Title: Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population

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Running title: Habitat drives clownfish local success

Abstract

Lifetime reproductive success (LRS), the number of offspring an individual contributes to the next generation, is of fundamental importance in ecology and evolutionary biology. LRS may be influenced by environmental, maternal and additive genetic factors, and the relative contributions of each are critical in determining whether species can adapt to rapid environmental change. However, studies quantifying LRS across multiple generations in wild populations are extremely rare, and to date, non-existent for marine species. Here we use pedigrees of up to 5 generations resolved from a 10-year data-set for a wild orange clownfish population from Kimbe Island (PNG) to assess the contribution of every breeder to the local population. We quantified the additive genetic, maternal and environmental contributions to variation in LRS for the self-recruiting portion of the population using a genetic linear mixed model approach. We found that the habitat of the breeder, including the anemone species and geographic location, made the greatest contribution to LRS, explaining ~97% of the variation. There were low to negligible contributions of genetic (1.3%) and maternal factors (1.9%) equating with low heritability and evolvability. Our findings imply our population will be extremely susceptible to short-term, small-scale changes in habitat structure and may have limited capacity to adapt to these changes.

Keywords: multi-generational pedigree, additive genetic variation, maternal effects, environmental effects, adaptation, selection, heritability, evolvability.

INTRODUCTION

Darwinian fitness or lifetime reproductive success (LRS) – the number of successful offspring an individual contributes to the next generation – is a critical variable underpinning ecological and evolutionary responses to the environment (Clutton-Brock 1988; Roff 2002; Clutton-Brock & Sheldon 2010; Hendry *et al.* 2018). LRS may be influenced by several factors including phenotypic responses to different environmental parameters, parental effects, and additive genetic variance (Kruuk *et al.* 2000; McCleery *et al.* 2004; McFarlane *et al.* 2014). Apportioning these contributions is critical to understanding the potential for short-term ecological effects and longer-term evolvability in response to rapid environmental change. If LRS is exclusively a phenotypic response to the conditions experienced by individuals, populations will be severely impacted by rapid environmental change and there is no prospect of adaptive microevolution. Maternal responses to environmental conditions may reduce the effect of those changes on the next generation through acclimation (Bernardo 1996; Mousseau & Fox 1998; Danchin *et al.* 2011; Donelson *et al.* 2017). However, it is the additive genetic variation in LRS that determines the rate of adaptation of a population to the environmental demand (Fisher 1930; Frank 1997; Lessard 1997; Crow 2002). To date, few studies have distinguished the relative importance of environmental and genetic contributions to LRS over multiple generations in wild populations, where genetic contributions to fitness may be complex (Kruuk & Hadfield 2007). This situation is changing as long-term, individual-based ecological studies in which multi-generational pedigrees have been established provide the necessary longitudinal information to quantify the different components of LRS (Pemberton 2008; Clutton-Brock & Sheldon 2010; Wolak *et al.* 2018; Cava *et al.* 2019). Such studies are imperative as we seek to understand the ability of species to withstand or adapt to accelerating climate change (Charmantier *et al.* 2008; Munday *et al.* 2017).

Intergenerational responses to selection are a product of the interplay between genetic and environmental mechanisms that ultimately shape the genetic variation in fitness-related traits.

Environmentally driven mechanisms (*e.g.*, phenotypic plasticity, genetic assimilation) can facilitate (Price *et al.* 2003; Ghalambor *et al.* 2007, Ledón-Rettig *et al.* 2014; Hoffmann & Merilä 1999; Danchin *et al.* 2019) or constrain the microevolutionary response to selection (Kruuk *et al.* 2003; Pujol *et al.* 2018). However, in the absence of genetic variation for LRS, these mechanisms will likely have little effect on a negligible rate of adaptive evolution. In quantifying additive genetic variation, it is important to distinguish between *heritability* and *evolvability* (Wheelwright *et al.* 2014; Cava *et al.* 2019). Narrow sense heritability, the additive genetic variance standardized by the total phenotypic variance, is widely used as a measurement of the population evolutionary potential to respond to selection (Falconer & Mackay 1996; Mousseau & Roff 1987; McCleery *et al.* 2004). It is directly affected both by the additive genetic variation and magnitude of direct environmental effects. Low heritability values can either reflect low additive genetic variance or large environmental, or residual effects (Price & Schluter 1991; Houle 1992; Hansen *et al.* 2011). Evolvability is the mean-standardized additive genetic variance (Houle 1992; Hansen *et al.* 2011). This is the expected proportional change per generation in population mean fitness given a unit strength of selection (Hendry *et al.* 2018). Evolvability is not affected by environmental or maternal effects, which makes it a more appropriate metric in the comparison of evolutionary potential between traits, populations and species. Heritability reveals whether the additive genetic variance for LRS represents a non-trivial proportion of the total variance of LRS in the actual environmental context of a given wild population. Together, evolvability and heritability inform us about how much environmental change a wild population can withstand on the basis of its evolutionary potential.

The few (n = 15) long-term, individual-based studies that have quantified additive genetic variation, heritability and evolvability of LRS in wild populations have all focused on terrestrial species (Postma 2014; Hendry *et al.* 2018; Table S1). These have largely confirmed that LRS have low additive genetic variation and evolvability (~0.08), which nevertheless reflects some evolutionary

potential (Burt 1995; Hendry *et al.* 2018). Until recently, quantifying LRS in marine organisms with a pelagic larval stage has been considered impossible because of the difficulties in following the fate of offspring from one generation to the next. However, there is increasing evidence of some degree of natal philopatry or self-recruitment in local marine populations (Jones *et al.* 1999; Swearer *et al.* 1999; Swearer *et al.* 2002; Jones *et al.* 2009). The application of genetic parentage analysis is making it possible to assign a significant proportion of successful offspring to their parents (Planes *et al.* 2009; Jones 2015; Le Port *et al.* 2017; Mobley *et al.* 2019) and construct multigenerational pedigrees (Salles *et al.* 2016a; Aykanat *et al.* 2014; Reed *et al.* 2019), at least for the offspring that return to their natal population. In quantitative genetic studies of LRS, it is impossible to measure the recruitment of dispersing juveniles at other locations. The regional component of LRS, which would inform us on fitness variation beyond the local scale is impossible to obtain. Measuring the local component of LRS in marine fish is an opportunity as in any other species and estimates the relative contribution of local fish to the population self-recruitment and replenishment.

For coral reef fishes, quantifying environmental and genetic components of LRS and assessing evolvability in wild populations is of great contemporary importance. Between 30 to 50% of the world's coral reefs have been lost and those remaining are considered highly vulnerable (Jackson 2010; De'ath *et al.* 2012; van Hooidonk *et al.* 2016). The rapid loss of suitable habitat is widely acknowledged to be contributing to a decline in reef fish populations and biodiversity (Jones *et al.* 2004; Wilson *et al.* 2006; Paddack *et al.* 2009; Pratchett *et al.* 2018). Laboratory studies have shown that near future environmental conditions predicted under climate change can have a dramatic effect on reef fish reproductive success, and despite some levels of phenotypic plasticity and transgenerational acclimation, the potential for adaptation is uncertain (Donelson *et al.* 2017; Munday *et al.* 2013; Munday *et al.* 2017). To date, environmental, maternal and additive genetic contributions to LRS in wild coral reef fish populations have not been assessed. However, recent

work establishing high levels of natal philopatry in some coral reef fishes (Jones *et al.* 2005, D'Aloia *et al.* 2015; Salles *et al.* 2015; Almany *et al.* 2017) and the success of parentage analysis in detecting family relationships across multiple generations (Salles *et al.* 2016a,b) opens the way for quantifying the local component of LRS for the first time.

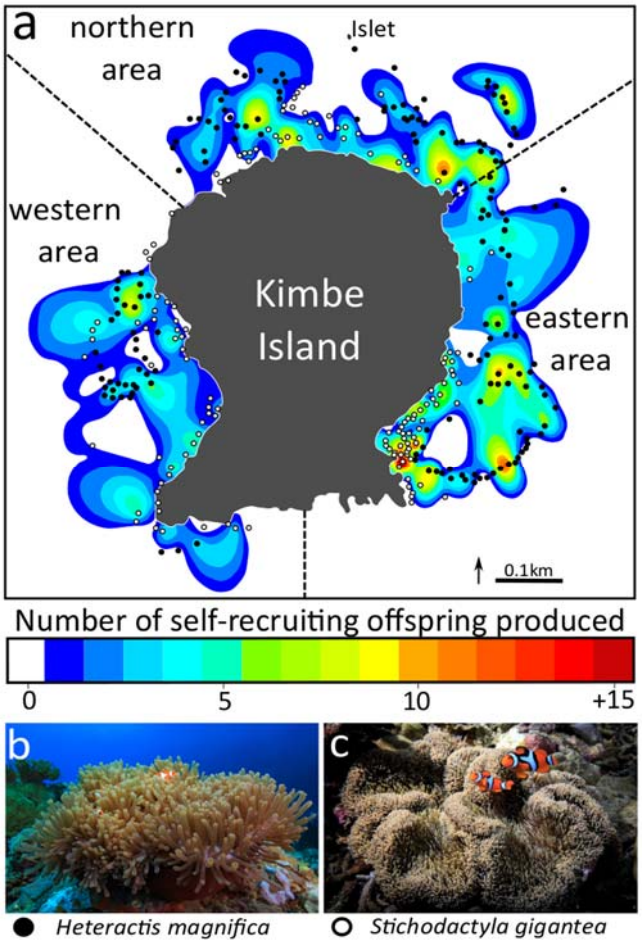
Here, we focus on the entire local population of the orange clownfish *Amphiprion percula* at Kimbe Island, Papua New Guinea where each year ~half the juveniles successfully recruiting are progeny of local breeding pairs (Salles *et al.* 2016a, Almany *et al.* 2017). We use multi-generational pedigrees of up to 5 generations obtained from biennial DNA sampling over 10 years (Salles *et al.* 2016a,b) and apply a quantitative genetic linear mixed model approach (Kruuk & Hill 2008) to quantify the additive genetic, maternal and environmental components of variation in LRS for the self-recruiting portion of the population. Habitat effects were quantified by examining this local LRS for individuals resident in two different anemone species and from different geographic locations around the island (Salles *et al.* 2016a). By integrating habitat data with the pedigree information in a quantitative genetic generalized linear mixed model, we were able to assess the relative contribution of additive genetic, maternal and habitat effects to local LRS. We also calculated the evolvability and heritability of local LRS to evaluate its evolutionary potential to respond to selection at the scale of the Kimbe island population.

