

Title	Attraction of other species by Bluethroat <i>Luscinia svecica</i> song playback during autumn migration: an experimental test using bird-ringing data
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Publication date	2016-10
Original Citation	de la Hera, I., Fontanilles, P., Delalande, L., Glad, A. and Sarraude, T. (2016) 'Attraction of other species by Bluethroat <i>Luscinia svecica</i> song playback during autumn migration: an experimental test using bird-ringing data', <i>Ardeola</i> , 64(1), pp. 91-99. doi:10.13157/arla.64.1.2017.sc4
Type of publication	Article (peer-reviewed)
Link to publisher's version	https://doi.org/10.13157/arla.64.1.2017.sc4 - 10.13157/arla.64.1.2017.sc4
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Download date	2023-09-29 09:25:03
Item downloaded from	https://hdl.handle.net/10468/7003

**HETEROSPECIFIC ATTRACTION BY BLUETHROAT *LUSCINIA SVECICA* SONG PLAYBACKS DURING AUTUMN MIGRATION:
AN EXPERIMENTAL TEST USING BIRD-RINGING DATA**

**ATRACCIÓN DE HETEROSPECÍFICOS POR REPRODUCCIONES DEL
CANTO DEL PECHIAZUL *LUSCINIA SVECICA* DURANTE LA MIGRACIÓN
OTOÑAL: UN TEST EXPERIMENTAL EMPLEANDO DATOS DE
ANILLAMIENTO**

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Short title: Heterospecific attraction by Bluethroat playbacks

Key words: Adour, conspecific attraction, lme4, tape-lure, Turdidae.

Word count: 2491 (main text without summaries)

1 SUMMARY.- Playback use of a particular avian species is well-known to have the
2 potential to bias the composition of conspecifics (with regard to sex, age or body
3 condition) that can be captured during mist-netting sessions. However, the possibility
4 that playbacks affect heterospecific captures has been less explored and lacks solid
5 experimental evidence. In this study, we explicitly tested through an experimental
6 approach whether the use of a Bluethroat *Luscinia svecica* playback altered the overall
7 number of heterospecifics captured during autumn migration in a wetland located in
8 southwestern France. We found that playback use increased the capture rates of species
9 that were not the direct target of the playback. This heterospecific attraction effect
10 should be assessed and carefully considered when designing any avian monitoring
11 program.

12

13 RESUMEN.- El uso de reproducciones sonoras de una especie de ave concreta es bien
14 conocido que tiene el potencial de sesgar la composición de conespecíficos (con
15 relación al sexo, edad o condición corporal) que pueden ser capturados durante las
16 sesiones de anillamiento con redes japonesas. Sin embargo, la posibilidad de que los
17 reclamos sonoros afecten a las capturas de heterospecíficos ha sido menos explorada y
18 carece de evidencias experimentales sólidas. En este estudio testamos explícitamente si
19 el uso de reclamos de Pechiazul *Luscinia svecica* alteraba el número total de
20 heterospecíficos capturados durante la migración otoñal en una zona húmeda localizada
21 en el suroeste de Francia. Nuestros resultados muestran que el uso de reproductores
22 sonoros incrementa las tasas de capturas de especies que no fueron el objetivo directo
23 del reproductor. Este efecto de atracción por heterospecíficos debería ser evaluado y
24 considerado cuidadosamente a la hora de diseñar cualquier programa de seguimiento de
25 aves.

26

27 Animals make use of different sensorial (e.g. acoustic, visual) stimuli coming from
28 other individuals to take behavioural decisions (Maynard-Smith & Harper, 2003). In
29 birds, the existence of conspecific and heterospecific acoustic interactions is well known
30 and is an important research area within social information theory (Nocera *et al.*, 2006;
31 Valone, 2007; Magrath *et al.*, 2009). Interestingly, avian bioacoustics also has a large
32 potential in practical applications, such as promoting the settlement of birds in particular
33 areas (Ward & Schlossberg, 2004; De Jong *et al.*, 2015), deterring species that are
34 conflictive for human activities (Ribot *et al.*, 2011) or increasing capture rates of rare
35 species in monitoring programs (Julliard *et al.*, 2006; Jiguet *et al.*, 2011). However, our
36 knowledge of how birds respond to different artificial aural attractants is still very
37 sparse and biased towards particular avian groups (e.g. colonial seabirds) and mostly
38 during reproduction (Ahlering *et al.*, 2010).

