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Rapid changes in dispersal on a small spatial scale at the range edge of an expanding population

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Abstract

In expanding populations, the allocation of resources to life-history traits is expected to change rapidly after the colonization of a new area. Understanding these changes is of crucial importance to predict the future changes in distribution ranges, and the possible impacts of expanding species on the colonized environments. Both theoretical and empirical studies have provided some evidence for an increased dispersal at the range edge of expanding populations. Because this phenomenon has been documented on large spatial scales, it seems difficult to determine what proportion of the phenotypic variation is due to the expansion process (spatial sorting) versus spatial variation in the environment (local adaptation). The aim of our study is to determine whether, in a small and recent expanding population, the dispersal capacity is increased at the range edge compared to the range core despite a minimal role of local adaptation. We studied the modification of dispersal capacity at the range edge of an expanding population of the African clawed frog, *Xenopus laevis* recently settled in Western France. To do so, we used experiments to compare movements of individuals depending on their location in the population, and capture–mark–recapture field surveys to estimate variation in traits related to dispersal across the invasive range. Both methods consistently showed significantly higher dispersal rates and distances, as well as in the relative length of the hind limb, at the range edge, for both sexes. This result is the first report suggesting that changes in allocation to dispersal, and not only traits associated with dispersal, can occur at a small geographical and temporal scale, where the role of local adaptation is likely minimal. This study fills a gap in an issue where it is currently crucial, for conservation purposes, to understand the mechanisms involved in range expansions.

Keywords Dispersal · Phenotypic plasticity · Range expansion · Spatial sorting · *Xenopus laevis*

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Introduction

On a global scale, an increasing number of species experience changes in their distributions. Range shifts can be the direct or indirect consequences of human activities (Channell and Lomolino 2000; Parmesan and Yohe 2003). These shifts are essentially driven by three parameters summarizing the trade-offs in the life-history traits of an individual in a population: density dependence, dispersal, and population growth (Burton et al. 2010). According to simulation and empirical studies, the allocation of resources to these traits is likely to change during the expansion of a population's range, resulting in different probabilities for an individual to reproduce, disperse, and survive depending on its location within its range, i.e. the core or the edge of the range (Burton et al. 2010). Empirical evidence abounds concerning the increased allocation to traits related to dispersal at the range edge for several taxonomical groups, but direct evidence of enhanced dispersal has more rarely been reported (Chuang and Peterson 2016). As underlined in previous studies on the dispersal behavior of individuals in expanding populations, great caution is necessary to correctly estimate dispersal rates at the range edge as underestimates may lead to an under-predicted expansion rate into new areas (Lindström et al. 2013).

Spatial sorting has been suggested to play a substantial role in the increased dispersal at the range edge to the detriment of local adaptation (Chuang and Peterson 2016; Shine et al. 2011). This phenomenon is described in the context of range expansions and can be defined as the accumulation of traits enhancing the dispersal rate of the population at the expanding range edge by repeated mating between long-dispersing individuals regardless of how this phenotype affects the survival and reproductive success of the organisms (Shine et al. 2011). But recent studies have demonstrated that other factors related to the variation in the environment play a role in the phenotypic plasticity observed in expanding populations through experiments (Van Petegem et al. 2017) and field studies (Stuart et al. 2019). Furthermore, other evolutionary mechanisms, such as local adaptation, can occur during range expansions, especially along environmental gradients (Colautti and Barrett 2013). But local adaptation has been shown to have a limited influence on phenotypes in contexts where individuals disperse a lot, such as metapopulations (Sultan and Spencer 2002).

Thus, discriminating the influence of spatial sorting and local adaptation in the modified phenotypes of the range edge individuals appears as a crucial element in the understanding of the phenomenon driving range expansions. To empirically study this issue, the choice of an accurate model must take into account the environmental context: no environmental gradient along the range expansion, and a significant dispersal rate in every area of the population, and not only at the range edge (Sultan and Spencer 2002; Colautti and Barrett 2013) to reduce the effect of local adaptation.

This is why, in this study, we used an invasive and expanding population of the African clawed frog, *Xenopus laevis*, introduced in France during the late 1980s (Fouquet 2001) to assess the changes in dispersal allocation during range expansion. This species is commonly used in research laboratories around the world and has been introduced on four continents (Measey et al. 2012). Yet, its ecology is poorly known and empirical data on overland movements and dispersal behavior of this species are surprisingly rare (Measey 2016). *Xenopus laevis*, was recently classified as one of the invasive amphibians with the most important ecological impacts in the world (Measey et al. 2016), and is likely to expand greatly in Europe over the next decades (Ihlow et al. 2016). An increased capacity for endurance and a longer relative length of the hind limbs at the range edge of an expanding population of *X. laevis* has been reported in France (Louppe et al. 2017). The species occupies a restricted geographic area in France (about 2000 km^2) with a very limited variation in climatic conditions (Joly et al. 2010), and no substantial variation in the landscape which is dominated by pastureland, vineyards, and crop fields. Thus, this expanding population represents an opportunity to empirically test the role of spatial sorting and local adaptation in the changes in dispersal allocation at the edge of its range.

