Reproductive benefits and reduced investment in parental care behavior associated with reproductive groups of males in *Abudefduf troschelii*

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Fishes of the family Pomacentridae present a wide diversity of mating systems, ranging from polygyny to promiscuity and from individual territorial defense to the establishment of reproductive colonies of males. The damselfish species *Abudefduf troschelii* has a reproductive colony mating system, in which males temporarily aggregate in reproductive areas to court and attract females. Males defend an individual territory where they receive eggs and perform paternal care behaviors for their offspring. The present study evaluated the advantages of the colonial mating system in *A. troschelii*. During an entire reproductive period, in a breeding colony within a rocky reef, we located, marked, geo-referenced, and measured the distances between the territories of all males. We quantified the variance among males in their patterns of paternal care investment, eggs acquired, hatching success, reproductive success, body size, and changes in body coloration. We found that males spatially distributed their nests in groups or independently (i.e. solitary nests). Nesting groups are formed by larger males that show intense nuptial coloration during the entire receptivity period. They are located centrally to the colony and consist of 3-6 males whose territories overlap. In contrast, small solitary males that fail to acquire or maintain nuptial coloration during the receptivity period establish their nests peripherally to the colony, away from the territories of other males. Our results highlight that the reproductive benefits of colonial nesting are unequal for males, as the spatial distribution of nests within the colony determines the reproductive success of males. Group nesting confers the highest reproductive benefits to males regarding eggs obtained, hatching success, and relative fitness and also enables males to reduce their parental investment in brood care behaviors. The preference of females for oviposition could be associated with greater intrasexual competitiveness, defense ability, body condition, or experience of group-nesting males located at the center of the colony or because their progeny will have

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a lower probability of predation than they would in solitary nests males.

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2 **reproductive groups of males in *Abudefduf troschelii*.**
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4 **Short title: Reproductive groups in *A. troschelii*.**

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47 **Abstract**

48 Fishes of the family Pomacentridae present a wide diversity of mating systems, ranging from
49 polygyny to promiscuity and from individual territorial defense to the establishment of
50 reproductive colonies of males. The damselfish species *Abudefduf troschelii* has a reproductive
51 colony mating system, in which males temporarily aggregate in reproductive areas to court and
52 attract females. Males defend an individual territory where they receive eggs and perform paternal
53 care behaviors for their offspring. The present study evaluated the advantages of the colonial
54 mating system in *A. troschelii*. During an entire reproductive period, in a breeding colony within
55 a rocky reef, we located, marked, geo-referenced, and measured the distances between the
56 territories of all males. We quantified the variance among males in their patterns of paternal care
57 investment, eggs acquired, hatching success, reproductive success, body size, and changes in body
58 coloration. We found that males spatially distributed their nests in groups or independently (i.e.
59 solitary nests). Nesting groups are formed by larger males that show intense nuptial coloration
60 during the entire receptivity period. They are located centrally to the colony and consist of 3-6
61 males whose territories overlap. In contrast, small solitary males that fail to acquire or maintain
62 nuptial coloration during the receptivity period establish their nests peripherally to the colony,
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64 colonial nesting are unequal for males, as the spatial distribution of nests within the colony
65 determines the reproductive success of males. Group nesting confers the highest reproductive
66 benefits to males regarding eggs obtained, hatching success, and relative fitness and also enables
67 males to reduce their parental investment in brood care behaviors. The preference of females for
68 oviposition could be associated with greater intrasexual competitiveness, defense ability, body
69 condition, or experience of group-nesting males located at the center of the colony or because their
70 progeny will have a lower probability of predation than they would in solitary nests males.

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72 **Key words:** mating system, breeding colony, Pomacentridae, parental care, reproductive
73 success.

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Introduction

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92 The spatial and temporal distribution of potential mates in a habitat can determine factors of great

93 importance on the fitness of individuals, including mate choice and variance in reproductive

94 success among individuals of a population (Emlen & Oring, 1977; Shuster and Wade, 2003; DuVal

95 et al., 2018). Mating systems (MS) that involve the grouping of males performing courtship

96 displays in adjacent areas to attract females are common in nature and perhaps the best studied

97 example of this is that of the Lek mating system, where males form groups during the mating

98 season, in such leks they court and are visited by the females for the sole purpose of mating

99 (Höglund & Alatalo, 1995).

100 The Lek mating system has been described in freshwater and marine fishes (McKaye,

101 1983; McKaye et al., 1990; Jan, 1991; Kellogg et al., 1995; Genner et al., 2005). However, in most

102 marine species, the males defend individual territories and receive eggs from the females within

103 these groups and are then left with exclusive responsibility for providing parental care to the

104 progeny. Paternal care represents an extra contribution of the males (in addition to their gametes)

105 and comes into conflict with the definition of Lek (Höglund & Alatalo, 1995). In this context,

106 different authors have opted instead to refer to them as "groups", "Lek-like" MS (Thresher, 1984),

107 "colonial nesting" (Tyler, 1995) or "colonial breeding" (Schütz et. al., 2016).

