

1           **Title: Determinants of lifetime reproductive success in a wild clownfish**  
2                           **population: strong habitat and weak genetic effects**

3  
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22   **Running title:** Habitat drives clownfish local success

## 23 **Abstract**

24 Lifetime reproductive success (LRS), the number of offspring an individual contributes to the next  
25 generation, is of fundamental importance in ecology and evolutionary biology. LRS may be  
26 influenced by environmental, maternal and additive genetic factors, and the relative contributions of  
27 each are critical in determining whether species can adapt to rapid environmental change. However,  
28 studies quantifying LRS across multiple generations in wild populations are extremely rare, and to  
29 date, non-existent for marine species. Here we use pedigrees of up to 5 generations resolved from a  
30 10-year data-set for a wild orange clownfish population from Kimbe Island (PNG) to assess the  
31 contribution of every breeder to the local population. We quantified the additive genetic, maternal  
32 and environmental contributions to variation in LRS for the self-recruiting portion of the population  
33 using a genetic linear mixed model approach. We found that the habitat of the breeder, including the  
34 anemone species and geographic location, made the greatest contribution to LRS, explaining ~97%  
35 of the variation. There were low to negligible contributions of genetic (1.3%) and maternal factors  
36 (1.9%) equating with low heritability and evolvability. Our findings imply our population will be  
37 extremely susceptible to short-term, small-scale changes in habitat structure and may have limited  
38 capacity to adapt to these changes.

39

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

## 42 INTRODUCTION

43 Darwinian fitness or lifetime reproductive success (LRS) – the number of successful offspring an  
44 individual contributes to the next generation – is a critical variable underpinning ecological and  
45 evolutionary responses to the environment (Clutton-Brock 1988; Roff 2002; Clutton-Brock &  
46 Sheldon 2010; Hendry *et al.* 2018). LRS may be influenced by several factors including phenotypic  
47 responses to different environmental parameters, parental effects, and additive genetic variance  
48 (Kruuk *et al.* 2000; McCleery *et al.* 2004; McFarlane *et al.* 2014). Apportioning these contributions  
49 is critical to understanding the potential for short-term ecological effects and longer-term  
50 evolvability in response to rapid environmental change. If LRS is exclusively a phenotypic response  
51 to the conditions experienced by individuals, populations will be severely impacted by rapid  
52 environmental change and there is no prospect of adaptive microevolution. Maternal responses to  
53 change environmental conditions may reduce the effect of those changes on the next generation  
54 through acclimation (Bernardo 1996; Mousseau & Fox 1998; Danchin *et al.* 2011; Donelson *et al.*  
55 2017). However, it is the additive genetic variation in LRS that determines the rate of adaptation of  
56 a population to the environmental demand (Fisher 1930; Frank 1997; Lessard 1997; Crow 2002).  
57 To date, few studies have distinguished the relative importance of environmental and genetic  
58 contributions to LRS over multiple generations in wild populations, where genetic contributions to  
59 fitness may be complex (Kruuk & Hadfield 2007). This situation is changing as long-term,  
60 individual-based ecological studies in which multi-generational pedigrees have been established  
61 provide the necessary longitudinal information to quantify the different components of LRS  
62 (Pemberton 2008; Clutton-Brock & Sheldon 2010; Wolak *et al.* 2018; Cava *et al.* 2019). Such  
63 studies are imperative as we seek to understand the ability of species to withstand or adapt to  
64 accelerating climate change (Charmantier *et al.* 2008; Munday *et al.* 2017).

65

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

68 Environmentally driven mechanisms (*e.g.*, phenotypic plasticity, genetic assimilation) can facilitate  
69 (Price *et al.* 2003; Ghalambor *et al.* 2007, Ledón-Rettig *et al.* 2014; Hoffmann & Merilä 1999;  
70 Danchin *et al.* 2019) or constrain the microevolutionary response to selection (Kruuk *et al.* 2003;  
71 Pujol *et al.* 2018). However, in the absence of genetic variation for LRS, these mechanisms will  
72 likely have little effect on a negligible rate of adaptive evolution. In quantifying additive genetic  
73 variation, it is important to distinguish between *heritability* and *evolvability* (Wheelwright *et al.*  
74 2014; Cava *et al.* 2019). Narrow sense heritability, the additive genetic variance standardized by the  
75 total phenotypic variance, is widely used as a measurement of the population evolutionary potential  
76 to respond to selection (Falconer & Mackay 1996; Mousseau & Roff 1987; McCleery *et al.* 2004).  
77 It is directly affected both by the additive genetic variation and magnitude of direct environmental  
78 effects. Low heritability values can either reflect low additive genetic variance or large  
79 environmental, or residual effects (Price & Schluter 1991; Houle 1992; Hansen *et al.* 2011).  
80 Evolvability is the mean-standardized additive genetic variance (Houle 1992; Hansen *et al.* 2011).  
81 This is the expected proportional change per generation in population mean fitness given a unit  
82 strength of selection (Hendry *et al.* 2018). Evolvability is not affected by environmental or maternal  
83 effects, which makes it a more appropriate metric in the comparison of evolutionary potential  
84 between traits, populations and species. Heritability reveals whether the additive genetic variance  
85 for LRS represents a non-trivial proportion of the total variance of LRS in the actual environmental  
86 context of a given wild population. Together, evolvability and heritability inform us about how  
87 much environmental change a wild population can withstand on the basis of its evolutionary  
88 potential.