We expect that the variation in locomotor performance observed in Louppe et al. (2017) is related to an actual increase in the dispersal components, the dispersal rate (the proportion of dispersing individuals) and the dispersal distance (Guillon and Bottein 2011) in this invasive population.

Material and methods

Study area: capture method

Xenopus laevis was introduced in Western France in the 1980's from a breeding facility in Bouillé-Saint-Paul (Fouquet 2001). The species has colonized a large part of the Deux-Sèvres and Maine-et-Loire departments, and expanded through the valleys of the Thouet and the Layon, two tributaries of the Loire river (Fig. 1). To capture frogs, fyke nets (60 cm length × 30 cm width, 6 mm mesh diameter) were introduced in ponds, with a constant capture effort fixed at one fyke net for every 50 m^2 of water surface. Individuals were removed from the fyke nets and used for the experiments or marked and released depending on the

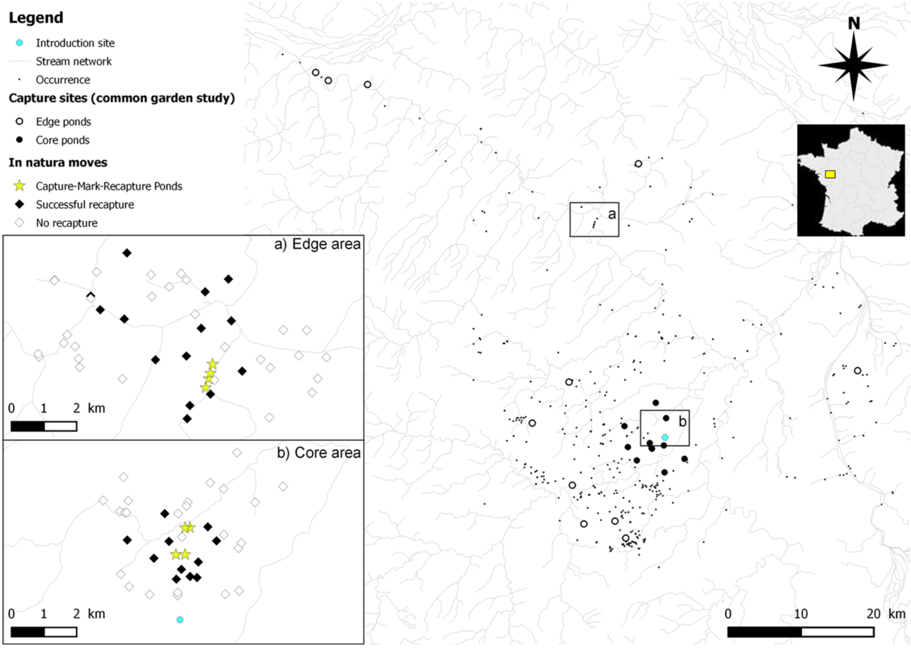

Fig. 1 Pond sampling for the field survey (detailed in **a**, **b**) and the experiments. For **a** and **b**, some ponds were located beyond the 4-km radius surrounding the surveyed ponds and are not drawn in the map

study. We selected ponds according to their location and to their characteristics (ponds in pasturelands, less than 500 m^2, with no detected fish, away from towns and large roads). Individuals used in experimental trials were euthanized by immersion in Tricaine metanosulfonate (MS222) after the trials (explained below) in accordance with French law. The release of the individuals for the capture–recapture survey was authorized through a permit delivered by the Préfet of the Deux-Sèvres department.

Capture–mark–recapture survey

Sampling design

A 3-year capture–mark–recapture (CMR) study was conducted in the area occupied by *X. laevis* in France, from 2014 to 2016. All ponds were visited eight times from early May each year, with a 3-day interval. On the first visit, each captured individual was sexed, measured for its Snout-vent length (SVL) and hind limb length with a digital caliper (Mitutoyo Absolute IP67—precision 0.01 mm). We took care to make individuals adopt a relaxed and flattened position before proceeding to any measurement in order to ensure constancy in the measured parameters. Individuals were weighed with an electronic scale (XL 2PP—precision 0.01 g), and marked with a passive integrated transponder (Loligo Systems, #AB10320) under the skin of their back, before being released in the pond where there were captured. On the next visits, individuals were checked for the presence of a transponder. The recaptures of marked individuals were recorded, if the previous capture occurred during the same year. New individuals were sexed, measured and marked. On the second and third year, on the first recapture of each individual, all measures (SVL, limb length, body mass) were repeated.