108 Reproductive group behavior has evolved in multiple species, frequently associated with

109 an increased individual fitness (Krause & Ruxton, 2002). However, few studies have provided

110 empirical data on how ecological factors (e.g. predation) or life history traits (e.g. body size) may

111 shape the distribution of males within breeding colonies or the fitness benefits of males practicing

112 colonial nesting (Tyler, 1995; Young et al., 2009, Rueger et al., 2021). Some authors have

113 empirically shown that models of lek evolution are applicable to explain colonial breeding models

114 (Schütz et al., 2016). The possible theoretical advantages proposed for the evolution of colonial

115 breeding include the indirect benefits of living in groups when closely related individuals live

116 together, increasing the inclusive fitness of close relatives (Dominey, 1981; Gross & McMillan,

117 1981; Tyler, 1995). In addition, it has been suggested that females prefer to appraise males in

118 groups (Bradbury, 1981; Fletcher & Miller, 2006). For this reason, male aggregations during the

119 breeding seasons have the benefit of increasing mate attraction and reproductive success per capita

120 (Gross & McMillan, 1981; Côté & Gross, 1993; Tyler, 1995). Within groups, females appear to

121 prefer males with centrally located nests compared to the peripheral males, which in this context

122 could act as a barrier against the intrusion of predators (Foster, 1989), and reduce egg loss (Gross

123 & McMillan, 1981; Tyler, 1992; Tyler, 1995). Furthermore, reproductive groups could improve

124 females' efficiency in evaluating phenotypic traits related to males' fitness or quality of parental

125 care, such as body size, aggressiveness, or territory size (Côté & Hunte, 1989). In some species,

126 the females also use male coloration as an estimator of hierarchy, aggressiveness, quality of

127 courtship (Seehausen & Alphen, 1998), parasitism level, quality of immune response (Möller et

128 al., 1999; Clotfelter et al., 2007) their capacity to defend the progeny and the quality of the territory

129 (Maan et al., 2004; Dijkstra et al., 2008; Genner et al., 2008). Even if males use fabricated

130 structures as extended phenotype signals, this could also be used for females to check male quality

131 economically (Schaedelin & Taborsky, 2006, Schaedelin & Taborsky, 2010).

132 The costs of colonial nesting include increased conspicuity as group size increases and,

133 therefore, an increased probability of predation for males and their progeny (Tyler, 1995).

134 Moreover, the closer proximity between nests increases the likelihood of parasite transmission,

135 intrasexual competition, reproductive interference during spawning and the risk of paternity loss

136 (Alexander, 1974; Brown & Brown, 1986; Tyler, 1995; Guillen-Parra et al., 2020). Because of the

137   cost-benefit trade-off of colonial nesting behavior, selective pressures to optimize nest distances

138   to maximize male reproductive success might be expected (Krause & Ruxton, 2002).

139   Reef fishes of the genus *Abudefduf* (family: Pomacentridae) engage in multiple reproductive

140   bouts throughout the year (Fishelson, 1970; Foster, 1987; Robertson et al., 1990). In the beginning,

141   males acquire a darker-bluish nuptial coloration (Bessa et al., 2007), establish and defend a

142   territory, prepare the nest area, court females and receive clutches of eggs from one or several

143   mates (Tyler, 1995; Lobel et al., 2019; Guillen-Parra et al., 2020). Males receive clutches for three

144   days (Foster, 1987; Tyler, 1995). Once oviposited, the eggs remain under the protection of the

145   male until the larvae hatch (Fishelson, 1970; Foster, 1987). Paternal care lasts 6 to 11 days; it is

146   costly since males suspend foraging (e.g. as in *A. abdominalis*, Tyler, 1995) to remain in their

147   territory, oxygenating and defending the eggs against possible predation (Fishelson, 1970; Foster,

148   1987, 1989; Pérez-Hernández, 2018). Fishes of this genus present different reproductive mating

149   systems, including the territorial defense of solitary or group nests within breeding colonies

150   (Foster, 1989; Tyler, 1992; Tyler, 1995). The number of individuals that form a group can vary,

151   as well as the distance at which the closest male is found (Foster, 1989; Tyler, 1995). Alternative

152   reproductive tactics have also been described, such as the presence of sneaking males that try to

153   fertilize the eggs under the guard of other males during oviposition (Dougherty et al., 2022). For

154   *Abudefduf* species, reported percentages of paternity theft range from 5% (in 15% of nests) in *A.*

155   *sordidus* (Lobel et al., 2019) to about 50% in *A. troschelii* (Guillen-Parra et al., 2020). However,

156   in other fish groups, the success rate of parasitic males (one or more per nest) can reach up to 78%

157   (Wirtz et al., 2014).

