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3 **SOCIAL INFORMATION AND BIOLOGICAL INVASIONS: CHORUS**

4 **SONGS ARE MORE ATTRACTIVE TO EUROPEAN STARLINGS IN MORE**

5 **RECENTLY ESTABLISHED POPULATIONS.**

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26 ABSTRACT

27

28 When biological invasions by animals occur, the individuals arriving in novel
29 environments can be confronted with unpredictable or unfamiliar resources and may
30 need social interaction to improve survival in the newly colonized areas. Gathering
31 with conspecifics and using social information about their activities may reveal the
32 location of suitable feeding and breeding sites. This could compensate for the absence
33 of individual information about new habitats and constitute an advantage for new
34 settlers. If a tendency to gather in response to social stimuli is transmitted from one
35 generation to the next, and if the benefit of gathering is lower in long time established
36 populations, there should be behavioural differences in receptivity to social cues in
37 populations with different colonizing histories. We hypothesized that individuals of a
38 social species like the European starling from relatively recently-established
39 populations would be more responsive to social cues than individuals belonging to
40 long-established populations. We conducted playback experiments using a starling
41 chorus to test its acoustic attractiveness to populations of starlings with different
42 colonizing histories. We compared the reaction of individuals from two populations
43 in rural Brittany, western France, established for a long time, with three more recently
44 settled ones: two populations from a propagation front in southern Italy and one urban
45 population from Rennes city in Brittany. Our data supported our hypothesis:
46 individuals from more recent populations were more responsive to the acoustic
47 stimulus, and gave more calls in flight than individuals from populations with an
48 older settlement history. We discuss the different behavioural responses we observed
49 in the different populations and the potential effects of habitat characteristics and
50 starling densities.

51 RESUMEN

52 Los individuos que llegan a un nuevo hábitat en las primeras etapas de una invasión
53 biológica pueden verse confrontados a una distribución impredecible de los recursos
54 y por ello pueden necesitar recurrir a interacciones sociales para aumentar su
55 probabilidad de supervivencia en las nuevas áreas colonizadas. Agruparse con otros
56 individuos de su misma especie y utilizar la información social producida por las
57 actividades de estos últimos puede permitir la localización de áreas ventajosas de
58 alimento o de reproducción. La información social obtenida de esta forma puede
59 constituir una ventaja y compensar la falta de información personal de los nuevos
60 individuos que llegan a ese nuevo hábitat. Si existe una tendencia a agruparse al
61 detectar señales sociales y si esta tendencia puede ser transmitida de una generación a
62 la otra podrían existir diferencias comportamentales en la receptividad a las señales
63 sociales entre poblaciones cuyas historias de colonización difieren.

64 Emitimos una hipótesis según la cual los individuos de poblaciones recientemente
65 establecidas en nuevas áreas geográficas serían más receptivos a señales sociales que
66 los individuos pertenecientes a poblaciones establecidas durante un largo lapso de
67 tiempo en un área bien conocida por la población. Para explorar esta hipótesis
68 llevamos a cabo un estudio sobre un ave social invasora, el Estornino pinto. Para ello
69 realizamos experimentos de difusión acústica gracias a grabaciones de un coro de
70 estorninos con el fin de evaluar la atractividad de los cantos ejercida sobre individuos
71 de poblaciones con historias diversas. Comparamos la reacción comportamental de
72 individuos pertenecientes a dos poblaciones antiguas situadas en las áreas rurales de
73 Bretaña, región del oeste francés con la reacción de aves pertenecientes a tres
74 poblaciones más recientes: dos poblaciones del frente de propagación situado al sur
75 de Italia y una población urbana reciente ubicada en el centro de la ciudad de Rennes.

76 Los resultados que obtuvimos apoyan la hipótesis emitida: los individuos
77 pertenecientes a las poblaciones más recientes fueron más reactivos al estímulo
78 acústico y emitieron más frecuentemente vocalizaciones durante el vuelo que los
79 individuos provenientes de poblaciones con un período mayor de asentamiento en sus
80 áreas. Discutimos las diferentes respuestas comportamentales observadas y
81 comentamos el posible efecto de otras variables como las características del hábitat y
82 las densidades poblacionales.

83

84 *Key words: social facilitation, biological invasions, vocal attractiveness,*

85 *Sturnus vulgaris, propagation front, local enhancement*

86

87 INTRODUCTION

88 Research on biological invasions by animals has recently focused on behavioural
89 approaches (Holway and Suarez 1999). Various studies have concentrated on aspects
90 of the social behaviour of invasive populations. Detailed studies of introduced
91 invasive ant species such as the Argentine ant *Linepithema humile* and the Fire ant
92 *Solenopsis invicta* (Holway et al. 1998, Suarez et al. 1999) found that introduced ants
93 from colonies in propagation fronts formed large supercolonies and presented lower
94 levels of intraspecific aggression than colonies from original anciently established
95 populations. This reduction in territorial behaviour between individuals of
96 neighbouring nests appears as one possible explanation for the establishment success
97 of this species in the areas of introduction. Social life and interactions with
98 conspecifics may be particularly relevant during the colonization process, as living in
99 groups may constitute an advantage when facing predators, looking for resources etc.
100 Animals can draw upon their own experience (Chesler 1969, Valone 1989) as well as
101 upon social transmission (e.g. by social facilitation, local enhancement, observational
102 learning) (Chesler 1969, Boyd and Richerson 1988, Galef 1993, Valone and
103 Templeton 2002) in order to acquire appropriate information about their environment.