METHODS

Study population and data collection

A natural population of orange clownfish (*A. percula*) living in the reef surrounding Kimbe Island (Fig. 1a; 5°12'22.56" S, 150°22'35.58" E), West New Britain Province of Papua New Guinea, was surveyed every second year from 2003 to 2013. Here, *A. percula* lives in a mutualistic association with one of two host sea anemone species, *Heteractis magnifica* (Fig. 1b) and *Stichodactyla gigantea* (Fig. 1c). We geographically located and tagged a total of 310 anemones (176 *H.*

146 *magnifica* and 134 *S. gigantea*) that were occupied by *A. percula* on the entire reef surrounding the
147 island.



148

149 **Figure 1**. **Variation of the total number of offspring orange clownfish produced on each anemone around Kimbe**
150 **Island between 2003 and 2013. (a)** The studied region was divided in three areas (northern, eastern and western areas).
151 Colors correspond to the variation of the total number of juveniles locally self-recruited that were produced on each
152 anemone (varying from 0 to 27) over a 10-year period. The expected value is interpolated from those around it (using
153 default algorithms implemented in *Origin* software). Dots correspond respectively to the location of the two host
154 anemones species: **(b)** *Heteractis magnifica* (black dots) and **(c)** *Stichodactyla gigantea* (white dots). Photos by Tane
155 Sinclair-Taylor.

156 These two anemone species are remarkably different in terms of the micro-habitat they provide,
157 including a wide range of shapes, sizes, depth distributions and surrounding substrata (Dunn 1981;
158 Chausson *et al.* 2018). Although we did not directly measure these variables (other than depth), the
159 combination of host anemone species (*H. magnifica* or *S. gigantea*) with one of the three
160 geographical areas covering the entire reef around the island (northern, western or eastern areas,

Figure 1a) where it is located describes a 'habitat' variable for each fish that encompasses a suite of biotic and abiotic environmental conditions. These geographical areas correspond to the different coasts of the island that reflect possible environmental effects of the geographic location (Salles *et al.* 2016b). In total, the combination of the two host anemone species with the three geographical areas allowed us to describe six different habitats.

Clownfish within one anemone live in group of typically three to five individuals in the Kimbe Island population (Salles *et al.* 2015). The size-based dominance hierarchy in *Amphiprion* allows us to determine the reproductive status of each individual (Fricke 1979). The female is the largest, the male is the second largest, and the non-breeders rank progressively lower in the hierarchy as they decrease in size. If the single female adult of a group dies, then the male changes sex to female, and the largest non-breeder from the anemone becomes sexually mature as male. Reproduction occurs year round, with females laying several hundred eggs in a clutch near the pedal disk of the host anemone each lunar month. The eggs hatch after ~7 days of paternal care into larvae that spend ~10 days in the pelagic environment (Berumen *et al.* 2010) before settling settling to an anemone, either at their natal location (Kimbe Island) or elsewhere (Planes *et al.* 2009).

Fish were captured by divers by using hand nets. Individuals were measured *in situ* using calipers, fin-clipped (size > 35mm) or collected whole (size < 35mm) for genetic analysis and then released back on the same anemone. Small pieces of fin tissue were preserved in 95% ethanol in 2-mL vials. The biggest fish in each anemone was identified as the female, the second largest individual was assumed to be the male, and all other individuals were classified as non-breeders. We extracted DNA from all samples at 22 polymorphic microsatellite loci (Bonin *et al.* 2015). Then, we identified the individuals sampled multiple times over the years by using the Excel macro GenAlex v6.5 (Peakall & Smouse 2012) to compare multilocus genotypes from 2003, 2005, 2007, 2009, 2011 and 2013. Individuals were in average sampled 2.88 ± 0.04 times (mean ± SE) over the six

surveys (1% of individuals persisted over the 10-yr period, Salles *et al.* 2016a). The 2-yr sampling scheme precluded calculating a precise measurement of the age of individuals (Salles *et al.* 2016b), in particular for fish sampled in 2003 during the first sampling period, which age was unknown. The total duration of this long term survey did not allow us to obtain many replicated measurements within individuals before and after sex change (n = 41 individuals). Estimating sex dependent additive genetic variance is precluded in this case because some effects cannot be disentangled as the clownfish only changes sex in one direction (from male to female). This change is always associated with a change of sexual partner and with an increase in female body size, which we expect to generate a confounding effect between a female condition and its genetic quality. We therefore did not consider sex in our model as a result of data and analytical limitations.

Pedigree used for quantitative genetic analysis

Pedigree reconstruction was conducted by assigning juvenile fish to parental pairs on the basis of their multilocus genotypes (Salles *et al.* 2016a). We used the software FaMoz (Gerber *et al.* 2003). This approach is based on the calculation of LOD scores (Log of the odd-ratio comparison) for any potential parentage relationship. It determined critical thresholds to accept or reject assignments by simulating true and false parent-offspring pairs. Further details on parentage analyses and pedigree reconstruction are given in Salles *et al.* (2016a). We kept assignments to known parental pairs, but rejected assignments to single adults. In the context of overlapping generations, we used the year of first sampling and the anemone of each parental couple as information to avoid possible false assignments. As a result, sibship links could not be confused with parental links. Because the sex changes through the life of the clownfish, the same individual can be related to its offspring with either a paternal or maternal link. Based on the size of the two parents and the year of first capture, we can identify the mother and the father. The original population pedigree includes 2927 clownfish over five generations including 121 families, 987 paternal, 987 maternal, 1809 full-sib, 412 maternal half-sibs, 248 paternal half-sib, 135 maternal grandmothers, 135 maternal grandfathers,

278 paternal grandmothers, 278 paternal grandfathers and 218 cousins (Salles *et al.* 2016a). For this study, we excluded from the original pedigree the 1192 individuals that were removed from the habitat at the juvenile stage (size < 35mm, 10 to 458 days old). The final pedigree used for this study includes 1735 individuals from five generations (Fig. S1). We used the R package 'pedantics' (Morrissey & Wilson 2010) to assess the power of the resolved pedigree to detect significant quantitative genetic parameters (Fig. S1).

LRS: the individual contribution to self-recruitment

LRS, which when measured at the scale of the local population is also the contribution of an individual to self-recruitment, corresponds to the total number of offspring produced during its lifetime and recruiting into Kimbe Island (*e.g.*, the local breeder population). To deal with the fact that some fish were still alive at the end of sampling and that some fish might have already reproduced before the first sampling year, we used biennial measurements of their reproductive success (using field-data from 2003, 2005, 2007, 2009, 2011 and 2013) to compare LRS between individuals. The LRS corresponds here to the total number of descendants produced on a biennial basis that successfully recruited into Kimbe Island population, which provided us with repeated measures over the period of the survey from 2003 to 2013. In the Supplementary information we present results from an alternative approach based on the De-lifing method (DL). The calculation of DL takes into account the temporal variation of the population growth and estimates the contribution of every clownfish to biennial changes in population size through both reproduction and survival (Coulson *et al.* 2016). Statistical problems potentially leading to precision issues and invalid conclusions have been associated with the use of DL (Dupont *et al.* 2017) but DL has only been used in two of the 15 studies where the genetic variation of fitness was quantified in wild populations (Table S1), which limits our ability to discuss its properties. We therefore also provided DL results in this study in the supplementary section.

Quantitative genetic generalized linear mixed model approach

Similarities between relatives living in contrasted micro-habitats allowed us to evaluate simultaneously the genetic and habitat components of LRS. Repeated 'records' on individuals made it possible to estimate permanent environmental effects, which allowed us to account for intra-individual and unmeasured environmental trait variation across time. Permanent environmental effects also account for a part of non-additive genetic effects (Wilson *et al.* 2010). The LRS variance was partitioned into six random effects: Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environment (V_{PE}) and Residual (V_R) variances by using the 'animal model' quantitative genetic approach (Kruuk 2004). This Linear Mixed Model (LMM) approach uses pedigree information to extract the additive genetic component. This approach is more powerful than traditional analyses (*e.g.*, parent–offspring regressions) because it takes into account every relationship link in a pedigree. Maternal variance was modeled using the mother's identity as a random effect, allowing maternal effects to include both genetic and environmental maternal effects. Permanent environmental effects were modeled by including the identity of individuals as a random effect. The LRS variance is the sum of six variance components:

$$V_{LRS} = V_A + V_M + V_{NH} + V_{RH} + V_{PE} + V_R \qquad (1)$$

Quantitative genetic models were computed as univariate GLMMs using the 'MCMCglmm' package (Hadfield 2010) in R version 3.5.1 (R.Core.Team 2018), with LRS as a Poisson response variable. Using this Bayesian framework facilitated parameter estimation for non-Gaussian traits. We used parameter expanded priors for all analyses (V=1, nu=0.02), which are often referred to as 'non informative' priors although such denomination can be debated, as we wanted posterior estimates to be determined from the data and not from the priors (Morrissey *et al.* 2014). We ran model MCMC chains over 1,000,000 iterations with initial burning of 10,000 iterations and a thinning of 1,000 iterations. Historically, the Deviance Information Criterion (DIC) was often used to compare models and assess the significance of the random variance components in this type of approach. However, it is becoming less commonly used since it was recognized as an inappropriate

tool for model comparisons of the same type than quantitative genetic GLMM analyses (Gelman *et al.* 2014; Spiegelhalter *et al.* 2014). Effects of variance components were considered statistically supported if their posterior distributions did not overlap zero (Wilson *et al.* 2010).