Study sites

Two groups of four ponds were selected at the range edge and core, respectively. The group of core ponds is located approximately two kilometers away from the introduction site, and is surrounded by a mosaic landscape dominated by pasture lands, scattered crop fields and woods. The edge group is located close to the northern margin in the Layon river valley, 25 km away from the introduction site. The landscape surrounding the ponds is dominated by pasture lands and vineyards, with scattered woods and crop fields. Both edge and core sampling areas are crossed by many temporary streams and surrounded by low-traffic roads.

Movement sampling

In 2016, after the end of the capture–mark–recapture survey, seven visits, with a 1-week interval between each visit, were performed in the ponds located in the area surrounding the core and edge groups of ponds (Fig. 1a, b). A radius of four kilometers around the CMR ponds was chosen for these visits (4.2 km and 5.1 km for the furthest pond at the range core and edge, respectively). Visits occurred in June and July 2016. On each visit, all individuals were checked for the presence of a transponder. For marked individuals, SVL and body mass were recorded, as well as limb length, the date and recapture site. The dispersal distance, D_{CMR}, was calculated by dividing the distance crossed by the pond density in the cluster, and is expressed in kilometers travelled per pond. This correction was made to control for the difference in pond density between areas as areas with more ponds per unit area may induce greater dispersal. This density was estimated by counting the ponds in a 50 km^2 buffer surrounding both sampling areas. We also ran analyses on the raw, uncorrected data. The dispersal rate, R_{CMR}, was estimated in each area by dividing the number of dispersing individuals by the total number of captured individuals.

Enclosure experiment

Experimental set-up

To experimentally estimate dispersal we constructed a track composed of two lanes (80 m length × 0.7 m width × 0.5 m high). The substrate of the experimental corridors was composed of grass, the height of which was maintained at 10 cm throughout the experiment. Plastic pools (30 × 20 × 15 cm) were filled with water and placed every 10 m with the surface of the pools at ground level. The water in pools was changed before every experiment.

Data collection

A total of 451 individuals were used for this experiment. Among them, 247 (116 females and 131 males) and 204 (117 females and 87 males) individuals were captured at the range core and the range edge, respectively, in 10 ponds for each area (Fig. 1) throughout the activity period (from April to September, Courant et al. 2017a). The individuals used for this experimental study were captured in different ponds than those of the CMR survey. During trials, individuals were introduced at one end of the track. Dispersal movements occurred at night, *X. laevis* being mainly active during this period (Ringeis et al. 2017). For each trial night, a group of five males was placed in a lane and five females were introduced in the other one. Thus, intersexual interference was avoided. From one night to the other, and for each lane, the sex and/or the end where individuals were introduced were changed. The distance crossed by each individual was recorded in the morning, 1 h after sunrise. For every individual, we noted the area (core or edge), the SVL and the length of the hind limb (femur, tibia, astragalus and the longest toe) with a digital caliper (Mitutoyo Absolute IP67—precision 0.01 mm). Body mass was measured using a digital scale (XL 2PP—precision 0.01 g).

Before each trial, several environmental and experimental parameters were collected. The starting end of the corridor (End) and the lane where individuals were introduced (Lane) were noted. These parameters were taken into account in the statistical analysis as they may allow the identification of a possible experimental bias. Meteorological parameters were also recorded during data sampling. They were sampled by collecting the daily online data for the closest meteorological station (N°47.08250; W°-0.19944), or directly on site. For each trial night, the cloud cover (CC) was noted as a three-category factor ("1" for a cloud-free or slight overcast, "2" for a partial overcast, and "3" for a completely covered sky). Similarly, for nocturnal wind strength (NWS), we noted the absence of wind as "1" and a strong wind with "3". The nocturnal rain (NR) was coded from "1" (no rain) to "3" (heavy rain). We also collected the maximal daily ambient temperature (MDT) and the moon phase. We considered the moonlight intensity (MI) following the relative brightness of the moon as a function of the lunar days (Nowinszky et al. 1979), i.e. the number of days since the last full moon.

Statistical analyses

Morphology

To test for the effect of the sampling area on the relative length of the hind limb (HindR), we used the residuals of the regression of the hind limb length on the SVL in a linear mixed model with the area and sex as fixed effects, and the pond as a random effect. Only individuals that dispersed were used for this analysis. The morphological measurements are provided in the results as means and standard deviations (SD).

Field survey

First, we made sure that the density of individuals in the ponds of the CMR survey did not influence their probability to emigrate from the pond of first capture. Thus, the density in each pond was estimated using the number of individuals captured in each pond and the pond surface area. The relationship between the density and the proportion of emigrating individuals recorded after the 3-year survey was assessed using a linear regression. To analyze differences in dispersal movements between populations of the core and the edge of the range, we used D_{CMR} in a linear mixed model with the cluster and the biological parameters of individuals, i.e. sex, SVL and HindR, as fixed effects. We used the capture site nested within the cluster as a random effect. We also calculated the dispersal rate R_{CMR} by dividing the number of records of moving individuals by the total number of individuals captured for a given cluster and a given sex. We performed similar analyses for D_{CMR}. Additionally, we focused on the sex-ratio of moving individuals by taking into account the number of captured individuals in each area during the initial CMR survey. To do so, we performed a Chi-Square test for each area with the number of moving individuals of each sex, with the proportion of individuals of each sex captured during the CMR survey.