104 The use of social cues from conspecifics or information obtained from other
105 species can be a mechanism allowing the establishment of new populations by local
106 enhancement at suitable sites or local avoidance of unsuitable ones (Smith et al. 1999,
107 Slaa et al. 2003). Some authors have started to study the use of information in
108 biological invasion contexts by comparing native and introduced species. For
109 example, Hazlett et al. (2003) found that two invasive crayfish species, the
110 Spinycheek crayfish *Orconectes limosus* and the Red swamp crayfish *Procambarus*
111 *clarkii*, were able to detect and react to the chemical alarm signals produced by

112 conspecifics and by other crayfish species in the presence of predators whereas the
113 native and non invasive species *Austropotomobius pallipes* was only sensitive to the
114 conspecifics' chemical signals. These results suggest that invasive species probably
115 use a broader range of interspecific information concerning predation risk than native
116 species. However no studies have compared in an intraspecific approach the degree of
117 use of information between populations settled in a well known and anciently
118 occupied environment and populations in more recently occupied sites as in
119 propagation fronts. In these last contexts individuals may be confronted with
120 unpredictable or sub-optimal environments (Boyd and Richerson 1988) and
121 information about non-toxic food, and suitable breeding and feeding sites may be
122 crucial (Galef and Laland 2005).

123 As different social cues can act as social aggregators, they may play an
124 important role in detecting food resources, the presence of predators and suitable
125 breeding sites (Gochfeld 1978). This assertion is supported by results on species
126 foraging in groups like the house sparrow *Passer domesticus* (Elgar 1986) or the
127 chicken *Gallus gallus domesticus* (Marler et al. 1986, Wauters and Richard-Yris
128 2003), where it has been shown that food calls induced flock formation or local
129 enhancement around the individual producing the calls, and therefore aggregation at
130 the food resource. The frequency of the food calls depends on the characteristics of
131 the food source (dispersed or concentrated, attractive or repulsive), the physiological
132 state of individuals (hungry or not) and is related to the amount of exploratory
133 behaviour (Elgar 1986, Wauters and Richard-Yris 2003).

134 Just as acoustic signals seem to be important in the location of food resources
135 in these cases, studies on colonial breeding behaviour have demonstrated that
136 individuals, in particular new settlers, could use acoustic stimuli as signals indicating

137 the presence of conspecifics in some potential breeding sites (Alatalo et al. 1982).
138 Mountjoy and Lemon (1991) demonstrated that both male and female starlings
139 *Sturnus vulgaris* were attracted by playback of male song near nest boxes, and
140 Alhering et al. (2006) were able to attract Baird's Sparrow males to suitable but
141 socially empty breeding sites with playbacks reproducing breeding male
142 vocalisations. In their experiment, they used as a control suitable and ecologically
143 similar sites where they did not playback calls, and no birds were attracted to these
144 sites. This confirmed that the acoustic signals were likely the key elements inducing
145 site choice and not the quality of surrounding vegetation.

146 The European starling is an invasive bird that has become successfully
147 established after its introduction to very different habitat types around the world, and
148 it continues to spread to the southern regions in Spain and Italy (Motis et al. 1983,
149 Feare 1984, Pasquali 1984). This bird has a complex social organization, where vocal
150 interactions are essential. In this species song seems to play a major role in mate
151 choice (Mountjoy and Lemon 1996) and song sharing reflects social affiliation
152 (Hausberger et al.1995, Hausberger 1997). Vocalisations may act as a group signature
153 as individuals of a same group share a same dialect (Adret-Hausberger 1983) and can
154 be a social "marker" that allows individuals of a same group to recognise and join
155 each other in roosts (Hausberger et al.2008). Acoustic social cues can thus be
156 considered as central parts of the flocking and social life in starlings. In previous
157 studies, it has been shown that starlings tended to react differently to familiar and less
158 familiar song (Hausberger et al. 1997). Starlings also recognize species-specific songs
159 and react appropriately to them despite local variations in dialect (Adret-Hausberger
160 1982).

161 We hypothesized that individuals from more recently established populations
162 in potentially unfamiliar, unpredictable or sub-optimal environments at propagation
163 fronts (Boyd and Richerson 1988) and in habitats disturbed by human activities, such
164 as towns, are more sensitive to social acoustic cues from individuals from other
165 groups than would be the case for individuals from long-established populations. In
166 order to test this hypothesis, we compared the reactions to an acoustic social stimulus
167 between various populations in different colonization phases. Responses of
168 individuals to the playback of a chorus of unfamiliar starling songs were observed in
169 more recently established populations in France and Italy (towns, propagation fronts)
170 and older rural populations in Brittany.