Variance Components

Variance components were estimated as the mode of the posterior distributions established on the MCMC sample and we reported the lower and the upper limits of the 95% credible interval. For the six variance components, we calculated their relative contribution to the sum of all variance components, thereby expressing their effects as percentages of the total phenotypic variance (V_{LRS}). As a result, we obtained standard narrow sense heritability estimates for LRS (h^2) by applying the basic formula ($h^2 = V_A / V_P$, see Falconer & McKay 1996), and similarly maternal effects by estimating the proportion of total phenotypic variance explained by the maternal variance ($m^2 = V_M / V_P$). Evolvability (I_A) of LRS, equal to the additive genetic variance divided by the squared mean of the LRS (Wagner & Altenberg 1996), was estimated to evaluate the capacity for adaptive evolutionary change of the number of offspring that self-recruit in the population. The analyses conducted in the 'MCMCglmm' framework assumed a Poisson distribution and therefore provided parameter estimates for evolutionary inference or future comparisons on a statistically convenient latent scale for non-Gaussian traits. We therefore endeavored to back-transform all the estimates of the latent scale variables included in the model (see equation 1) onto the observed data scale to improve our inferences. We used the 'QGlmm' package (de Villemereuil *et al.* 2016) to back-transform the estimates, specifically the function 'QGparams' to estimate additive components such as V_A and h^2, and 'QGicc' to estimate broader sense components such as V_M and m^2, V_{NH}, V_{RH}, V_{PE} and V_R. Although parameter estimates transformed back on the data-scale are expected to be upward biased, their ratio is reliable, and hence the estimators derived from their relative proportions such as h^2. It is necessary to point out two specific aspects of the back transformation on the observed data scale. First, V_R is estimated on the basis of the additive over-dispersion term in the nonlinear

model and its value cannot be interpreted similarly to the usual residual variance term estimated by classical quantitative genetics generalized linear mixed models. Second, the sum of the variance components estimated on the data scale are not additive and therefore not expected to sum up to the value of the phenotypic variance calculated directly on the raw data. For the sake of clarity and comparison, we present the results on the latent scale and the observed data scale. We calculated the 95% credibility intervals from the posterior distributions of observed parameters for all the variance components and other estimates expressed on their basis by using the 'HDInterval' package (Meredith & Kruschke 2016).

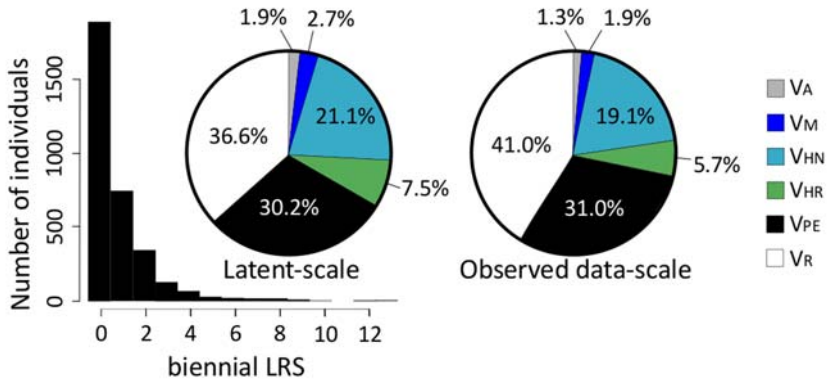
RESULTS

Habitats dominantly shape the Lifetime Reproductive Success in the clownfish population

Biennial estimates of the Lifetime Reproductive Success (LRS) estimated inside the area of the Kimbe island population ranged from 0 to 13, with a phenotypic variance V_{LRS}=1.31 and an average value of 0.54 ± 0.05 (mean ± SE) offspring per individual for a two-year period. Because clownfish live in strong association with their anemone, we were able to identify and geo-locate the precise position and habitat where breeders contributed more to the local replenishment of the population (Fig. 1a). For example, breeders that produced more self-recruiting offspring lived in Kimbe Island's eastern area and mostly in *S. gigantea* anemones. Our analysis also revealed fish that did not contribute at all to the local replenishment of the population over the 10-year monitoring period. These fish were located in 48 *H. magnifica* and 30 *S. gigantea* of the 310 anemones monitored in both deep and shallow waters (Fig. 1a). We found that 25% of the pairs of local breeders did not contribute at all to the renewal of the population over a period of 10 years.

Quantitative genetic linear mixed models on the latent and the observed data scale gave very close results. Our results on the scale of observed data showed that Natal Habitat and Resident Habitat explained respectively 19.1% and 5.7% of the variance in local LRS, furthermore, residual and

317 permanent environment explained respectively 41.0% and 31.0%, whereas additive genetic effects
318 and maternal effects were very weak and explained 1.3% and 1.9% respectively (Fig. 2a, variances
319 on observed data-scale). Similar results were obtained for DL (see Supplementary Information for
320 more details).



321

322 **Figure 2. Sources of variation in the biennial estimate of the local Lifetime Reproductive Success (LRS) of the**
323 **Kimbe Island orange clownfish.** Distribution of the biennial estimate of the LRS (histograms). Variance components
324 on both latent-scale and observed data-scale (pie charts) for the biennial estimate of the LRS explained by Additive
325 genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environmental (V_{PE}) and
326 Residual (V_R) variances. These proportions were calculated from the values of the posterior modes of a quantitative
327 genetics generalized linear mixed model analysis (for details see Table 1).

328

329 ## Low evolvability and low heritability for LRS

330 The modes of the posterior distributions estimating additive genetic variance, expressed on
331 observed data-scale, were extremely small for the two measures of self-recruitment (Table 1).

332

333 **Table 1. Sources of variation in Lifetime Reproductive Success (LRS) for the Kimbe Island orange clownfish.**
334 Here we reported variance component estimates quantified by using the animal model approach: Additive genetic (V_A),
335 Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environmental (V_{PE}) and Residual (V_R)
336 Variances. We also report size effects as proportions of explained phenotypic variance: narrow-sense heritability (h^2),
337 maternal effects (m^2) and the mean standardized additive genetic variance: evolvability (I_A) for biennial LRS. Measures
338 are expressed on a latent-scale (direct *MCMCglmm* R results) and the observed data-scale (*QGglmm* R back-
339 transformation). 95% credible intervals (CI) are reported for each estimate.

	LRS **Latent scale**	**LRS** **Observed data-scale**
V_A	0.046	0.030
(CI)	(1.381×10^{-3} to 0.146)	(4.94×10^{-4} to 0.060)
V_M	0.067	0.046
(CI)	(2.000×10^{-3} to 0.211)	(8.822×10^{-3} to 0.287)
V_{NH}	0.516	0.450
(CI)	(0.015 to 1.529)	(0.126 to 1.524)
V_{RH}	0.184	0.135
(CI)	(0.264 to 0.473)	(0.038 to 0.457)
V_{PE}	0.737	0.726
(CI)	(0.496 to 0.952)	(0.203 to 2.460)
V_R	0.894	0.963
(CI)	(0.717 to 1.105)	(0.270 to 3.264)
V_{LRS}	2.44	2.35
(CI)	(1.71 to 3.65)	(0.65 to 8.05)
h^2	0.019	0.013
(CI)	(6.827×10^{-4} to 0.057)	(4.951×10^{-5} to 1.227×10^{-2})
m^2	0.027	0.019
(CI)	(9.157×10^{-4} to 0.083)	(2.966×10^{-5} to 2.044×10^{-2})
I_A	0.154	0.103
(CI)	(4.643×10^{-4} to 0.492)	(1.661×10^{-3} to 0.511)

We found V_A=0.030 ($CI_{95\%}$ 4.94×10^{-4} to 0.060). This could be linked to the statistical power of our pedigree (Fig. S1). Our model nevertheless placed fairly restricted bands on the 95% credible intervals (Table 1). Credible intervals did not overlap the zero but were close. The extent to which these very low values of genetic estimates are not null must therefore be considered with caution. LRS evolvability estimated on the observed data-scale, which evaluated the micro-evolutionary change of the number of self-recruiting offspring that can be reached by the population, was equal to 0.103 ($CI_{95\%}$ 1.661×10^{-3} to 0.511). In other words, 0.104 additional juveniles were added to the

348 average number of juveniles originating and recruiting in the population per generation. The
349 heritability estimate expressed on the observed data-scale was h^2=0.013 ($CI_{95\%}$ 4.951×10^{-5} to
350 1.227×10^{-2}) for LRS (Table 1). We can therefore estimate the maximum response (R) to selection
351 (S), in the presence of strong selection pressures acting on the Kimbe Island orange clownfish
352 population by using the Breeder's equation $R=h^2\times S$ (Falconer & Mackay 1996; Lush 2008). The
353 low to negligible value of the LRS heritability means that the maximum genetic change of the
354 population average LRS would never exceed ~0.020 offspring per generation. Similar results were
355 obtained for DL (see Supplementary Information for more details).
356
357 **Low maternal effects for LRS**
358 We found that maternal variance for the LRS was extremely small, to the extent that it might be
359 considered as null (Table 1): V_M=0.019 ($CI_{95\%}$ 2.966×10^{-5} to 2.044×10^{-2}). While our analysis
360 detected maternal variance, it made very little contribution to the total variance in LRS (m^2=1.9%,
361 expressed on observed data-scale, Fig. 2). The habitat occupied by the mother (Natal Habitat) had a
362 stronger effect on LRS than the mother herself. The relative contribution of individuals to the
363 population replenishment was indeed influenced by the Natal Habitat to an extent of 19.1% for
364 LRS. Similar results were obtained for DL (see Supplementary Information for more details).
365
366 # DISCUSSION
367 *Strong habitat and weak genetic effects on LRS*
368 Our study revealed that LRS in the Kimbe Island orange clownfish population quantified over five
369 generations was largely explained by host anemone species and geographical location (~97%), with
370 only weak maternal (1.9%) and additive genetic effects (1.3%). The strong effects of habitat can be
371 attributed to the intrinsic biological characteristics of the anemone species (*e.g.*, size, shape and
372 toxicity) and their effects of on life-history traits of their resident clownfish (Salles *et al.* 2016b;
373 Chausson *et al.* 2018). In addition, the higher toxicity of *S. gigantea* (Nedosyko *et al.* 2014) might

provide better protection against predators of eggs attached near the pedal disk of the host anemone, but this hypothesis remains to be tested. The geographical location of the different host-anemones also appears to be important, with more successful individuals in shallow water, close to the land on *S. gigantea* and in deeper lagoons for *H. magnifica*, which might promote greater local retention of larvae. To date, the mechanisms responsible for geographical differences in LRS around Kimbe Island remain unknown (Berumen *et al.* 2010). It is likely that some breeders have a different reproductive success beyond the sampled population, through dispersers rather than self-recruiters. The weak genetic effects on LRS that shows a very low to negligible rate of adaptation inside the Kimbe island population raise concern about the ability of this reef fish population to exhibit longer-term adaptive evolution in response to rapid climate change.

Susceptibility to habitat change

Habitat is clearly the main driver of the variation in LRS and individuals that happen to settle on particular anemones and particular places do well. The dependence of LRS on habitat quality inside the Kimbe island population suggests this species will be extremely susceptible to habitat degradation over ecological time scales. Direct and indirect human impacts on clownfish populations and their anemone habitats are already affecting the habitat quality for numerous clownfish species (Jones *et al.* 2008; Saenz-Agudelo *et al.* 2011; Bonin *et al.* 2016). *S. gigantea* anemones located in shallow waters are likely to be disproportionately more impacted by increasing water temperatures and irradiance (Bak *et al.* 2005; Hobbs *et al.* 2013). If these locations are differentially impacted, this will affect the individual contribution to the local replenishment of the population and compromise population persistence.