158   *Abudefduf troschelii* is a reef fish with diurnal habits. It moves in shoals on mid-depth water

159   without establishing territories and feeds mainly on plankton (Foster, 1987; Aguilar-Medrano et

160   al., 2011). At the beginning of the mating season, males separate from the conspecific school. They

161   display a conspicuous coloration change (i.e. sexual dichromatism) from yellow darkening until

162   reaching a bluish tone (Tyler, 1995), which has been suggested as nuptial coloration (e.g. *A.*

163   *saxatilis*, Bessa et al., 2007). Breeding colonies in this species are formed by groups of males

164   nesting simultaneously (from 1 to over 50 males) with a very short distance to the nearest

165   neighbor's nest (0.48 ± 0.25 m; Foster, 1989). Territorial males court females and, if they receive

166   egg clutches, are exclusively responsible for the parental care of the immature until the pelagic

167   larvae hatch (Fishelson, 1970; Foster, 1987; Pérez-Hernández, 2018). For *A. troschelii* males, the

168   reproductive period lasts about 7-11 days and includes a brief three-day spawning period (3.67 d,

169   SD =1.29; Foster, 1987), during which they court females and receive egg clutches from one or

170   more females (Guillen-Parra et al., 2020). After this period, males invest all their parental effort in

171   guarding their territories and the progeny in them until larval hatching typically occurs four or five

172   days after spawning (Fishelson, 1970; Foster, 1987).

173   In this context, this work aims to evaluate the benefits of colonial nesting and the traits

174   contributing to its evolution in damselfishes. Therefore, we studied nesting and parental care

175   patterns in a male breeding colony of the damselfish *Abudefduf troschelii* to evaluate: 1) Whether

176   the spatial distribution of nests is random or shows aggregation patterns within the colony. 2) The

177   effect of phenotypic characteristics of males on the spatial distribution patterns of their nests within

178   the colony. 3) If male nesting decisions determine the reproductive benefits (e.g. reproductive

179   success, parental investment) associated with colonial breeding.

180   **Materials & Methods**

181   **Study site**

182   The study was conducted between September 19th and October 4th, 2016, in an *A. troschelii*

183   breeding colony located in a homogeneous and continuous rocky reef in the bay of La Paz, Baja

184   California Sur, Mexico (24°9'22.32"N, 110°19'28.00"W), at a water depth of between 1 and 5 m.

185   We monitored the area daily starting 5 days before the full moon (i.e. non-nesting period, Tyler

186   1995) and until males began nest preparation behavior (September 25-26). All of the initiated

187   territories (i.e. areas of the reef cleaned by a male) were marked with a numbered rock, geo-

188   referenced and the inter-nest euclidean distances were measured with a 100 m measuring tape to

189   determine the male spatial nesting patterns and generate a detailed map with the spatial distribution

190   of all nests in the colony (Figure 1). The distribution of the territories was used to determine

191   whether the males of *A. troschelii* in this population establish group territories or conduct solitary

192   nesting (see Foster, 1989; Tyler, 1995): 1) Nesting groups are formed by the territories of three or

193   more individuals that simultaneously initiate nest preparation and egg reception. The maximum

194   distance to the center of the nearest neighbor's nest is less than 1m (see Foster, 1989; Tyler, 1995),

195   and the areas defended by males overlapped (see below for the male's maximum attack distance

196   definition). and 2) Solitary nesting is performed by males who initiate a nest at a distance larger

197   than 2.5 meters to the center of the nearest neighbor's nest. Therefore their defended areas do not

198   overlap with those of other males in the breeding colony.

199   **Observations of reproductive behavior**

200   All territories were monitored using daily 15-minute video recordings made over the entire

201   reproductive period (i.e. from spawning until larval hatching 4-5 days). These recordings were

202   made with waterproof cameras (GoPro Hero 4 Silver), located 50 cm from the center of each

203   territory, to avoid agonistic behavior of the male towards the camera and a loss of detail in the

204   recording associated with the water depth and focus of the cameras. Each video featured a size

205 reference placed within the frame to estimate the male's size and territory (see below). The daily

206 order of video recording was randomized between 9:00 and 14:00 hrs. We used these videos to

207 quantify the time spent on parental care behaviors and the reproductive success of each individual.

208 The videos of each male (i.e. one per nesting day) were viewed second by second to quantify the

209 time (in minutes) spent by each male on the different parental care behaviors. As an estimator of

210 the investment in parental care performed by males, we used the time (in minutes) allocated by

211 each male to the main parental care behaviors previously reported at the study site by Pérez-

212 Hernández (2018), both per nesting day and per entire nesting period (sum of seconds allocated

213 daily). We also estimated the proportion (i.e. percentage) of the total time allocated by each male

214 to these behaviors. Blinded methods were used when all parental care behaviors were quantified

215 from all video recordings to minimize observer bias (the observers knew neither the individual

216 identity, the order of the videos, nor the strategy of each male). The patterns into which we

217 organized the parental care behavior were the following:

218   **Chasing :** The male chases away an intruder that enters his territory.