171

172 MATERIAL AND METHODS

173 ANIMALS AND SITES

174 We compared the reactions of starlings from five geographical areas where

175 populations had different colonisation histories (Figure 1):

176 - Two “old” populations from western France, Brittany, 110 km apart, where starlings
177 became established more than five centuries ago (Richard 1826) and which have
178 abundant food and nesting resources (enough insects and enough available nesting
179 holes) (Clergeau, 1981),

180 - Rural Rennes: rural population in the country surrounding Rennes city

181 - Rural St Brieuc: rural population in the country surrounding Saint

182 Brieuc city

183 - Three “more recent” populations where resources are scarce and less predictable and

184 where starlings have been established for less than 80 years:

- 185 - Urban Rennes: 30-80 year old breeding population (Clergeau 1981). This
186 population uses habitats frequently disturbed by anthropogenic activities and
187 with scarce resources particularly during the breeding period (Mennechez and
188 Clergeau 2006).
- 189 - Rural Italy: rural populations in the Apuglia region in the recent colonization
190 front established less than 30 years ago (Castiglia and Tabarrini 1982)
- 191 - Urban Italy: urban populations of Bari and Mola di Bari cities in Apuglia, also
192 belonging to the colonization front, and established for less than 40 years
193 (Pasquali 1984)

194

195 BEHAVIOURAL TESTS

196 Selected sites were short grass areas (park lawns, football areas, grazed grass
197 fields) as similar as possible (size between 60m x 45m and 120m x 90m). The study
198 was conducted during the breeding period (April 2008) and during hours of intense
199 foraging and social activity: from 06h30 to 12h00 and from 15h00 to 19h00 (Clergeau
200 1981, Feare 1984). We placed a playback speaker at each site where starlings had
201 been observed and begun playback without preidentified individuals.

202 In order to make sure that it was the song chorus as such that was attractive
203 rather than local song characteristics, we broadcasted a chorus of distant unfamiliar
204 birds (8 North American starlings: 4 males and 4 females) presenting distant songs.
205 The song structures within the chorus were equally different from both Brittany and
206 Italian local songs (Henry 1994, 1998) and they contained only songs of class II and
207 III (Hausberger 1997) constituting whistles and warbling that do not provide dialectal
208 information. The chorus consisted of continuous singing for 3 min 26 that was
209 repeated for the duration of the test (30 min) between one display and the follower

210 there were only two seconds of pause. This procedure allowed flying birds to
211 randomly hear several different whistles and warbling songs as they could arrive in
212 the observation area at any moment during the chorus. The intensity of playback
213 diffusion was 85 dB when measured at 1m from the loudspeaker. The loudspeaker
214 was placed on the ground one meter from a tree or an electric line in order to allow
215 birds to perch nearby, and it was hidden under a khaki coat. The observer (A.R.)
216 remained 20m away from the loudspeaker and observed and noted the number and
217 behaviour of starlings flying over the observation area (2500m² around the
218 loudspeaker). We chose to test starlings on ten to fifteen sites in each area rather than
219 to focus on only one group per population and we could thus take into account the
220 distribution and density of the colonies. Only one test was performed per site. More
221 than 700 birds were sampled (100 to 180 per population) (Table 1).

222

223 BEHAVIOURAL RESPONSES

224 Previous studies on behavioural responses of birds to playback experiments had
225 identified different degrees of reaction. In studies of parent recognition by penguin
226 chicks, the authors distinguished various responses that differed in strength (Aubin
227 and Jouventin 1998, Jouventin et al. 1999). Following this method, we classified the
228 observed behaviours (see Table 1) into 4 categories which could reflect different
229 levels of reactivity:

- 230 - no reaction: the bird flew over with no change in direction or speed;
- 231 - reactions during flight: the bird could turn its head towards the loudspeaker, or
232 make a detour over the loudspeaker or descend towards it (without landing),
233 or stationary flight over it, or vocalize during flight or even decelerate;

- 234 - perching: the bird could simply perch on the tree or electric pole near
235 loudspeaker or perch and turn head searching in many directions, or perch and
236 emit contact calls or sing;
237 - landing near the loudspeaker.

238 The experiments were conducted near breeding areas where birds had
239 previously been observed making flights to search food or nest material; they were
240 mainly observed alone or in pairs. In a few cases we observed groups of more than
241 two birds. In any case we considered that a bird was attracted by the sound source
242 only if it was flying and reacting alone or if it was among the first simultaneous birds
243 reacting. We did not consider individuals following their group members as
244 individuals attracted by the chorus in order to avoid an overestimation of the number
245 of reactive birds to the external stimulus. The follower birds were considered as birds
246 who did not react to the chorus. Each observation session lasted 30 minutes. We
247 checked the direction of birds' flight to avoid recounting the same bird in a same
248 session and only one session was conducted per site in order to avoid recounting the
249 same birds twice. If we were in an area with apparently low bird density and if some
250 birds stayed in the observation area, we stopped the observation earlier to avoid
251 pseudoreplication by this way, we avoid counting the birds more than one time.
252 During the observations, single birds or birds in little groups flew over the
253 experimental area and we counted carefully the number of flying birds and the
254 number of them who reacted to the chorus.

