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Research

Informed dispersal based on prospecting impacts the rate and shape of range expansions

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Rapid progress is being made in understanding how dispersal strategies influence the spread of species whose ranges are expanding. However, potentially vital dispersal behaviours have so far been neglected. Social species have been demonstrated to use their own breeding performance (personal information) and the breeding performance of their conspecifics (public information) to inform both their emigration and settlement decisions. Here, to provide insight into how these behaviours may impact range expansion dynamics, we extend a recently-developed individual-based model that incorporates the use of personal and public information in emigration decisions and a prospecting phase informing settlement decisions. We find that compared to non-informed emigration, informed emigration results in slower range expansions, except when individuals prospect a high number of patches or when their perceptual range is high. Spread rate and also the extent of the front strongly depend upon the willingness of individuals to settle in an empty patch. Given the likely prevalence of prospecting and informed dispersal across a wide range of taxa, these results indicate an urgent need for further empirical and modelling studies to improve our understanding and predictive capability of how species exhibiting this informed dispersal strategy will respond to environmental changes.

Keywords: breeding success, colonization, individual-based model, information use, invasion rates, spread rate

Introduction

Dispersal is a key ecological process that determines the speed of range expansion. Classical theoretical models of population spread demonstrated that the intrinsic growth rate of a population together with its dispersal ability should determine the equilibrium rate at which it should spread (Skellam 1951, Hastings et al. 2005). A rich literature now exists on how specific individual behaviours and life history traits associated with dispersal influence range dynamics but model results are sometimes contrasting (Neubert and Caswell 2000, Holt et al. 2005, Dytham 2009, Williams et al. 2016, Miller et al. 2020). For example, Kot et al. (1996) demonstrated that a fat-tailed



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dispersal kernel could theoretically yield ever accelerating rates of expansion, while Clark et al. (2001) highlighted that discrete unusually long-distance dispersal events could result in substantially higher spread rates that reach an asymptote. As well as advances in incorporating the statistical properties of dispersal into models of range expansion, progress has been made in explicitly incorporating population processes and individual behaviours. For wind-dispersed plants, mechanistic models for seed dispersal have been coupled with demographic models to project spread rates (reviewed by Nathan et al. 2011). For actively dispersing animals, models have started incorporating density-dependence in emigration and settlement rules (Kun and Scheuring 2006, Best et al. 2007, Altwegg et al. 2013), as well as explicitly representing the movement of individuals between habitat patches (Bocedi et al. 2014). Furthermore, there has been increasing attention paid to understanding how spread rates vary according to spatial patterns of environmental suitability (King and With 2002, Henry et al. 2014, Fronhofer et al. 2017). However, to date there is a surprising lack of work on what, for many colonial and territorial species, may be key features of their dispersal behaviours: the gathering and use of information to make emigration and settlement decisions (Reed et al. 1999).

There has been a long-standing understanding that individuals of many species make context dependent emigration decisions based upon social information (Clobert et al. 2012). However it is only in more recent years that knowledge on the acquisition and use of information based on the performance of conspecifics or heterospecifics, namely public information (*sensu* Danchin et al. 2004), has begun to be gained in relation to emigration and settlement decisions (Clobert et al. 2009). These strategies are based on information gathering that provides an individual with lower uncertainty on the relative qualities of alternative potential breeding patches when the environment is spatially heterogeneous and temporally predictable (Boulinier and Danchin 1997, Doligez et al. 2003, Bocedi et al. 2012, Oro 2020). It typically includes a prospecting phase where individuals gather personal and public information in other breeding areas which helps them settle in more productive patches (Reed et al. 1999). Individuals also acquire information from their own experience and interaction with the environment (personal information), to inform their emigration decision (Dall et al. 2005). Overall, these so-called informed dispersal strategies, where individuals use information in both emigration and settlement decisions, have been described in the field in many taxa but theoretical models still overlook them (Ponchon et al. 2021).

Furthermore, the balance between the use of personal versus public information is still unclear when it comes to individuals colonizing empty patches at the range front, which is clearly a critical component of any range expansion dynamic (Oro 2020). Indeed, for a range to expand, the first colonizers have to settle in empty patches, where no public information is available. Thereby, those individuals have to rely on personal information obtained from their direct interaction with

the environment through visual, chemical and/or auditory cues to decide where to settle (Dall et al. 2005). But how is range expansion supposed to happen when individuals prefer relying on the breeding performance of their conspecifics to make their settlement decision? As there are no conspecifics, individuals relying on prospecting and public information use are unlikely to colonize new patches and the lack of public information would constitute a barrier for range expansion.

Here, our aim is to demonstrate how the use of personal and public information in both emigration and settlement decisions is likely to influence the speed and shape of range expansion. We do so by extending a recently developed individual-based model incorporating information use and prospecting in an eco-evolutionary dynamics model (Ponchon et al. 2021). We adapt it to run ecological experiments in which we ask: 1) how does information use in emigration or settlement decisions influence the dynamics of range expansion compared to non-informed emigration and settlement?, 2) how does informed dispersal influence the population density of individuals as a function of distance from the front?, and 3) how does the relative preference of individuals for settling in occupied versus empty patches affect the speed and shape of range expansion?

Material and methods

Overview of modelling approach

The spatially-explicit individual-based model we use is based on the one recently described in Ponchon et al. (2021). This model was inspired from the life cycle of a long-lived colonial species such as a seabird but could be applied to any social species that acquires a breeding site or territory and lives in a spatially heterogeneous and temporally predictable environment. The model includes three life stages (juveniles, pre-breeders and adults), overlapping generations, a negative effect of density-dependence on fecundity, an emigration probability depending both on personal (individual breeding success or failure at producing offspring) and public information (local conspecific breeding success) and a prospecting phase during which individuals use either personal (local environmental quality) or public information (conspecific breeding success) for settlement decisions. The one necessary and key addition to the model for this study is the relative preference of individuals for settling in an already occupied patch from which they would have access to both personal and public information versus an empty patch from which they would only have access to personal information, as there are no other conspecifics to provide public information. For further model details, an Overview, Design concepts and Details protocol (ODD) is available as Supporting information.