Experiments

The effect of the capture area (range edge or range core) was tested on the dispersal rate, R_{EXPE}, calculated as the ratio between the number of individuals that moved and the number of individuals used in the experiment. The effect of the capture area was also calculated on the dispersal distance, D_{EXPE}, calculated as the ratio between the estimated distance and the maximal distance (80 meters) that animals could cross. These effects were tested using a linear mixed model for each of these dispersal traits. Environmental (CC, MDT and MI), biological (SVL, Body mass, Sex, HindR) and experimental (Month, End and Lane) parameters were used as covariates for both models. We added the interactions between CC and MI, MDT and NWS, and NWS and MI as covariates. The capture site nested in the area was used as a random predictor. To select the parameters significantly influencing dispersal traits, we used a backward stepwise selection, following the recommendations of Hegyi and Laczi (2015) by using the stepwise-reintroduction for parameter estimation (SRPE), because the original method is largely criticized (Whittingham et al. 2006). This method implies to first perform a stepwise regression with a linear mixed model to obtain a first model with the selected parameters. Then, each unselected parameter is added one by one to the model with the selected parameters. For parameters improving the model and having a significant effect (using the Akaike Information Criterion, AIC), we implemented them in the final model shown in the results.

Graphics and statistical analyses were performed in R 3.5.1 (R Core Team 2019), using the nlme package (Pinheiro et al. 2013) to perform linear mixed models with backward stepwise selections and ggplot2 (Wickham 2009) to build the graphs. The map and the distances traveled by free-ranging frogs from the pond of first capture to the pond of last capture were respectively built and measured using the Quantum GIS software (QGD Team 2019).

Results

Morphology

For females, the mean SVL reached 87.23 mm (± 2.29 mm SD; $N = 84$) and 83.89 mm (± 1.50 mm SD; $N = 117$) at the range core and the range edge, respectively. For males, it reached 70.86 mm (± 0.97 mm SD; $N = 111$) and 69.49 mm (± 0.88 mm SD; $N = 91$) at the range core and the range edge, respectively. The area (core vs. edge) had a significant effect on the variation in relative hind limb length of individuals measured in the field survey and the experiment (linear mixed model: $F_{1,27} = 11.03$, $p < 0.005$), with a significantly higher relative hind limb length at the range edge (Fig. 2). It also differed between sexes (linear mixed model: $F_{2,378} = 125.71$, $p < 0.0001$), with a significantly longer relative hind limb length for males in each cluster (Fig. 2).

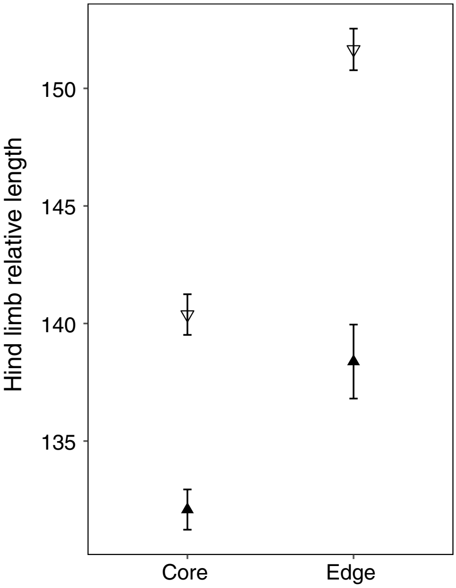

Fig. 2 Variation in relative hind limb length (limb length/snout-vent length × 100) for males (unfilled triangles) and females (filled triangles) of *Xenopus laevis* captured at the range edge and the range core of the population introduced in Western France for animals included in the experiments and in the field surveys. Symbols and error bars represent the means and the standard deviations, respectively

Dispersal estimates from the field survey

The proportion of individuals leaving the ponds where they were first captured ranged from 8.51 to 31.48% in the ponds at the range edge, and from 4.48 to 15.18% at the range core (Table 1). There was no significant relationship between the animal density in a pond and the proportion of individuals leaving the pond ($R^2 = 0.31$; $F_{3,4} = 0.59$; $p = 0.65$).