255 As almost all the birds were flying alone or in groups of 2 or 4 individuals (only
256 four groups of more than 5 individuals) we did not test the effect of group size.

257

258

259 STATISTICAL ANALYSIS

260 We have considered the percentage of birds that responded per site. We used pairwise
261 chi square tests (Siegels and Castellon 1988) to compare the differences in acoustic
262 attractiveness between pairs of populations and the differences in response types.

263

264 RESULTS

265 OVERALL REACTION TO CHORUS

266 We observed substantial differences in how birds responded to the acoustic stimulus
267 among our different study populations ($\chi^2 = 27.31$, $df = 4$, $p < 0.001$). In Urban
268 Rennes, about 64% of tested birds reacted to the stimulus whereas in Italian
269 populations we observed between 40 and 45 % of birds reacting. Finally, in Rural
270 Brittany populations less than 26% of the birds expressed a reaction to the playback
271 (Table 1).

272

273 In pair-wise comparisons, birds in Rural Italy appeared to be significantly
274 more reactive than those from Rural Rennes and Rural St Brieuc (respectively
275 $\chi^2 = 8.24$, $df = 1$, $p < 0.01$ and $\chi^2 = 4.32$, $df = 1$, $p < 0.05$). Similarly, the population
276 from Urban Italy showed more reactions than the population from Rural Brittany but
277 this difference was significant only in the pairwise comparison with the Rural
278 Rennes, not with the Rural St Brieuc (respectively $\chi^2 = 6.77$, $df = 1$, $p < 0.01$ and
279 $\chi^2 = 3.51$, ns). The Urban Rennes population appeared to be significantly more
280 reactive than the Rural Rennes and the Rural St Brieuc ones (respectively $\chi^2 = 17.81$,
281 $df = 1$, $p < 0.001$ and $\chi^2 = 11.1$, $df = 1$, $p < 0.001$). Finally, the Rural Rennes population
282 and the Rural St Brieuc population appeared to behave similarly ($\chi^2 = 0.13$ ns).

283 In conclusion, more recently established populations appeared to be more reactive
284 towards the playbacks than long-settled ones (Figure 1).

285 As a corollary of these observations, we observed a gradient of “No reaction”
286 response with three levels:

- 287 - the Rural Brittany populations are those that present the highest percentages
- 288 for this category (around 75% of no reaction).
- 289 - the Italian populations with an intermediate level: around 56 % of no reaction
- 290 - the Urban Rennes population with a lower absence of reaction: 36 % of no
- 291 reaction

292

293 REACTIONS IN FLIGHT

294 Flight reactions differed across populations ($\chi^2 = 47.25$, $df = 4$, $p < 0.001$) (Table 1):
295 The Rural Italian population was the most reactive in flight (39% of birds); the Urban
296 Italian and the Urban Rennes populations had intermediate levels of response (near
297 30% of birds); the Rural Rennes and the Rural St Brieuc populations presented the
298 lowest levels of response (10% of birds). We obtained here a gradient of response
299 corresponding to the gradient of age of the populations, the more recent ones being
300 the more reactive.

301 Making detours and decelerations over the experimental area were the most
302 frequent behaviours observed in all the populations but they were more frequent in
303 recent populations than in older ones (Figures 3A and B, Table 1).

304 In the Rural Italian population significant more birds made detours than in
305 Rural Rennes and in Rural St Brieuc ($\chi^2 = 15.43$ $df = 1$ $p < 0.001$ and $\chi^2 = 6.57$ $df = 1$
306 $p < 0.02$ respectively). Urban Italian birds made also significant more detours than
307 Rural Rennes and Rural St Brieuc ($\chi^2 = 13.66$, $df = 1$, $p < 0.001$ and $\chi^2 = 5.65$, $df = 1$,

308 $p < 0.02$). Urban Rennes population performed significant more detours than Rural
309 Rennes population ($\chi^2 = 9.72$, $df = 1$, $p < 0.01$). The other pair-wise comparisons on
310 detour behaviour were not significant ($\chi^2 < 3.74$, $df = 1$, $p > 0.05$).

311 Concerning decelerations, Rural Italy birds decelerated significantly more frequently
312 than Rural Rennes birds ($\chi^2 = 7.57$, $df = 1$, $p < 0.01$) and Urban Italy birds decelerated
313 significantly more frequently than Rural Saint Brieuc birds ($\chi^2 = 4.56$, $df = 1$,
314 $p < 0.05$). The other pair-wise comparisons were not significantly ($\chi^2 < 2.22$, $df = 1$,
315 $p > 0.05$) or the data were inadequate for statistical testing.