Low to negligible evolutionary potential

Our findings provide the first empirical support for a wild marine population to Fisher's fundamental theorem of selection that additive genetic variance in fitness is depleted under

400 selection and tends towards zero in a population reaching evolutionary equilibrium (Fisher 1930;
401 Gustafsson 1986; Falconer 1989). Although normal and expected, low heritability and evolvability
402 in LRS is concerning giving the increasing rate of environmental change. The low to negligible
403 scope for adaptive evolution (estimated by evolvability) and the low to negligible genetic potential
404 for responding to selection (estimated by heritability) may not be a problem for gradual
405 environmental change. At this rate, it would take around at least 10 generations for the population
406 average LRS to increase by one juvenile, which highlights the stability of the demographic rate of
407 self-recruitment in this population. Our results therefore support the hypothesis that the population
408 is at evolutionary equilibrium (no genetic changes) in a context of environmental stability over the
409 timescale of the survey.
410
411 *Connectivity as a plausible cause*
412 Our finding that the Kimbe Island clownfish population harbored low to negligible additive genetic
413 variation for LRS over a ten-year period was at first surprising because immigration accounts for on
414 average 44% of the juvenile recruitment (Salles *et al.* 2015; 2016a). The average dispersal distance
415 in Kimbe Bay is between 10 and 20km, providing substantial connectivity among adjacent reefs and
416 potential dispersal of up to 100km (Almany *et al.* 2017; Pinsky *et al.* 2017). The associated gene
417 flow would be expected to bring new genetic variants and thereby increase genetic variation for
418 LRS (Keller *et al.* 2001; Lavergne & Molofsky 2007; Facon *et al*. 2008). Under such scenario,
419 selection for self-recruitment, and thereby against migrants, would have to be strong to keep the
420 population at evolutionary equilibrium. An alternative scenario is that homogenization by gene flow
421 results in most immigrants sharing a similar genetic background. As a result, low genetic variation
422 would be maintained because no new genetic variants were brought in the population by gene flow
423 (Pujol *et al.* 2010). Low genetic variation for LRS implies that evolution by selection at the local
424 scale is extremely limited in its current state. However, this does not imply a dead end for the

adaptive evolution of this population because several mechanisms can provide adaptive evolutionary potential over the long term (Pujol *et al.* 2018).

Slight but probably negligible maternal genetic effect

Additional adaptive evolutionary potential can in theory be provided to a population by maternal effects (Räsänen & Kruuk 2007). In the Kimbe Island orange clownfish, we found that maternal effects explained up to 2.7% of the LRS variance, which is quite small, even if it was more than additive genetic effects. Our findings thereby revealed that maternal effects increased slightly the low to negligible rate of LRS change by adaptive evolution. One should note that this increase was nearly negligible. It is likely that this low value represents the genetic component of the maternal effect because the identity of each mother was taken into account. The habitat of birth, on the other hand, which is also the maternal habitat, might encompass some direct effect of the maternal environment (Germain & Gilbert 2014). The environmental component can represent a non-negligible part of parental effects (Chirgwin *et al.* 2017). In fact, there is growing awareness that maternal environmental effects can contribute to adaptation in natural populations, especially when maternal and offspring environments are positively correlated (Burgess & Marshall 2014; Shama 2015; Dey *et al.* 2016). It might even buy some time for adaptive evolution through slow genetic change to occur (Levis & Pfenning 2016).

Towards a wider sample of contemporary rates of adaptive evolution in the wild

In our study, LRS estimates the individual fish contribution to the local population replenishment. This excludes the dispersal fitness because the amount of offspring produced and which dispersed to live somewhere else is unknown on wild population pedigrees (Kruuk *et al.* 2000; Merilä & Sheldon 2000, McCleery *et al.* 2004). Its genetic variation evaluates the rate of adaptive evolution inside the Kimbe island population. While there are no comparable data from marine systems, 15 studies conducted on terrestrial vertebrates have also estimated the additive genetic variation and

451 the heritability of LRS (Table S1). It is noteworthy that the number of estimates of maternal effects
452 on LRS variation are extremely rare (Kruuk *et al.* 2000, Foerster *et al.* 2007; Schroeder *et al.* 2012;
453 McFarlane *et al.* 2014). A majority of these studies similarly found low to negligible contributions
454 of additive genetic effects, while the situation is less clear for maternal effects, partly because
455 studies remain scarce. The existence of additive and maternal genetic variation for fitness, even
456 when very low, implies that the population was not totally at equilibrium because there was a small
457 genetic change in the wild population over the course of the long term survey. It also implies very
458 limited genetic adaptive potential.
459

460 # CONCLUSION

461 The major outcome of this study is that the heterogeneity of the habitat of the Kimbe Island orange
462 clownfish had a profound influence on the individual contribution to the local population
463 replenishment over five generations. This finding implies that habitat ecology is crucial for this
464 clownfish population. In terms of future persistence, expected changes in habitat quality and
465 configuration over relatively short time scales might affect the ability of fish to self-recruit. This
466 ability harbored low to negligible additive genetic and maternal genetic variation. As a
467 consequence, this population potential for rapid evolutionary change of LRS by selection, and
468 therefore its rate of adaptive evolution, can be considered negligible in the current state of the
469 population. This finding, which is in line with other studies on the topic, stresses the importance of
470 environmental mechanisms (*e.g.*, plasticity) that have the potential to enable rapid adaptive
471 responses (Donelson *et al.* 2017; Munday *et al.* 2017). Our findings suggest a further evaluation of
472 maternal environmental effects is needed to better evaluate their role in the resilience of wild
473 populations (Shama 2015; Chirgwin *et al.* 2017). From the perspective of management, our results
474 caution against hoping for local adaptive responses and lend support to focusing conservation
475 efforts on maintaining habitat quality.
476

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AUTHORSHIP

GPJ, SLRT, and SP designed the research program; OCS, BP, GRA, and MLB contributed new reagents/analytic tools; OCS and BP analyzed data; OCS, BP et SP wrote the manuscript and all authors contributed substantially to revise the paper.

DATA ACCESSIBILITY STATEMENT

Data from this study can be obtained by using the CRIOBE data portal (http://www.criobe.pf). R programming protocol can be obtained on the Zenodo repository DOI

CONFLICT OF INTEREST DISCLOSURE

The authors of this preprint declare that they have no financial conflict of interest with the content of this article.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

The Additional Supporting Information file contains:

- **Table S1.** Previous estimates of fitness heritability and maternal effects on fitness in 15 wild populations.
- **Figure S1.** Pedigree data and power analysis for the Kimbe Island orange clownfish population.
- **Supplementary methods, results and discussion** on De-lifing measures.

Supporting Information

Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population

Océane C. Salles, Glenn R. Almany, Michael L. Berumen, Geoffrey P. Jones, Pablo Saenz-Agudelo, Maya Srinivasan, Simon R. Thorrold, Benoit Pujol*, and Serge Planes*

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This file contains:

- **Table S1.** Previous estimates of fitness heritability and maternal effects on fitness in 15 wild populations.
- **Figure S1.** Pedigree data and power analysis for the Kimbe Island orange clownfish population.
- **Supplementary methods, results and discussion** on De-lifing measures.

Table S1. Previous estimates of fitness heritability and maternal effects on fitness in wild populations. Different fitness measures are denoted as lifetime reproductive success (LRS), De-lifing or relative RS (LRS/mean of LRS in the population). ♀ corresponds to female, ♂ corresponds to male and ⚥ corresponds to female and male confounded. NA indicates that maternal effects were not estimated or dropped from the quantitative genetic models.

Study organism	Location	Years of monitoring	Heritability estimate ± SE or 95%SI	Maternal effects estimate	Fitness measure	Reference
Collared flycatcher	Gotland Is.	1980 to 1984	♀ 0.01 ± 0.16 ♂ 0.01 ± 0.13	NA NA	LRS	(Gustafsson 1986)
Red deer	Isle of Rum	1971 to 1999	♀ 0.00 ± 0.05 ♂ 0.02 ± 0.06	0.16 ± 0.041 NA	LRS	(Kruuk *et al.* 2000)
		1971 to 2005	♀ 0.21 ± 0.06 ♂ 0.07 ± 0.06	0.0021 0.0045	De-lifing	(Foerster *et al.* 2007)
Collared flycatcher	Gotland Is.	1980 to 1997	♀ 0.21 ± 0.06 ♂ 0.07 ± 0.06	NA NA	LRS	(Merila & Sheldon 2000)
Bighorn sheep	Ram Mountain Sheep River	1973 to 1998 1981 to 1998	♀ 0.66 ± 0.32 ♀ 0.19 ± (0.50)	NA NA	LRS LRS	(Réale & Festa-Bianchet 2000)
Cheetahs	Serengeti park	1970 to 1994	♀ 0.88 ± ?	NA	LRS	(Kelly 2001)
Great tit	Wytham Wood	1960 to 1998	♀ 0.00 ± 0.04 ♂ 0.02 ± 0.04	NA NA	LRS	(McCleery *et al.* 2004)
Bighorn sheep	Ram Mountain	1971 to 2003	♀ 0.00 ± 0.00 ♂ 0.00 ± 0.00	NA NA	LRS	(Coltman *et al.* 2005)
Red billed gulls	Kaikoura	1958 to 2004	♀ 0.36 ± 0.29 ♂ 0.00 ± 0.00	NA NA	LRS	(Teplitsky *et al.* 2009)
Rhesus macaques	Cayo Is.	1959 to 1990	♀ 0.36 ± 0.081	NA	LRS	(Blomquist 2010)
House sparrow	Lundy Is.	2000 to 2011	⚥ 0.09 (0.03 to 0.18)	0.33 (0.14 to 0.51)	De-lifing	(Schroeder *et al.* 2012)
Soay sheep	St Kilda	1985 to 2002	⚥ 0.03 ± 0.01	NA	Relative RS	(Morrissey *et al.* 2012)
Red squirrels	Yukon	1987 to 2011	⚥ 4.90×10^{-04} (3.0×10^{-08} to 0.07) ♀ 6.80×10^{-04} (8.5×10^{-11} to 0.10) ♂ 4.90×10^{-04} (1.1×10^{-03} to 0.39)	0.07 (0.02 to 0.14) 0.08 (0.01 to 0.14) 0.10 (0.10 to 0.37)	LRS	(McFarlane *et al.* 2014)
Savannah sparrow	Kent Is.	1987 to 2005	♀ 0.002 ± 0.036 ♂ 0.000 ± 0.036	NA NA	LRS LRS	(Wheelwright *et al.* 2014)
Brown anole lizard	Kidd Cay	2005 to 2008	⚥ 1.40 (8.0×10^{-10} to 0.023)	NA	RS	(Calsbeek *et al.* 2015)
Song sparrow	Mandarte Island	1993-2015	♀ 0.5 ± 0.21 ♂ 0.44 ± 0.74	NA NA	LRS	(Wolak *et al.* 2018)

