

1 Running head: Breeding systems and dispersibility

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3 **The link between selfing and greater dispersibility in a heterocarpic Asteraceae¹**

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37 **SUMMARY**

38 **PREMISE OF THE STUDY:** Although evolutionary link between breeding systems
39 and dispersibility has been proposed, to date empirical data and theoretical models on
40 plants show contrasting trends, sometimes associating selfing and non-dispersal, and
41 others selfing and dispersal.

42 **METHODS:** We tested two competing hypotheses for the association between
43 breeding systems and dispersibility in the heterocarpic *Hypochaeris salzmanniana*
44 (Asteraceae) by using both an experimental approach and surveys in five natural
45 populations occurring in a gradient of pollinator availability over two years.

46 **KEY RESULTS:** *H. salzmanniana* produced two types of fruits, beaked (BF) and non-
47 beaked (NBF), differing in dispersal ability. BF were lighter and showed a lower
48 dropping velocity and higher dispersal distance than NBF. Potential for long dispersal,
49 measured as BF ratio per head, had high narrow-sense heritability. Greater dispersibility
50 and selfing ability were linked at all the scales studied. Both selfed BF and NBF fruits
51 exhibited longer plumes and lower plume loading than outcrossed, characteristics
52 promoting farther dispersal. Natural populations with higher percentage of self-
53 compatible plants showed higher BF ratio. Moreover, selfing led to higher BF ratio than
54 outcrossing.

55 **CONCLUSIONS:**

56 The avoidance of inbreeding depression seems to be the most plausible selective
57 pressure for greater dispersibility traits of selfed seeds. Furthermore, the ability to
58 modulate the BF ratio and thus, the potential for long dispersal of offspring, based on its
59 selfed or outcrossed origin could be advantageous, and therefore selected, under
60 unpredictable pollination environments that favors higher dispersive selfers that
61 overcome both pollen limitation and inbreeding avoidance.

62 INTRODUCTION

63 Breeding systems and seed dispersal are key factors modeling plant metapopulation
64 dynamics and species' distributions, and can be affected by several factors that are
65 omnipresent in the current global change, as habitat loss, fragmentation or pollinator
66 decline. Breeding system and dispersal ability are anatomically and ontogenetically
67 linked, and selective pressures on breeding systems can generate consequences for
68 dispersal, and vice versa (Primack, 1987; Rubio de Casas et al., 2012; Auld and Rubio
69 de Casas, 2013). Both reproductive traits impact gene flow, genetic diversity and
70 colonization ability of flowering plants, and thus may affect potentiality for adaptation
71 of their populations; therefore, an evolutionary association between both reproductive
72 traits could be expected (de Waal et al., 2014). However, the association between
73 breeding systems and dispersal has not a clear pattern, and opposing links (low or high
74 dispersal and selfing) are predicted (Auld & Rubio de Casas, 2013; de Waal et al,
75 2014).

76 Inbreeding avoidance and environmental stochasticity are two explanatory hypotheses
77 for the correlated evolution of these traits (Olivieri et al., 1995; Perrin and Goudet,
78 2001; Guillaume and Perrin, 2006; Ronce, 2007; Auld and Rubio de Casas, 2013). In
79 species suffering high inbreeding depression (i.e. fitness reduction due to the expression
80 of homozygote recessive alleles; Charlesworth & Willis, 2009), dispersal would reduce
81 the chance of mating between genetically close individuals (Waser, 1993), which could
82 constitute a selective force favoring high dispersibility of selfed progeny. Several
83 theoretical studies predict that dispersal is favored by high inbreeding depression
84 (Perrin & Mazalov, 1999; Perrin & Goudet, 2001; Roze & Rousset, 2005).

85 In contrast, theoretical models based on pollinator availability, predicted a strict
86 association between obligate outcrossing and greater dispersibility under random

87 pollination fluctuations (Cheptou and Massol, 2009). Stochasticity in pollination
88 regimes, which are widespread in natural populations (Burd 1994) is central to
89 interpreting the association of mating system and dispersal traits (Massol & Cheptou,
90 2011a). In their theoretical models, Cheptou and Massol found that dispersal was never
91 associated with selfing (Cheptou and Massol 2009; Massol & Cheptou, 2011a). These
92 authors argued that uncertainty in pollination triggers a lethal cost for non-dispersing
93 outcrossers, which could be overcome either by dispersing, or by selfing (Massol &
94 Cheptou, 2011b). Both mechanisms have costs: the former implies paying the cost of
95 dispersal, and the latter, paying the cost of inbreeding. For that reason, the authors argue
96 that selfers with greater dispersibility could not evolve since they would be
97 outcompeted by mutants that disperse or self-fertilize less (Massol & Cheptou, 2011b).
98 Heterocarpic species constitute excellent systems to test dispersibility and mating
99 systems. Heterocarpic species produce at least two fruit types differing in dispersal
100 ability, which have been seen as an adaptive strategy for plants dealing with
101 heterogeneous environments (Lloyd, 1968). Heterocarpy, described in 18 families, is
102 especially common in Asteraceae family, which accounts over the half of the described
103 species (Imbert, 2002). In heterocarpic Asteraceae, the link between selfing-
104 dispersibility may be due to different trait associations. Within the flower head, less
105 dispersible fruits are always located at the periphery and, according to the centripetal
106 phenological flowering pattern, they are produced first (Imbert, 2002). These less
107 dispersive fruits are only produced at the first flower rows within the flower head and
108 are much less numerous than inner fruits. In fact, the number of outer flowers,
109 controlled by the number of parastichies (i.e. the number of phyllotactic spirals of
110 flowers that composes the flower head), is expected to show no genetic variance (Imbert
111 & Ronce, 2001). In radiate Asteraceae species, the two types of fruits are associated

112 with different flower types: outer female ray flowers and inner hermaphrodite disk
113 flowers (Venable and Levin, 1985). Thus, outer fruits come from female flowers, which
114 necessarily have higher outcrossing rates than inner ones (Marshall and Abbott, 1982,
115 1984), and this leads to the association between outcrossing and non-dispersibility (but
116 see Gibson, 2001; Gibson, Tomlinson, 2002 for similar outcrossing rates in ray and disk
117 flowers). In contrast, in other heterocarpic Asteraceae with only hermaphrodite flowers,
118 contrasting associations have been found in relation to mating system and flower
119 position. Thus, in *Carduus* species, protandry along with centripetal head phenology,
120 makes selfing more likely in outer flowers, leading to the link between selfing and non-
121 dispersibility (Olivieri et al., 1983; Ravigné et al., 2006). However, in *Crepis sancta*
122 (L.) Babc., with similar protandry and head phenology, higher outcrossing levels using
123 allozymes markers have been found in outer flowers, giving rise to the link between
124 outcrossing and non-dispersibility (Cheptou et al., 2001). The association between
125 selfing and greater dispersibility is also found in a multi-species study of Asteraceae
126 from South Africa (de Waal et al., 2014).