316 Descent flights towards the loudspeaker and turning the head during flight
317 were rare and only expressed in recently colonized habitats. In addition, we observed
318 more vocalisations during flight in recent populations than in older ones. Italian Rural
319 population (with almost 8% of birds vocalizing in flight) vocalised significantly more
320 than Rural Rennes birds ($\chi^2 = 5.84$, $df = 1$, $p < 0.01$) and than Rural St Brieuc birds that
321 never vocalised in flight ($\chi^2 = 7.46$, $df = 1$, $p < 0.01$) (figure 2C).

322

323 PERCHING BEHAVIOURS

324 Italian populations perched the least (11% of the birds). About 18 % of Rural Brittany
325 birds perched. Urban Rennes population perched the most frequently (31%) (Figure
326 2).

327 Some birds, mostly from Brittany populations moved their head in many
328 directions as if they were searching for the singing individuals of the chorus. This
329 behaviour tended to be more frequent in Brittany populations than in Italian ones
330 (Figure 3D) but there were not enough data to conduct pair-wise comparisons. Other
331 individuals vocalized or sang after perching with no differences among populations
332 (Figure 3E).

333 LANDING REACTIONS

334 Landing on the ground close to the loudspeaker was a rare behaviour and almost only
335 observed in Urban Rennes population (Table 1, Figure 1).

336 DISCUSSION

337 Our experiments show that the studied populations reacted differently to broadcasts
338 of chorus songs. For the first time a higher sensitivity to this kind of social cue was
339 observed in more recent populations than in populations living in long-colonized
340 environments. In a related study, inter-individual differences in sensitivity to social
341 cues were observed by Hahn and Silverman (2006) who observed the reaction of
342 migratory adults of the American redstart (*Setophaga ruticilla*) to song playbacks in
343 order to test the influence of social acoustic cues on habitat selection. They compared
344 experimental plots with playback stimulus and control plots without the acoustic
345 stimulus. They found that experimental plots attracted more adult males that were
346 new immigrants in this geographic area than the control plots, indicating that the
347 settlement in the new habitat by naïve individuals who did not know the area was
348 enhanced by these social cues.

349 Detecting predators, finding conspecifics, and locating breeding and foraging
350 areas may be crucial when establishing in new environments. Being more reactive to
351 social stimuli could have been an advantage for the ancestors of the more recent
352 populations and could have acted as a mechanism allowing groups' formation during
353 the settlement process. If this behavioural character was transmitted from the settler
354 generations to the next, the higher sensitivity to social cues observed in recent
355 populations is probably a consequence of this mechanism. It has been shown that
356 invasive ants form large colonies presenting low levels of territoriality that allow
357 proximal gathering between neighbour nests (Holway et al. 1998, Suarez et al. 1999).

358 In our case, gathering with conspecifics seems to have been a factor allowing colony
359 formation in the past which is still observed today.

360 Propagation fronts are the expanding edges of a species distribution. The
361 proportion of immigrant individuals can be higher than in long-colonized habitats
362 where on the contrary immigrants are probably less frequent and where the proportion
363 of long time residents can be higher. By consequence, propagation fronts can present
364 higher proportions of naïve individuals that do not know well these areas. Studies on
365 different taxa like bats and birds have shown that naïve, inexperienced or
366 unsuccessful individuals tended to follow successful foraging individuals that had
367 previously located suitable breeding or feeding sites (Wilkinson 1992, Marzluff et
368 al. 1996, Kert and Reckardt 2003). In some species as in greater spear-nosed bats
369 (*Phyllostomus hastatus*) vocalizations such as contact calls increase the attractiveness
370 of suitable foraging or roosting sites (Wilkinson and Wenrick Bougman 1998).
371 Sensitivity to social, and in the present case, to acoustic cues is therefore probably an
372 advantage for invasive species.

373 In their study on responses to shared and non shared song types, Hausberger et
374 al. (1997) found that captive male starlings reacted little to an unfamiliar female song,
375 and that females reacted mostly to song-types they shared with their social partners
376 when these song-types were reproduced by a playback. Here we found that
377 individuals from more recently established populations were very sensitive to the
378 playback even if it was a chorus produced by unfamiliar birds, which means that
379 these starlings react more to the social information even when produced by unknown
380 individuals. Hazlet et al. (2003) had observed this kind of phenomenon at an
381 interspecific scale; they found that two species of introduced invasive crayfish were
382 able to use a broader range of chemical cues than two non invasive species.

383 Here we interpreted the high levels of response in propagation fronts or in new
384 contexts (like in cities) as the consequence of the recent history of the populations and
385 as a way facilitating colonization. However, the differences of response may be due
386 to differences in food resources or by differences in levels of competition to obtain
387 these resources. Moreover we did not control for ambient noise levels, so this factor
388 could be acting on birds receptivity. Mockford and Marshall (2009) observed that
389 male Great tits from quiet territories reacted significantly stronger when hearing song
390 from another territory holder with low background noise than from those with high
391 background noise. Urban environments are usually noisier than rural ones so birds
392 our birds could have been less responsive in urban areas but it was not the case
393 which means that even with noise birds from the recent populations of the urban areas
394 heard well the playback and were more reactive. However more studies controlling
395 both for food resources and background noise should be conducted to confirm if the
396 history of population is really the factor influencing the responses.