Environment

We assume a grid of 20 columns and 300 rows. The expanding front is occurring towards upper rows, which are sufficiently

high in numbers to prevent individuals to reach the top of the grid. Each cell defines a discrete habitat patch where local environmental quality $Q_{x,y,t}$ varies every year independently and is temporally auto-correlated. At time $t=0$, each patch x, y is given a local environmental quality $Q_{x,y,0}$ based on a value $w_{x,y,0}$ drawn from a normal distribution $N^-(0,\sigma)$ so that initial conditions are:

$$Q_{x,y,0} = w_{x,y,0} \quad (1)$$

At $t+1$, the local environmental quality $Q_{x,y,t+1}$ depends on $Q_{x,y,t}$ and $w_{x,y,t}$ is resampled from a normal distribution $N^-(0,\sigma)$ and associated with an auto-correlation coefficient α so that:

$$Q_{x,y,t+1} = \alpha \times Q_{x,y,t} + w_{x,y,t} \times \sqrt{1-\alpha^2} \quad (2)$$

The carrying capacity of each patch $K_{x,y,t}$, which is always ≥ 0 , is directly affected by the local environment quality so that:

$$K_{x,y,t} = K_0 + K_0 \times Q_{x,y,t} \quad (3)$$

Reproduction

The annual cycle of individuals in patch x, y starts with reproduction. Each female i produces a number of offspring sampled from a Poisson distribution with a mean μ_{Off} given by:

$$\mu_{\text{Off}} = \frac{\text{Off}_{\text{max}}}{\left(1 + (\text{Off}_{\text{max}} - 1) \times \frac{N_{x,y,t}}{K_{x,y,t}}\right)} \quad (4)$$

where Off_{max} is the maximum mean number of offspring produced per female and $N_{x,y,t}$ is the number of adults present in patch x, y in year t . If females successfully produce one or more offspring, they are successful breeders. Otherwise, they are failed breeders. The local breeding success $\text{LBS}_{x,y,t}$ is calculated as the ratio of the number of successful breeders to the number of adults $N_{x,y,t}$.

Life stages

Juveniles have a probability S_j of surviving at birth and becoming pre-breeders (Table 1). Age at recruitment, i.e. age at which pre-breeders become adults and attempt to breed for the first time, is generated at birth from a Poisson distribution with a mean of 5. As long as pre-breeders do not reach age at recruitment, they experience a survival probability S_j (Table 1) and remain pre-breeders. They neither breed nor disperse. When they recruit and become adult, they can disperse to select their first breeding patch (see below). Adults have an annual survival probability S_A (Table 1).

Emigration, prospecting and settlement

Dispersal is decomposed into three steps: prospecting, emigration decision and settlement decision. The emigration probability can either be fixed for all individuals (non-informed) or it can depend on both personal and public information (informed), which respectively correspond to individual and local conspecific breeding success. Successful breeders have a very low emigration probability E_{succ} while that of failed individuals E_{fail} depends on a fixed parameter E_{fail} and the local breeding success of conspecific $\text{LBS}_{x,y,t}$ in their current breeding patch so that:

$$E'_{\text{fail}} = E_{\text{fail}} - E_{\text{fail}} \times \text{LBS}_{x,y,t} \quad (5)$$

As such, all individuals use their own breeding success as personal information when deciding whether to emigrate. Failed breeders additionally use the breeding success of conspecifics in their own breeding patch as public information when deciding whether to emigrate.

When pre-breeders become adult, they can choose where to recruit and breed for the first time. As they have not reproduced yet, they have no past breeding performance. Nevertheless, they are assigned the emigration probability of failed breeders E_{fail} , as they are assumed to use the same public information to make their emigration decisions.

The prospecting phase, which is independent from emigration decision, consists for individuals of visiting a specific number of patches N_p chosen randomly within a prospecting window defined by the perceptual range PR (Fig. 1). Note that individual movements within the grid are not explicit

Table 1. Main parameters used in the model.

Model parameters	Abbreviation	Value
Carrying capacity in bad environment	K_0	20
Maximum mean number of offspring produced by female	Off_{max}	2
Juvenile survival	S_j	0.6
Pre-breeder survival	S_j	0.7
Adult survival	S_A	0.85
Standard deviation for the environment	σ	1
Temporal auto-correlation coefficient	α	0.8
Non-informed emigration probability	E	0.5
Intercept of informed emigration probability for failed breeders	E_{fail}	0.85
Informed emigration probability for successful breeders	E_{succ}	0