127 Evidence for the link between selfing and non-dispersibility comes mainly from
128 cleistogamous or amphicarpic plants exhibiting mixed-mating systems (Cheplick,
129 1987). In these species, diaspores from cleistogamous or basal flowers have no dispersal
130 mechanism and can even be buried just beneath the mother plants, whereas those from
131 chasmogamous or aerial flowers possess some dispersive mechanism. This happens in
132 several grasses (Cheplick, 1993a, b; Clay, 1983; McNamara and Quinn, 1977) and also
133 in cleistogamous Asteraceae, as *Centaurea melitensis* L., in which less dispersible fruits
134 are associated with cleistogamous heads, which has been considered as an adaptation to
135 unstable environment (Porras and Muñoz, 2000). Selfing and reduced dispersal

136 potential as a consequence of an increase in fruit size was also found in the non-
137 cleistogamous *Hypochoeris radicata* L., (Mix et al., 2006).

138 No doubt further empirical work is needed to get a deeper insight into the links between
139 breeding system and dispersibility, a need also claimed by other authors (Auld and
140 Rubio de Casas, 2013; Iritani and Cheptou, 2017). Very few studies have tested for
141 differences in seed dispersal potential between closely related selfing vs outcrossing
142 populations (but see Darling et al., 2008), so no empirical generalization is currently
143 possible.

144 Here, we documented the association between selfing and dispersibility by monitoring,
145 for two consecutive years, five natural populations of *Hypochoeris salzmanniana* DC.
146 (Asteraceae) distributed along a gradient of pollinator availability, as well as by using
147 an experimental approach. It has a sporophytic self-incompatibility system (Ortiz et al.,
148 2006), by which self-fertilization is prevented by the inherited capacity of flowers to
149 reject incompatible pollen (including its own), based on the sporophytic (i.e diploid)
150 genetic control of pollen and pistil by means of recognition and associated self-
151 rejection processes (de Nettancourt, 2001).

152 Populations of *H. salzmanniana* are self-incompatible in North Africa and presumably
153 lost its self-incompatibility system when the species migrated to SW Spain, where they
154 show a mixture of self-incompatible, partially self-compatible and fully self-compatible
155 plants (Ortiz et al., 2006). Self-compatible plants are able to self-fertilize automatically
156 even without any pollinator attendance (Arista et al. 2017). In SW Spain, pollination
157 environment varies at a few kilometers distance from west toward east due to extreme
158 winds in the Strait of Gibraltar area, making spatial differences in pollinator
159 environment higher than temporal ones (Arista et al., 2017). Populations occupying
160 areas with extreme winds (pollination-limited environments) are mainly composed of

161 self-compatible individuals and show low genetic diversity (Ortiz et al., 2006; Arista et
162 al., 2017). This geographic variation in self-incompatibility has been associated with
163 reproductive assurance due to lack of mate availability caused by both low genetic
164 diversity and unfavorable pollinator environment (Ortiz et al., 2006; Arista et al., 2017).
165 *Hypochoeris salzmanniana* is an endangered species with a distribution area restricted
166 to coastal sand dunes, habitat that have suffered in Spain an impressive reduction in the
167 last 40 years mainly due to real estate constructions along the coastline (Ortiz et al.,
168 2003). We chose *H. salzmanniana* as a model system to test the association between
169 selfing ability and dispersibility because it occurs along a pollination-environment
170 gradient, and exhibits variability in its reproductive system that shows clear patterns of
171 inheritance (progeny after selfing are mostly self-compatible; Arista et al., 2017).
172 Moreover, the species shows inbreeding depression, which varies spatially and
173 temporally in intensity (Arista et al., 2017). Lastly, plants produce two types of fruits
174 that presumably differ in dispersal distance and fruit-morph ratio can give an estimator
175 of dispersibility of the progeny. Changes in fruit-morph ratio may affect fitness through
176 changes in the dispersal rate of the progeny (Venable, 1985; Olivieri et al., 1995), and it
177 could evolve if it is heritable. The combination of mixed mating systems and
178 heterocarpy could give rise to either of two contrasting associations between selfing and
179 lower/greater dispersibility, as mentioned above. On one hand, given the high level of
180 inbreeding depression of *H. salzmanniana*, a strong selection for greater dispersibility
181 of selfed progeny is expected to lower the risk of inbreeding. On the other hand, under
182 conditions of pollination environment fluctuations, outcrossers would benefit from
183 dispersal, and consequently the link between selfing and non-dispersal (or lower
184 dispersal) is to be expected.

185 We use a combination of observations of natural populations and experimental hand

186 pollinations to test for heritability and changes in dispersibility in relation to breeding
187 system (i.e. among-individual level) and pollen source (i.e. within-individual level).
188 Specifically, we want to answer the following questions: 1) Is fruit-morph ratio a
189 heritable trait? This is a necessarily condition for a trait to evolve 2) Does selfing affect
190 fruit production and fruit traits affecting dispersal ability? If so, is this a consequence of
191 inbreeding depression or a strategy to avoid it? 3) Are there differences in fruit-morph
192 ratios between self-compatible and self-incompatible plants? and 4) Does pollen source
193 (self vs. cross) affect fruit-morph ratio in self-compatible plants? The ability to
194 increased fruit-morph ratio after selfing could represent an advantage to avoid
195 inbreeding depression, while an increased fruit morph ratio after outcrossing could be
196 seen as a selective pressure favoring outcrossers in unfavorable pollination
197 environments.

198 MATERIAL AND METHODS

199 *Study species and populations studied*—*Hypochoeris salzmanniana* is an annual
200 species belonging to the tribe Lactuceae from the Asteraceae family, endemic to a
201 restricted area in both sides of the strait of Gibraltar (SW Spain – NW Morocco). Its
202 fruit heads produce two wind-dispersed fruit types (achenes with plumes; Fig. 1): non-
203 beaked plumed fruits at the periphery of the head, and beaked plumed fruits at the
204 center.

205 Field study was carried out for two consecutive years in five natural populations of *H.*
206 *salzmanniana* occurring along an environmental cline in southwestern Spain (Cádiz
207 province). These populations were from West to East: Conil (36.21° N, 6.06° W), Caños
208 (36.20° N, 6.05° W), Barbate, (36.21° N, 5.93° W), Zahara (36.14° N, 5.86° W), and
209 Tarifa (36.13° N, 5.84° W). All of them occur on the first sand dune of the coast, with

210 the exception of Barbate, where plants grow in a fixed dune under a forest of *Pinus*
211 *pinea* L., about 2 km from the sea shore. These populations show important differences
212 in self-incompatibility, with self-incompatible plants decreasing in frequency towards
213 the east due to an increase of winds during flowering which affect pollinator activity
214 (Arista et al., 2017). Self-incompatibility of these populations was studied in 2002,
215 2003, 2014 and 2015; in all years, Tarifa and Zahara were composed mainly of self-
216 compatible plants, while Conil, Caños and Barbate of self-incompatible ones (Ortiz et
217 al., 2006; Arista et al., 2017).