39 Playback use is a common practice in scientific mist-netting (Redfern & Clark,
40 2001). It is often accepted that this method increases the number of captures of target
41 species (conspecific attraction), although sound experimental studies are still scarce
42 (e.g. Mukhin *et al.*, 2008; Arizaga *et al.*, 2015). Much less understood, and often
43 overlooked, is the potential impact of playbacks on capture rates of non-target species
44 through heterospecific attraction. The possibility that this effect occurs during migration
45 has been raised by several authors (Herremans, 1990; Wojczulanis-Jakubas *et al.*,
46 2016). However, it has not been explicitly tested experimentally, let alone using a
47 design that accounts for the spatial and temporal variation in bird abundance and
48 capture rates. Thus, most relevant studies on this matter have been carried out without
49 alternating treatments between study plots (i.e. overlooking spatial variation, e.g.
50 Mukhin *et al.*, 2008) or without overlapping in time treatment and control captures (i.e.
51 ignoring temporal variation; e.g. Wojczulanis-Jakubas *et al.*, 2016). Formally, the

52 robustness of this type of experimental designs would be compromised since observed
53 patterns can be alternatively explained by, for example, differences between plots in
54 habitat features or by temporal differences in the influx of migrants stopping over at the
55 study site.

56 The Bluethroat (*Luscinia svecica*) is a migratory species whose stopover ecology has
57 recently attracted much attention in North Western Europe (Arizaga *et al.*, 2013; 2015).
58 Thus, some ringing stations use audio-players of this species to maximize its captures
59 during migration, but the consequences of this methodology on the catchability of other
60 species remains unknown. In order to clarify this issue, we performed a playback
61 experiment in a wetland located in southwestern France, where studies on the stopover
62 ecology of Bluethroats and other species are carried out using aural attractants.

63 This study took place in Villefranque, Quartier-bas (43°27'N, 01°28'W, France), a
64 locality situated in the lower basin of Nive river, near the Adour mouth in Bayonne city.
65 The study site is a wetland dominated by reed bed (*Phragmites australis*) and other less
66 common plants associated with damp meadows, and scattered by some native (mostly
67 Willows *Salix* spp.) and exotic trees (mainly Elder *Acer negundo*) (see Fontanilles *et al.*,
68 2014). We placed three triplets of mist-nets (triplet A, B and C) in the area, separated
69 each other by more than 70 m. Each triplet consisted of three 12-m mist-nets positioned
70 in straight line (36 m of overall length per triplet) and always in the same fixed
71 positions. We made 21 ringing sessions (i.e. 21 ringing days) between August 18th and
72 October 2nd, 2015, when migrating Bluethroats stopover in this region during their post-
73 breeding migratory period. During each session, we used two playbacks, each one
74 placed in two of the three triplets, while the triplet without playback was used as a
75 control. Both playbacks had the same characteristics and consisted in an mp3 (Intenso
76 music walker) containing a male Bluethroat song connected to an amplifier (18W Kemo

77 #M033) and a speaker (DB Sonic 6010). The playback installed in one triplet rarely
78 could be heard from the other triplets. We used exactly the same commercial male song
79 used in the ringing campaigns performed in our study site and other areas (Arizaga *et*
80 *al.*, 2015), which was extracted from Roché (2009). This song recording was played
81 repeatedly from approximately 30 minutes before dawn (when mist-nets were open)
82 until the end of the ringing session (when mist-nets were furled). Playbacks were
83 located at the midpoint of the corresponding 36-m mist-net line at volume 28 out of the
84 32 levels of the mp3. Whether the control triplet was on triplet A, B or C (see Fig. 1)
85 was selected randomly when possible, but it was conditional on two requirements. First,
86 each one of the three triplets was the control once every three ringing sessions and,
87 second, we avoided that the same triplet was used as control in two consecutive
88 sessions. This decision was taken in order to have each experimental set-up
89 homogeneously distributed over time. According to this, each triplet was the control
90 triplet seven days throughout the study period.