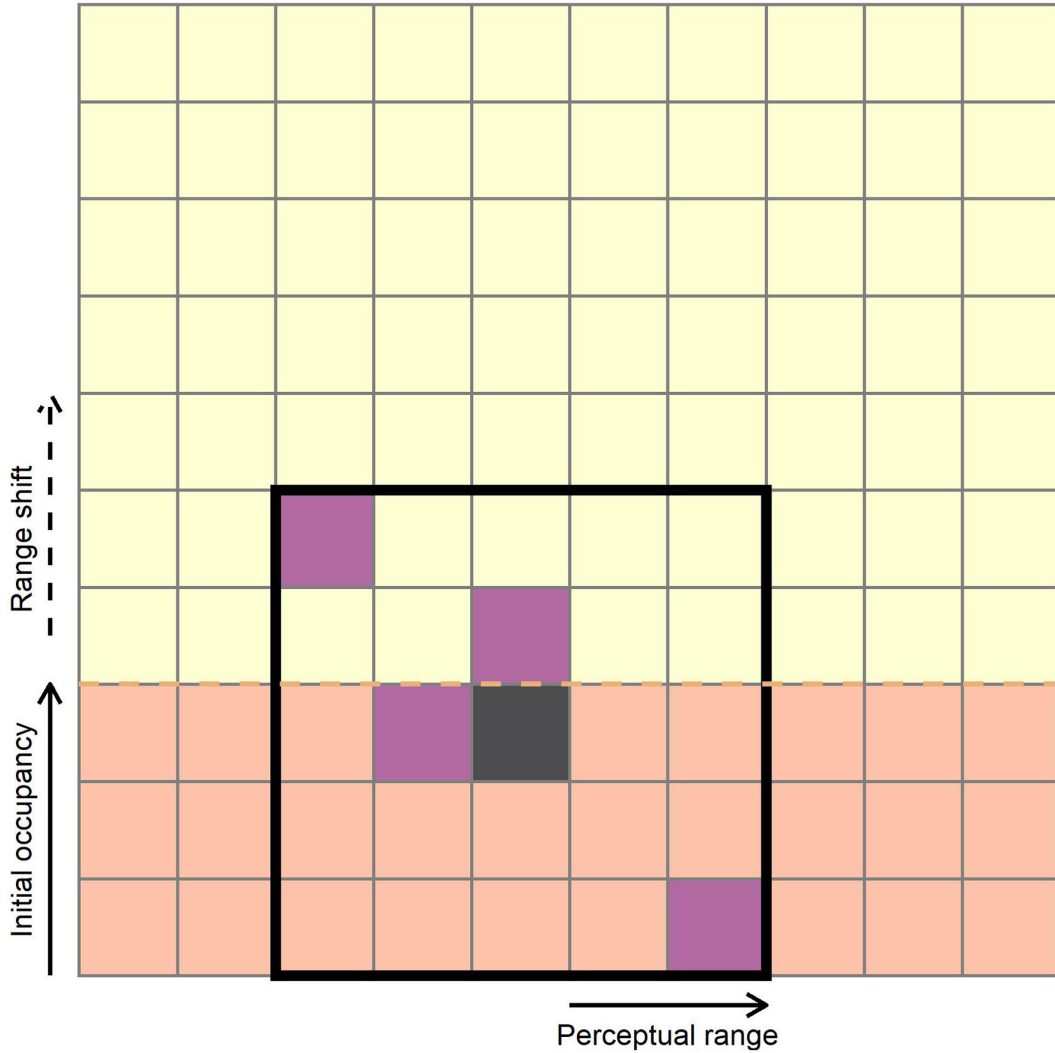


Figure 1. Illustration of how prospecting is implemented. Occupied patches are represented in orange and empty patches, in yellow. Individuals have access to a specific number of patches around their current breeding patch (dark grey cell) determined by the perceptual range PR . Within this prospecting window (black square), they visit a specific number of patches (purple cells) which can be occupied or empty. Their settlement preference probability P_s determines whether they settle in the most productive occupied patch they have prospected or the empty patch with highest environmental quality they have prospected. The range shift is occurring towards upper rows.

– thus there is no spatial autocorrelation between the patches that are prospected. The prospected patches are ranked according either to their local breeding success for occupied patches (public information use) or by their environmental quality for empty patches (personal information use).

A key component of individuals' behaviour is their willingness to settle in an empty patch, since only personal information is available in empty patches. Given the low availability of empirical data which could inform our model choices, we represent it as simply as possible by introducing a single new parameter, the settlement preference probability P_s . As long as individuals have prospected at least one occupied and at least one empty patch, P_s is the probability that individuals settle in the empty patch with the highest local environmental quality that they prospected. Alternatively, with probability $1 - P_s$, they settle in the occupied patch with the highest local breeding

success that they prospected. When individuals prospect only occupied patches but their settlement preference dictates they should settle in an empty patch, they do not emigrate and stay in their current patch. The same rule apply when individuals prospect only empty patches but have a settlement preference that dictates they should settle in an occupied patches. The lower the value of P_s , the more likely individuals are to use public information and settle in already occupied patches and thus, the harder the colonization of empty patches.

When individuals do not prospect ($N_p=0$), individuals settle randomly in a patch within the prospecting window, regardless of local breeding success nor environmental quality.

Simulation experiments

At initialisation, only the first three rows of the grid hold some populations and individuals are not allowed to move between

patches for 200 years so that local populations are at equilibrium. After this burn-in, simulations are run for a further 100 years during which individuals are allowed to disperse to a new breeding patch based on their emigration strategy, perceptual range and defined number of prospected patches.

We considered two emigration strategies: in the first one, emigration depends on information use, as described above (informed emigration), with $E_{succ} = 0$ and E_{fail} depending on the local breeding success of conspecifics (Eq. 5) and intercept $E_{fail} = 0.85$ (Table 1). The second emigration strategy is non-informed, meaning that all individuals have the same constant emigration probability $E = 0.5$ regardless of their own breeding success or the one of their conspecifics. Those emigration values were chosen based on the values of emigration probabilities obtained in evolutionary stable strategies of informed dispersal (Ponchon et al. 2021).

Along with emigration strategies, we tested six different settlement strategies: a random settlement, when individuals do not prospect ($N_p = 0$) and five settlement strategies based on prospecting, where individuals can gather information on either 2, 4, 8, 12 or 16 patches within the prospecting window. We tested these informed dispersal strategies with 3 values of perceptual range (2, 4 or 8) and 11 values of settlement preference probabilities P_s (0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1). Overall, this resulted in 374 scenarios which were ran over 300 years and replicated 10 times. For a better readability, some results are only presented for a subset of P_s and N_p . The rest of scenarios can be found in the Supporting information. The speed of range expansion is calculated as the mean number of rows colonized per year and the extent of the front is calculated as the difference between the maximum and minimum rows with < 100 individuals.