218 ***Fruit traits affecting dispersal ability and differences between the two types of***
219 ***fruits***— Traits that could affect fruit dispersal ability were recorded in the two types of
220 fruits by measuring the lengths of the plume, the beak and the fruit, the opening
221 diameter of the plume, the width of the fruit and the total weight of the fruit (Fig. 1).
222 These traits were measured in 6-15 fruits coming from 18 plants from Zahara and
223 Barbate populations (in total, 75 beaked and 77 non-beaked, hereafter BF and NBF).
224 Plume loading was calculated as fruit weight/plume area (Andersen, 1993). Plume
225 shape was assumed as the lateral surface of an inverted cone, with the cone base area as
226 the plume area. Note that plume loading is not calculated with plume length.
227 To determine the relative wind dispersal ability of both types of fruits, we used two
228 estimates: dropping velocity and dispersal distance. Dropping velocity was calculated
229 by taking the fall time of each fruit at 2m height. The same observer recorded the time
230 in each case. Although fall time is considered a proxy for dispersal distance in many
231 studies (e.g. Cody and Overton, 1996; Fresnillo and Ehlers, 2008), we also estimated
232 differences in dispersal distance between fruits by using a wind tunnel. The wind tunnel
233 consisted of a transparent tube 8m long, with an industrial fan placed at one end,
234 producing a simulated wind source of 2.5 m/s measured by a Brunton Sherpa

235 anemometer (Louisville, Colorado, USA). In the tube, just at the top of the fan, a small
236 hole permitted the release of each fruit, which was dragged along the tube. Distances
237 reached by each fruit through the tube were then recorded.

238 **Potential for long dispersal in wild populations**—For two consecutive years in the five
239 aforementioned natural populations, 35 to 61 plants were marked, and one head per
240 plant was tagged at the beginning of flowering time. After flowering and before fruit
241 ripening, the heads were bagged in order to avoid fruit loss. Fruits were collected when
242 ripe and the number of beaked and non-beaked fruits per flower head was counted. Both
243 types of fruits in *H. salzmanniana* have plumes but, as will be shown in the results, BF
244 disperses at longer distances than NBF. Thus, for each plant we calculated the
245 proportion of BF per head (hereafter BF ratio) as an estimate of long-dispersal potential
246 (Imbert, 2001; Cheptou *et al.*, 2008). BF ratio ranges from zero to one, and the higher
247 BF ratio is, the higher mean dispersal ability will be.

248 **Heritability of BF ratio** — To establish an evolutionary association between mating
249 systems and the potential for long dispersal, both traits have to be heritable. Self-
250 incompatibility is a known heritable trait but, to our knowledge, the heritability of the
251 potential for long dispersal has only been demonstrated once (Imbert, 2001); thus, it
252 needs to be investigated in this species. To estimate the heritability of BF ratio, we used
253 F₁ and F₂ plants growing in a common glasshouse to avoid the effects of different
254 environments (Holland *et al.*, 2003). In summer 2014, fruit heads were collected from
255 marked plants of two natural populations of *H. salzmanniana* (Barbate and Zahara). In
256 each population, ten plants separated at least 20m from each other were selected, and
257 one fruit head was collected from each. All the fruits on each head represented a family,
258 totaling ten families per population. Ripe fruits were stored in the laboratory until

259 autumn, when they were germinated in a growing chamber and the plants were sown in
260 a glasshouse. In spring 2015, one flowering plant from each family was randomly
261 chosen to study the heritability of dispersal ability. The remaining plants were used to
262 study the link between dispersibility and breeding system (see below). The selected
263 plants (F_1) were hand-pollinated in a diallel cross design with plants from the other
264 families. Given that *H. salzmanniana* plants produced between 5-7 flower heads in the
265 glasshouse and that some plants were self-incompatible, the cross design was
266 incomplete. The final sample size was ten families, six from Barbate and four from
267 Zahara. Fruit heads resulting from these pollinations were collected, their production of
268 BF and NBF was counted, and BF ratios were calculated. All these fruits were sown,
269 and the resulting F_2 plants cultivated in the glasshouse (n=44 plants from families of
270 Barbate, and n=33 plants from families of Zahara); in spring 2016, two flower heads
271 from each plant were hand-pollinated with a mixture of pollen from three plants of the
272 other families to ensure pollination with compatible pollen. Each flower head was
273 pollinated twice during its anthesis to ensure all the flowers on the heads received
274 pollen; they were then bagged to avoid fruit loss when ripe. These fruit heads were
275 collected, and the mean number of BF and NBF per head and BF ratio in each plant
276 were calculated.

277 ***Dispersibility and its relationship with breeding systems*** — The link between breeding
278 system and BF ratio was studied at two different levels: we determined the possible
279 differences in BF ratio between self-incompatible (SI) and self-compatible (SC) plants,
280 and between outcrossed and selfed heads on SC plants. We used the remaining 134
281 plants from the heritability study, as described above, grown in a glasshouse from fruit
282 heads of 12 plants collected in 2014 from two wild populations (Barbate and Zahara; 6
283 families per population, 6-15 plants per family). On each plant, two flower heads were

284 tagged at the beginning of the flowering period, one was hand cross-pollinated twice
285 during its anthesis with pollen from three different donors, and the other was self-
286 pollinated. The number of flowers and fruits of both selfed- and cross-pollinated heads
287 were recorded. Fruits were categorized as BF or NBF, and BF ratio was calculated for
288 each fruit head. Additionally, to test differences linked to pollen source in fruit traits
289 affecting dispersal ability, some of those fruits were weighed (n=581) and their plume
290 lengths were measured (n=129).

291 For each plant grown in the glasshouse, we calculated the fruit set (i.e. fruit to flower
292 ratio) per head of each treatment. With those data, the index of self-incompatibility (ISI)
293 was calculated using the formula $ISI = \text{fruit set in self-pollinated heads} / \text{fruit set in}$
294 $\text{cross-pollinated heads}$ (Zapata and Arroyo, 1978). A plant is considered fully self-
295 compatible (FSC) when ISI is ≥ 1 , partially self-compatible (PSC) when ISI is ≥ 0.2 but
296 < 1 , and fully self-incompatible (SI) when ISI is < 0.2 (Zapata and Arroyo, 1978). Given
297 that we want to assess the importance of selfing versus outcrossing in BF ratio, we will
298 consider all plants with any degree of self-compatibility together, and they will be
299 referred to as self-compatible plants (SC).