219   **Oxygenation of eggs:** Propulsion of water towards the eggs by fanning the pectoral fins

220 or propelling water using the mouth.

221   **Guarding:** The male is located over the nest (at an approximate distance of no more than

222 20 cm) while regularly changing body orientation to cover a 360° field of view and toward the

223 clutches and the surface.

224   The time the male leaves the nest area was recorded (i.e. beyond the video frame), with no

225 association to any parental care behavior (e.g. chasing). Therefore, we label this time as absence

226 since we have no direct evidence of males' behavior (e.g., foraging, courtship) when they are absent

227 from the nest.

228   To estimate male size from the videos, we took several photographs of the complete

229   individual besides the size reference. From these images, we measured each male's total length

230   (TL: the distance from the mouth to the tip of the longest lobule of the caudal fin). For all videos,

231   we measured the distance from the nest's center to the maximum point at which the male chased

232   an intruder and used it as the male's maximum attack distance (MDA) radius. If the male left the

233   video frame during a chase, the distance from the nest's center to the last observable point in the

234   video frame (i.e. 98 cm) was considered the MDA radius. The MDA diameter was used to estimate

235   the territory size for each male. Finally, in all videos, we recorded whether the male presented

236   nuptial coloration.

237   In order to estimate the number of eggs received by each male, daily photographs were taken

238   twice a day (9:00 and 16:00 hrs) from the day the males received their first egg clutch until the

239   hatching of all larvae. The camera (Olympus TG-5 camera) was positioned parallel 30 cm from

240   the egg clutch (i.e. nest), and a size scale was placed next to the eggs for size reference. If the male

241   nest consisted of egg clutches located on separate rocks (i.e. sections), a photograph was taken in

242   each section. The program ImageJ ver. 1.53. was used to estimate the area occupied by eggs, and

243   daily variations in this value were recorded (Guillen-Parra et al., 2020). We also employed in situ

244   macro-photography of a 1 cm^2 area (with an Olympus TG-5 camera), to quantify twice a day (9:00

245   and 16:00 hrs) the number of eggs per cm^2 in each nest. We take one macro-photograph at the

246   center of the egg clutch and two more at 10 cm from (in each section of the nest). These macro-

247   photographs allowed us to make an estimate of egg density per cm^2 and a rough estimate of the

248   number of eggs received by the male (total area of egg clutch x egg density). In addition, macro-

249   photographs at the center of the nest allowed us to document egg development time; from

250   spawning to hatching (Figure 2), which confirmed that larvae hatch on the 4th or 5th day after egg

251 oviposition (at night). Following Foster (1989), we considered the hatching success of each male

252 as the total area of the egg clutch present in the last photograph of the afternoon of the fourth and

253 fifth nesting day that is no longer present in the first photograph of the following morning

254 (penultimate and last nesting day).

255   To evaluate the effect of the reproductive strategies on the male's reproductive success, we

256 used three independent fitness estimators: 1) Total area of eggs received; 2) Hatching success, the

257 proportion of the total area of eggs received from which larvae hatched (area with hatched

258 eggs/total area of received eggs); 3) Relative hatching success (total area of eggs hatched from

259 each male/mean area of eggs hatched from the total males of the population) (Gillespie, 2004).

260   This study was carried out in strict accordance with the recommendations of the "Regulation

261 of the Institutional Ethics Committee" of the Universidad Michoacana de San Nicolás de Hidalgo.

262 **Data analysis**

263 The nests of all males in the breeding colony were spatially mapped in a two-dimensional space

264 (x-y coordinates point pattern) in order to determine whether, within the breeding colony, males

265 distribute their nests in a continuous (i.e., complete spatial randomness, CSR) or clustered manner.

266 We performed a Ripley's K function, using the Monte Carlo method and 1000 simulated CSR, and

267 corrected for any border effect in the spatstat package in R software.

268   In order to obtain a more detailed description of the contribution of male quality, parental

269 care and the reproductive strategy on the reproductive success of the males, and to compare the

270 effect in terms of reproductive success of the nesting strategies practiced by the males of *A.*

271 *troschelii* in the study population, three independent generalized linear mixed models (GLMM)

272 were generated using the identity of the groups as a random variable and a Normal distribution of

273 errors. These models used the following estimators of fitness as response variables: generalized

274 linear mixed model of the total area occupied by eggs ($GLMM_{TA}$), generalized linear mixed model

275 of hatching success ($GLMM_{HS}$) and generalized linear mixed model of relative hatching success

276 ($GLMM_{RHS}$). Reproductive strategy (i.e. grouped males or solitary nesting), investment in

277 behaviors of parental care (i.e. time assigned to each of the behaviors of parental care), absence of

278 the nest and male size were used as independent variables. Because all three response variables

279 contain zero values, GLMMs were performed in R software using the glmmTMB function of the

280 glmmTMB package (Bolker, 2003), which allows the modeling of zero-inflated continuous data.