Results

Information use, the range over which individuals prospect, the number of sites they prospect and their willingness to settle in empty patches all have major impacts on the rate of range expansion. When emigration is informed, speeds of range expansion are roughly twice as slow as when emigration is non-informed, that is when individuals emigrate regardless of their own breeding success. This difference in rates of expansion between informed and non-informed is maintained with increasing perceptual range and with the number of prospected patches (Fig. 2). An increase in the number of prospected patches and perceptual range increases the rate of expansion, often substantially. For example, after informed emigration, when individuals prospect 2 patches and have a preference settlement probability of 0.5, the rate of expansion is 0.2 row year⁻¹ when the perceptual range is 2, 0.4 row year⁻¹ when it is 4 and 0.8 row year⁻¹ when it is 8. This rate of expansion further increases to 1 when 12 patches are prospected with a perceptual range is 8. This increase is even more visible with a non-informed emigration.

All settlement strategies based on prospecting can, under some conditions, outperform random settlement (black horizontal lines in Fig. 2). There is a threshold in preference settlement probability P_s above which informed settlement results in a higher rate of expansion than random settlement. This threshold highly depends on the number of prospected patches and the perceptual range: the higher the number of prospected patches and the higher perceptual range, the lower the threshold in preference settlement probability. This means that even when individuals prefer settling in occupied patches, the speed of range expansion can be boosted

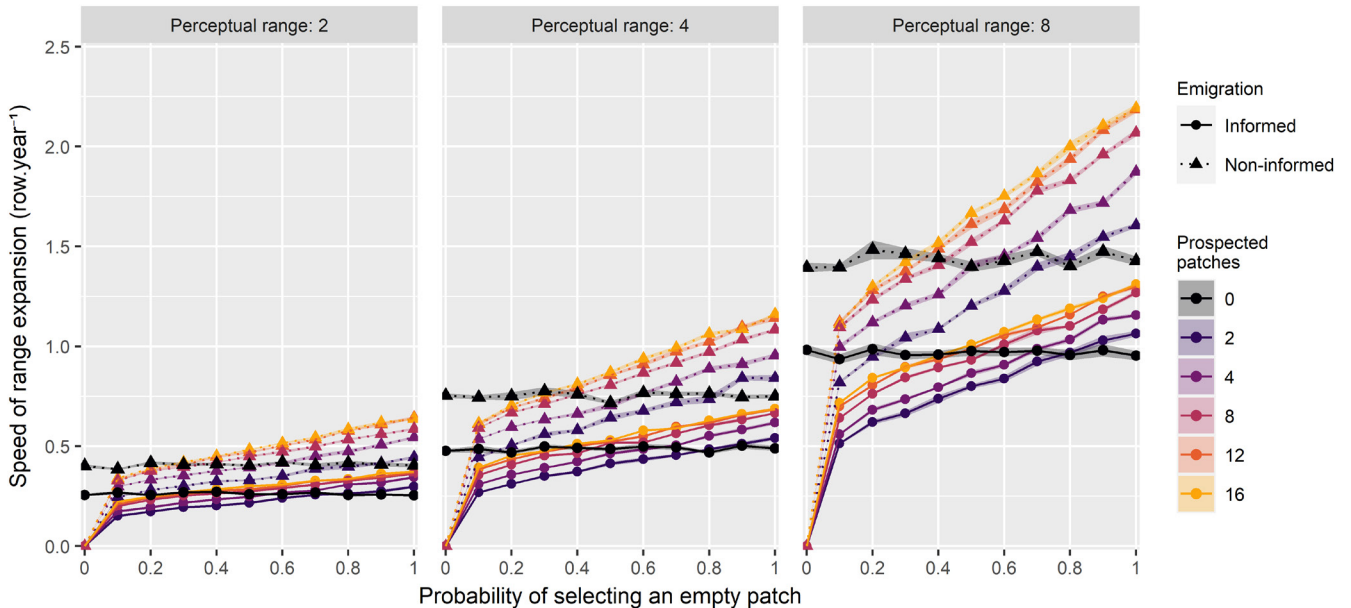


Figure 2. Speed of mean \pm SE of range expansion (row year⁻¹) over 10 replicates depending on the perceptual range, the number of prospected patches and the probability of individuals to choose an empty patch when emigration is non-informed (dotted lines/triangles) or informed (solid lines/points). Note that a settlement strategy based on 0 prospected patch corresponds to random settlement.

by prospecting with a high perceptual range and/or a high number of patches.

When looking at how individuals are distributed in the patches (Fig. 3; see the Supporting information for all scenarios), with an informed emigration, densities are higher at the core of the range but they drop abruptly towards the expanding margin. In the case of non-informed emigration, densities at the core are generally lower, but they decrease more gradually towards the expanding margin and they have longer fronts. When the probability of choosing an empty patch increases, a high number of prospected patches leads to lower densities at the core and extended fronts with very low densities, especially with non-informed emigration and the highest number of prospected patches (16). When the perceptual range increases, these patterns are qualitatively the same but populations spread faster and further.

The extent of the front over years is highly sensitive to emigration and settlement strategies, the perceptual range and individual willingness to settle in empty patches (Fig. 4). In general, informed emigration along with prospecting (solid colored lines, Fig. 4) leads to relatively short fronts regardless of either the number of prospected patches or the settlement preference probability. They are always shorter compared to non-informed emigration (dotted colored lines; Fig. 4). Contrastingly, a random settlement strategy (black lines, Fig. 4) leads to different front extents. When the preference

for empty patches is low, fronts are much longer than with prospecting but this reverts when individuals prefer settling in empty patches. Fronts become longer with prospecting, especially with a non-informed emigration (dotted coloured lines) and the difference between the number of prospected patches is accentuated with a high perceptual range. The dynamics of the front extent over time is relatively stable, rapidly reaching an asymptote for most scenarios, except when the perceptual range is high. In this case, the front extent increases rapidly over the first 20 years and slows down gradually afterwards. When the preference for empty patches is low, the front extent even decreases when individuals prospect a high number of patches after a non-informed emigration (dotted coloured lines; Fig. 4).

