc	W_t	ΔAICc	W_t
Colonisation	1	$s(\text{OCC})$	6	0	0.27	2.96	0.06	2.50	0.10
	2	$s(\text{OCC}) + s(\text{Q})$	9	4.55	0.03	3.28	0.05	4.75	0.03
	3	$s(\text{OCC}) + \text{QSEC}$	7	0.58	0.21	0	0.24	1.87	0.13
	4	$s(\text{OCC}) + \text{QSEC}:\text{OCC1000}$	8	2.58	0.08	0.39	0.20	2.54	0.10
	5	$s(\text{OCC}) + \text{Q500}$	7	1.87	0.11	2.24	0.08	3.06	0.07
	6	$s(\text{OCC}) + \text{Q500}:\text{OCC1000}$	8	3.82	0.04	2.89	0.06	4.45	0.04
	7	$s(\text{OCC}) + \text{Q750}$	7	0.64	0.20	0.71	0.17	0	0.34
	8	$s(\text{OCC}) + \text{Q750}:\text{OCC1000}$	8	2.61	0.07	0.95	0.16	1.09	0.20
	9	QSEC	4	49.14	0.00	57.76	0	54.43	0.00
	10	Q500	4	49.66	0.00	58.96	0	55.07	0.00
	11	Q750	4	49.71	0.00	59.09	0	54.97	0.00
	12	$s(\text{Q})$	6	52.73	0.00	61.40	0	57.50	0.00
	13	Intercept only	3	47.74	0.00	57.19	0	53.04	0.00
Persistence	1	$s(\text{OCC})$	6	2.37	0.12	3.48	0.08	3.03	0.09
	2	$s(\text{OCC}) + s(\text{Q})$	9	3.73	0.06	5.04	0.04	2.83	0.10
	3	$s(\text{OCC}) + \text{QSEC}$	7	2.52	0.11	2.75	0.12	4.32	0.05
	4	$s(\text{OCC}) + \text{QSEC}:\text{OCC1000}$	8	4.13	0.05	5.08	0.04	6.75	0.01
	5	$s(\text{OCC}) + \text{Q500}$	7	0	0.39	0	0.46	0	0.42
	6	$s(\text{OCC}) + \text{Q500}:\text{OCC1000}$	8	2.32	0.12	2.26	0.15	2.12	0.15
	7	$s(\text{OCC}) + \text{Q750}$	7	2.53	0.11	3.06	0.1	2.24	0.14
	8	$s(\text{OCC}) + \text{Q750}:\text{OCC1000}$	8	4.83	0.04	5.39	0.03	4.62	0.04
	9	QSEC	4	21.67	0.00	26.41	0	15.56	0.00
	10	Q500	4	21.05	0.00	26.45	0	14.05	0.00
	11	Q750	4	23.86	0.00	28.44	0	16.07	0.00
	12	$s(\text{Q})$	6	20.05	0.00	26.05	0	18.55	0.00
	13	Intercept only	3	22.02	0.00	26.3	0	14	0.00

Table 3. Parameter estimates for colonisation and persistence. We show estimates for the fixed effects (not including smoothers) of the best models from the candidate set ($\Delta\text{AICc} < 2$), across the three assumptions of closure period (10, 20 and 30 days), where closure period refers to the length of time over which we assumed that the occupancy status of a cell did not change. QSEC = habitat quality of focal patch, Q500 = average habitat quality of all patches within a 500 m radius, Q750 = average habitat quality of patches within 750 m, OCC1000 = mean proportion occupancy within a 1000 m radius. Models including OCC1000 include the habitat main effect, and an interaction (:) between the habitat covariate and OCC1000

	Parameter	10DAYS		20DAYS		30DAYS	
		Estimate	SE	Estimate	SE	Estimate	SE
COLONISATION	QSEC	0.07	0.06	0.13	0.06	0.09	0.06
	Q500	0.04	0.10				
	Q750	0.16	0.14	0.30	0.15	0.30	0.14
	QSEC:OCC1000			0.28	0.23		
	Q750:OCC1000			0.70	0.52	0.47	0.49
PERSISTENCE	Q500	0.36	0.17	0.62	0.27	0.51	0.24