For females, the dispersal rate, R_{CMR}, was significantly different between the range core and the range edge ($Chi^2 = 10.52$, $df = 1$, $p = 0.001$), with 7.69% (12 moves) and 15.25% (34 moves) of the females moving at the range core and at the range edge, respectively. The dispersal rate was not different for males, however ($Chi^2 = 0.28$, $df = 1$, $p = 0.559$), with 13.36% (31 moves) and 14.40% (27 moves) for the range core and range edge, respectively. The sex ratio was significantly male-biased at the range core ($Chi^2 = 7.13$; $df = 1$; $p = 0.008$), with 59.79% of males (N = 232) and 40.21% of females (N = 156). However, the sex-ratio was not biased at the range edge, with 53.54% (N = 257) and 46.46% (N = 223) of males and females, respectively ($Chi^2 = 1.07$; $df = 1$; $p = 0.301$). In agreement with these results, we found that the dispersal rate was not significantly male-biased at the range edge ($Chi^2 = 0.0002$; $df = 1$; $p = 0.989$) and nearly significantly male-biased at the range core ($Chi^2 = 3.81$; $df = 1$; $p = 0.051$).

During a 2 years time period, females travelled between 0.15 and 1.29 km at the range core and between 0.12 and 4.01 km at the range edge. During the same time period, males travelled between 0.15 and 1.52 km at the range core and between 0.20 and 3.63 km at the range edge. The analysis performed on the raw Euclidean distances showed that the distances crossed by individuals from the range edge were significantly longer than the distances crossed by individuals from the range core (linear mixed model: $F_{1,97} = 16.36$, $p < 0.01$). A similar result was obtained when considering the distance travelled corrected by pond density D_{CMR} (linear mixed model: $F_{1,97} = 8.67$, $p < 0.05$; Fig. 3b). For both response variables, we observed no effect of sex (linear mixed model: $F_{1,97} = 0.45$, $p = 0.64$) or relative hind limb length (linear mixed model: $F_{1,97} = 0.02$, $p = 0.90$) on D_{CMR}.

Experimental estimates of dispersal traits

The proportion of moving individuals in the experimental set-up varied significantly (Table 2) between core ($R_{EXPE} = 62.07\%$; N = 72) and edge females ($R_{EXPE} = 71.79\%$; N = 84). For males, the pattern was analogous, with $R_{EXPE} = 61.07\%$ (N = 80) and

Table 1 Emigration estimates after the capture–mark–recapture survey

Population	Pond ID	N_{Total}	$N_{Emigration}$	Emigration (%)	Pond surface	Density
Edge	1	376	32	8.51	315	1.19
Edge	2	79	8	11.39	466	0.17
Edge	3	54	17	31.48	504	0.11
Edge	4	30	3	10	636	0.05
Core	1	112	17	15.18	66	1.70
Core	2	67	3	4.48	491	0.14
Core	3	111	15	13.51	211	0.53
Core	4	88	9	10.23	236	0.37

Densities were calculated as the ratio between N_{Total} and the pond surface area

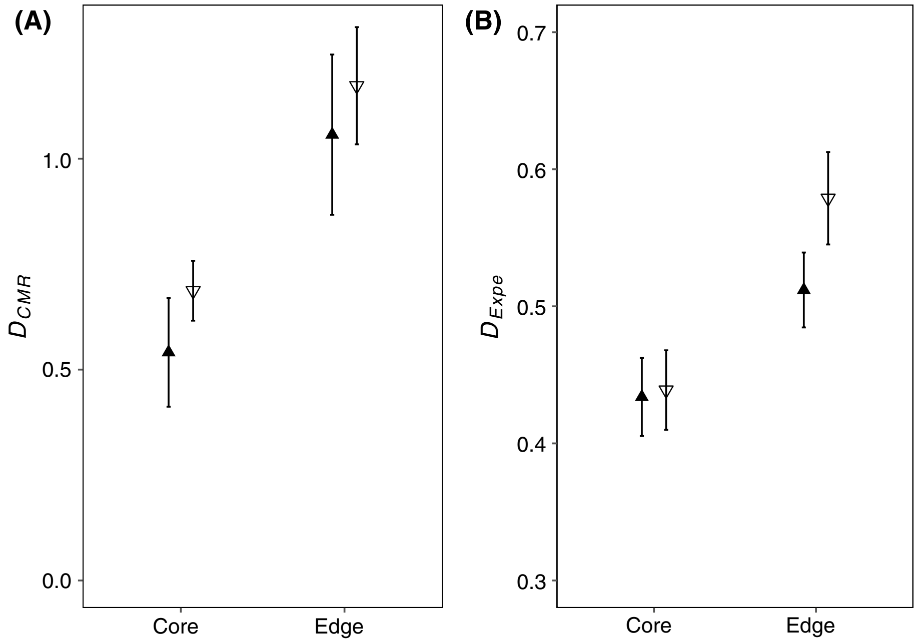

Fig. 3 Estimates of dispersal distances for males (unfilled triangles) and females (filled triangles) from the range core and the range edge of the invasive populations of *Xenopus laevis* in Western France. For the field survey, distances were corrected by the density of the ponds, and are reported as D_{CMR} (**a**). They were transformed to vary between 0 and 1 and are reported as D_{EXPE} in the experimental design (**b**). Symbols and error bars represent the means and the standard deviations, respectively

R_{EXPE}=73.56% (N=64) for the males of the range core and the range edge, respectively. There was no effect of sex on R_{EXPE}, but some environmental parameters had a significant effect (Table 2).