Discussion

We have used an individual-based model incorporating emigration decisions and a prospecting phase conditioning settlement to determine the effects of information use on the speed and shape of range expansion. Our results highlight that emigration strategy, prospecting behaviours and the willingness to settle in empty patches all have major impacts on the rate at which species expand their range. They also illustrate that the shape of species' expanding ranges are

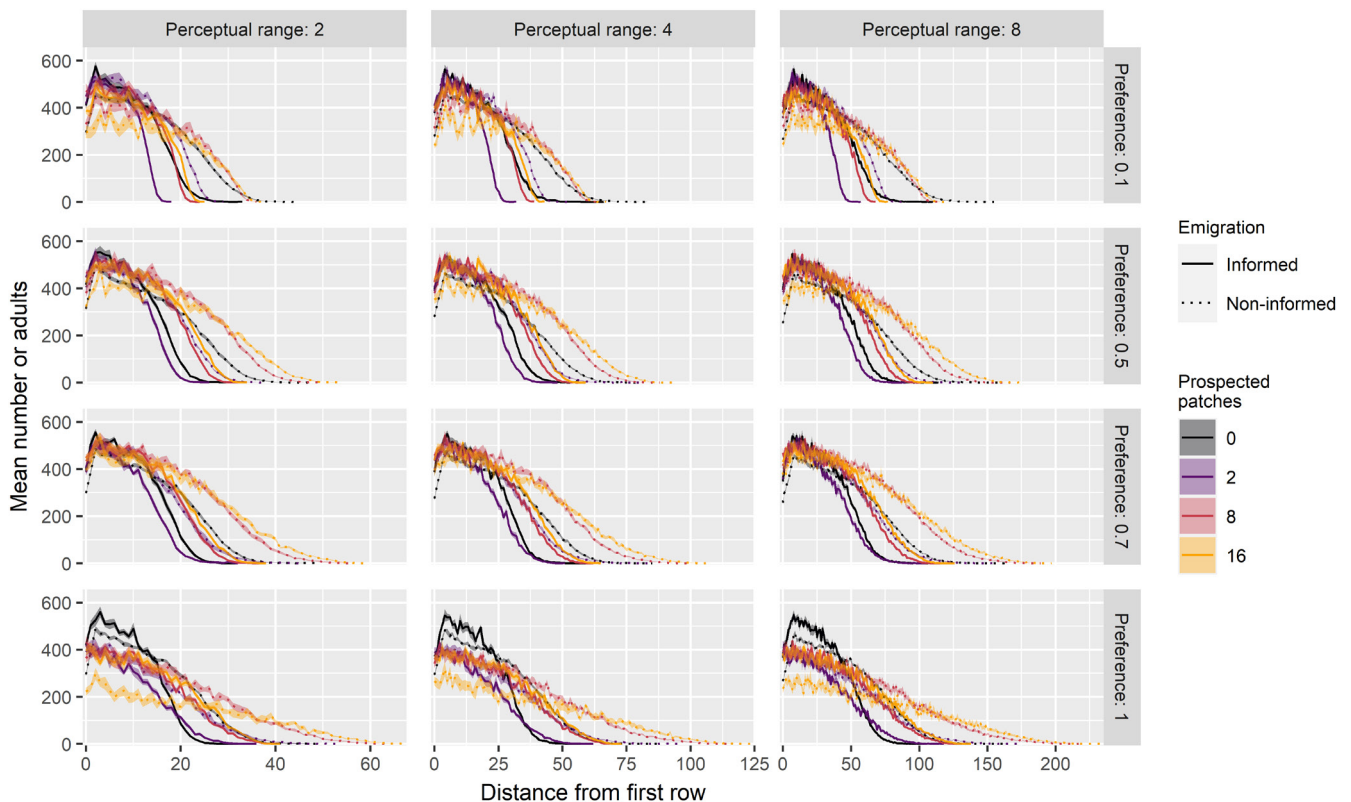


Figure 3. Mean \pm SE of population densities over 10 replicates from range core to the front after 100 years depending on the perceptual range, number of prospected patches and the preference probability of individuals to settle in an empty patch when emigration is non-informed (dotted lines) or informed (solid lines). A settlement strategy based on 0 prospected patch corresponds to random settlement.