397 Finally, there is an alternative hypothesis to explain the higher sensitivity of
398 birds from recently-established populations. It has been demonstrated that density can
399 influence the use of social acoustic cues (Fletcher 2007). We can thus not exclude the
400 possibility that the higher levels of sensitivity in propagation fronts (southern Italy)
401 are due to the fact that starling density is moderate in this region compared to the
402 higher densities in Rural Brittany. Fletcher (2007) has found that individuals were
403 more sensitive to acoustic cues in habitats with moderate density values. Birds less
404 habituated to hearing unfamiliar songs in areas with low densities during the breeding
405 period may be in consequence more sensitive to social acoustic cues from unfamiliar
406 birds. However this hypothesis can not be applied to the urban Brittany population
407 where bird densities are equivalent to those of the older Rural Brittany population

408 (Mennechez 1999). In this case the higher levels of reactivity might also be due to the
409 fact that city is a sub-optimal environment where food for nestlings is difficult to find
410 (Mennechez and Clergeau 2006), probably increasing the value of social information.

411

412 BEHAVIOURAL DIFFERENCES IN POPULATION REACTIONS TOWARDS 413 THE CHORUS

414 Populations differed not only in their overall response but also in their modalities of
415 response. Individuals from more recently established populations reacted mostly by
416 modifying the direction of their flight, perching and vocalising, whereas the major
417 response of older populations was perching with little interaction with the sound
418 source.

419 In contrast to studies involving visual cues (Clergeau 1981, 1982) where
420 starling decoys were put on the ground, we observed very few landing responses
421 perhaps because the individuals could not visually detect the birds that sang the
422 chorus.

423 Individuals from more recently established populations tended to vocalise
424 more during flight in response to the acoustic stimulus than individuals from long-
425 established populations. We suggest that individuals may search actively for
426 gatherings of conspecifics and seek out vocal interaction, as they both receive and
427 produce acoustic cues or that calling is contagious as observed in Pampas
428 Meadowlarks (*Sturnella defilippii*) (Gochfeld 1978).

429 Some individuals moved their head in many directions. Vocal and visual
430 reactions are probably used to obtain additional information and detect and locate the
431 singers. Studies conducted on primates indicated that in the absence of visual
432 obstacles or when inter-individual distances were short, animals used predominantly

433 visual contact to detect and locate conspecifics. On the contrary, when confronted
434 with a habitat containing various visual obstacles (trees or buildings for example)
435 individuals produced contact calls more frequently (Snowdon and Hodun 1981, Koda
436 et al. 2008). In our study flying individuals from Rural Italy tended to vocalize more
437 than individuals from Urban Italy whereas individuals from Urban Rennes vocalized
438 more than those from Rural Brittany. Nevertheless, populations in more recently
439 colonized habitats (either rural or urban) vocalized more than those from older
440 populations, probably looking for more vocal contact. Population history may play a
441 more important role in actively searching for contact than habitat characteristics, but
442 we cannot exclude the possibility that some landscape features could have had an
443 effect on head-turning and vocalising.

444 These results imply that the use of social cues may act as a major mechanism
445 in social aggregation during colonization or invasion processes and that it is probably
446 a mechanism allowing individuals to join conspecifics in potentially suitable sites
447 (Clergeau 1981, 1982). During establishment in a new area individuals can be
448 confronted with many unknown and novel contexts, new landscapes, new food
449 resources, unpredictable resources, lack of information about predator location, etc.
450 One possible way to compensate for this lack of information is the use of social
451 information gathered from conspecifics, which allows them to settle more easily in
452 the new habitats. Even if other studies are needed to corroborate our results
453 (especially translocation experiments or integration of the levels of inter-individual
454 competition), we can conclude that cues like acoustic signals could play an important
455 role in the colonisation process for gregarious birds such as the European starling.

456

457

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607

608 LEGENDS

609

610 FIGURE 1: Levels of overall responsiveness to the acoustic stimulus by five

611 populations with different histories

612

613 FIGURE 2: Qualitative and quantitative differences in the expression of

614 responsiveness to the acoustic stimulus. A: Birds making a detour. B: Birds

615 decelerating. C: Birds vocalizing in flight. D: Birds turning the head in many

616 directions when perched. E: Birds singing when perched.

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618 TABLE 1: Percentages of individuals that reacted with each kind of behaviour to the