According to the linear mixed model the variables related to the experimental device (End and Lane), cloud cover (CC), nocturnal rain (NR), sex, snout-vent length (SVL) and sampling were not selected in the backward stepwise selection (Table 2). The cluster effect on D_{EXPE} was, however, significant (Table 2), with a higher D_{EXPE} for individuals from the range edge (Fig. 3a). The mean D_{EXPE} at the range edge was 14.34% higher for males and 8.25% higher for females compared to the range core. Nocturnal wind strength (NWS), moonlight intensity (MI), their interaction, and the interaction of maximal daily temperature (MDT) with nocturnal wind strength (NWS) had significant effects on D_{EXPE} (Table 2).

Discussion

We report consistent variation in the dispersal capacity of individuals captured at the edge and range core of the invasive range of *Xenopus laevis* in Western France using two different approaches, experimental and observational. These results are based on the measurement of one-time movements in an experimental track and movements detected during a multi-year field survey. In the experimental study, we recorded a significant increase in

Table 2 Model output of the linear mixed models run to test the effect of the cluster on the proportion of moving individuals R_{EXPE} and the distance travelled by these individuals D_{EXPE}, taking into account environmental parameters

Fixed effects	*df*	F	*p*	Fixed effects	*df*	F	*p*
R_{EXPE}				D_{EXPE}			
Intercept	1–420	232.512	**< 0.0001**	Intercept	1–269	1235.91	**< 0.0001**
Cluster	1–19	8.671	**0.0083**	Cluster	1–18	16.031	**0.0008**
Relative hind limb length	1–420	0.971	0.3249	Relative hind limb length	1–269	11.964	**0.0006**
Maximal daily temperature (MDT)	1–420	15.686	**0.0001**	Maximal daily temperature (MDT)	1–269	0.0001	0.9942
Moonlight intensity (MI)	1–420	7.712	**0.0057**	Nocturnal wind strength (NWS)	2–269	2.913	0.0561
Nocturnal rain (NR)	2–420	3.523	**0.0304**	Moonlight intensity (MI)	1–269	0.794	0.3738
Cloud cover (CC)	2–420	0.827	0.4381	Month	1–18	3.743	0.0689
Sex	1–420	2.554	0.1107	Nocturnal rain (NR)	2–269	3.055	**0.0487**
MI × CC	2–420	2.451	0.0874				
MDT × NWS	2–269	7.991	**0.0004**				
NWS × MI	2–269	1.951	0.1441				

The morphological and environmental parameters shown in the table were selected among all the parameters using a backward stepwise selection, followed by a check of the effect size of each unselected parameter. For the parameters exhibiting a significant effect on the distance crossed, the associated *p*-value is indicated in bold both dispersal rate and dispersal distance from the core to the range edge. For both sexes, the D_{CMR} for range-edge individuals was almost twice as high as for range-core individuals. The French invasive population of *X. laevis* is located in a relatively small area and the landscape is composed of a mosaic of pastureland and crop fields. The variation of climatic conditions is very limited across the range (Joly et al. 2010). Thus, this population is unlikely to face different environmental constraints across its range which could induce local adaptation. The introduction is also recent (30–40 years), which probably limits the scope for divergent selection to generate different phenotypes. The only remaining source of natural selection would be due to the environmental conditions at the pond level that could differ between clusters. We were, however, cautious in selecting ponds with environmental characteristics that were as similar as possible. Moreover, the individuals occupying the core ponds were also dispersing at a non negligible rate. This supports the idea of a population where gene flow is important in the core areas, with a possible but not confirmed metapopulation organisation, which does not favour local adaptation (Sultan and Spencer 2002). Thus, the changes in dispersal allocation at the range edge reported in this study likely result from spatial sorting, as predicted by theory (Burton et al. 2010; Shine et al. 2011).

Despite these results, we cannot state completely on the absence of local adaptation amongst the drivers of the expansion of the *X. laevis* populations. Thus, the respective role of each evolutionary mechanism should be assessed using common garden experiments coupled with individual-based models such as those performed on the spider mite by Van Petegem et al. (2016). Independent of the capture area, the rates of moving individuals were high enough to suggest that this species does not exhibit strong site fidelity, an extremely variable trait among amphibians (Gamble et al. 2007), and that it may be structured in metapopulations, as many other amphibians species (Smith and Green 2005). Further analyses on the capture–mark–recapture survey may provide useful insights concerning the way that the populations of *X. laevis* are structured. The movement rate reported here appears larger than the values reported in the native area of *X. laevis* (De Villiers and Measey 2017). This difference may partially result from different densities in the hydrographic systems between Western France and the Cape region in South Africa. *Xenopus laevis* is known as principally aquatic, but the fact that our survey ponds were not connected by rivers or streams shows that it is capable of frequent overland movements as observed in the native population in South Africa (De Villiers and Measey 2017). Thus, our results and other empirical data (Measey 2016; De Villiers and Measey 2017) highlight the importance of overland movements for this species.