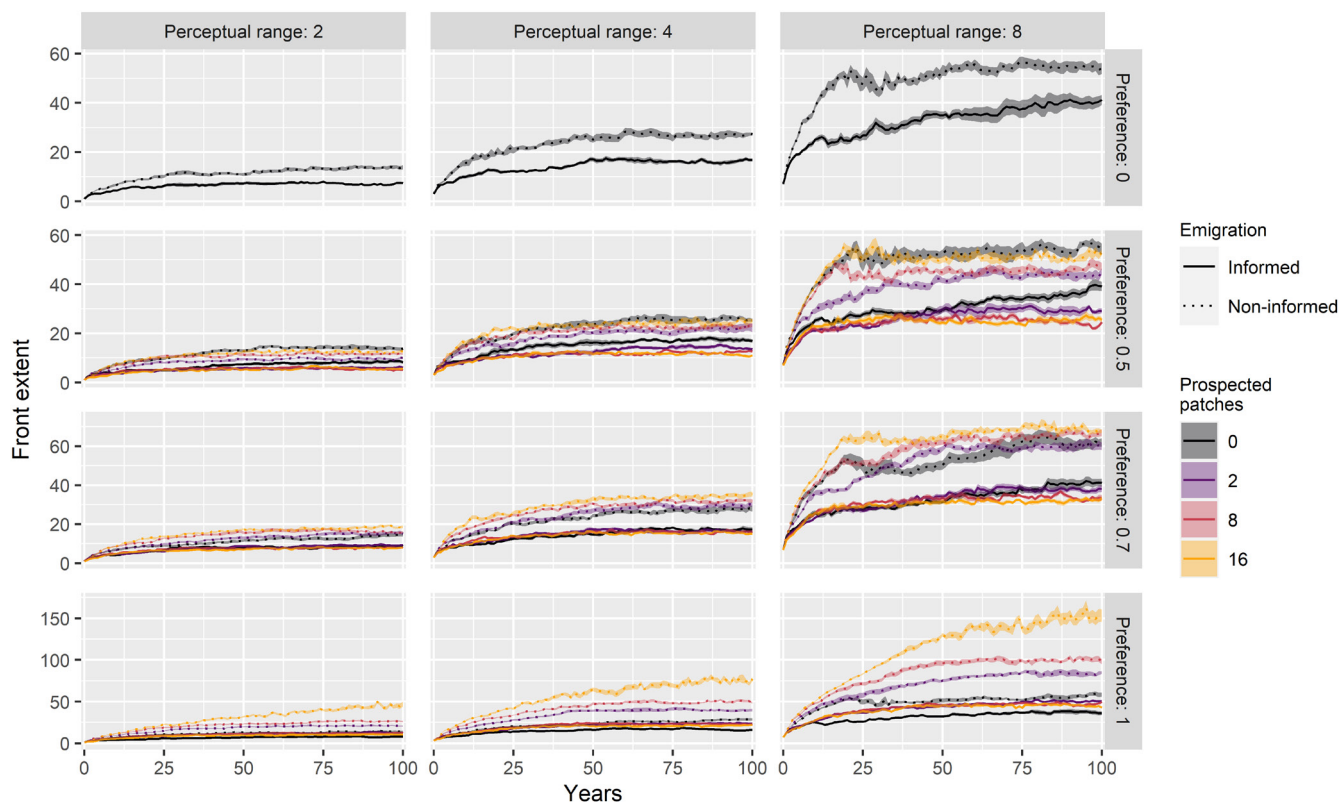


Figure 4. Mean \pm SE of extent of the front (difference between the minimum and maximum row with < 100 individuals) over time depending on the perceptual range, number of prospected patches and the preference probability of individuals to settle in an empty patch when emigration is non-informed (dotted lines) or informed (solid lines). A settlement strategy based on 0 prospected patch corresponds to random settlement.

highly sensitive to the type of information acquisition and use during dispersal.

First, we show that emigration alone has a crucial impact on the speed of range expansion, as rates of expansion under informed emigration are generally half as fast as those obtained under non-informed emigration. This is because with informed emigration, individuals successfully breeding are very unlikely to disperse and the ones failing breeding have a low probability of dispersing when they are in a productive patch (Ponchon et al. 2021). With a lower number of dispersing individuals, the probability to successfully colonize more distant patches is lower and thus, the speed of range expansion is slowed down. These results align with earlier models that demonstrated that under positively density-dependent emigration, range expansions are typically slower than when emigration is density-independent (Best et al. 2007, Bocedi et al. 2014). It also aligns with Altwegg et al. (2013) who additionally found slower speeds of range expansion when settlement was positively correlated with local densities (more individuals settling in patches of high densities). The same trend was found in empirical studies (Fernández-Chacón et al. 2013, Brown 2016, De Bona et al. 2019).

We address an additional crucial factor for the successful colonization of empty patches: the settlement preference for occupied or empty patches. Indeed, if all individuals used

solely public information on local breeding success to settle in occupied patches, range expansion would be impossible, as confirmed when $P_s=0$ (Fig. 2). For new empty suitable patches to be colonized, at least a small number of individuals have to rely on personal information acquired directly from the local environment in order to settle in empty patches and the number of individuals doing so has to be sufficiently high and sustained over time for the range to expand (Zador et al. 2009). This point is particularly intriguing as it is still unclear in the field how species generally using public information manage to colonize new empty patches. Some empirical studies have shown that, for example, seabird colonies could be formed by groups of experienced breeders or skipping breeders with a potential lag between the first observation of individuals in the new patch and first successful breeding (Munilla et al. 2016, Payo-Payo et al. 2017). It has also been shown that habitat quality is key in colonization of new patches (Zador et al. 2009). Yet, some newly formed colonies go extinct a few years after colonization (Payo-Payo et al. 2017), especially when the initial number of founders is low (Zador et al. 2009). Logically, the process of colony foundation should be extremely sensitive to how individuals acquire and use different types of information. While there are a handful of empirical studies examining the dynamics of colony foundation in empty patches (Calabuig et al. 2010, Munilla et al. 2016, VanderWerf et al. 2019, Oro 2020,

Oro et al. 2021) and the early growth dynamics of recently established colonies (Oro and Ruxton 2001, Santoro et al. 2016, Tenan et al. 2017, Lee et al. 2018), further empirical studies are required across a greater range of systems to better predict the range expansion dynamics of social species using informed dispersal (e.g. in bats, Santos et al. 2016).

In our scenarios, we have shown that with high numbers of prospected patches and perceptual range, higher rates of range expansion can be obtained. However, a recent evolutionary model has shown that individuals were unlikely to prospect a high number of prospecting patches, including when prospecting was costly (Ponchon et al. 2021). This theoretical result aligns with the existing empirical evidence in prospecting which suggests that individuals may typically only prospect a relatively small number of colonies among the ones situated within reach (Votier et al. 2011, Boulinier et al. 2016, Campioni et al. 2017, Ponchon et al. 2017a, b, Oro et al. 2021). Therefore, species that exhibit informed emigration and prospecting with a low probability of settling in empty patches and low perceptual range (i.e. low displacement ability) may be less likely to respond quickly to environmental change and could be more at risk for population extinction.