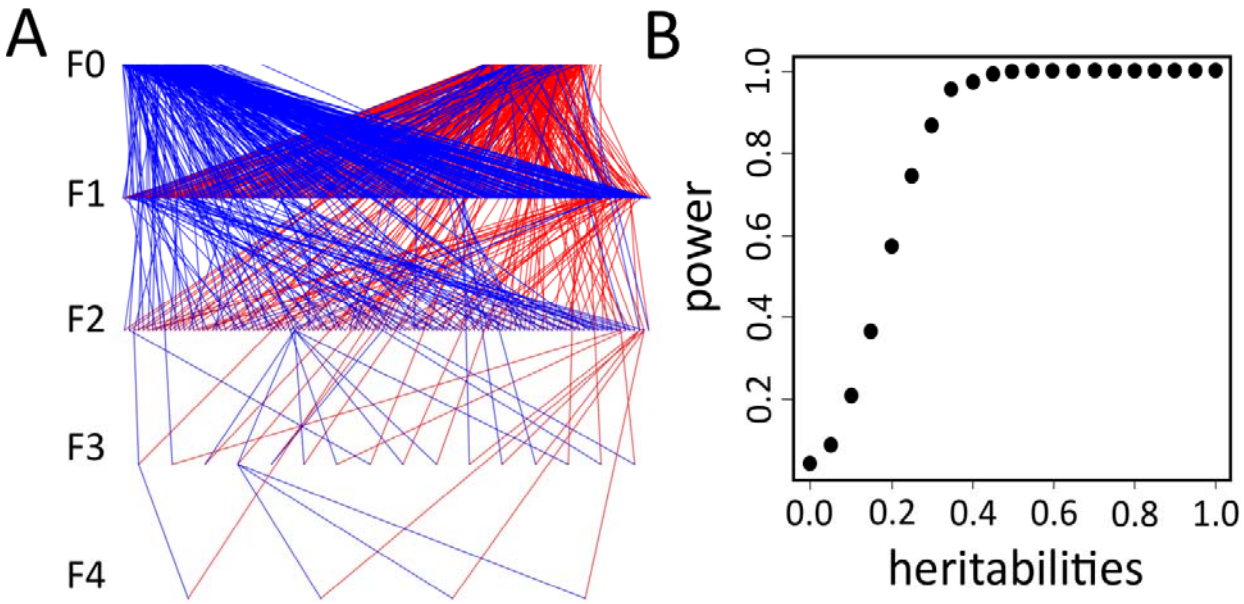

Figure S1. Pedigree data of the Kimbe Island orange clownfish population. **(A)** Pedigree representation of the orange clownfish *Amphiprion percula* in Kimbe Island (n= 1735, excluding new-recruits). Each line connects a parent with one of its offspring (blue and red lines represent respectively paternal and maternal links). It is important to note that an individual can be father then mother. The generation is indicated on the left from first generation (F0, n=502) to fifth generation (F4). **(B)** Power analysis of the pedigree.

SUPPLEMENTARY METHODS

Individual's contribution to biennial population growth rate

We estimated the De-lifing (DL), which is the individual's contribution to the biennial population growth rate. DL was calculated following Coulson *et al.* (2006). This index can be considered as the realized fitness of an individual over the given period of time (here two years) by including survival and success to local recruitment. This index offers great opportunities to empirically study ecological and evolutionary changes in stochastic environments (Dupont *et al.* 2017).

According to Coulson *et al.* (2006), an individual's biennial fitness is measured by its contribution DL_{ti} to the growth rate of the population between t and $t+1$.

$$DL_{ti} = \frac{s_{ti}-\bar{s}_t}{N_t-1} + \frac{F_{ti}-\bar{F}_t}{N_t-1} \qquad (1)$$

where N_t is the population size at time t; s_{ti} is the survival of individual i between t and $t+1$ (1 if it survived and 0 otherwise); $\bar{S}_t$ is the mean survival rate in the population between t and $t+1$; F_{ti} is the fecundity of the individual i defined as the number of offspring born between t and $t+1$ and

still alive at $t + 1$ and $\bar{F}_t$ is the mean individual fecundity in the population. A negative value of DL represents an individual that performed worse than the population mean while a positive value represents one that performed better.

Quantitative genetic generalized linear model approach

As for the IIRS variance, the DL variance was partitioned into six random effects: Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environment (V_{PE}) and Residual (V_R) variances by using the 'animal model' quantitative genetic approach (Kruuk 2004).

The DL variance is the sum of six variance components:

$$V_{DL} = V_{A_{DL}} + V_{M_{DL}} + V_{NH_{DL}} + V_{RH_{DL}} + V_{PE_{DL}} + V_{R_{DL}} \quad (2)$$

We used a quantitative genetics model as univariate GLMMs using the 'MCMCglmm' package (Hadfield 2010) in R version 3.5.1 (R Core Team 2018), with DL as a Gaussian response variable. We used parameter expanded priors for all analyses (V=1, nu=0.02), which are often referred to as 'non informative' priors although such denomination can be debated, as we wanted posterior estimates to be determined from the data and not from the priors (Morrissey *et al.* 2014). We ran model MCMC chains over 1,000,000 iterations with initial burning of 10,000 iterations and a thinning of 1,000 iterations.

Variance components were estimated as the mean of the posterior distributions (the mean of the MCMC sample). and we reported the lower and the upper limits of the 95% credible interval. For the six variance components, we calculated their relative contribution to the sum of all variance components, thereby expressing their effects as percentages of the total phenotypic variance (V_{DL}). As a result, we obtained standard heritability estimates for DL (h^2_{DL}) by applying the basic formula ($h^2 = V_A / V_P$, see Falconer & McKay 1996), and similarly maternal effects by estimating the proportion of total phenotypic variance explained by the maternal variance ($m^2 = V_M / V_P$). Because DL is Gaussian variable, we reported a standard heritability and a standard maternal effects. We calculated the 95% credibility intervals from the posterior distributions of observed parameters for

all the variance components and other estimates expressed on their basis by using the 'HDInterval' package (Meredith & Kruschke 2016).

SUPPLEMENTARY RESULTS

Habitats dominantly shape the De-lifing in the clownfish population.

De-lifing (DL) varied from -2.56 $\times 10^{-3}$ to 1.81 $\times 10^{-2}$ (Figure S2, histogram), which illustrates that there is variation in the individual contribution to the population demographic growth through reproduction and survival. Its average value at the population level was $2.16 \times 10^{-5} \pm 8.04 \times 10^{-5}$ units. When considering DL, 43.1% of its variance was explained by Natal Habitat (Figure S2, pie chart) and 55.3% by Resident Habitat, again with minor contributions from Additive genetic effects (0.3%) and Maternal effects (1.0%).

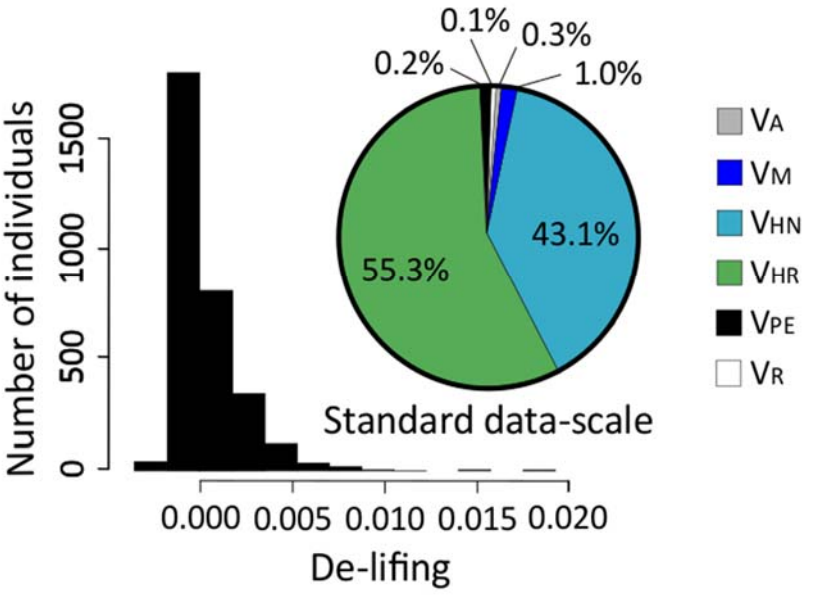

Figure S2. Sources of variation in De-lifing (DL) variance of the the Kimbe Island orange clownfish. Distribution (histograms) and variance components on standard data-scale (pie chart) for biennial DL explained by Additive genetic (V_A), Maternal (V_M), Natal Habitat (V_{NH}), Resident Habitat (V_{RH}), Permanent Environment (V_{PE}) and Residual (V_R) variances. These proportions were calculated from the values of the posterior mode of a quantitative genetics generalized linear mixed model analysis.

We found that Additive genetic variance was extremely low: $V_{A,DL}$=3.151 $\times$ 10^{-5} ($CI_{95\%}$ 2.897×10^{-5} to 3.470×10^{-5}, Table S2). Consequently, heritability estimates expressed on the standard data-scale was h^2_{DL} =0.003 ($CI_{95\%}$ 2.432 $\times$ 10^{-3} to 0.0261, Table S2) for DL. We also found that maternal was

extremely small, to the extent that it might be considered as null: $V_{M,DL}$=1.190×10^{-4} ($CI_{95\%}$ 9.974×10^{-5} to 1.434×10^{-4}, Table S2). While our analysis detected maternal variance, it made very little contribution to the total variance in DL estimate (m^2_{DL}=1.0%, Figure S2). The relative contribution of individuals to the population replenishment was indeed influenced by the Natal Habitat to an extent of 43.1% for DL.

Table S2. Sources of variation in De-lifing (DL) for the Kimbe Island orange clownfish. Here we reported variance component estimates quantified by using the animal model approach: Additive genetic effect (V_A), Maternal effect (V_M), Natal Habitat (V_{NH}) and Resident Habitat (V_{RH}) effects, Permanent Environmental (V_{PE}) effect and Residual Variance (V_R) and heritability (h^2) and maternal effects (m^2) for biennial DL. 95% credible intervals (CI) are reported for each estimate.