According to the field survey, our data suggest that females move less frequently than males at the range core. Male-biased dispersal rates have been reported for various species, and are mostly associated with sexual dimorphism, mating system, parental care, or territoriality (Trochet et al. 2016). As far as we know, *X. laevis* does not display parental care, as it commonly consumes its own eggs and larvae (Vogt et al. 2017; Courant et al. 2017b; Thorp et al. 2018). Moreover, we also did not record strong changes in sexual dimorphism that could explain the disappearance of the male-biased dispersal rate at the range edge. Male *X. laevis* are known to defend territories from one to five square meters (Ringeis et al. 2017), however. In contrast, enhanced competition for resources with other native species may occur at the range edge (Brown et al. 2013) and lead to an increased proportion of dispersing individuals of both sexes at the range edge. Competition for resources is indeed known to influence resource allocation to dispersal, especially in expanding populations (Burton et al. 2010). Alternatively, spatial sorting may lead to selection for individuals that are behaviourally more inclined to move, as recorded for the invasive cane toad in Australia

(Gruber et al. 2017a, b). Future empirical studies investigating the changes in competitive ability and studies into the behavioural tendency to move at the range edge are needed.

Conclusions

Our results suggest that the increased dispersal at the range edge of expanding populations can occur at a small spatial scale in recently founded populations, thus underscoring the role of spatial sorting in the expansion dynamics. Taking into account the role of this evolutionary process in species distribution models and conservation plans for biological invaders or endangered species experiencing range shifts becomes crucial as a number of empirical studies confirm the occurrence of this process at various spatial scales and even after a few generations. Hence, the colonization of *X. laevis* in Europe, likely enhanced by climate change (Ihlow et al. 2016), may be further accelerated by the increased dispersal in peripheral populations. Spatial sorting is expected to affect the trade-offs involving dispersal, with reproduction or survival, eventually imposing an upper limit to the colonization capacity of a population. By focusing on cases where local adaptation is unlikely to drive phenotypic divergence, we may gain insights into the evolutionary processes occurring during range expansion.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

References

Brown GP, Kelehear C, Shine R (2013) The early toad gets the worm: cane toads at an invasion front benefit from higher prey availability. J Anim Ecol 82:854–862. https://doi.org/10.1111/1365-2656.12048

Burton OJ, Phillips BL, Travis JMJ (2010) Trade-offs and the evolution of life-histories during range expansion. Ecol Lett 13:1210–1220. https://doi.org/10.1111/j.1461-0248.2010.01505.x

Channell R, Lomolino MV (2000) Dynamic biogeography and conservation of endangered species. Nature 403:84–86. https://doi.org/10.1038/47487

Chuang A, Peterson CR (2016) Expanding population edges: theories, traits, and trade-offs. Glob Change Biol 22:494–512. https://doi.org/10.1111/gcb.13107

Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. Science (80–) 342:364–366. https://doi.org/10.1126/science.1242121

Courant J, Secondi J, Bereiziat V, Herrel A (2017a) Resources allocated to reproduction decrease at the range edge of an expanding population of an invasive anuran. Biol J Linn Soc 122:157–165. https://doi.org/10.1093/biolinnean/blx048

Courant J, Vogt S, Marques R et al (2017b) Are invasive populations characterized by a broader diet than native populations? PeerJ 5:e3250. https://doi.org/10.7717/peerj.3250

De Villiers FA, Measey J (2017) Overland movement in African clawed frogs (*Xenopus laevis*): empirical dispersal data from within their native range. PeerJ 5:e4039. https://doi.org/10.7717/peerj.4039

Fouquet A (2001) Des clandestins aquatiques. Zamenis 6:10–11

Gamble LR, McGarigal K, Compton BW (2007) Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: implications for spatio-temporal population dynamics and conservation. Biol Conserv 139:247–257. https://doi.org/10.1016/j.biocon.2007.07.001

Gruber J, Brown G, Whiting MJ, Shine R (2017a) Geographic divergence in dispersal-related behaviour in cane toads from range-front versus range-core populations in Australia. Behav Ecol Sociobiol 71:38. https://doi.org/10.1007/s00265-017-2266-8

Gruber J, Brown G, Whiting MJ, Shine R (2017b) Is the behavioural divergence between range-core and range-edge populations of cane toads (*Rhinella marina*) due to evolutionary change or developmental plasticity? R Soc Open Sci. https://doi.org/10.1098/rsos.170789