281 In addition, for the data analysis, the total time of nesting by the males was divided into two

282 periods: 1) receptivity period (from the day males concluded nest cleaning and received their first

283 eggs, until the last day on which they performed courtship behavior and received clutches of eggs);

284 and 2) hatching period (from the day after the end of receptivity to eclosion of the last larvae). In

285 the case of $GLMM_{TA}$, only the receptivity period was used for the investment of parental care

286 behaviors, since these could influence mate selection and oviposition preference on the part of the

287 females. Non-significant explanatory variables in each full model were backward eliminated to

288 simplify the model.

289   We compare male size, durations, and frequencies of behavioral patterns of parental care

290 and absence of the nest between group nesting and solitary nesting males of *A. troschelii*

291 performing a series of generalized linear mixed models (GLMM) using the identity of the groups

292 as a random variable. We use a normal distribution for the male size response variable and a

293 Poisson distribution of errors for all behavioral response variables. The analyses were performed

294 in R software.

295   Due to conspicuous egg coloration in *A. troschelii*, females could visually quantify the total

296   number of eggs in the nest of each male and prefer nests with more eggs. Bias in female oviposition

297   preferences for traits such as the presence, size, and color of egg clutches has been previously

298   reported in teleost fish species with exclusive paternal care, including *A. sexfasciatus* and *A.*

299   *luridus* (Afonso & Santos, 2005; Goldberg et al., 2020). We evaluated whether females thus biased

300   their oviposition preferences across receptivity days. We performed a linear mixed-effects model

301   (GLMM$_{EP}$) using the total number of eggs in each nest per day as the response variable (during

302   the 3 days of receptivity); as fixed effects, we considered the nesting day, the number of eggs

303   gained and the interaction day*eggs gained, and as random effects the intercept and the nesting

304   day within each male. Since many solitary males did not receive eggs, we used only group-nesting

305   males.

306   From the distribution of the groups, we evaluated whether the relative position of each

307   male's nest influences his reproductive success (e.g., female preference for centrally located nests).

308   We used the center of each nest in a group to draw an irregular polygon, calculate its centroid and

309   use it as the group's center. Next, we measured the distance between this point to the center of all

310   the group nests and the center of the nearest solitary nests. Using these distances we evaluated: 1)

311   the relationship between male size and the location of their nesting territories in the breeding

312   colony; 2) the effect on individual success of the position of the territory of each male relative to

313   the centroid of its group (for Group nesting males) or to the centroid of the nearest group (for

314   solitary nesting males). For this, because the relationship between the variables is not linear we

315   used Spearman rank correlations, with distance from the center of the territory of each male to the

316   centroid of the group as an independent variable (in the case of solitary nesting males, the distance

317   to the centroid of the nearest group was used), male size (i.e. total length) and the three fitness

318   estimators as dependent variables. Furthermore, to evaluate whether there is an effect of the

319   position of the territory of each male relative to the center of the territory of the most successful

320   male in each group (i.e. the male with the largest area of nesting territory occupied by eggs), we

321   repeated the Spearman rank correlation analysis described above, but using the distance from the

322   center of the territory of each male to the center of the territory of the most successful male in each

323   group as the independent variable. For all analyses, Bonferroni corrections were applied to correct

324   the no independence between variables.

325   **Results**

326   More than 2,300 minutes of video were analyzed, corresponding to the behaviors of parental care

327   in 31 custodian males that could be observed daily over the entire course of their reproductive

328   period (mean = 3 days, range 1-6). Two types of nest spatial distribution were observed: 1) males

329   exhibiting group nesting behavior (n = 21 individuals), with an average distance to the nearest

330   neighbor of 70.8 cm (± 14.4), which presented nuptial coloration and maintained it during the 3

331   days of receptivity; and 2) those practicing solitary nesting SN (n = 10 individuals), with an

332   average distance to the nearest neighbor of 296. 4 cm (± 66.3), of these, 50% showed nuptial

333   coloration and only 10% maintained it for at least the first 2 days of receptivity; Figure 1. The 21

334   Group nesting males were found in five independent groups (G1 = 6 inds., G2 = 4 inds., G3 = 4

335   inds., G4 = 4 inds., G5 = 3 inds.). The mean length of all males was 13.54 cm (range 10.98-17.3

336   cm). The Kolmogorov-Smirnov spatial test of CSR (Ripley's K function) showed that nests were

337   not continuously distributed (D = 0.678, p < 0.001). Ripley's K function strongly suggests that the

338   highest proportion of *A. troschelii* males nest near their neighbors, closer than would be expected

339   by chance(Figure S2 supplementary material).