Components	DL Standard scale
V_A **(CI)**	3.151×10^{-5} (2.897×10^{-5} to 3.470×10^{-5})
V_M **(CI)**	1.190×10^{-4} (9.974×10^{-5} to 1.434×10^{-4})
V_{NH} **(CI)**	5.022×10^{-3} (9.972×10^{-4} to 0.012)
V_{RH} **(CI)**	6.443×10^{-3} (1.13×10-3 to 0.017)
V_{PE} **(CI)**	3.016×10^{-5} (2.72× 10^{-5} to 3.25×10^{-5})
V_R **(CI)**	2.978×10^{-5} (1.15×10^{-5} to 1.29×10^{-5})
h^2 **(CI)**	0.003 (6.506×10^{-4} to 6.712×10^{-3})
m^2 **(CI)**	0.010 (2.432×10^{-3} to 0.0261)

SUPPLEMENTARY DISCUSSION

Because of the different proprieties of the two measures of individual reproductive success (i.e., IIRS, which is the Intra-population Individual Reproductive Success, and DL), the results obtained on the DL highlights that the residual variance of SLR can be implicitly explained by annual environmental variation. The model decomposing the variance in DL measured a larger effect of the habitat, which is likely due to the fact that DL has different statistical properties. DL accounts for

reproductive success, survival and population size. DL is expected to smooth out changes in demographic population growth and to account for the individuals that did not produce offspring but contributed to the population stability or growth by their own survival. Recruitment and population size vary through time in this population (Salles *et al.* 2015), which might explain why more variance in DL was explained by the model. This difference in outcomes among these two estimators of the individual contribution to the local replenishment of the population supports the hypothesis that a part of the self-recruitment variation explained by the habitat is confounded with temporal heterogeneity in population growth and survival.

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#####   Heritability Local Fitness Data Clownfish Kimbe Island       #####
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####################################
############ PACKAGES ##############

library(tnet)
library(pedantics)
library(ggplot2)
library(wesanderson)
library(scales)
library(RColorBrewer)
library(gplots)
library(shape)
library(proxy)
library(MCMCglmm)

library(nadiv)
library(igraph)
library(lme4)
library(lmerTest)
library(arm)
library(sp)
library(spdep)
library(splm)
library(ape)
library(vegan)
library(ade4)

library(Cairo)
library(geoR)
library(proxy)
library(pedigree)

library(FactoMineR)
library(MasterBayes)
library(QGglmm)
library(HDInterval)

#####################################################
############ PEDIGREE + INVERSE ####################

Ped=as.data.frame(read.table(file="D:/Documents/POSTDOC_TOULOUSE/Publications/T
ransmissionNiche/Data/PED_CLOWNFISH_FINAL_sansNR.txt",header=TRUE,
na.string="NA"))
```

```
Ped$ID=as.factor(Ped$ID)
Ped$FATHER=as.factor(Ped$FATHER)
Ped$MOTHER=as.factor(Ped$MOTHER)

#Orders the pedigree so that parents come before their offspring

library(MasterBayes)
Ped=orderPed(Ped)
#possibility to order the pedigree using fixPedigree if orderPed doesnt work...
Ped=fixPedigree(Ped)
for(x in 1:3) Ped[,x]<-as.factor(Ped[,x])
write.table(Ped,
"D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data/OrderPed.txt
", sep="\t")


#we keep only informative individuals from the pedigree
Ped=prunePed(Ped, Ped$ID)

#Gets the inverse of the relatedness matrix
library(pedantics)
Ainv=inverseA(Ped)$Ainv
drawPedigree(Ped)

#draw the matrix of genetic similarity
library(nadiv)
pedigree=prepPed(Ped)

#save the figure

jpeg(filename="Models/Figs/Pedigreeall.jpg",
     width=900, height=1000,units="px")
drawPedigree(Ped)
dev.off()


#########################################################
############ DATA REPEATED MEASURES ###############

setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data")


Aperc=as.data.frame(read.table(file="D:/Documents/POSTDOC_TOULOUSE/Publications
/TransmissionNiche/Data/DATA_CLOWNFISH_FINAL_sansNR_REPEATED_MEASURES.txt",head
er=TRUE,na.string="NA"))

#gets ID/dam/sire as factors
Aperc$ANIMAL=as.factor(Aperc$ID)
Aperc$MOTHER=as.factor(Aperc$MOTHER)
Aperc$FATHER=as.factor(Aperc$FATHER)

#these need to be repeated for connection to the extra matrices in the models
Aperc$ANIMAL2=as.factor(Aperc$ID)
```

```
Aperc$animal=as.factor(Aperc$ID)
Aperc$MOTHER2=as.factor(Aperc$MOTHER)
Aperc$FATHER2=as.factor(Aperc$FATHER)


#these need to be repeated for connection to the extra matrices in the models
Aperc$ANIMAL2=as.factor(Aperc$ID)
Aperc$MOTHER2=as.factor(Aperc$MOTHER)
Aperc$FATHER2=as.factor(Aperc$FATHER)
Aperc$HABITATVIE=as.factor(Aperc$HABITATVIE)
Aperc$HABITATMOTHER=as.factor(Aperc$HABITATMOTHER)

# gets factor or numeric for each parameters
Aperc$sex=as.factor(Aperc$sex)
Aperc$cohort=as.factor(Aperc$cohort)
Aperc$SuccessReproAR=as.numeric(Aperc$SuccessReproAR)
Aperc$Survival=as.numeric(Aperc$Survival)
Aperc$LRS=as.numeric(Aperc$LRS)
Aperc$occurrence=as.numeric(Aperc$occurrence)
Aperc$HabitatBirth=as.numeric(Aperc$HabitatBirth)
Aperc$HabitatResident=as.numeric(Aperc$HabitatResident)
Aperc$LRSbin=as.numeric(Aperc$LRS)
Aperc$LRSbin[Aperc$LRSbin>0]<-1

Aperc$delifing=as.numeric(Aperc$delifing)

Aperc$DepthAnemone=as.numeric(Aperc$DepthAnemone)
Aperc$CodespAnemone=as.factor(Aperc$CodespAnemone)
Aperc$CodeArea=as.factor(Aperc$CodeArea)
Aperc$PropDeadCorals=as.numeric(Aperc$PropDeadCorals)
Aperc$PropCorals=as.numeric(Aperc$PropCorals)
Aperc$PropSand=as.numeric(Aperc$PropSand)
Aperc$PropRock=as.numeric(Aperc$PropRock)
Aperc$PropAlgae=as.numeric(Aperc$PropAlgae)

Aperc$DepthAnemoneParents=as.numeric(Aperc$DepthAnemoneParents)
Aperc$CodeAreaParents=as.factor(Aperc$CodeAreaParents)
Aperc$CodespAnemoneParents=as.factor(Aperc$CodespAnemoneParents)
Aperc$PropDeadCoralsParents=as.numeric(Aperc$PropDeadCoralsParents)
Aperc$PropCoralsParents=as.numeric(Aperc$PropCoralsParents)
Aperc$PropSandParents=as.numeric(Aperc$PropSandParents)
Aperc$PropRockParents=as.numeric(Aperc$PropRockParents)
Aperc$PropAlgaeParents=as.numeric(Aperc$PropAlgaeParents)


#Visualisation des données + sauvegarde
setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data")
jpeg("Models/Figs/delifingRM.jpg")
hist(Aperc$delifing)
dev.off()

jpeg("Models/Figs/histLRSRM.jpg")
hist(Aperc$LRS)
dev.off()
```

```
jpeg("Models/Figs/LRSbinRM.jpg")
hist(Aperc$LRSbin)
dev.off()


###################################
############ MODELS ###############

#########################"
#### PCI PAPER

library(MCMCglmm)

prior5=list(G=list(G1=list(V=1, nu=0.02),
                   G2=list(V=1, nu=0.02),
                   G3=list(V=1, nu=0.02),
                   G4=list(V=1, nu=0.02),
                   G5=list(V=1, nu=0.02)),
            R=list(V=1, nu=0.02))

MCMCglmm_LRS_pnas5<-MCMCglmm(LRS  ~ 1
                             , random=~ANIMAL + MOTHER + HabitatBirth +
HabitatResident + ID
                             , family="poisson"
                             , data= Aperc
                             , ginverse=list(ANIMAL=Ainv)
                             , prior=prior5
                             , nitt = 1000000
                             , burnin = 1000
                             , thin = 1000)
save(MCMCglmm_LRS_pnas5,
file=paste("Models/","Figs/","MCMCglmm_LRS_pnas5.Rdata",sep=""))

prior4=list(G=list(G1=list(V=1, nu=0.02),
                   G2=list(V=1, nu=0.02),
                   G3=list(V=1, nu=0.02),
                   G4=list(V=1, nu=0.02)),
            R=list(V=1, nu=0.02))

MCMCglmm_LRS_pnas4<-MCMCglmm(LRS  ~ 1
                             , random=~ANIMAL + MOTHER + HabitatBirth + ID
                             , family="poisson"
                             , data= Aperc
                             , ginverse=list(ANIMAL=Ainv)
                             , prior=prior4
                             , nitt = 1000000
                             , burnin = 1000
                             , thin = 1000)
save(MCMCglmm_LRS_pnas4,
file=paste("Models/","Figs/","MCMCglmm_LRS_pnas4.Rdata",sep=""))


MCMCglmm_LRS_pnas4b<-MCMCglmm(LRS  ~ 1
```

```
                              , random=~ANIMAL + MOTHER + HabitatResident +  ID
                              , family="poisson"
                              , data= Aperc
                              , ginverse=list(ANIMAL=Ainv)
                              , prior=prior4
                              , nitt = 1000000
                              , burnin = 1000
                              , thin = 1000)
save(MCMCglmm_LRS_pnas4b,
file=paste("Models/","Figs/","MCMCglmm_LRS_pnas4b.Rdata",sep=""))

MCMCglmm_LRS_pnas4c<-MCMCglmm(LRS  ~ 1
                               , random=~ANIMAL + HabitatBirth + HabitatResident
+  ID
                               , family="poisson"
                               , data= Aperc
                               , ginverse=list(ANIMAL=Ainv)
                               , prior=prior4
                               , nitt = 1000000
                               , burnin = 1000
                               , thin = 1000)
save(MCMCglmm_LRS_pnas4c,
file=paste("Models/","Figs/","MCMCglmm_LRS_pnas4c.Rdata",sep=""))