Guillon JM, Bottein J (2011) A spatially explicit model of sex ratio evolution in response to sex-biased dispersal. Theor Popul Biol 80:141–149. https://doi.org/10.1016/j.tpb.2011.04.003

Hegyi G, Laczi M (2015) Using full models, stepwise regression and model selection in ecological data sets: Monte Carlo simulations. Ann Zool Fennici 52:257–279. https://doi.org/10.5735/086.052.0502

Ihlow F, Courant J, Secondi J et al (2016) Impacts of climate change on the global invasion potential of the African clawed frog *Xenopus laevis*. PLoS ONE 11:e0154869. https://doi.org/10.1371/journal.pone.0154869

Joly D, Brossard T, Cardot H et al (2010) Les types de climats en France, une construction spatiale. Cybergeo Eur J Geogr. https://doi.org/10.4000/cybergeo.23155

Lindström T, Brown GP, Sisson SS et al (2013) Rapid shifts in dispersal behavior on an expanding range edge. Proc Natl Acad Sci USA 110:13452–13456. https://doi.org/10.1073/pnas.1303157110

Louppe V, Courant J, Herrel A (2017) Differences in mobility at the range edge of an expanding invasive population of *Xenopus laevis* in the West of France? J Exp Biol 220:278–283

Measey GJ (2016) Overland movement in African clawed frogs (*Xenopus laevis*): a systematic review. PeerJ 4:e2474. https://doi.org/10.7717/peerj.2474

Measey GJ, Rödder D, Green SL et al (2012) Ongoing invasions of the African clawed frog, *Xenopus laevis*: a global review. Biol Invasions 14:2255–2270. https://doi.org/10.1007/s10530-012-0227-8

Measey GJ, Vimercati G, de Villiers FA et al (2016) A global assessment of alien amphibian impacts in a formal framework. Divers Distrib. https://doi.org/10.1017/CBO9781107415324.004

Nowinszky L, Szabó S, Toth G et al (1979) The effect of the moon phases and of the intensity of polarized moonlight on the light-trap catches. Z Angew Entomol 88:337–353. https://doi.org/10.1111/j.1439-0418.1979.tb02512.x

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. https://doi.org/10.1038/nature01286

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2013) nlme: linear and nonlinear mixed effects models. R package version 3.1-139. Available at: https://CRAN.Rproject.org/package=nlme

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2019) R: a language and environment for statistical computing. R Foundation Statistical Computing, Vienna. ISBN 3-900051-07-0

Ringeis A, Krumscheid B, Bishop PJ et al (2017) Acoustic communication and reproductive behaviour in the aquatic frog *Xenopus laevis* (Pipidae), a field study. Afr J Herpetol 66:122–146. https://doi.org/10.1080/21564574.2017.1381649

Shine R, Brown GP, Phillips BL (2011) An evolutionary process that assembles phenotypes through space rather than through time. Proc Natl Acad Sci USA 108:5708–5711. https://doi.org/10.1073/pnas.1018989108

Smith AM, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography (Cop) 28:110–128. https://doi.org/10.1111/j.0906-7590.2005.04042.x

Stuart KC, Shine R, Brown GP (2019) Proximate mechanisms underlying the rapid modification of phenotypic traits in cane toads (*Rhinella marina*) across their invasive range within Australia. Biol J Linn Soc 126:68–79

Sultan SE, Spencer HG (2002) Metapopulation struture favors plasticity over local adaptation. Am Nat 160:271–283

Thorp CJ, Vonesh JR, Measey J (2018) Cannibalism or congeneric predation ? The African clawed frog, *Xenopus laevis* (Daudin), preferentially predates on larvae of Cape platannas, *Xenopus gilli* Rose & Hewitt. Afr J Ecol. https://doi.org/10.1111/aje.12577

Trochet A, Courtois EA, Stevens VM et al (2016) Evolution of sex-biased dispersal. Q Rev Biol 91:297–320. https://doi.org/10.1086/688097

Van Petegem KHP, Boeye J, Stoks R, Bonte D (2016) Spatial selection and local adaptation jointly shape life-history evolution during range expansion. Am Nat 188:485–498. https://doi.org/10.1086/688666

Van Petegem K, Moerman F, Dahirel M et al (2017) Kin competition accelerates experimental range expansion in an arthropod herbivore. Ecol Lett 21:225–234. https://doi.org/10.1111/ele.12887

Vogt S, De Villiers FA, Ihlow F et al (2017) Competition and feeding ecology in two sympatric *Xenopus* species (Anura:Pipidae). PeerJ 5:e3130. https://doi.org/10.7717/peerj.3130

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182–1189. https://doi.org/10.1111/j.1365-2656.2006.01141.x

Wickham H (2009) ggplot2: Elegant graphics for data analysis. Springer, Berlin

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