91 Our study was performed within a radio-tracking-based project studying the spatial
92 ecology of Bluethroats stopping over in the area during their autumn migration, so that
93 the ringing dates selected to perform the experiment and the duration of each ringing
94 session was constrained by the monitoring necessities of this more general and priority
95 project. Thus, the number of days elapsed between consecutive ringing sessions (range:
96 1-11 days) and the duration of each ringing session differed (range: 150-360 min).
97 However, the opening and closing time of each triplet was virtually the same within
98 each day, so that differences in the patterns of captures observed in this study cannot be
99 attributed to methodological biases.

100 Each bird captured during a ringing session was ringed, and its species, age and sex
101 were determined based on available literature (Svensson, 1992; Jenni & Winkler, 1994).

102 We decided to not consider the re-traps of individuals previously captured within the
103 same day in order to avoid pseudo-replication. Playbacks might affect each species
104 differently depending on their phylogenetic or trophic similarity to the Bluethroat
105 (DeJong *et al.*, 2015). Likewise, playbacks might affect the proportion of age and sex
106 groups captured for a particular species (Arizaga *et al.*, 2015). Our sample size was too
107 small to test all these specific effects reliably. Consequently, we opted for restricting our
108 analyses to: the overall number of captures (excluding Bluethroats), the number of
109 captures of species not included in *Muscicapidae* (the family the Bluethroat belongs to)
110 and the closely-related family *Turdidae* (see Gill & Donsker, 2016), and specific
111 analyses for Bluethroats and for the most commonly trapped species in this study (the
112 Reed Warbler *Acrocephalus scirpaceus*).

113 We used Generalized Linear Mixed models (GLMM) with Poisson error distribution
114 to test the hypothesis that the overall number of captures per triplet per day (either,
115 among and within triplets) would be larger when using the aural attractant. In this
116 analysis, we included the overall number of captures (excluding captures of Bluethroats)
117 per triplet as dependent variable, triplet (three levels: A, B and C), playback (whether a
118 particular triplet had playback on a particular day or not) and their interaction as fixed
119 effects. The day was included as a random factor, since the number of captures can
120 greatly vary between days depending on the prevailing meteorological conditions and
121 other factors that affect landing decisions of migrating birds. We performed the same
122 model using the number of captures of species not belonging to the families *Turdidae* or
123 *Muscicapidae* (see Table 1 to identify these species) and the captures of the Reed
124 Warbler as dependent variables. Finally, a similar model with binomial error
125 distribution was performed for the capture or not of at least one Bluethroat in each
126 particular triplet per day, with the purpose of exploring the existence of conspecific

127 attraction in this species. All statistical tests were performed using the *R* package *lme4*
128 (Bates & Maechler, 2010) and considering a threshold of $P = 0.05$.

129 We made a total of 574 captures from 21 different avian species during our 21
130 ringing sessions (Table 1). The Reed Warbler was by far the most commonly mist-
131 netted species, followed in numbers by the Cetti's Warbler and the Sedge Warbler. All
132 other species, including the Bluethroat, accounted for less than 5% of the overall
133 number of captures (Table 1). Mean number of captures per day excluding the
134 Bluethroats was 26.6 birds (range= 8-144; ± 6.4 se). We detected a significant effect of
135 the Bluethroat playback on the number of heterospecifics captured (Table 2), as it can
136 also be noted in Figure 1, where –for illustrative purposes– the percentage of captures
137 made in each triplet per day was represented under the three different experimental set-
138 ups (note also that the experimental set-up was not an effect to be estimated in the
139 statistical tests; see Table 2). The effect of the playback did not differ between triplets as
140 it can be deduced from the lack of statistically significant interactions between the terms
141 ‘playback’ and ‘triplet’ (see Table 2). Results were qualitatively the same when only
142 captures of individuals belonging to species not included within the families *Turdidae*
143 or *Muscicapidae* were analysed (‘playback’ effects: Estimate = 0.64 ± 0.19 se, *Z-value*
144 = 3.33, $P < 0.001$). Additionally, this pattern does not seem to be only mediated by the
145 most commonly trapped species, since the effect of the playback on the number of Reed
146 Warblers trapped was marginally non-significant (‘playback’ effects: Estimate = $0.46 \pm$
147 0.25 se, *Z-value* = 1.82, $P = 0.069$).

148 We captured more Bluethroats in triplets with ($n = 14$) than in triplets without
149 playback ($n = 2$), but this difference was not significant when tested by a GLMM with
150 binomial error distribution (‘playback’ effects: Estimate = 0.7 ± 1.49 se, *Z-value* = 0.47,
151 $P = 0.638$).