300 **Statistical analyses**— Differences in morphological traits (weight, length and width of
301 the fruit, plume length and diameter, and plume loading) and dispersal abilities
302 (dropping velocity and dispersal distance) between types of fruits (NBF vs. BF) were
303 tested using different linear mixed-effects models (LMM), including the fruit and
304 family as random effects nested within population (trait ~
305 fruit_type+Plant+Population+1|Fruit/Plant/Population). For this purpose, we used the
306 *lme* function of the *nlme* package (Pinheiro et al., 2017) in R software (R Core Team,
307 2017). Moreover, we performed linear regressions to test which morphological
308 variables of fruits were important predictors of 1) dropping velocity and 2) the dispersal

309 distance of fruits. Two different models were used in each case, including the following
310 predictors: a) plume loading, plume length and population, and b) fruit weight, fruit
311 length, plume length and population. Additionally, Pearson correlations between fruit
312 morphological traits were also tested.

313 To estimate the heritability of BF ratio we used parent-offspring linear regressions of F₂
314 offspring over the F₁ mother plants using *lm* function in R software. Heritability (h^2)
315 was estimated using the regression coefficient (Lynch and Walsh, 1998). Spearman
316 correlations between the production of each fruit type of F₁ and F₂, and between the BF
317 ratio of F₁ and F₂ were also performed.

318 Differences in BF ratio in natural populations were tested using generalized linear
319 models (*glm* function in R) with binomial distribution, considering population and year
320 as main factors, and the interaction between them (BFratio~pop+year+pop:year).

321 Comparisons among populations and years were performed by calculating the estimated
322 marginal means using the *emmeans* package (Lenth, 2018), and the *cld* function of the
323 *multcomp* package in R (Hothorn *et al.*, 2008).

324 Differences in BF ratio according to breeding system were tested with generalized
325 linear mixed-effects models (GLMM) with binomial distribution, including the family
326 as random effect nested within population (BF ratio~SI_system+1|family/population),
327 using the *glmer* function from the *lme4* package in R (Bates *et al.*, 2015). The effect of
328 self-incompatibility system was tested by two different ways: 1) using outcrossed heads
329 of SI plants, and both outcrossed and selfed heads of SC plants; this situation is likely
330 realistic, as in the field SC plants would produce a mixture of outcrossed and selfed
331 fruits, while SI plants would produce only outcrossed fruits, and 2) using outcrossed
332 heads of both SI and SC plants, in order to compare the effect of the self-incompatibility
333 system in heads exposed to a similar pollen source. Both treatments had similar results,

334 and only the first one is exposed in the results.
335 Moreover, we also assessed differences in BF ratio according to pollination type (self or
336 cross) in SC plants by a GLMM with binomial distribution
337 ($\text{BFratio} \sim \text{pollination_type} + (1 | \text{family/population})$) using *glmer* function in R. Lastly,
338 differences in the weight and plume length of both types of fruits (BF and NBF)
339 resulting from selfing or outcrossing were also tested with LMM, including the family
340 as random effect nested within population ($\text{trait} \sim \text{fruit_type} + (1 | \text{family/population})$).
341 The effect of self incompatibility or pollination type (selfing vs outcrossing) on other
342 response variables normally distributed (number of NBF and BF, and total number of
343 fruits per head) were tested with General Mixed-Effects Models, including the family as
344 random effect nested within population ($\text{response_var} \sim \text{treatment} + \text{population} + \text{year}$,
345 ($\text{random} = \sim 1 | \text{family/population}$)), with *lme* function in R.
346 To check for linear model assumptions, Shapiro-Wilk tests for normality and Levene
347 tests for homocedasticity were performed. Models were compared after re-estimating
348 them using maximum likelihood by the *update* function in R. In order to get the best fit,
349 non-significant fixed factors were dropped out the model. The models with lower AIC
350 were selected for this study.

351 **RESULTS**

352 ***Fruit traits affecting dispersal ability and differences between the two types of***
353 ***fruits***— The types of fruits differed in all the morphological traits, except fruit length,
354 and in the two estimates of dispersal ability (Table 1).

355 Beaked fruits (BF) were significantly thinner and slighter, and had longer plumes with a
356 wider opening diameter than non-beaked fruits (LMM, $P < 0.01$; Table 1). Beaked fruits
357 showed lower dropping velocity (0.44 ± 0.01 m/s BF vs. 0.60 ± 0.01 m/s in NBF; $P <$

358 0.001; Table 1) and reached higher dispersal distances in the wind tunnel (1.76 ± 0.07 m
359 BF vs. 1.58 ± 0.06 m NBF; $P < 0.05$; Table 1). Plume loading was significantly lower in
360 BF (0.006 ± 0.002 mg/mm²) than in NBF (0.012 ± 0.005 mg/mm²; $P < 0.001$; Table 1).
361 Linear regressions showed that plume loading significantly affected fruit dropping
362 velocity ($F_{1, 149} = 217.12$, $P < 0.001$) and dispersal distance reached in the wind tunnel
363 ($F_{1, 149} = 9.97$, $P = 0.002$). In the model including all fruit traits, fruit dropping velocity
364 was significantly affected plume diameter ($F_{1, 148} = 163.23$, $P < 0.001$), fruit weight ($F_{1, 148} = 156.63$, $P < 0.001$) and plume length ($F_{1, 148} = 38.05$, $P < 0.001$). In contrast, the
365 sole predictor of dispersal distance was plume diameter ($F_{1, 150} = 14.47$, $P < 0.001$). No
366 effect of the population of origin was observed in those models ($P > 0.05$).
367
368 Significant negative correlations were found between fruit weight and plume diameter
369 ($r = -0.24$, $P = 0.003$, $n = 152$), and between fruit weight and plume length ($r = -0.20$, $P =$
370 0.015 , $n = 152$). Additionally, fruit dropping velocity was negatively correlated to
371 dispersal distance ($r = -0.29$, $P < 0.001$, $n = 152$).
372 **Potential for long dispersal in wild populations**— The BF ratio of *H. salzmanniana*
373 significantly differed among populations (Wald χ^2 test, $P < 0.001$) and between years (P
374 < 0.001). The two easternmost populations, Zahara and Tarifa, showed the highest BF
375 ratio (Fig. 2). The population-by-year interaction was significant (Wald χ^2 test, $P <$
376 0.001), since in 2015 BF ratio decreased in three populations but increased in the other
377 two (Fig. 2).
378 **Heritability of each fruit type and of BF ratio**— All studied plants produced both
379 types of fruits, but we observed heads with only one type of fruit, especially with only
380 BF ($n = 12$), but also with only NBF ($n = 2$). When both types of fruits were produced in
381 the heads (93% of the analyzed heads), NBF were always located at the periphery,
382 although their number was extremely variable among heads (range: 1-53; mean: 15).