MCMCglmm_LRS_pnas4d<-MCMCglmm(LRS  ~ 1
                               , random=~MOTHER + HabitatBirth + HabitatResident
+  ID
                               , family="poisson"
                               , data= Aperc
                               , ginverse=list(ANIMAL=Ainv)
                               , prior=prior4
                               , nitt = 1000000
                               , burnin = 1000
                               , thin = 1000)
save(MCMCglmm_LRS_pnas4d,
file=paste("Models/","Figs/","MCMCglmm_LRS_pnas4d.Rdata",sep=""))

###############

MCMCglmm_delifing_pnas5<-MCMCglmm(delifing  ~ 1
                              , random=~ANIMAL + MOTHER + HabitatBirth +
HabitatResident + ID
                              , family="gaussian"
                              , data= Aperc
                              , ginverse=list(ANIMAL=Ainv)
                              , prior=prior5
                              , nitt = 1000000
                              , burnin = 1000
                              , thin = 1000)
save(MCMCglmm_delifing_pnas5,
file=paste("Models/","Figs/","MCMCglmm_delifing_pnas5.Rdata",sep=""))

prior4=list(G=list(G1=list(V=1, nu=0.02),
```

```
                  G2=list(V=1, nu=0.02),
                  G3=list(V=1, nu=0.02),
                  G4=list(V=1, nu=0.02)),
           R=list(V=1, nu=0.02))

MCMCglmm_delifing_pnas4<-MCMCglmm(delifing  ~ 1
                             , random=~ANIMAL + MOTHER + HabitatBirth + ID
                             , family="gaussian"
                             , data= Aperc
                             , ginverse=list(ANIMAL=Ainv)
                             , prior=prior4
                             , nitt = 1000000
                             , burnin = 1000
                             , thin = 1000)
save(MCMCglmm_delifing_pnas4,
file=paste("Models/","Figs/","MCMCglmm_delifing_pnas4.Rdata",sep=""))


MCMCglmm_delifing_pnas4b<-MCMCglmm(delifing  ~ 1
                              , random=~ANIMAL + MOTHER + HabitatResident +  ID
                              , family="gaussian"
                              , data= Aperc
                              , ginverse=list(ANIMAL=Ainv)
                              , prior=prior4
                              , nitt = 1000000
                              , burnin = 1000
                              , thin = 1000)
save(MCMCglmm_delifing_pnas4b,
file=paste("Models/","Figs/","MCMCglmm_delifing_pnas4b.Rdata",sep=""))

MCMCglmm_delifing_pnas4c<-MCMCglmm(delifing  ~ 1
                              , random=~ANIMAL + HabitatBirth + HabitatResident
+  ID
                              , family="gaussian"
                              , data= Aperc
                              , ginverse=list(ANIMAL=Ainv)
                              , prior=prior4
                              , nitt = 1000000
                              , burnin = 1000
                              , thin = 1000)
save(MCMCglmm_delifing_pnas4c,
file=paste("Models/","Figs/","MCMCglmm_delifing_pnas4c.Rdata",sep=""))


MCMCglmm_delifing_pnas4d<-MCMCglmm(delifing  ~ 1
                              , random=~MOTHER + HabitatBirth + HabitatResident
+  ID
                              , family="gaussian"
                              , data= Aperc
                              , ginverse=list(ANIMAL=Ainv)
                              , prior=prior4
                              , nitt = 1000000
                              , burnin = 1000
                              , thin = 1000)
```

```
save(MCMCglmm_delifing_pnas4d,
file=paste("Models/","Figs/","MCMCglmm_delifing_pnas4d.Rdata",sep=""))



setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data/Models
/Figs")

load("MCMCglmm_delifing_pnas5.Rdata")
load("MCMCglmm_delifing_pnas4.Rdata")
load("MCMCglmm_delifing_pnas4.Rdata")
load("MCMCglmm_delifing_pnas4b.Rdata")
load("MCMCglmm_delifing_pnas4c.Rdata")
load("MCMCglmm_delifing_pnas4d.Rdata")


load("MCMCglmm_LRS_pnas5.Rdata")
load("MCMCglmm_LRS_pnas4.Rdata")
load("MCMCglmm_LRS_pnas4.Rdata")
load("MCMCglmm_LRS_pnas4b.Rdata")
load("MCMCglmm_LRS_pnas4c.Rdata")
load("MCMCglmm_LRS_pnas4d.Rdata")

summary(MCMCglmm_delifing_pnas5)
posterior.mode(MCMCglmm_delifing_pnas5$VCV)
HPDinterval(MCMCglmm_delifing_pnas5$VCV)



summary(MCMCglmm_delifing_pnas4)
posterior.mode(MCMCglmm_delifing_pnas4$VCV)
HPDinterval(MCMCglmm_delifing_pnas4$VCV)
VA_delifing4= MCMCglmm_delifing_pnas4$VCV[,"ANIMAL"]
VM_delifing4=MCMCglmm_delifing_pnas4$VCV[,"MOTHER"]
VNH_delifing4=MCMCglmm_delifing_pnas4$VCV[,"HabitatBirth"]
VPE_delifing4=MCMCglmm_delifing_pnas4$VCV[,"ID"]
VR_delifing4=MCMCglmm_delifing_pnas4$VCV[,"units"]

#heritability
H2_delifing4=VA_delifing4/(VA_delifing4 + VM_delifing4 + VNH_delifing4 +
VPE_delifing4 + VR_delifing4)
posterior.mode(H2_delifing4)
HPDinterval(H2_delifing4,0.95)

summary(MCMCglmm_delifing_pnas4)


summary(MCMCglmm_delifing_pnas4b)
posterior.mode(MCMCglmm_delifing_pnas4b$VCV)
HPDinterval(MCMCglmm_delifing_pnas4b$VCV)
VA_delifing4b= MCMCglmm_delifing_pnas4b$VCV[,"ANIMAL"]
VM_delifing4b=MCMCglmm_delifing_pnas4b$VCV[,"MOTHER"]
VNH_delifing4b=MCMCglmm_delifing_pnas4b$VCV[,"HabitatBirth"]
VRH_delifing4b=MCMCglmm_delifing_pnas4b$VCV[,"HabitatResident"]
```

```
VPE_delifing4b=MCMCglmm_delifing_pnas4b$VCV[,"ID"]
VR_delifing4b=MCMCglmm_delifing_pnas4b$VCV[,"units"]

#heritability
H2_delifing4b=VA_delifing4b/(VA_delifing4b + VM_delifing4b + VRH_delifing4b +
VPE_delifing4b + VR_delifing4b)
posterior.mode(H2_delifing4b)
HPDinterval(H2_delifing4b,0.95)



summary(MCMCglmm_delifing_pnas4c)
posterior.mode(MCMCglmm_delifing_pnas4c$VCV)
HPDinterval(MCMCglmm_delifing_pnas4c$VCV)
VA_delifing4c= MCMCglmm_delifing_pnas4c$VCV[,"ANIMAL"]
VM_delifing4c=MCMCglmm_delifing_pnas4c$VCV[,"MOTHER"]
VNH_delifing4c=MCMCglmm_delifing_pnas4c$VCV[,"HabitatBirth"]
VRH_delifing4c=MCMCglmm_delifing_pnas4c$VCV[,"HabitatResident"]
VPE_delifing4c=MCMCglmm_delifing_pnas4c$VCV[,"ID"]
VR_delifing4c=MCMCglmm_delifing_pnas4c$VCV[,"units"]

#heritability
H2_delifing4c=VA_delifing4c/(VA_delifing4c + VNH_delifing4c + VRH_delifing4c+
VPE_delifing4c + VR_delifing4c)
posterior.mode(H2_delifing4c)
HPDinterval(H2_delifing4c,0.95)


summary(MCMCglmm_delifing_pnas4d)
posterior.mode(MCMCglmm_delifing_pnas4d$VCV)
HPDinterval(MCMCglmm_delifing_pnas4d$VCV)

summary(MCMCglmm_LRS_pnas5)
posterior.mode(MCMCglmm_LRS_pnas5$VCV)
HPDinterval(MCMCglmm_LRS_pnas5$VCV)



summary(MCMCglmm_LRS_pnas4)
posterior.mode(MCMCglmm_LRS_pnas4$VCV)
HPDinterval(MCMCglmm_LRS_pnas4$VCV)


summary(MCMCglmm_LRS_pnas4b)
posterior.mode(MCMCglmm_LRS_pnas4b$VCV)
HPDinterval(MCMCglmm_LRS_pnas4b$VCV)

summary(MCMCglmm_LRS_pnas4c)
posterior.mode(MCMCglmm_LRS_pnas4c$VCV)
HPDinterval(MCMCglmm_LRS_pnas4c$VCV)

summary(MCMCglmm_LRS_pnas4d)
posterior.mode(MCMCglmm_LRS_pnas4d$VCV)
HPDinterval(MCMCglmm_LRS_pnas4d$VCV)
```

```
load("MCMCglmm_delifing_pnas5.Rdata")


summary(MCMCglmm_delifing_pnas5)
VA_delifing= MCMCglmm_delifing_pnas5$VCV[,"ANIMAL"]
mean(VA_delifing)

VM_delifing=MCMCglmm_delifing_pnas5$VCV[,"MOTHER"]
mean(VM_delifing)

VNH_delifing=MCMCglmm_delifing_pnas5$VCV[,"HabitatBirth"]
mean(VNH_delifing)

VRH_delifing=MCMCglmm_delifing_pnas5$VCV[,"HabitatResident"]
mean(VRH_delifing)

VPE_delifing=MCMCglmm_delifing_pnas5$VCV[,"ID"]
mean(VPE_delifing)

VR_delifing=MCMCglmm_delifing_pnas5$VCV[,"units"]
mean(VR_delifing)

posterior.mode(MCMCglmm_delifing_pnas5$VCV)
HPDinterval(MCMCglmm_delifing_pnas5$VCV)
mean(MCMCglmm_delifing_pnas5$VCV)


#heritability
H2_delifing=VA_delifing/(VA_delifing + VM_delifing + VNH_delifing +
VRH_delifing + VPE_delifing + VR_delifing)
mean(H2_delifing)
posterior.mode(H2_delifing)
HPDinterval(H2_delifing,0.95)

#mother effects
M2_delifing=VM_delifing/(VA_delifing + VM_delifing + VNH_delifing +
VRH_delifing + VPE_delifing + VR_delifing)
posterior.mode(M2_delifing)
HPDinterval(M2_delifing,0.95)
mean(M2_delifing)
#evolvability
mdelifing=mean(Aperc$delifing)
Ia_delifing=VA_delifing/(mdelifing*mdelifing)


posterior.mode(Ia_delifing)
HPDinterval(Ia_delifing,0.95)