340   The generalized linear models revealed that the male reproductive strategies showed significant

341   differences in the three estimators of fitness considered. The $GLMM_{TA}$ to evaluate differences in

342   mating success, showed significant effects of the strategy, male size and guarding parental care

343   (Table 1), higher egg production success was observed in males nesting in groups (Table 2, Figure

344   3). The $GLMM_{HS}$ revealed significant effects of the strategy, guarding and absence behavior

345   during the final day of the nesting period (Table 1), with group-nesting males having the highest

346   hatching success (Table 2, Figure 3). The $GLMM_{RHS}$ to evaluate the differences in relative

347   hatching success revealed significant effects of the strategy and guarding parental care behavior

348   (Table 1), the highest relative success is achieved by group-nesting males (Table 2, Figure 3). The

349   general patterns of the parental care behaviors of all males that received eggs show that the males

350   of the population assign most of their time to guarding behavior (*ca*. 70%), although they also

351   spend some time absent from the nest (*ca*. 25%). The mean area occupied by eggs per nest was

352   416.93 cm^2 (range = 0-969.02 cm^2), the mean area of eggs under guard by the males at the end of

353   the hatching period was 139.07 cm^2 (range = 0-672.73 cm^2), while the mean hatching success of

354   the males of the population was 27% (range = 0-91%).

355   Results of GLMM analyses to compare morphological traits, parental care behaviors, and

356   fitness estimators between group nesting and solitary nesting males showed that group-nesting

357   males spent significantly a higher percentage of parental care time on guarding behavior (Estimate

358   = 24.61, S.E. = 6.26, t-value = 3.93, p = 0.00048), they lost a lower percentage of eggs (Estimate

359   = -6.74, S.E. = 0.56, z-value = 11.88, p < 0.001) and spent a higher percentage of time absent

360   from the nest (Estimate = -5.64, S.E. = 1.29, t-value = -4.46, p < 0.001). However, no significant

361   differences were observed for male size (Estimate = -0.996, S.E. = 0.76, t-value = -1.308, p =

362   0.212), offspring oxygenation (Estimate = 0.036, S.E. = 0.04, t-value = 0.91, p = 0.358), nor

363   intruder chasing (Estimate = 0.591, S.E. = 0.569, z-value = 1.038, p = 0.299), (Table 2, Figure 4).

364   The GLMM$_{EP}$ model to assess whether females might bias their oviposition preferences based

365   on eggs owned by a male in the nest showed significant differences in the receptivity day (Estimate

366   = 20295, E.E. = 3668. 8, t-value = 5.53, p < 0.05), and the eggs obtained per day per male (Estimate

367   = 0.725, E.E. = 0.156, t-value = 4.65, p < 0.05), but not of the interaction day*eggs obtained

368   (Estimate = 0.001, E.E. = 0.087, t-value = 0.012, p = 0.9905). The fact that the interaction is not

369   significant suggests that although there are daily differences among males in their mating success,

370   the daily probability of success for each male is not determined by the number of eggs obtained

371   on the previous day (Supplementary Figure S3).

372   The Spearman rank correlation analyses did not indicate any significant relationships between

373   the distances from the center of each territory (Group nesting and solitary nesting males) to the

374   center of the territory of the most successful male in each group and the total length of the males

375   (TL: S= 6444.1, r = -0.298, p= 0.102). However, significant and negative relationships were

376   observed between the distance to the center of the territory of the most successful male in each

377   group and the center of the individual territories of the Group nesting and solitary nesting males,

378   for all of the estimators of reproductive success (total area occupied by eggs: S = 8152.2, r = -

379   0.643, p < 0.001; hatching success: S = 8348.3, r = -0.683, p< 0.001; relative hatching success: S

380   = 8630.4, r = -0.739, p < 0.001, Figure 5). We did not observe a significant relationship between

381   the distances from the center of each territory (Group nesting and solitary nesting) to the centroid

382   of the group and the total length of the males (TL: S = 5786.1, r = -0.166, p = 0.3705). In contrast,

383   significant and negative relationships were observed between the distance to the centroid of the

384   group and the center of the individual territories of the Group nesting and solitary nesting males,

385   for all of the estimators of reproductive success (total area occupied by eggs: S = 7434.2, r = -

386   0.498, p < 0.001, hatching success: S = 8228.1, r = -0.659, p < 0.001, relative hatching success: S

387   = 8149.1, r = -0.643, p < 0.001, Figure S1 Supplementary material).

388

389   **Discussion**

390

391   The results of this study regarding the reproductive advantages of the breeding colony mating

392   systems for *A. troschelii* males confirm the theoretical expectation and previous empirical evidence

393   (Foster, 1989). Furthermore, our results suggest that, although within the breeding colony, there

394   appears to be a continuous and homogeneous distribution of available nesting habitat (although

395   there could undoubtedly be subtle variations in the substrate that we did not measure), *A. troschelii*

396   males do not distribute their territories randomly. Spatial analysis of male territories within this

397   population suggests that larger males perform group nesting behavior, locating their nests closer

398   together than would be expected by chance and these groups are in the central part of the colony.