383 Beaked fruits were produced at the center of the head, and their number was also
384 extremely variable (range: 1-96; mean: 37). The number of both types of fruits were
385 markedly correlated with total fruit production ($P < 0.001$), but the correlation
386 coefficient of BF was higher ($\rho = 0.81$; $n = 74$) than that of NBF ($\rho = 0.63$; $n=74$).
387 The mean number of BF per head of the progeny (F_2) were directly correlated with
388 those of their F_1 mother plants ($\rho=0.54$, $n=74$, $P < 0.001$). Similarly, a significant
389 correlation was found between the mean number of NBF per head of F_1 and F_2 ($\rho=0.61$,
390 $n=74$, $P < 0.001$). Mean BF ratio of F_1 plants was 0.579 ± 0.022 , while for F_2 , mean BF
391 ratio was 0.662 ± 0.016 . The BF ratio of F_2 plants were positive and significantly
392 correlated with those of their F_1 mothers ($\rho=0.62$, $P < 0.001$, $n=74$). A significant linear
393 regression BF ratio of F_2 to F_1 showed that heritability (h^2) was 0.51 (Fig. 3).

394 *Dispersibility and its relationship with breeding systems*

395 In self-compatible plants, the type of pollen received by a flower head (self or outcross)
396 influenced BF ratio of the fruit head, as well as fruit traits affecting dispersibility (fruit
397 weight and plume length). Fruit production was slightly higher in outcrossed heads than
398 in selfed ones, but this result was only marginally significant ($F_{1, 118} = 3.55$, $P = 0.062$).
399 Although the production of each fruit type was similar between selfing and outcrossing
400 treatments (NBF: $F_{1, 118} = 3.06$, $P = 0.083$; BF: $F_{1, 118} = 2.62$, $P = 0.110$), fruit heads
401 produced by selfing showed significantly higher BF ratio than those produced by
402 outcrossing ($Z = 2.46$, $P = 0.014$; Fig. 4A).

403 In relation to fruit traits, after accounting for genetic family, fruits produced after selfing
404 were markedly lighter than after outcrossing ($F_{1, 540} = 117.03$, $P < 0.001$), and BF were
405 always lighter than NBF ($F_{1, 540} = 275.14$, $P < 0.001$); the fruit type by cross type
406 interaction was not significant ($P > 0.05$). BF had a mean weight of 1.4 ± 0.029 mg
407 after selfing, and of 1.8 ± 0.027 mg after outcrossing, while NBF had 2.04 ± 0.35 mg

408 and 2.46 ± 0.26 mg after selfing and outcrossing respectively. Plume length of fruits
409 after selfing were also significantly different than after outcrossing, but the tendency
410 was opposite to that found in fruit weight: after accounting for genetic family, BF had
411 always longer plume lengths than NBF ($F_{1, 114} = 35.67$, $P < 0.001$), and plume length
412 was significantly longer in fruits after selfing (13.44 ± 0.18 mm) than after outcrossing
413 (12.49 ± 0.17 mm; $F_{1, 114} = 7.28$, $P = 0.008$), a trend which was maintained in both BF
414 and NBF types (fruit type by cross type interaction not significant; $P > 0.05$).
415 Models for total fruit production, number of BF and number of NBF as response
416 variables revealed that self-incompatibility was not a significant predictor ($P > 0.05$).
417 Average BF ratio was higher in self-compatible plants, but the GLMM model did not
418 show significant differences among incompatibility types ($P > 0.05$; Fig. 4B).

419 **DISCUSSION**

420 This work provides empirical evidence about the differences in dispersal ability of fruits
421 in the annual heterocarpic *Hypochoeris salzmanniana*, and about the link between
422 selfing and greater dispersibility at different levels. In this species, both types of fruits
423 differed in beak presence, and beaked fruits (BF) were lighter, and produced longer
424 plumes with a wider aperture diameter than NBF. Plume loading affected dropping
425 velocity, as has been previously found in other Asteraceae (Andersen, 1993), and also
426 dispersal distance of fruits. While analyzing traits separately, fruit weight, plume
427 diameter and plume length affected dropping velocity. In contrast, the diameter of the
428 plume was the sole trait affecting fruit dispersal distance. Fruit weight was negatively
429 correlated with both plume length and plume diameter, leading to the following
430 tendencies: the lighter the fruits, the larger the length and diameter of plume, and thus
431 the lower the dropping velocity and the longer the dispersal distance. In fact, we have

432 found experimentally that BF had a lower dropping velocity and a longer dispersal
433 distance than NBF. This suggests that in the field, BF are responsible for the long-
434 distance dispersal, while NBF disperse more locally. Thus, the percent of beaked fruits
435 (BF ratio) is a good estimate of the potential capacity for long dispersal of a plant. Our
436 study also demonstrates that fruit dropping velocity is negatively correlated to dispersal
437 distance, and thus dropping velocity is a useful trait as a surrogate of dispersal distance
438 in wind-dispersed species (Cody and Overton, 1996; Fresnillo and Ehlers, 2008; de
439 Waal et al., 2014).

440 BF ratio in *H. salzmanniana* is a trait with a high narrow-sense heritability, as h^2 for
441 mid-parent regression was 0.51. From this result, we can conclude that phenotypic
442 variance for dispersal ability has a genetic component. However, we must take into
443 account that genetic variance depends on allelic frequencies, and thus, estimation of h^2
444 is population-dependent. As our experimental design included crosses of plants from
445 two different populations, the heritability level found in *H. salzmanniana* could be
446 overestimated. In the other sole species to our knowledge in which the heritability of a
447 dispersal ratio has been measured, *Crepis sancta*, narrow-sense heritability was higher
448 than 0.2, despite the ontogenetic contingency observed in this species (Imbert, 2001).

449 This suggests that dispersibility is heritable in Asteraceae.

450 The most important result we have found is a strong link between selfing and greater
451 dispersibility at two scales. Selfing leads to 1) a higher proportion of long-dispersible
452 progeny (i.e. higher BF ratio), and 2) fruits with traits that increase dispersal ability. In
453 our study species, selfed and outcrossed fruits differed markedly in mass, selfed fruits
454 being much lighter but with longer plumes, irrespective of position in the head. Given
455 that fruit weight and plume diameter were negatively correlated, and that plume loading
456 was the most important variable affecting dispersibility, lighter fruits dispersed at longer

457 distances. Thus, both selfed BF and NBF dispersed at longer distances than those from
458 outcrossing. Differences in mass could be due to inbreeding depression, as this species
459 shows high levels of inbreeding depression at different life-stages as well as throughout
460 the total life cycle (Arista et al., 2017); but inbreeding depression cannot account for the
461 longer plumes of selfed fruits as they would be more costly. Iritani and Cheptou (2017)
462 proposed that, alternatively to the inbreeding depression interpretation, the lower size of
463 selfed seeds could be an adaptive trait mediating differential seed dispersal. In our
464 studied species, the fact that plume length of selfed fruits was significantly longer than
465 that of outcrossed fruits, promoting a higher dispersibility, also supports the adaptive
466 significance of the greater dispersal ability of selfers.