QGparams(mu=mu,var.a=va,var.p=vp,model="Poisson.log") #regarder si mean.obs et
var.obs sont proches des données obs

mean(Aperc$LRS)
```

```
var(Aperc$LRS)

summary(MCMCglmm_delifing_pnas5)

# model complets MCMCglmm_LRS_pnas5 et MCMCglmm_delifing_pnas5
#Diagnostic of the MCMC

setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data")
jpeg("Models/Figs/MCMCglmm_LRS_PLOTVCV.jpg")
plot(MCMCglmm_LRS_pnas5$VCV)
dev.off()

jpeg("Models/Figs/MCMCglmm_delifing_PLOTVCV.jpg")
plot(MCMCglmm_delifing_pnas5$VCV)
dev.off()

#Results from the MCMCglmm
posterior.mode(MCMCglmm_LRS_pnas5$VCV)
HPDinterval(MCMCglmm_LRS_pnas5$VCV)

summary(MCMCglmm_LRS_pnas5)

VA_LRS= MCMCglmm_LRS_pnas5$VCV[,"ANIMAL"]
VM_LRS=MCMCglmm_LRS_pnas5$VCV[,"MOTHER"]
VNH_LRS=MCMCglmm_LRS_pnas5$VCV[,"HabitatBirth"]
VRH_LRS=MCMCglmm_LRS_pnas5$VCV[,"HabitatResident"]
VPE_LRS=MCMCglmm_LRS_pnas5$VCV[,"ID"]
VR_LRS=MCMCglmm_LRS_pnas5$VCV[,"units"]

mean(VA_LRS)
mean(VM_LRS)
mean(VNH_LRS)
mean(VRH_LRS)
mean(VPE_LRS)
mean(VR_LRS)

#heritability
H2_LRS=VA_LRS/(VA_LRS + VM_LRS + VNH_LRS + VRH_LRS + VPE_LRS + VR_LRS)
mean(H2_LRS)
posterior.mode(H2_LRS)
HPDinterval(H2_LRS,0.95)

#mother effects
M2_LRS=VM_LRS/(VA_LRS + VM_LRS + VNH_LRS + VRH_LRS + VPE_LRS + VR_LRS)
mean(M2_LRS)
posterior.mode(M2_LRS)
HPDinterval(M2_LRS,0.95)

#evolvability equation: Ia=Va/m² with m the mean of the trait
mLRS=mean(Aperc$LRS)
Ia_LRS=mean(VA_LRS)/(mLRS*mLRS)
mean(Ia_LRS)
posterior.mode(Ia_LRS)
HPDinterval(Ia_LRS,0.95)
```

```
library(QGglmm)
library(MCMCglmm)
#heritability estimate using de Villmereuille et al 2016 Genetics
mu= mean(MCMCglmm_LRS_pnas5[["Sol"]][,"(Intercept)"])
va= mean(MCMCglmm_LRS_pnas5[["VCV"]][,"ANIMAL"])
vm=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"MOTHER"])
vnh=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"HabitatBirth"])
vrh=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"HabitatResident"])
vpe=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"ID"])
vr=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"units"])
vp=mean(rowSums(MCMCglmm_LRS_pnas5[["VCV"]]))

QGparams(mu=mu,var.a=va,var.p=vp,model="Poisson.log") #héritabilité
QGparams(mu=mu,var.a=vm,var.p=vp,model="Poisson.log") # effets maternels
QGparams(mu=mu,var.a=vnh,var.p=vp,model="Poisson.log") #HabitatBirth
QGparams(mu=mu,var.a=vrh,var.p=vp,model="Poisson.log") #HabitatResident
QGparams(mu=mu,var.a=vpe,var.p=vp,model="Poisson.log") #ID
QGparams(mu=mu,var.a=vr,var.p=vp,model="Poisson.log") #units


QGicc(mu=mu,var.comp=vm,var.p=vp,model="Poisson.log") # effets maternels
QGicc(mu=mu,var.comp=vnh,var.p=vp,model="Poisson.log") #HabitatBirth
QGicc(mu=mu,var.comp=vrh,var.p=vp,model="Poisson.log") #HabitatResident
QGicc(mu=mu,var.comp=vpe,var.p=vp,model="Poisson.log") #ID
QGicc(mu=mu,var.comp=vr,var.p=vp,model="Poisson.log") #units

QGicc(mu = mu, var.p = vp, var.comp = va, model = "Poisson.log")#Computing the
broad - sense heritability
QGicc(mu = mu, var.p = vp, var.comp = vm, model = "Poisson.log")


#réccupérer les posteriors distributions

df= data.frame(mu = as.vector(MCMCglmm_LRS_pnas5[["Sol"]][, "(Intercept)"]),
                  va = as.vector(MCMCglmm_LRS_pnas5[["VCV"]][, "ANIMAL"]),
                  vm= as.vector(MCMCglmm_LRS_pnas5[["VCV"]][, "MOTHER"]),
                  vnh=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"HabitatBirth"]),
                  vrh=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"HabitatResident"]),
                  vpe=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"ID"]),
                  vr=mean(MCMCglmm_LRS_pnas5[["VCV"]][,"units"]),
                  vp = rowSums(MCMCglmm_LRS_pnas5[["VCV"]]))
head(df)


# on calcule les posterior distribution pour h²
post= do.call("rbind", apply(df, 1, function(row){
               QGparams(mu=row[["mu"]],
               var.a=row[["va"]],
               var.p=row[["vp"]],
               model="Poisson.log", verbose= FALSE)
              }))

head(post) # on regarde la tête du tableau
```

```
post.h2.obs=as.matrix(post$h2.obs) # on sélectionne la colonne h²
mean(post.h2.obs)
post.var.a.obs=as.matrix(post$var.a.obs)
hdi(post.var.a.obs, credMass = 0.95)# on mesure la CI95%
hdi(post.h2.obs, credMass = 0.95)

#estimation de l'évolvabilité du trait LRS
post_Ia_LRS_obervedscale= post$var.a.obs / (mLRS*mLRS)
mean(post_Ia_LRS_obervedscale)
posterior.mode(post_Ia_LRS_obervedscale)
hdi(post_Ia_LRS_obervedscale,0.95)
```

```
# on calcule les posterior distribution pour m²
postm= do.call("rbind", apply(df, 1, function(row){
  QGparams(mu=row[["mu"]],
           var.a=row[["vm"]],
           var.p=row[["vp"]],
           model="Poisson.log", verbose= FALSE)
}))

head(postm) # on regarde la tête du tableau
postm.h2.obs=as.matrix(postm$h2.obs) # on sélectionne la colonne h²
postm.var.a.obs=as.matrix(postm$var.a.obs)
hdi(postm.h2.obs, credMass = 0.95)# on mesure la CI95%
hdi(postm.var.a.obs, credMass = 0.95)


# on calcule les posterior distribution pour m² avec QGicc
postm= do.call("rbind", apply(df, 1, function(row){
  QGicc(mu=row[["mu"]],
           var.comp=row[["vm"]],
           var.p=row[["vp"]],
           model="Poisson.log", verbose= FALSE)
}))

head(postm) # on regarde la tête du tableau
postm.var.comp.obs=as.matrix(postm$var.comp.obs)
hdi(postm.var.comp.obs, credMass = 0.95)

postm.m2.obs=as.matrix(postm$icc.obs) # on sélectionne la colonne h²
hdi(postm.m2.obs, credMass = 0.95)# on mesure la CI95%



# on calcule les posterior distribution pour vnh
postvnh= do.call("rbind", apply(df, 1, function(row){
  QGicc(mu=row[["mu"]],
           var.comp=row[["vnh"]],
           var.p=row[["vp"]],
```

```
           model="Poisson.log", verbose= FALSE)
            }))
head(postvnh) # on regarde la tête du tableau
postvnh.var.comp.obs=as.matrix(postvnh$var.comp.obs) # on sélectionne la
colonne h²
hdi(postvnh.var.comp.obs, credMass = 0.95)# on mesure la CI95%

# on calcule les posterior distribution pour vrh
postvrh= do.call("rbind", apply(df, 1, function(row){
  QGicc(mu=row[["mu"]],
           var.comp=row[["vrh"]],
           var.p=row[["vp"]],
           model="Poisson.log", verbose= FALSE)
}))
head(postvrh) # on regarde la tête du tableau
postvrh.var.comp.obs=as.matrix(postvrh$var.comp.obs) # on sélectionne la
colonne h²
hdi(postvrh.var.comp.obs, credMass = 0.95)# on mesure la CI95%




# on calcule les posterior distribution pour vpe
postvpe= do.call("rbind", apply(df, 1, function(row){
  QGicc(mu=row[["mu"]],
           var.comp=row[["vpe"]],
           var.p=row[["vp"]],
           model="Poisson.log", verbose= FALSE)
}))

head(postvpe) # on regarde la tête du tableau
postvpe.var.comp.obs=as.matrix(postvpe$var.comp.obs) # on sélectionne la
colonne h²
hdi(postvpe.var.comp.obs, credMass = 0.95)# on mesure la CI95%



# on calcule les posterior distribution pour vr
postvr= do.call("rbind", apply(df, 1, function(row){
  QGicc(mu=row[["mu"]],
           var.comp=row[["vr"]],
           var.p=row[["vp"]],
           model="Poisson.log", verbose= FALSE)
}))

head(postvr) # on regarde la tête du tableau
postvr.var.comp.obs=as.matrix(postvr$var.comp.obs) # on sélectionne la colonne
h²
hdi(postvr.var.comp.obs, credMass = 0.95)# on mesure la CI95%




posterior.mode(MCMCglmm_LRS_pnas5$VCV)#estimation of additive genetics ans
```

```
residual variance
HPDinterval(MCMCglmm_LRS_pnas5$VCV) #interval de confiance (95%) du mod
distribution.

######### Utiliser QGparams pour vérifier que Poisson log est bien pour LRS
# QGparams renvoie moyenne et variance des données qui correspondent à
l'estimation du modèle

setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data/Models
/Figs")
load("MCMCglmm_LRS_pnas5.Rdata")
QGparams(mu=mu,var.a=va,var.p=vp,model="Poisson.log") #regarder si mean.obs et
var.obs sont proches des données obs

mean(Aperc$LRS)
var(Aperc$LRS)

summary(MCMCglmm_delifing_pnas5)
setwd("D:/Documents/POSTDOC_TOULOUSE/Publications/TransmissionNiche/Data/Models
/Figs")

##############################################################################
###
```