399   On the other hand, smaller males perform solitary nesting behavior, locating their territories in the

400   periphery of the colony and far away from the groups and nests of other solitary males.

401   The effect of male body size and total number of eggs obtained suggests that larger

402   individuals perform group nesting behavior in *A. troschelii*, which may reflect their higher

403   intrasexual competitiveness, defense ability, body condition, or experience (Côté & Hunte, 1989;

404   Maan et al., 2004; Dijkstra et al., 2008; Genner et al., 2008). Although we do not know the age

405   classes in *A. troschelii*, the average body size difference between group and solitary males (ca. 1

406   cm) is consistent with the differences between the two older age classes of *A. saxatilis* males

407   (Villegas-Hernández et al., 2022), which along *A. hoefleri* form the sister clade of *A. troschelii*.

408   Supporting that group nesting males are of a different age class (i.e. one year older) than solitary

409   males. Older and more experienced males apparently prefer to establish their nests near other males

410   of the same status. Whereas younger males have to establish solitary territories near these groups

411   as part of their learning process or because they are excluded from the groups.

412   Besides larger males, only grouping males maintained their nuptial coloration during the 3

413   days of receptivity. In contrast, only 50% of solitary males adopted nuptial coloration, and just 1

414   maintained it until the second day of receptivity. The change in body coloration associated with

415   reproduction (i.e. nuptial coloration) occurs in multiple species of marine and freshwater fishes. It

416   has been described as having functions both in agonistic interactions among males and female

417   attraction (Kodric-Brown, 1998). In addition, male coloration ornaments often reflect body

418   condition (Candolin, 1999; Velando et al., 2006), the intensity of parasitism or the condition of the

419   immune response (Moller et al., 1999; Clotfelter et al., 2007), oxidative damage (Pike et al., 2007)

420   and territory quality (Kodric-Brown, 1983).

421   Our results show that males with group nesting MS have territories in the center of the colony

422   and closer to the centroid of their group while presenting higher success in all fitness estimators.

423   This oviposition preference for males occupying central territories within a colony has been

424   reported in this same species (Foster, 1989). In our study, the relatively small number of males per

425   group makes it difficult to analyze whether the factors determining the fitness advantage of group-

426   nesting males is territory position or simply group membership. However, although we did not

427   measure other phenotypic traits of males, the fact that distance to the centroid is not related to male

428   size could partially support the hotshot model in which the oviposition preference of females is for

429   nests located within the breeding colony and not for male phenotypic traits (Beehler & Foster,

430   1988) nor the presence/number of eggs in the nest.

431   Similar behaviors have been described in fishes; for example, in cichlids with cooperative

432   colonial breeding males with shorter distances to the nearest neighbor have fitness advantages

433   (Jungwirth et al., 2015; Schütz et al., 2016). Also, a preference for male settlement within dense

434   colonies has also been experimentally demonstrated (Heg et al., 2008). The same advantage of

435   reproductive groups has been described in *Amphiprion frenatus* and *Dascyllus aruanus*

436   (Pomacentridae); where males maintain territories adjacent to that of other breeding pairs and

437   whose group size varies depending on shelter size (e.g., anemone or coral) or food availability

438   (Williams & Sale, 1981; Hattori ,1991; Kobayashi & Hattori, 2006; Hattori & Cassadeval, 2016).

439   The influence of group size on male reproductive success has been previously evaluated in

440   *Abudefduf* breeding colonies. However, the effect of solitary nesting has not been analyzed so far,

441   although what we call solitary males have been previously described as "groups of 1 individual"

442   for several species (Foster, 1989; Tyler, 1992; Tyler ,1995; Young et al., 2009).

443   Due to our methodology, we cannot affirm that grouped males have higher number of mates.

444   Nonetheless, considering that the average potential fecundity of the females has been estimated to

445   be close to 21,000 oocytes in the ovary per spawning batch of mature females, both for the species

446   *A. saxatilis* (Villegas-Hernández et al., 2022) and *A. abdominalis* (Helfrich, 1958); grouped males

447   received at least clutches from 3.4 females per nest, and solitary males on average received eggs

448   from 0.96 mates. Thus, as the female preference model proposed, group-nesting males are

449   preferred (i.e. higher mating success, higher total eggs) because their progeny have a lower

450   probability of predation than in solitary male nests. Similar advantages on the survival of progeny

451   to predation have also been observed in other taxa, such as insects (Strassman et al., 1988) and

452   birds (Riehl, 2020).