152 Our study shows luring effects of Bluethroat song playbacks on other avian species,
153 which increased the overall number of birds trapped during bird-ringing sessions at
154 mist-nets fitted with a playback. Interestingly, observed patterns cannot be explained
155 only by the attraction of individuals phylogenetically more closely related to the
156 Bluethroat, since results did not change qualitatively when captures of birds belonging
157 to the families *Turdidae* and *Muscicapidae* were not considered in the analyses. Thus,
158 our experimental study demonstrates with a proper spatial and temporal control that a
159 specific playback can increase the captures of heterospecific (non-phylogenetically-
160 related) birds.

161 The heterospecific attraction hypothesis was originally formulated to describe the
162 fact that some migratory bird species use local resident birds from other species as cues
163 to make habitat-selection decisions for breeding (Monkkonen *et al.*, 1997; Thomson *et*
164 *al.*, 2003). However, their basic principles might be extrapolated to other periods of the
165 annual cycle of birds (i.e. migration or wintering), as well as to other zoological groups
166 (e.g. amphibians; Pupin *et al.*, 2007). Our data support the idea that birds also include
167 the acoustic emissions of other bird species in their decision-making process at their
168 stopover sites. In our study area, birds might be using heterospecific cues in order to
169 track suitable patches for foraging, since avian songs could indicate areas where
170 individuals are in good nutritional condition (Van Hout *et al.*, 2012). This interpretation
171 would be supported by the fact that the majority of the birds occurring in our study site
172 are likely to be actively migrating birds that stopped over in the area during their post-
173 breeding migration. This is difficult to elucidate for each particular individual to test
174 this possibility formally, especially for migratory or partial migratory species that show
175 some local breeding pairs (e.g. Reed Warbler, European Robin *Erithacus rubecula*). In
176 any case, it is expected that a high percentage of captured birds corresponded to

177 recently-arrived individuals that were completely unfamiliar with the area and, hence,
178 would make use of available social information (heterospecific songs) to track food
179 resources (Wojczulanis-Jakubas *et al.*, 2016).

180 We acknowledge that our study possesses two limitations that lead us to take our
181 results and interpretations with some caution. First, observed patterns might be
182 mediated by the specific nature of the single male song selected to be broadcasted in
183 Villefranque. And, second, we lacked an additional non-natural noisy control (e.g.
184 classic music) that helped us to rule out the possibility that birds were attracted by any
185 type of playback.

186 We failed to detect a significant conspecific attraction effect of Bluethroat playbacks.
187 This was probably mediated by the relatively low number of Bluethroats captured that
188 year, which only allowed us to perform a less powerful GLMM with binomial error
189 distribution to test this hypothesis. However, our rough figures suggest a potential effect
190 since 14 out of the 16 Bluethroats were trapped in triplets with playback (Table 1). If we
191 consider that the null hypothesis would be the capture of twice more Bluethroats in
192 mist-nets with playback (i.e. two triplets with playback versus one triplet without
193 playback each day), we would obtain a marginally non-significant effect using a Chi-
194 Square test ($\chi_1 = 3.15$, $P = 0.076$). A recent study suggests the possibility that Bluethroat
195 playbacks would only increase autumn capture rates of conspecifics at particular
196 locations, probably those having also local breeding populations (Arizaga *et al.*, 2015).
197 Breeding Bluethroats have not been recorded in our study site, so individuals of this
198 species in Quartier-bas are considered migrating birds. Consequently, the causes
199 determining the among-site differential response of Bluethroats to their own aural
200 attractant during autumn migration is still an open question.