Our model only examined the ecological consequences of different emigration, prospecting and settlement strategies and there was no inter-individual variation in the perceptual range, number of prospected patches, preference for empty patches or emigration probabilities. In future work, it will be important to address the question of how these different traits underlying those informed behaviours jointly evolve during range expansions. We know that dispersal strategies can come under strong selection at the front of an expanding range (Travis and Dytham 2002). Theory has predicted increased emigration probabilities at an expanding margin, especially when local densities are low (Travis et al. 2009). Further theory has highlighted that different individual behaviours during the transience phase of dispersal are likely to be selected for at expanding fronts compared to the core of stationary range (Bartoń et al. 2012). Increasingly, empirical studies are demonstrating that these predictions are borne out in the real world (Duckworth 2008, Phillips et al. 2010, Brown et al. 2014, Myles-Gonzalez et al. 2015, Tabassum and Leishman 2018). Verbally, we can predict that during a period of range expansion, there will likely be a spatial sorting for individuals using informed dispersal that is likely to lead them being colonisers of empty patches beyond the existing front, or at least early joiners. These individual traits would include higher propensity to emigrate (even at low density or after successful breeding), inability to successfully compete with local conspecifics, propensity to prospect over longer distances and visit a greater number of patches and willingness to settle in empty patches. If there is a heritable component to these traits as there is for dispersal (Hansson et al. 2003, Ochocki and Miller 2017, Saastamoinen et al. 2018), then it is likely that over a number of generations, the range front will become increasingly dominated by individuals possessing these traits and the range is thus likely to expand at

an accelerating rate, facilitating species response to environmental changes.

Our results further highlight that not only the rate of range expansion, but also the shape of the front, is highly sensitive to how individuals acquire and use information during dispersal. When individuals prospect further, in many patches and are willing to settle in empty patches, the front has a very long tail but only with a non-informed emigration, as the number of dispersers is higher (Fig. 4). This scenario has two main effects: first, colonisation into new regions is faster (extending the front even further) and second, local population growth rates are effectively reduced in newly colonised patches, as emigrants from those patches are more likely to settle in empty patches than they are to reinforce the populations in other recently colonised patches (Zador et al. 2009, Payo-Payo et al. 2017). In contrast, when individuals prefer to settle in patches that are already colonised, the front expands more slowly but the effective growth rate of recently colonised patches are elevated due to their high attractiveness to potential prospectors (see Santoro et al. 2016 for an empirical example). Hence, under these conditions, the front has a shorter tail, especially when individuals prospect (Fig. 4). Importantly, we suggest that these distinct front shapes over time can provide a means to infer how individuals disperse. It is of course challenging to directly study the formation of new colonies in the field, in particular the process by which the very first individuals settle in a new patch. So developing methods to indirectly infer the processes from the spatial density patterns at expanding margins could be a highly fruitful direction for future work. Bayesian inference would provide a means for formally doing this and linking empirical data on density structure towards range margins with individual based models through approximate Bayesian computation (Dominguez Almela et al. 2020) would be one exciting avenue our current work could be taken in.

Overall, we demonstrate that informed dispersal can drastically slow down range expansion, especially when individuals use public information on conspecific breeding success to inform their settlement decisions and when the probability of settling in an empty patch is low. Moreover, the speed of range expansion is likely to be lower when emigration is informed, because fewer individuals disperse. Therefore, our results highlight the crucial effect of information use in both emigration and settlement phases on the speed of range expansion and population distribution. We also stress the need to implement complex ecological processes like dispersal more realistically to be able to better understand, predict and ultimately manage more effectively species' responses to environmental change (Pellerin et al. 2019).

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Author contributions

Aurore Ponchon: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Justin M. J. Travis:** Conceptualization (supporting); Funding acquisition (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.06190>>.

Data availability statement

The source code and outputs are available from the Zenodo Repository (<<https://doi.org/10.5281/zenodo.5643574>>). Codes for extracting model variables and making figures are also freely available at <https://github.com/auponchon/Prospecting_Invasions>.

Supporting information

The supporting information associated with this article is available from the online version.

References

- Altwegg, R. et al. 2013. Density-dependent dispersal and the speed of range expansions. – *Divers. Distrib.* 19: 60–68.
- Bartoń, K. A. et al. 2012. Risky movement increases the rate of range expansion. – *Proc. R. Soc. B* 279: 1194–1202.
- Best, A. S. et al. 2007. Which species will successfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. – *Oikos* 116: 1531–1539.
- Bocedi, G. et al. 2012. Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. – *Am. Nat.* 179: 606–620.
- Bocedi, G. et al. 2014. Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. – *Ecography* 37: 1240–1253.
- Boulinier, T. and Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial species. – *Evol. Ecol.* 11: 505–517.
- Boulinier, T. et al. 2016. Migration, prospecting, dispersal? What host movement matters for infectious agent circulation? – *Integr. Comp. Biol.* 56: 330–342.
- Brown, C. R. 2016. The ecology and evolution of colony-size variation. – *Behav. Ecol. Sociobiol.* 70: 1613–1632.
- Brown, G. P. et al. 2014. The straight and narrow path: the evolution of straight-line dispersal at a cane toad invasion front. – *Proc. R. Soc. B* 281: 20141385.
- Calabuig, G. et al. 2010. Colony foundation in the lesser kestrel: patterns and consequences of the occupation of empty habitat patches. – *Anim. Behav.* 80: 975–982.
- Campioni, L. et al. 2017. Albatrosses prospect before choosing a home: intrinsic and extrinsic sources of variability in visit rates. – *Anim. Behav.* 128: 85–93.
- Clark, J. S. et al. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. – *Am. Nat.* 157: 537–554.
- Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecol. Lett.* 12: 197–209.
- Clobert, J. et al. 2012. Dispersal ecology and evolution. – Oxford Univ. Press.
- Dall, S. R. X. et al. 2005. Information and its use by animals in evolutionary ecology. – *Trends Ecol. Evol.* 20: 187–193.
- Danchin, E. et al. 2004. Public information: from nosy neighbors to cultural evolution. – *Science* 305: 487–491.
- De Bona, S. et al. 2019. Spatio-temporal dynamics of density-dependent dispersal during a population colonisation. – *Ecol. Lett.* 22: 634–644.
- Doligez, B. et al. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density-dependence. – *Anim. Behav.* 66: 973–988.
- Dominguez Almela, V. et al. 2020. Integrating an individual-based model with approximate Bayesian computation to predict the invasion of a freshwater fish provides insights into dispersal and range expansion dynamics. – *Biol. Invas.* 22: 1461–1480.
- Duckworth, R. A. 2008. Adaptive dispersal strategies and the dynamics of a range expansion. – *Am. Nat.* 172: S4–S17.
- Dytham, C. 2009. Evolved dispersal strategies at range margins. – *Proc. R. Soc. B* 276: 1407–1413.
- Fernández-Chacón, A. et al. 2013. When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population. – *Ecography* 36: 1117–1126.
- Fronhofer, E. A. et al. 2017. Information use shapes the dynamics of range expansions into environmental gradients. – *Global Ecol. Biogeogr.* 26: 400–411.
- Hansson, B. et al. 2003. Heritability of dispersal in the great reed warbler. – *Ecol. Lett.* 6: 290–294.
- Hastings, A. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. – *Ecol. Lett.* 8: 91–101.
- Henry, R. C. et al. 2014. Inter-annual variability influences the eco-evolutionary dynamics of range-shifting. – *Peer J.* 1: e228.
- Holt, R. D. et al. 2005. Theoretical models of species' borders: single species approaches. – *Oikos* 108: 18–27.
- King, A. W. and With, K. A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? – *Ecol. Model.* 147: 23–39.
- Kot, M. et al. 1996. Dispersal data and the spread of invading organisms. – *Ecology* 77: 2027–2042.
- Kun, A. and Scheuring, I. 2006. The evolution of density-dependent dispersal in a noisy spatial population model. – *Oikos* 115: 308–320.
- Lee, D. E. et al. 2018. Initial growth of northern fur seal *Callorhinus ursinus* colonies at the South Farallon, San Miguel and Bogoslof Islands. – *J. Mammal.* 99: 1529–1538.
- Miller, T. E. X. et al. 2020. Eco-evolutionary dynamics of range expansion. – *Ecology* 101: e03139.
- Munilla, I. et al. 2016. Colony foundation in an oceanic seabird. – *PLoS One* 11: e0147222.
- Myles-Gonzalez, E. et al. 2015. To boldly go where no goby has gone before: boldness, dispersal tendency and metabolism at the invasion front. – *Behav. Ecol.* 26: 1083–1090.