619 playback

620 () = number of birds tested for each population

621 - = not enough individuals to conduct chi² analysis

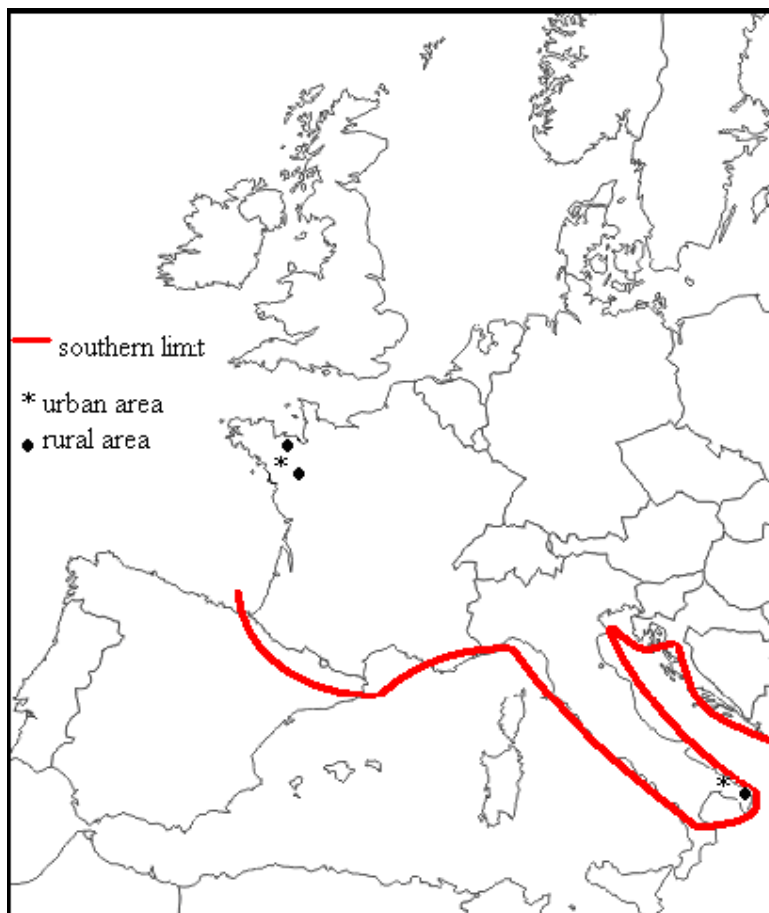
622 *** p<0.001

623 ** p<0.01

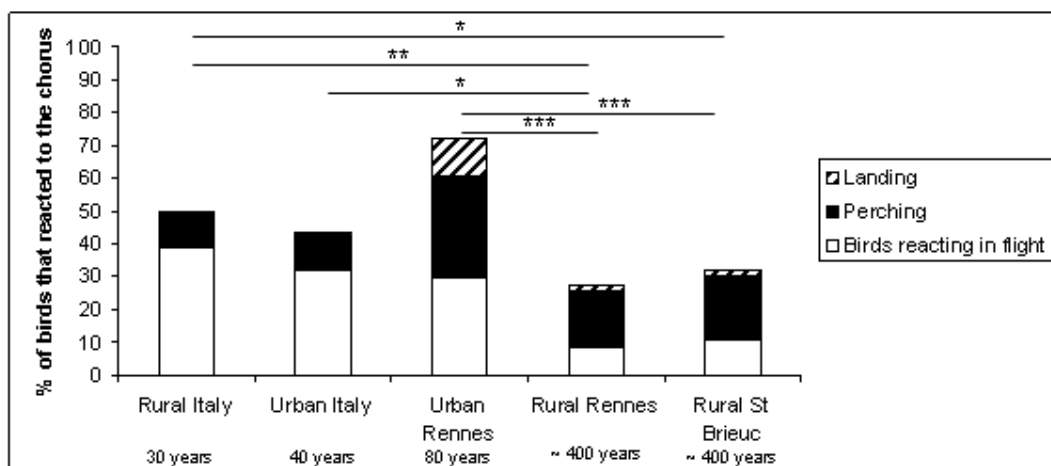
624 * p<0.05

625 df = degrees of freedom

626 FIGURE 1

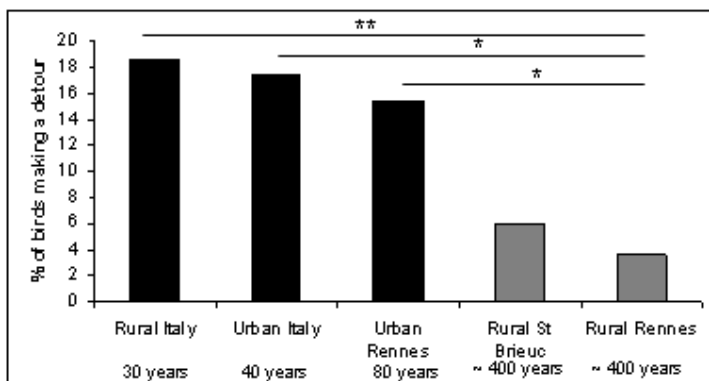


629 FIGURE 2



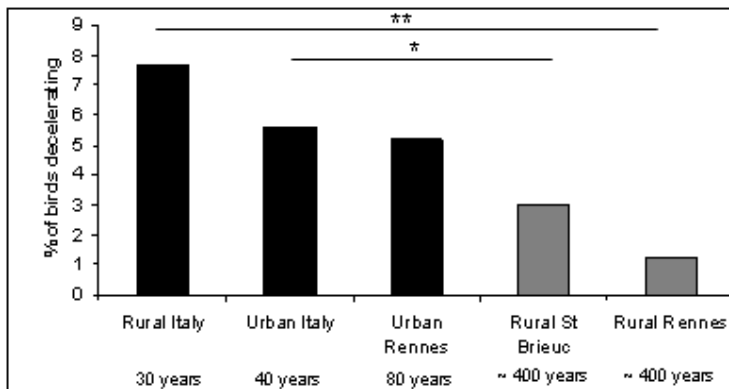
632 FIGURE 3

633 A.



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635 B.