89

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

94 potential (Burt 1995; Hendry *et al.* 2018). Until recently, quantifying LRS in marine organisms with  
95 a pelagic larval stage has been considered impossible because of the difficulties in following the  
96 fate of offspring from one generation to the next. However, there is increasing evidence of some  
97 degree of natal philopatry or self-recruitment in local marine populations (Jones *et al.* 1999;  
98 Swearer *et al.* 1999; Swearer *et al.* 2002; Jones *et al.* 2009). The application of genetic parentage  
99 analysis is making it possible to assign a significant proportion of successful offspring to their  
100 parents (Planes *et al.* 2009; Jones 2015; Le Port *et al.* 2017; Mobley *et al.* 2019) and construct  
101 multigenerational pedigrees (Salles *et al.* 2016a; Aykanat *et al.* 2014; Reed *et al.* 2019), at least for  
102 the offspring that return to their natal population.

103

104 For coral reef fishes, quantifying the environmental and genetic components of LRS and assessing  
105 evolvability in wild populations is of great contemporary importance. Between 30 to 50% of the  
106 world's coral reefs have been lost and those remaining are considered highly vulnerable (Jackson  
107 2010; De'ath *et al.* 2012; van Hooijdonk *et al.* 2016). The rapid loss of suitable habitat is widely  
108 acknowledged to be contributing to a decline in reef fish populations and biodiversity (Jones *et al.*  
109 2004; Wilson *et al.* 2006; Paddock *et al.* 2009; Pratchett *et al.* 2018). Laboratory studies have  
110 shown that near future environmental conditions predicted under climate change can have a  
111 dramatic effect on reef fish reproductive success, and despite some levels of phenotypic plasticity  
112 and transgenerational acclimation, the potential for adaptation is uncertain (Donelson *et al.* 2017;  
113 Munday *et al.* 2013; Munday *et al.* 2017). To date, environmental, maternal and additive genetic  
114 contributions to LRS in wild coral reef fish populations have not been assessed. However, recent  
115 work establishing high levels of natal philopatry in some coral reef fishes (Jones *et al.* 2005,  
116 D'Aloia *et al.* 2015; Salles *et al.* 2015; Almany *et al.* 2017) and the success of parentage analysis in  
117 detecting family relationships across multiple generations (Salles *et al.* 2016a,b) opens the way for  
118 quantifying LRS for the first time.

119

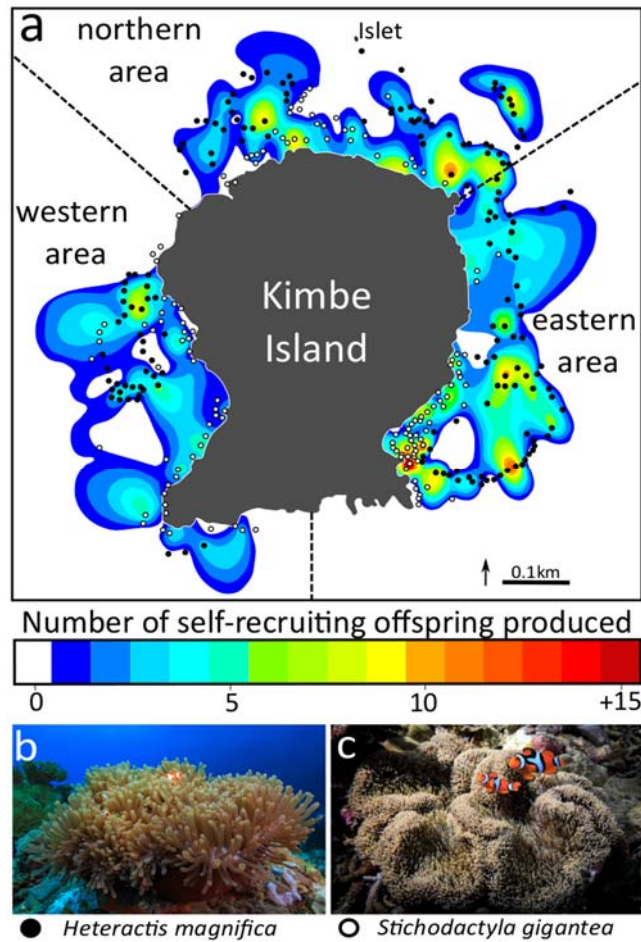
120 Here, we focus on the entire population of the orange clownfish *Amphiprion percula* at Kimbe  
121 Island, Papua New Guinea where each year ~half the juveniles successfully recruiting are progeny  
122 of local breeding pairs (Salles *et al.* 2016a, Almany *et al.* 2017). We use multi-generational  
123 pedigrees of up to 5 generations obtained from biennial DNA sampling over 10 years (Salles *et al.*  
124 2016a,b) and apply a quantitative genetic linear mixed model approach (Kruuk & Hill 2008) to  
125 quantify the additive genetic, maternal and environmental components of variation in LRS for the  
126 self-recruiting portion of the population. Habitat effects were quantified by examining LRS for  
127 individuals resident in two different anemone species and from different both geographic locations  
128 around the island (Salles *et al.* 2016a). By integrating habitat data with the pedigree information in a  
129 quantitative genetic generalized linear mixed model, we were able to assess the relative contribution  
130 of additive genetic, maternal and habitat effects to local LRS. We also calculated the evolvability  
131 and heritability of LRS to evaluate its evolutionary potential to respond to selection at the local  
132 population scale.