- Nathan, R. et al. 2011. Mechanistic models of seed dispersal by wind. – *Theor. Ecol.* 4: 113–132.
- Neubert, M. G. and Caswell, H. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. – *Ecology* 81: 1613–1628.
- Ochocki, B. M. and Miller, T. E. X. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. – *Nat. Commun.* 8: 14315.
- Oro, D. 2020. Perturbation, behavioural feedbacks and population dynamics in social animals. – Oxford Univ. Press, pp. 126.
- Oro, D. and Ruxton, G. D. 2001. The formation and growth of seabird colonies: Audouin's gull as a case study. – *J. Anim. Ecol.* 70: 527–535.
- Oro, D. et al. 2021. High frequency of prospecting for informed dispersal and colonisation in a social species at large spatial scale. – *Oecologia* 197: 395–409.
- Payo-Payo, A. et al. 2017. Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers. – *Sci. Rep.* 7: 42866.
- Pellerin, F. et al. 2019. Matching habitat choice promotes species persistence under climate change. – *Oikos* 128: 221–234.
- Phillips, B. L. et al. 2010. Evolutionarily accelerated invasions: the rate of dispersal evolves upwards during the range advance of cane toads. – *J. Evol. Biol.* 23: 2595–2601.
- Ponchon, A. et al. 2017a. Spatial overlaps of foraging and resting areas of black-legged kittiwakes breeding in the English Channel with existing marine protected areas. – *Mar. Biol.* 164: 119.
- Ponchon, A. et al. 2017b. Intense prospecting movements of failed breeders nesting in an unsuccessful breeding subcolony. – *Anim. Behav.* 124: 183–191.
- Ponchon, A. et al. 2021. Prospecting and informed dispersal: understanding and predicting their joint eco-evolutionary dynamics. – *Ecol. Evol.* 11: 15289–15302.
- Reed, J. M. et al. 1999. Informed dispersal: prospecting by birds for breeding sites. – *Curr. Ornithol.* 15: 189–259.
- Saastamoinen, M. et al. 2018. Genetics of dispersal. – *Biol. Rev.* 93: 574–599.
- Santoro, S. et al. 2016. Immigration enhances fast growth of a newly established source population. – *Ecology* 97: 1048–1057.
- Santos, J. D. et al. 2016. Dispersal and group formation dynamics in a rare and endangered temperate forest bat (*Nyctalus lasiopterus*, Chiroptera: Vespertilionidae). – *Ecol. Evol.* 6: 8193–8204.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. – *Biometrika* 38: 196–218.
- Tabassum, S. and Leishman, M. R. 2018. Have your cake and eat it too: greater dispersal ability and faster germination towards range edges of an invasive plant species in eastern Australia. – *Biol. Invas.* 20: 1199–1210.
- Tenan, S. et al. 2017. Conspecific and not performance-based attraction on immigrants drives colony growth in a waterbird. – *J. Anim. Ecol.* 86: 1074–1081.
- Travis, J. M. J. and Dytham, C. 2002. Dispersal evolution during invasions. – *Evol. Ecol. Res.* 4: 1119–1129.
- Travis, J. M. J. et al. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. – *J. Theor. Biol.* 259: 151–158.
- VanderWerf, E. A. et al. 2019. Establishing Laysan and black-footed albatross breeding colonies using translocation and social attraction. – *Global Ecol. Conserv.* 19: e00667.
- Votier, S. et al. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. – *Mar. Biol.* 158: 355–362.
- Williams, J. L. et al. 2016. The influence of evolution on population spread through patchy landscapes. – *Am. Nat.* 188: 15–26.
- Zador, S. G. et al. 2009. Factors influencing subcolony colonization and persistence in a colonial seabird, the common murre *Uria aalge*. – *Mar. Ecol. Prog. Ser.* 376: 283–293.