467 Although the numbers of NBF and BF fruits were similar after both pollination
468 treatments in SC plants, we found that the BF ratio of *H. salzmanniana* was
469 significantly higher in selfed than in outcrossed heads. This suggests that, after selfing,
470 plants could reallocate resources to increase their BF ratio. Changes in BF ratio due to
471 resource reallocation has been documented in other Asteraceae, leading to an increased
472 dispersal rate of their progeny under stressful conditions (Imbert & Ronce, 2001) or to a
473 decreased wind dispersal rate with increased density (Baker and O'Dowd, 1982; Ruiz de
474 Clavijo and Jimenez, 1998). However, in both cases it is not possible to reject
475 developmental constraints as a source of variation in fruit morph proportions (Imbert &
476 Ronce, 2001). In fact, in the tribe Lactuceae, the number of peripheral flowers in a head
477 is expected to be bounded to 13 (Imbert & Ronce, 2001). However, in *H. salzmanniana*,
478 we found a wide range of NBF (up to 53), and significant correlations between
479 peripheral NBF and total fruits, and between NBF of mother plants and progeny were
480 observed, suggesting maternal effects. Thus, in our study, developmental constraints do
481 not seem the main source of variation in fruit morph proportions. Rather, the differences

482 in BF ratio could be seen as an ability to modulate the potential for long dispersal of
483 offspring based on its selfed or outcrossed origin. This ability would be advantageous,
484 and therefore could be selected, under unpredictable pollination conditions. However,
485 further observations in fruit-development phenology within the flower heads would be
486 necessary to check whether a resource allocation adjustment among fruit types is acting.
487 In any case, the adaptive significance of the response of BF ratio to pollen source is
488 difficult to interpret, since fruit types could differ by other characteristics, as dormancy
489 (Venable and Levin 1985; Picó et al., 2003), that could provide distinct ecological
490 differences to each fruit type (Gibson, 2001).

491 The results recorded in five natural populations of *H. salzmanniana* over two years also
492 uphold the link between selfing and dispersibility found glasshouse experiments.

493 Populations with a high proportion of SC plants and worse pollinator environment due
494 strong winds (Zahara and Tarifa) showed higher BF ratio than more self-incompatible
495 populations (Conil and Barbate; Ortiz et al., 2006; Arista et al., 2017). Thus, high
496 potential for long dispersal appears to be associated with self-compatibility and worse
497 pollinator environment. These results do not support the local adaptation hypothesis
498 which predicts that selfed progeny will perform better in the local area because they
499 conserve a genetic combination adapted to the present environment (Schmitt and
500 Gamble, 1990). Our results are also opposed to those of the extension of Cheptou-
501 Massol models (Cheptou and Massol, 2009; Massol and Cheptou, 2011; Sun and
502 Cheptou, 2012). In these models, self-fertilization evolves when environment limits
503 pollination, as has been suggested in natural populations of *H. salzmanniana* (Arista et
504 al., 2017). However, those theoretical models assume a decrease in inbreeding
505 depression in self-pollinating plants, and thus a low pressure for dispersal. This situation
506 is not found in *H. salzmanniana* where self-compatible plants suffer inbreeding

507 depression (Arista et al., 2017). Given the high cost of inbreeding in this species, the
508 greater dispersibility of selfed progeny could represent a strategy to avoid that cost.
509 Moreover, seedlings resulting from inbreeding are closely related; therefore, the
510 avoidance of sib-competition cannot be ruled out as a selective pressure for dispersal
511 (Cheplick, 1993a). In fact, the consequences of inbreeding depression for the evolution
512 of dispersal cannot be understood without taking into account its complex interactions
513 with sib competition (Ronce, 2007).

514 The link of selfing and greater dispersibility found in *H. salzmanniana* is also supported
515 by a theoretical study which predicts that selfing selects for and is selected for an
516 increased seed dispersal, although the evolutionary outcome is strongly influenced by
517 the relative cost of pollen vs. seed dispersal (Ravigné et al., 2006). More recently, Iritani
518 and Cheptou (2017) developed several theoretical models, with increasing complexity,
519 for the evolution of mating system and differential seed dispersal in metapopulations,
520 incorporating heterogeneous pollination, dispersal cost, outcrossing cost and
521 environment-dependent inbreeding depression. In those models dealing with the joint
522 evolution of multiple traits, evolutionary patterns not predicted on previous simpler
523 models (Cheptou and Massol, 2009; Massol and Cheptou, 2011a) arise and show that,
524 when selfing and dispersal evolve together, evolution would lead to higher or equal
525 dispersal rate for selfed seeds compared to that for outcrossed (Iritani and Cheptou,
526 2017).

527 Within-species variability in dispersal traits indicates that dispersal strategies can be
528 evolutionarily labile (Van Den Elzen et al., 2016). In our study species, the heritability
529 of dispersibility and the existence of variability in BF ratio in natural populations
530 suggest that changes in long-distance dispersibility over a few generations of selection
531 are possible in this species, as demonstrated in *Crepis sancta* (Cheptou et al., 2008).

532 The heritable character of self-compatibility in *H. salzmanniana* (Arista et al., 2017)
533 also implies that more dispersible fruits produced after selfing give rise preferentially to
534 self-compatible plants, which would be more successful in founding new colonies than
535 self-incompatible ones, due to reproductive assurance by uniparental reproduction
536 (Pannel, 2015). This is crucial for an annual plant whose populations shows high
537 stochasticity in pollinator conditions.

538 In conclusion, our study shows that the two types of fruits of *H. salzmanniana* differ in
539 dispersal availability and that BF ratio is a heritable trait related with long dispersal
540 potential. The link found experimentally between selfing and greater BF ratio has also
541 been recorded in natural populations over two years, and seems to have been selected as
542 a way of avoiding inbreeding depression of selfers. Self-fertilization in *H. salzmanniana*
543 could enhance the colonization of vacant habitat patches, sustaining metapopulations
544 (Olivieri et al., 1983, 1995; Pannell and Barrett, 1998, Pannell et al., 2015), and the
545 potential expansion of the species' geographic distribution at range margins (Thomas et
546 al., 2001; Travis and Dytham, 2002; Darling et al., 2008). The enhanced dispersal rates
547 observed at range margins, as detected in *Abronia umbellata* (Nyctaginaceae; Darling et
548 al., 2008) and also in exotic ranges of invasive species such as de congeneric
549 *Hypochaeris glabra* (Martín-Fores et al., 2018) confirms the importance of dispersal
550 modeling plant distributions. Moreover, dispersal plays a key role in species' responses
551 disturbances (Harveargres and Eckert, 2014), as habitat loss or fragmentation, which
552 represent current conservation problems that involve changes in species' distributions
553 (Sexton et al., 2009). This work contributes to understanding the link between mating
554 systems and dispersal adaptation in an endangered species inhabiting a fragile habitat
555 with unfavorable pollinator environment, and highlight the association between selfing
556 and higher dispersibility. Our contribution can also give insights to understand the joint

557 evolution of selfing and dispersibility and its influence plant distributions in ways that
558 are important in the current context of environmental challenges, such as the decline of
559 pollinators and habitat loss.