133

## 134 **METHODS**

### 135 **Study population and data collection**

136 A natural population of orange clownfish (*A. percula*) living in the reef surrounding Kimbe Island  
137 (Fig. 1a; 5°12'22.56" S, 150°22'35.58" E), West New Britain Province of Papua New Guinea, was  
138 surveyed every second year from 2003 to 2013. Here, *A. percula* lives in a mutualistic association  
139 with one of two host sea anemone species, *Heteractis magnifica* (Fig. 1b) and *Stichodactyla*  
140 *gigantea* (Fig. 1c). We geographically located and tagged a total of 310 anemones (176 *H.*  
141 *magnifica* and 134 *S. gigantea*) that were occupied by *A. percula* on the entire reef surrounding the  
142 island.



143

144 **Figure 1. Variation of the total number of offspring orange clownfish produced on each anemone around Kimbe**

145 **Island between 2003 and 2013. (a)** The studied region was divided in three areas (northern, eastern and western areas).

146 Colors correspond to the variation of the total number of juveniles locally self-recruited that were produced on each

147 anemone (varying from 0 to 27) over a 10-year period. The expected value is interpolated from those around it (using

148 default algorithms implemented in *Origin* software). Dots correspond respectively to the location of the two host

149 anemones species: (b) *Heteractis magnifica* (black dots) and (c) *Stichodactyla gigantea* (white dots). Photos by Tane

150 Sinclair-Taylor.

151 These two anemone species are remarkably different in terms of the micro-habitat they provide,

152 including a wide range of shapes, sizes, depth distributions and surrounding substrata (Dunn 1981;

153 Chausson *et al.* 2018). Although we did not directly measure these variables (other than depth), the

154 combination of host the anemone species (*H. magnifica* or *S. gigantea*) with one of the three

155 geographical areas covering the entire reef around the island (northern, western or eastern areas,

156 Figure 1a) where it is located describes a ‘habitat’ variable for each fish that encompasses a suite of

157 biotic and abiotic environmental conditions. These geographical areas correspond to the different

158 coasts of the island that reflect possible environmental effects of the geographic location (Salles *et*  
159 *al.* 2016b). In total, the combination of the two host anemone species with the three geographical  
160 areas allowed us to describe six different habitats.

161

162 Clownfish within one anemone live in group of typically three to five individuals in the Kimbe  
163 Island population (Salles *et al.* 2015). The size-based dominance hierarchy in *Amphiprion* allows us  
164 to determine the reproductive status of each individual (Fricke 1979). The female is the largest, the  
165 male is the second largest, and the non-breeders rank progressively lower in the hierarchy as they  
166 decrease in size. If the single female adult of a group dies, then the male changes sex to female, and  
167 the largest non-breeder from the anemone becomes sexually mature as male. Reproduction occurs  
168 year round, with females laying several hundred eggs in a clutch near the pedal disk of the host  
169 anemone each lunar month. The eggs hatch after ~7 days of paternal care into larvae that spend ~10  
170 days in the pelagic environment (Berumen *et al.* 2010) before settling on an anemone that may or  
171 may not be in the population (Planes *et al.* 2009).