201 There is increasing evidence suggesting that the information obtained in bird-ringing
202 monitoring programs can be altered by the use of playbacks and, hence, their use is
203 normally prohibited when birds are more sensitive to them (e.g. breeding period;
204 Redfern & Clark, 2001) or within ringing coordinated programs (DeSante *et al.*, 2015).
205 The most commonly described alterations are related to modifications in the proportions
206 of the different population groups (i.e. age, sex or birds with different body condition)
207 that can be captured within the target species (Figuerola & Gustamante, 1995; Brotons,
208 2000; Lecoq & Catry, 2003). Although the potential of playbacks to alter heterospecific
209 captures had been timidly suggested in some studies (Mukhin *et al.*, 2008; Wojczulanis-
210 Jakubas *et al.*, 2016), this has not been broadly acknowledged. Our study provides
211 substantial empirical evidence of the existence of heterospecific attraction during
212 autumn migration by using a more robust experimental design. Thus, overall captures in
213 the mist-nets equipped with Bluethroat playbacks in our study site are surely
214 overestimated. An interesting remaining question is to address whether this playback
215 effects are homogeneous across species, which could not be tested in our study due to
216 sample size limitations, but would have important implications for bird community
217 comparisons. If the heterospecific attraction effects we found for the Bluethroat also
218 take place with the playbacks of other species, any inference made between sites (or
219 between periods within the same locality) in the capture rates of any species would be
220 compromised if playback protocols are not standardized in time and space.
221 Consequently, the effects of aural attractants on heterospecific captures should be also
222 assessed and carefully considered by ornithologists when designing any avian
223 monitoring program.

224

225 ACKNOWLEDGEMENTS.- We are grateful to the funders of the project and all members of OISO
226 association who made this research possible, especially François Lartigau and Kevin Sourdrille. This study

227 was funded by the Conseil Départemental des Pyrénées Atlantiques, Syndicat de la Nive Maritime, and
228 Villefranque council. National Museum of Natural History from Paris authorized the bird-ringing
229 activities. We also want to thank María Torres-Sánchez for her help in the field, and an anonymous
230 reviewer for useful comments on an earlier version of the manuscript.

231

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311 warbler and sedge warbler to acoustic playback in relation to age, sex, and body
312 condition. *Journal of Ornithology*, 157: 137-143.

313 **Table 1.** Number of captures in control and playback triplets and overall number of
 314 captures for each of the 21 avian species trapped during the autumn migration period in
 315 Quartier-bas (Southwestern France). Species belonging to the *Turdidae* or
 316 *Muscicapidae* families are indicated in the first column by ‘[TURD.]’ or ‘[MUSC.]’,
 317 respectively. Note that playbacks were used in two out of the three mist-net triplets in
 318 each ringing session.

319 **Tabla 1.** Número de capturas en tripletes control y con reclamo, así como número total
 320 de capturas para cada una de las 21 especies de aves capturadas durante el periodo de
 321 migración otoñal en Quartier-bas (Suroeste de Francia). Especies pertenecientes a las
 322 familias *Turdidae* y *Muscicapidae* están indicadas en la primera columna como
 323 ‘[TURD.]’ o ‘[MUSC.]’ respectivamente. Nótese que los reclamos se emplearon en dos
 324 de los tres tripletes de redes en cada jornada de anillamiento.

<i>Species (Scientific name)</i>	<i>Control captures</i>	<i>Playback captures</i>	<i>Total captures</i>
Reed Warbler (<i>Acrocephalus scirpaceus</i>)	89	233	322
Cetti's Warbler (<i>Cettia cetti</i>)	7	30	37
Sedge Warbler (<i>Acrocephalus schoenobaenus</i>)	5	27	32
European Robin (<i>Erithacus rubecula</i>) [MUSC.]	9	16	25
Common Grasshopper Warbler (<i>Locustella naevia</i>)	3	20	23
Common Whitethroat (<i>Sylvia communis</i>)	2	21	23
Eurasian Blackcap (<i>Sylvia atricapilla</i>)	4	17	21
Eurasian Blue Tit (<i>Cyanistes caeruleus</i>)	3	15	18
Bluethroat (<i>Luscinia svecica</i>) [MUSC.]	2	14	16
Willow Warbler (<i>Phylloscopus trochilus</i>)	3	9	12
European Pied Flycatcher (<i>Ficedula hypoleuca</i>) [MUSC.]	3	7	10
Garden Warbler (<i>Sylvia borin</i>)	1	6	7
Great Tit (<i>Parus major</i>)	3	3	6
Melodious Warbler (<i>Hippolais polyglotta</i>)	4	1	5
Common Blackbird (<i>Turdus merula</i>) [TURD.]	3	2	5
Chiffchaff (<i>Phylloscopus collybita</i>)	0	4	4
Eurasian Wryneck (<i>Jynx torquilla</i>)	0	3	3
Song thrush (<i>Turdus philomelos</i>) [TURD.]	0	2	2
Nightingale (<i>Luscinia megarhynchos</i>) [MUSC.]	0	1	1
Whinchat (<i>Saxicola rubetra</i>) [MUSC.]	0	1	1

Eurasian Wren (<i>Troglodytes troglodytes</i>)	1	0	1
<hr/> <i>Total</i>	142	432	574

325

326

327 **Table 2.** Results of the GLMM effects model that analysed the number of birds
 328 captured, excluding Bluethroats.