560

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756 **Table 1.** Morphological traits and differences in dispersal ability of beaked and non-
 757 beaked fruits of *H. salzmanniana*. Differences are tested using Linear Mixed-Effects
 758 Models, including the family as random effect nested within population.
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 760

Trait	Fruit type	Mean \pm SE	F-value	numDF	denDF	<i>P</i>
Weight (mg)	BF	1.89 \pm 0.03	253.17	1	149	***
	NBF	2.92 \pm 0.06				
Fruit length (mm)	BF	5.05 \pm 0.05	0.69	1	149	ns
	NBF	5.02 \pm 0.05				
Fruit width (mm)	BF	0.78 \pm 0.01	25.67	1	150	***
	NBF	0.68 \pm 0.01				
Beak length (mm)	BF	3.63 \pm 0.11	1108.35	1	150	***
	NBF	0.00 \pm 0.00				
Plume length (mm)	BF	14.59 \pm 0.18	7.38	1	149	**
	NBF	13.68 \pm 0.17				
Plume diameter (mm)	BF	20.10 \pm 0.30	25.67	1	150	***
	NBF	17.99 \pm 0.29				
Plume loading (mg/mm ²)	BF	0.006 \pm 0.002	97.53	1	150	***
	NBF	0.012 \pm 0.005				
Dropping velocity (m/s)	BF	0.44 \pm 0.01	144.30	1	150	***
	NBF	0.60 \pm 0.01				
Dispersal distance (m)	BF	1.76 \pm 0.07	3.99	1	150	*
	NBF	1.58 \pm 0.06				

761
 762 * *P* < 0.05; ** *P* < 0.01 ****P* < 0.001; ns, *P* > 0.05
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 765

766 **Figure captions:**

767

768 **Figure 1.** Types of fruits of *Hypochoeris salzmanniana*. A) Beaked fruit (BF); B) Non-
769 beaked fruit (NBF). Measures performed to characterize both types of fruits are shown.
770 pl, plume length; be, beak length; ac, achene length; fw, fruit width, pd, plume diameter.
771 All measures except beak length were performed in both types of fruits.

772

773 **Figure 2.** BF ratio (calculated as the percentage of beaked fruits per head for each
774 plant) in five natural populations during the years 2014 and 2015. Error bars represent
775 standard errors of the means. Different letters indicate significant differences among
776 populations and years, calculated from estimated marginal means of the glm model ($P <$
777 0.05).

778

779 **Figure 3.** BF ratio of the parental plants (F1) over their progeny (F2), showing the
780 heritability of potential for long dispersal. Regression line and statistical test results are
781 shown.

782

783 **Figure 4.** Boxplots of showing BF ratios (percentage of beaked fruits per head for each
784 plant) in A) self-compatible plants after selfing and outcrossing pollination treatments;
785 and B) self-compatible (SC) and self-incompatible (SI) plants. Asterisk shows
786 significant difference among treatments based on a GLMM model with binomial
787 distribution.