172

173 Fish were captured by divers by using hand nets. Individuals were measured *in situ* using calipers,  
174 fin-clipped (size > 35mm) or collected whole (size < 35mm) for genetic analysis and then released  
175 back on the same anemone. Small pieces of fin tissue were preserved in 95% ethanol in 2-mL vials.  
176 The biggest fish in each anemone was identified as the female, the second largest individual was  
177 assumed to be the male, and all other individuals were classified as non-breeders. We extracted  
178 DNA from all samples at 22 polymorphic microsatellite loci (Bonin *et al.* 2015). Then, we  
179 identified the individuals sampled multiple times over the years by using the Excel macro GenAlex  
180 v6.5 (Peakall & Smouse 2012) to compare multilocus genotypes from 2003, 2005, 2007, 2009,  
181 2011 and 2013. Individuals were in average sampled  $2.88 \pm 0.04$  times (mean  $\pm$  SE) over the six  
182 surveys (1% of individuals persisted over the 10-yr period, Salles *et al.* 2016a). The 2-yr sampling  
183 scheme precluded calculating a precise measurement of the age of individuals (Salles *et al.* 2016b),



184 in particular for fish sampled in 2003 during the first sampling period, which age was unknown.  
185 The total duration of this long term survey did not allow us to obtain many replicated measurements  
186 within individuals before and after sex change ( $n = 41$  individuals). Estimating sex dependent  
187 additive genetic variance is precluded in this case because some effects cannot be disentangled as  
188 the clownfish only changes sex in one direction (from male to female). This change is always  
189 associated with a change of sexual partner and with an increase in female body size, which we  
190 expect to generate a confounding effect between a female condition and its genetic quality. We  
191 therefore did not consider sex in our model as a result of data and analytical limitations.

192

### 193 **Pedigree used for quantitative genetic analysis**

194 Pedigree reconstruction was conducted by assigning juvenile fish to parental pairs on the basis of  
195 their multilocus genotypes (Salles *et al.* 2016a). We used the software FaMoz (Gerber *et al.* 2003).  
196 This approach is based on the calculation of LOD scores (Log of the odd-ratio comparison) for any  
197 potential parentage relationship. It determined critical thresholds to accept or reject assignments by  
198 simulating true and false parent-offspring pairs. Further details on parentage analyses and pedigree  
199 reconstruction are given in Salles *et al.* (2016a). Assignments to single parents were rejected. We  
200 kept assignments of parental pairs. In the context of overlapping generations, we used the year of  
201 first sampling and the anemone of each parental couple as information to avoid possible false  
202 assignments. As a result, sibship links could not be confused with parental links. Because the sex  
203 changes through the life of the clownfish, the same individual can be related to its offspring with  
204 either a paternal or maternal link. Based on the size of the two parents and the year of first capture,  
205 we can identify the mother and the father. The original population pedigree includes 2927 clownfish  
206 over five generations including 121 families, 987 paternal, 987 maternal, 1809 full-sib, 412  
207 maternal half-sibs, 248 paternal half-sib, 135 maternal grandmothers, 135 maternal grandfathers,  
208 278 paternal grandmothers, 278 paternal grandfathers and 218 cousins (Salles *et al.* 2016a). For this  
209 study, we excluded from the original pedigree the 1192 individuals that were removed from the

210 habitat at the juvenile stage (size < 35mm, 10 to 458 days old). The final pedigree used for this  
211 study includes 1735 individuals from five generations (Fig. S1). We used the R package ‘pedantics’  
212 (Morrissey & Wilson 2010) to assess the power of the resolved pedigree to detect significant  
213 quantitative genetic parameters (Fig. S1).

214

### 215 **Individual contribution to self-recruitment**

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

231

### 232 **Quantitative genetic generalized linear mixed model approach**

233 Similarities between relatives living in contrasted micro-habitats allowed us to evaluate  
234 simultaneously the genetic and habitat components of LRS. Repeated ‘records’ on individuals made  
235 it possible to estimate permanent environmental effects, which allowed us to account for intra-

236 individual and unmeasured environmental trait variation across time. Permanent environmental  
 237 effects also account for a part of non-additive genetic effects (Wilson *et al.* 2010). The LRS  
 238 variance was partitioned into six random effects: Additive genetic ( $V_A$ ), Maternal ( $V_M$ ), Natal  
 239 Habitat ( $V_{NH}$ ), Resident Habitat ( $V_{RH}$ ), Permanent Environment ( $V_{PE}$ ) and Residual ( $V_R$ ) variances  
 240 by using the ‘animal model’ quantitative genetic approach (Kruuk 2004). This Linear Mixed Model  
 241 (LMM) approach uses pedigree information to extract the additive genetic component. This  
 242 approach is more powerful than traditional analyses (*e.g.*, parent–offspring regressions) because it  
 243 takes into account every relationship link in a pedigree. Maternal variance was modeled using the  
 244 mother’s identity as a random effect, allowing maternal effects to include both genetic and  
 245 environmental maternal effects. Permanent environmental effects were modeled by including the  
 246 identity of individuals as a random effect. The LRS variance is the sum of six variance components:

$$247 \quad V_{LRS} = V_A + V_M + V_{NH} + V_{RH} + V_{PE} + V_R \quad (1)$$

248 Quantitative genetic models were computed as univariate GLMMs using the ‘MCMCglmm’  
 249 package (Hadfield 2010) in R version 3.5.1 (R.Core.Team 2018), with LRS as a Poisson response  
 250 variable. Using this Bayesian framework facilitated parameter estimation for non-Gaussian traits.  
 251 We used parameter expanded priors for all analyses ( $V=1$ ,  $nu=0.02$ ), which are often referred to as  
 252 ‘non informative’ priors although such denomination can be debated, as we wanted posterior  
 253 estimates to be determined from the data and not from the priors (Morrissey *et al.* 2014). We ran  
 254 model MCMC chains over 1,000,000 iterations with initial burning of 10,000 iterations and a  
 255 thinning of 1,000 iterations. Historically, the Deviance Information Criterion (DIC) was often used  
 256 to compare models and assess the significance of the random variance components in this type of  
 257 approach. However, it is becoming less commonly used since it was recognized as an inappropriate  
 258 tool for model comparisons of the same type than quantitative genetic GLMM analyses (Gelman *et*  
 259 *al.* 2014; Spiegelhalter *et al.* 2014). Effects of variance components were considered statistically  
 260 supported if their posterior distributions did not overlap zero (Wilson *et al.* 2010).

261

## 262 Variance Components

263 Variance components were estimated as the mode of the posterior distributions established on the  
264 MCMC sample and we reported the lower and the upper limits of the 95% credible interval. For the  
265 six variance components, we calculated their relative contribution to the sum of all variance  
266 components, thereby expressing their effects as percentages of the total phenotypic variance ( $V_{LRS}$ ).  
267 As a result, we obtained standard narrow sense heritability estimates for LRS ( $h^2$ ) by applying the  
268 basic formula ( $h^2 = V_A / V_P$ , see Falconer & McKay 1996), and similarly maternal effects by  
269 estimating the proportion of total phenotypic variance explained by the maternal variance ( $m^2 = V_M /$   
270  $V_P$ ). Evolvability ( $I_A$ ) of LRS, equal to the additive genetic variance divided by the squared mean of  
271 the LRS (Wagner & Altenberg 1996), was estimated to evaluate the capacity for adaptive  
272 evolutionary change of the number of offspring that self-recruit in the population. The analyses  
273 conducted in the ‘MCMCglmm’ framework assumed a Poisson distribution and therefore provided  
274 parameter estimates for evolutionary inference or future comparisons on a statistically convenient  
275 latent scale for non-Gaussian traits. We therefore endeavored to back-transform all the estimates of  
276 the latent scale variables included in the model (see equation 1) onto the observed data scale to  
277 improve our inferences. We used the ‘QGlmm’ package (de Villemereuil *et al.* 2016) to back-  
278 transform the estimates, specifically the function ‘QGparams’ to estimate additive components such  
279 as  $V_A$  and  $h^2$ , and ‘QGicc’ to estimate broader sense components such as  $V_M$  and  $m^2$ ,  $V_{NH}$ ,  $V_{RH}$ ,  $V_{PE}$   
280 and  $V_R$ . Although parameter estimates transformed back on the data-scale are expected to be upward  
281 biased, their ratio is reliable, and hence the estimators derived from their relative proportions such  
282 as  $h^2$ . It is necessary to point out two specific aspects of the back transformation on the observed  
283 data scale. First,  $V_R$  is estimated on the basis of the additive over-dispersion term in the nonlinear  
284 model and its value cannot be interpreted similarly to the usual residual variance term estimated by  
285 classical quantitative genetics generalized linear mixed models. Second, the sum of the variance  
286 components estimated on the data scale are not additive and therefore not expected to sum up to the  
287 value of the phenotypic variance calculated directly on the raw data. For the sake of clarity and

288 comparison, we present the results on the latent scale and the observed data scale. We calculated the  
289 95% credibility intervals from the posterior distributions of observed parameters for all the variance  
290 components and other estimates expressed on their basis by using the ‘HDInterval’ package  
291 (Meredith & Kruschke 2016).