329 **Tabla 2.** Resultados del modelo GLMM que analizó el número de aves capturadas una
 330 vez se excluyeron las capturas correspondientes al Pechiazul.

331

<i>Random Effects</i>	<i>Variance ± Std. Dev.</i>			
Day	0.497 ± 0.705 (63 observations, 21 days)			
<i>Fixed effects:</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Z</i>	<i>P-value</i>
Intercept (Triplet A, Control)	1.67	0.21	7.97	<0.001
Triplet B	-0.08	0.24	-0.34	0.733
Triplet C	-0.35	0.28	-1.25	0.213
Playback (Playback)	0.61	0.19	3.28	0.001
Triplet B × Playback	-0.16	0.32	-0.50	0.618
Triplet C × Playback	-0.24	0.35	-0.69	0.488

332

333

FIGURE LEGENDS

334

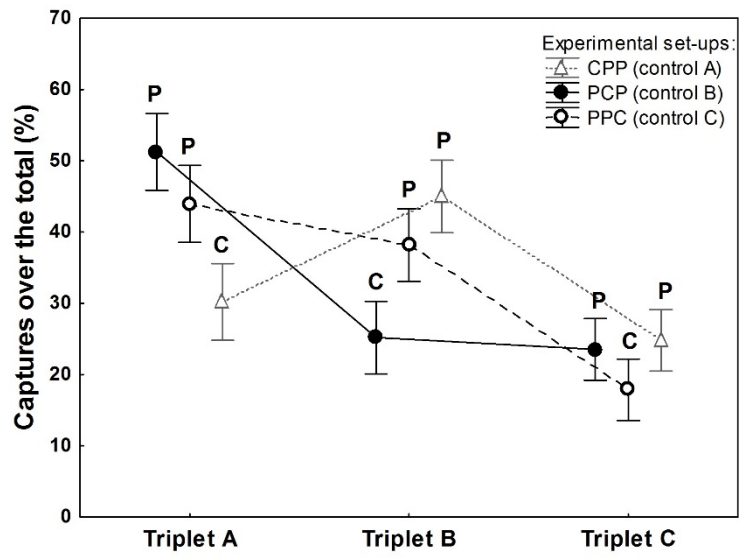
335

336 **Figure 1.** Percentage of birds captured in each triplet over the total number of daily
337 captures for each of the three experimental set-ups that were possible during each
338 ringing day (control in triplet A, B or C). Whether within each set-up the triplet has a
339 playback or not (control) is indicated in the graph by P or C, respectively. Graph shows
340 means and SE. In all cases the sample size for each bar in the graph is the same ($n = 7$).
341 Note that the percentage of captures was used for illustrative purposes in order to
342 account for between-day differences in the number of captures, but raw values of
343 captures were used in the statistical analyses (Table 2). Likewise, the experimental set-
344 up was not a main effect to be tested in the statistical analyses, but was also used in this
345 graph to better represent the between and within-triplet variation in capture rates.

346

347 **Figura 1.** Porcentaje de aves capturadas en cada triplete de redes sobre el número total
348 de capturas diarias para cada una de las tres configuraciones experimentales posibles
349 durante cada jornada de anillamiento (control en triplete A, B o C). Si dentro de cada
350 configuración el triplete tenía reclamo sonoro o no (control) se indica en el gráfico
351 como P o C, respectivamente. La gráfica muestra medias y errores estándar. En todos
352 los casos, el tamaño de muestra para cada barra en el gráfico es el mismo ($n = 7$).
353 Nótese que el porcentaje de capturas sólo se empleó con fines ilustrativos para controlar
354 por las diferencias diarias en el número de capturas, pero fueron los valores originales
355 los utilizados en los análisis estadísticos. Igualmente, la configuración experimental no
356 fue un efecto a testar en los análisis estadísticos (Tabla 2), sino que también se empleó
357 en la gráfica para representar más adecuadamente la variación entre y dentro de tripletes
358 en las tasas de capturas.

359



360

361 De la Hera et al. Figure 1