788

789

Fig. 1

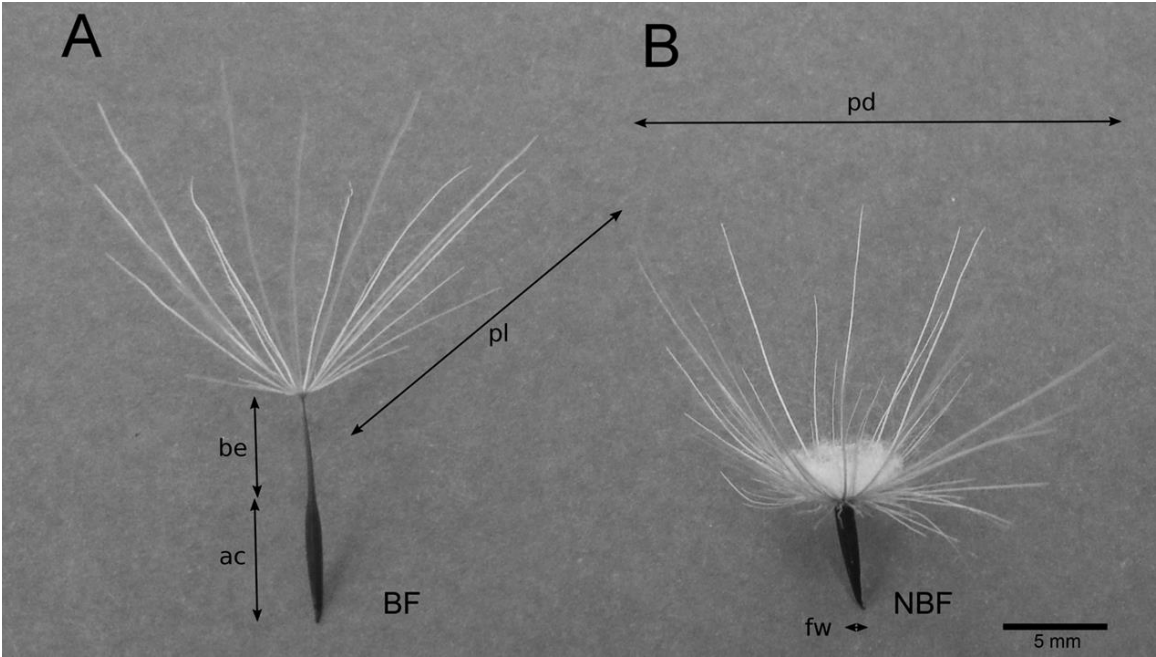


Fig. 2

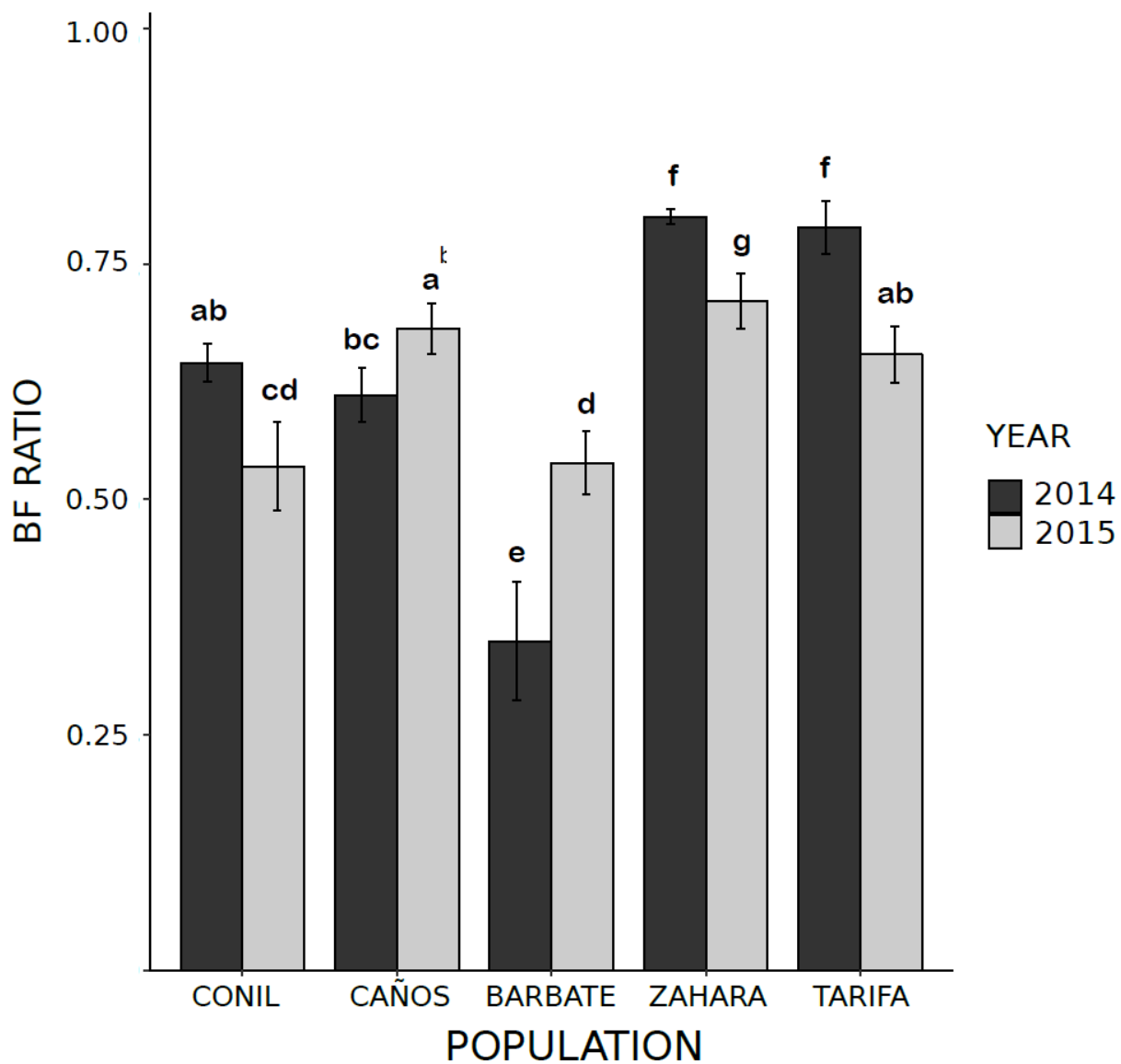


Fig. 3

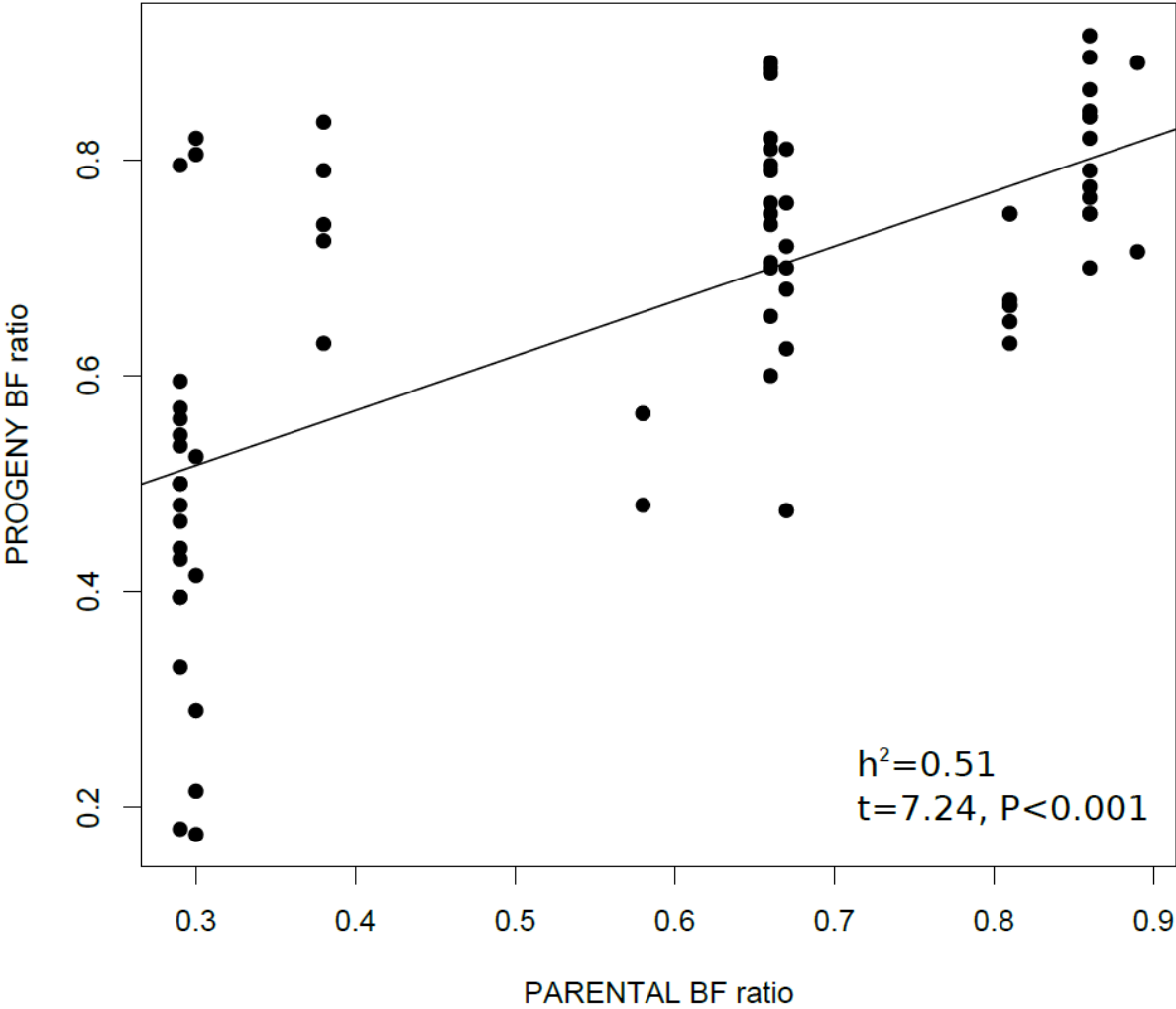


Fig. 4