292

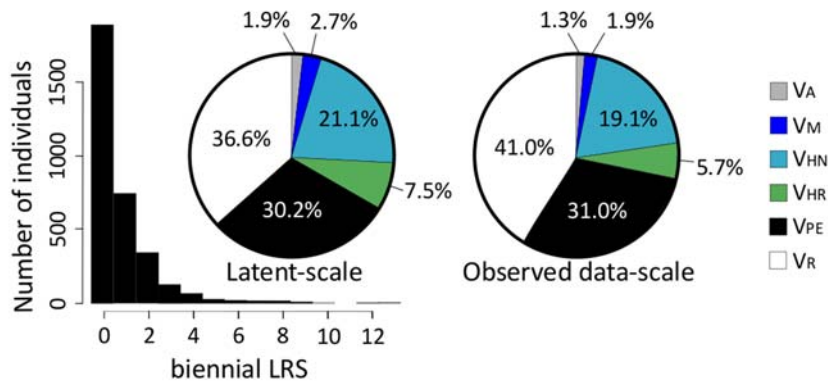
## 293 **RESULTS**

### 294 **Habitats dominantly shape the Lifetime Reproductive Success in the clownfish population**

295 Biennial estimates of the Lifetime Reproductive Success (LRS) ranged from 0 to 13, with a  
296 phenotypic variance  $V_{LRS}=1.31$  and an average value of  $0.54 \pm 0.05$  (mean  $\pm$  SE) offspring per  
297 individual for a two-year period. Because clownfish live in strong association with their anemone,  
298 we were able to identify and geo-locate the precise position and habitat where breeders contributed  
299 more to the local replenishment of the population (Fig. 1a). For example, breeders that produced  
300 more self-recruiting offspring lived in Kimbe Island’s eastern area and mostly in *S. gigantea*  
301 anemones. Our analysis also revealed fish that did not contribute at all to the local replenishment of  
302 the population over the 10-year monitoring period. These fish were located in 48 *H. magnifica* and  
303 30 *S. gigantea* of the 310 anemones monitored in both deep and shallow waters (Fig. 1a). We found  
304 that that 25% of the pairs of local breeders did not contribute at all to the renewal of the population  
305 over a period of 10 years.

306

307 Quantitative genetic linear mixed models on the latent and the observed data scale gave very close  
308 results. Our results on the scale of observed data showed that Natal Habitat and Resident Habitat  
309 explained respectively 19.1% and 5.7% of the variance in LRS, furthermore, residual and  
310 permanent environment explained respectively 41.0% and 31.0%, whereas additive genetic effects  
311 and maternal effects were very weak and explained 1.3% and 1.9% respectively (Fig. 2a, variances  
312 on observed data-scale). Similar results were obtained for DL (see Supplementary Information for  
313 more details).



314

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

321

### 322 Low evolvability and low heritability for LRS

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

325

### 326 Table 1. Sources of variation in Lifetime Reproductive Success (LRS) for the Kimbe Island orange clownfish.

327 Here we reported variance component estimates quantified by using the animal model approach: Additive genetic ( $V_A$ ),  
 328 Maternal ( $V_M$ ), Natal Habitat ( $V_{NH}$ ), Resident Habitat ( $V_{RH}$ ), Permanent Environmental ( $V_{PE}$ ) and Residual ( $V_R$ )  
 329 Variances. We also report size effects as proportions of explained phenotypic variance: narrow-sense heritability ( $h^2$ ),  
 330 maternal effects ( $m^2$ ) and the mean standardized additive genetic variance: evolvability ( $I_A$ ) for biennial LRS. Measures  
 331 are expressed on a latent-scale (direct *MCMCglmm* R results) and the observed data-scale (*QGglmm* R back-  
 332 transformation). 95% credible intervals (CI) are reported for each estimate.

	LRS	LRS
	Latent scale	Observed data-scale
$V_A$	0.046	0.030
(CI)	( $1.381 \times 10^{-3}$ to 0.146)	( $4.94 \times 10^{-4}$ to 0.060)

$V_M$	0.067	0.046
(CI)	( $2.000 \times 10^{-3}$ to 0.211)	( $8.822 \times 10^{-3}$ 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)	( $6.827 \times 10^{-4}$ to 0.057)	( $4.951 \times 10^{-5}$ to $1.227 \times 10^{-2}$ )
$m^2$	0.027	0.019
(CI)	( $9.157 \times 10^{-4}$ to 0.083)	( $2.966 \times 10^{-5}$ to $2.044 \times 10^{-2}$ )
$I_A$	0.154	0.103
(CI)	( $4.643 \times 10^{-4}$ to 0.492)	( $1.661 \times 10^{-3}$ to 0.511)