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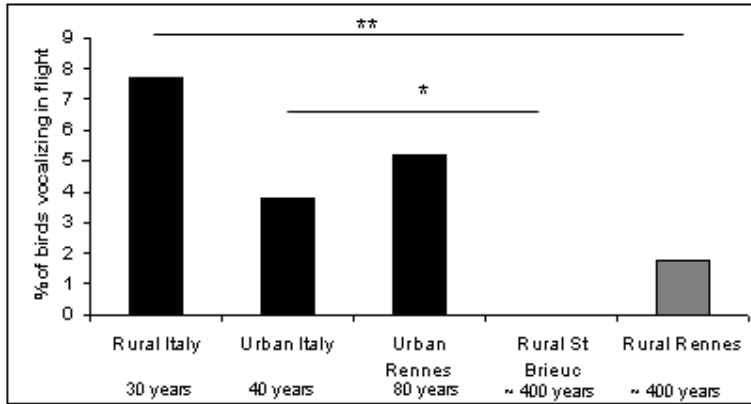
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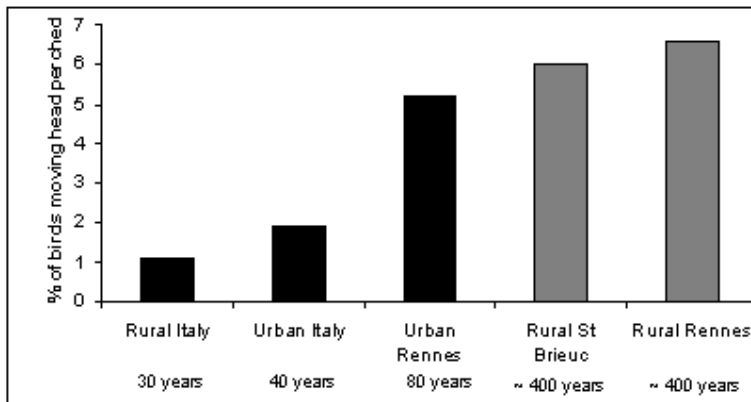
645 C.



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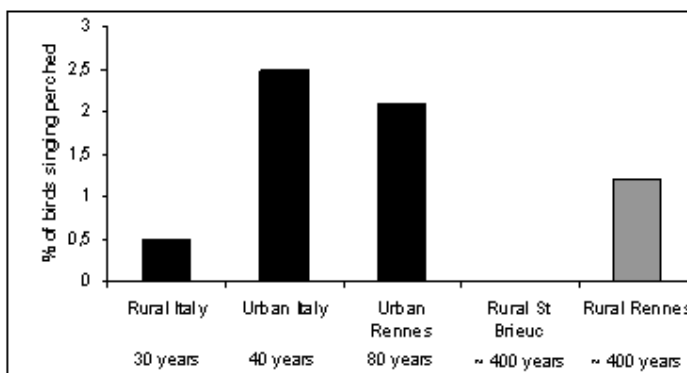
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648 D.



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650 E.



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653 TABLE 1

Population	Populations in new habitats			Populations in old habitats	
	Rural Italy	Urban Italy	Urban	Rural	Rural St

	13 sites (183 birds)	10 sites (160 birds)	Rennes 11 sites (97 birds)	Rennes 13 sites (166 birds)	Briec 13 sites (100 birds)
Total birds reacting	44.3 %	42.5 %	63.9 %	23.5 %	26 %
1. Birds reacting in flight	38.7 %	31.9 %	29.9 %	8.4 %	11 %
Descent towards the loudspeaker	3.83 %	4.4 %	2.1 %	0 %	0 %
Detour over the loudspeaker	18.6 %	17.5 %	15.5 %	3.6 %	6 %
Stationary flight over the loudspeaker	0 %	0 %	1 %	1.2 %	3 %
Deceleration	7.7 %	5.6 %	5.2 %	1.2 %	3 %
Turn head in flight	1.1 %	0.6 %	1 %	0 %	0 %
Vocalises in flight	7.7 %	3.8 %	5.2 %	1.81 %	0 %
2. Birds perching	10.9 %	11.3 %	30.9 %	17.5 %	19 %
Individuals only perching	8.2 %	5.6 %	15.5 %	9.4 %	13 %
Individuals perching and moving head in many directions	1.1 %	1.9 %	5.2 %	6.6 %	6 %
Individuals perching and emitting contact calls	1.1 %	1.25 %	8.24 %	0.6 %	0 %
Individuals perching and singing	0.56 %	2.5 %	2.1 %	1.2 %	0 %
3. Birds landing	0 %	0.6 %	11.3 %	1.2 %	2 %