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333

334 We found  $V_A=0.030$  (CI<sub>95%</sub>  $4.94 \times 10^{-4}$  to 0.060). This could be linked to the statistical power of our  
335 pedigree (Fig. S1). Our model nevertheless placed fairly restricted bands on the 95% credible  
336 intervals (Table 1). Credible intervals did not overlap the zero but were close. The extent to which  
337 these very low values of genetic estimates are not null must therefore be considered with caution.  
338 LRS evolvability estimated on the observed data-scale, which evaluated the micro-evolutionary  
339 change of the number of self-recruiting offspring that can be reached by the population, was equal  
340 to 0.103 (CI<sub>95%</sub>  $1.661 \times 10^{-3}$  to 0.511). In other words, 0.104 additional juveniles were added to the  
341 average number of juveniles originating and recruiting in the population per generation. The  
342 heritability estimate expressed on the observed data-scale was  $h^2=0.013$  (CI<sub>95%</sub>  $4.951 \times 10^{-5}$  to  
343  $1.227 \times 10^{-2}$ ) for LRS (Table 1). We can therefore estimate the maximum response ( $R$ ) to selection

344 (*S*), in the presence of strong selection pressures acting on the Kimbe Island orange clownfish  
345 population by using the Breeder's equation  $R=h^2 \times S$  (Falconer & Mackay 1996; Lush 2008). The  
346 low to negligible value of the LRS heritability means that the maximum genetic change of the  
347 population average LRS would never exceed  $\sim 0.020$  offspring per generation. Similar results were  
348 obtained for DL (see Supplementary Information for more details).

349

### 350 **Low maternal effects for LRS**

351 We found that maternal variance for the LRS was extremely small, to the extent that it might be  
352 considered as null (Table 1):  $V_M=0.019$  ( $CI_{95\%} 2.966 \times 10^{-5}$  to  $2.044 \times 10^{-2}$ ). While our analysis  
353 detected maternal variance, it made very little contribution to the total variance in LRS ( $m^2=1.9\%$ ,  
354 expressed on observed data-scale, Fig. 2). The habitat occupied by the mother (Natal Habitat) had a  
355 stronger effect on LRS than the mother herself. The relative contribution of individuals to the  
356 population replenishment was indeed influenced by the Natal Habitat to an extent of 19.1% for  
357 LRS. Similar results were obtained for DL (see Supplementary Information for more details).

358

## 359 **DISCUSSION**

### 360 *Strong habitat and weak genetic effects on LRS*

361 Our study revealed that LRS in the Kimbe Island orange clownfish population quantified over five  
362 generations was largely explained by host anemone species and geographical location ( $\sim 97\%$ ), with  
363 only weak maternal (1.9%) and additive genetic effects (1.3%). The strong effects of habitat can be  
364 attributed to the intrinsic biological characteristics of the anemone species (*e.g.*, size, shape and  
365 toxicity) and their effects of on life-history traits of their resident clownfish (Salles *et al.* 2016b;  
366 Chausson *et al.* 2018). In addition, the higher toxicity of *S. gigantea* (Nedosyko *et al.* 2014) might  
367 provide better protection against predators of eggs attached near the pedal disk of the host anemone,  
368 but this hypothesis remains to be tested. The geographical location of the different host-anemones  
369 also appears to be important, with more successful individuals in shallow water, close to the land on



370 *S. gigantea* and in deeper lagoons for *H. magnifica*, which might promote greater local retention of  
371 larvae. To date, the mechanisms responsible for geographical differences in LRS around Kimbe  
372 Island remain unknown (Berumen *et al.* 2010). The weak genetic effects on LRS that shows a very  
373 low to negligible rate of adaptation raise concern about the ability of this reef fish population to  
374 exhibit longer-term adaptive evolution in response to rapid climate change.

375

#### 376 *Susceptibility to habitat change*

377 Habitat is clearly the main driver of the variation in LRS and individuals that happen to settle on  
378 particular anemones and particular places do well. The dependence of LRS on habitat quality  
379 suggests this species will be extremely susceptible to habitat degradation over ecological time  
380 scales. Direct and indirect human impacts on clownfish populations and their anemone habitats are  
381 already affecting the habitat quality for numerous clownfish species (Jones *et al.* 2008; Saenz-  
382 Agudelo *et al.* 2011; Bonin *et al.* 2016). *S. gigantea* anemones located in shallow waters are likely  
383 to be disproportionately more impacted by increasing water temperatures and irradiance (Bak *et al.*  
384 2005; Hobbs *et al.* 2013). If these locations are differentially impacted, this will affect the  
385 individual contribution to the local replenishment of the population and compromise population  
386 persistence.

387

#### 388 *Low to negligible evolutionary potential*

389 Our findings provide the first empirical support for a wild marine population to Fisher's  
390 fundamental theorem of selection that additive genetic variance in fitness is depleted under  
391 selection and tends towards zero in a population reaching evolutionary equilibrium (Fisher 1930;  
392 Gustafsson 1986; Falconer 1989). Although normal and expected, low heritability and evolvability  
393 in LRS is concerning given the increasing rate of environmental change. The low to negligible  
394 scope for adaptive evolution (estimated by evolvability) and the low to negligible genetic potential  
395 for responding to selection (estimated by heritability) may not be a problem for gradual

396 environmental change. At this rate, it would take around at least 10 generations for the population  
397 average LRS to increase by one juvenile, which highlights the stability of the demographic rate of  
398 self-recruitment in this population. Our results therefore support the hypothesis that the population  
399 is at evolutionary equilibrium (no genetic changes) in a context of environmental stability over the  
400 timescale of the survey.

401

#### 402 *Connectivity as a plausible cause*

403 Our finding that the Kimbe Island clownfish population harbored low to negligible additive genetic  
404 variation for LRS over a ten-year period was at first surprising because immigration accounts for on  
405 average 44% of the juvenile recruitment (Salles *et al.* 2015; 2016a). The average dispersal distance  
406 in Kimbe Bay is between 10 and 20km, providing substantial connectivity among adjacent reefs and  
407 potential dispersal of up to 100km (Almany *et al.* 2017; Pinsky *et al.* 2017). The associated gene  
408 flow would be expected to bring new genetic variants and thereby increase genetic variation for  
409 LRS (Keller *et al.* 2001; Lavergne & Molofsky 2007; Facon *et al.* 2008). Under such scenario,  
410 selection for self-recruitment, and thereby against migrants, would have to be strong to keep the  
411 population at evolutionary equilibrium. An alternative scenario is that homogenization by gene flow  
412 results in most immigrants sharing a similar genetic background. As a result, low genetic variation  
413 would be maintained because no new genetic variants were brought in the population by gene flow  
414 (Pujol *et al.* 2010). Low genetic variation for LRS implies that evolution by selection at the local  
415 scale is extremely limited in its current state. However, this does not imply a dead end for the  
416 adaptive evolution of this population because several mechanisms can provide adaptive  
417 evolutionary potential over the long term (Pujol *et al.* 2018).

418

#### 419 *Slight but probably negligible maternal genetic effect*

420 Additional adaptive evolutionary potential can in theory be provided to a population by maternal  
421 effects (Räsänen & Kruuk 2007). In the Kimbe Island orange clownfish, we found that maternal

422 effects explained up to 2.7% of the LRS variance, which is quite small, even if it was more than  
423 additive genetic effects. Our findings thereby revealed that maternal effects increased slightly the  
424 low to negligible rate of LRS change by adaptive evolution. One should note that this increase was  
425 nearly negligible. It is likely that this low value represents the genetic component of the maternal  
426 effect because the identity of each mother was taken into account. The habitat of birth, on the other  
427 hand, which is also the maternal habitat, might encompass some direct effect of the maternal  
428 environment (Germain & Gilbert 2014). The environmental component can represent a non-  
429 negligible part of parental effects (Chirgwin *et al.* 2017). In fact, there is growing awareness that  
430 maternal environmental effects can contribute to adaptation in natural populations, especially when  
431 maternal and offspring environments are positively correlated (Burgess & Marshall 2014; Shama  
432 2015; Dey *et al.* 2016). It might even buy some time for adaptive evolution through slow genetic  
433 change to occur (Levis & Pfenning 2016).

434

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

436 In our study, LRS estimates the individual fish contribution to the local population replenishment.  
437 This excludes the dispersal fitness because the amount of offspring produced and which dispersed  
438 to live somewhere else is unknown on wild population pedigrees (Kruuk *et al.* 2000; Merilä &  
439 Sheldon 2000, McCleery *et al.* 2004). Its genetic variation evaluates the rate of adaptive evolution.  
440 While there are no comparable data from marine systems, 15 studies conducted on terrestrial  
441 vertebrates have also estimated the additive genetic variation and the heritability of LRS (Table S1).  
442 It is noteworthy that the number of estimates of maternal effects on LRS variation are extremely  
443 rare (Kruuk *et al.* 2000, Foerster *et al.* 2007; Schroeder *et al.* 2012; McFarlane *et al.* 2014). A  
444 majority of these studies similarly found low to negligible contributions of additive genetic effects,  
445 while the situation is less clear for maternal effects, partly because studies remain scarce. The  
446 existence of additive and maternal genetic variation for fitness, even when very low, implies that  
447 the population was not totally at equilibrium because there was a small genetic change in the wild

448 population over the course of the long term survey. It also implies very limited genetic adaptive  
449 potential.

450

## 451 **CONCLUSION**

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

467

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## 482 **AUTHORSHIP**

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

## 486 **DATA ACCESSIBILITY STATEMENT**

487 All data from this study are available on the CRIOBE data portal (<http://www.criobe.pf>)

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736 **SUPPORTING INFORMATION**

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

738 The Additional Supporting Information file contains:

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

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