453   Our result is consistent with the reduced predation on eggs of males nesting in larger groups

454   observed in species of *Abudefduf* (Foster, 1989; Tyler, 1995). Although, it is possible that some of

455   this predation could be associated with filial cannibalism by the male, as has been reported in

456   species such as *A. luridus* (Afonso & Serra 2005) and *A. sexfasciatus* where about 13% has been

457   reported (Manica, 2003). However, during the evaluation of paternal care behaviors, we did not

458   observe any filial cannibalism behavior (i.e. nips to eggs), which coincides with the results of

459   previous work in the same population (Pérez-Hernández 2018), suggesting that the frequency of

460   filial cannibalism in this population of *A. troschelii* is relatively low. Considering the level of

461   predation is essential because some solitary nesting males obtained eggs at the receptivity stage,

462   but almost all (i.e. 89%) lost them before hatching. The average percentage of oviposited eggs that

463   reached the end of the nesting phase was only 1% for the solitary nesting males, compared to 40%

464   for the Group nesting males. It has been reported for this same species that the males with closer

465   neighbors have greater success in the eclosion of larvae than those for which the nearest neighbors

466   are located at longer distances (< 1 m; Foster, 1989).

467   Because of the high predation pressure that colonies suffer, only group defense may guarantee

468   egg hatching. However, solitary nesting at a breeding colony may be maintained in the population

469   if solitary males exploit the efforts of group males by establishing close territories within the

470   breeding colony. Locating their territories close to the groups allows them to act opportunistically

471   by intercepting females attracted to the colony and obtaining some egg clutches or even stealing

472   the paternity of some group nests, which according to previous results in this population of *A.*

473   *troschelii* could represent the potential of sneaker males to sire up to 50% of the clutches (Guillen-

474   Parra et al., 2020). Furthermore, both could be sequential strategies associated with changes in

475 ontogeny (i.e., size) or changes in the status of individuals that could be maintained in the

476 population as an optimal response (Brockman & Taborsky, 2008).

477   It is notable that, contrary to that described by Tyler (1995) in *A. Abdominalis*, the *A. troschelii*

478 males with the solitary nesting lost almost all of the eggs they received. The males of the study

479 population nest on an apparently substrate continuum and are thus probably just as visible and

480 possibly detectable by the predators as the grouped males, and the additive defense of group

481 nesting seems to provide a significant advantage in reducing predation. In order to determine

482 whether it is the female preference or hotshot model that best explains the formation of the Nesting

483 groups, follow-up or experimental manipulations are required in order to observe whether it is the

484 successful males that attract the females to the Nesting group or whether it is the size of the group

485 itself that is the attractant (Alatalo et al., 1992).

486   The GLMM results indicate that male size and parental care investment are important factors

487 in explaining differences in reproductive success and predation reduction between group-nesting

488 and solitary-nesting males. Our results strongly suggest that group nesting is advantageous for *A.*

489 *troschelii* males in addition to advantages in reproductive success because it markedly reduces the

490 cost of investment in parental care behaviors. We observed a reduction in the time allocated to

491 guarding behaviors, as well as in the time and number of aggressive interactions against intruders.

492 Similar results have been reported in cooperatively breeding colonies of cichlids, with larger

493 groups reducing their investment in anti-predator behaviors (Jungwirth et al., 2015). It remains to

494 be determined whether this reduction in the energy budget associated with the cost of paternal care

495 allows individuals with group nesting behavior to maximize their fitness by allowing them

496 increased participation in successive reproductive events. Spatial patterns of nesting show that the

497 proximity of nests to the center of groups confers significant fitness advantages on males.

498   However, there is a need to determine the patterns that govern group establishment (e.g. phenotype

499   matching ; also whether these groups maintain their stability over time, and the mechanisms that

500   may shape the patterns of association within these groups (e.g., familiarity), as well as to deepen

501   our understanding of female choice mechanisms.

502   The documentation of alternative reproductive tactics, such as those displayed by the males of

503   this population, has been reported in multiple species that exhibit territorial and parental care

504   behaviors (e.g. in families such as Cichlidae, Labridae, Gasterosteidae and Pomacentridae). The

505   section above, supports the theoretical prediction that exclusive paternal care of progeny can be

506   exploited by competing males and promotes the evolution of alternative reproductive tactics

507   (ARTs, Taborsky, 2008).

508   The two nesting strategies described in this study (group nesting and solitary nesting) involve

509   territorial defense and parental care of the progeny, and have been suggested indirectly in

510   *Abudefduf saxatilis*, *Abudefduf troschelii* (Foster, 1989) and *Abudefduf abdominalis* (Tyler, 1995),

511   although the previous operational definition of "groups of males" in this genus does include groups

512   formed by a single individual (Tyler, 1995), which corresponds to the definition used in this study

513   of the solitary nesting. This study is therefore the first documentation of two territorial strategies

514   in the same population of pomacentrid fish with a breeding colony mating system, as well as the

515   differential parental investment associated with each of these strategies. In this same context, the

516   wide variance in reproductive success among the males of the study population seems to promote

517   the appearance of alternative reproductive tactics (Mendoza-Cuenca & Macías-Ordóñez, 2010),

518   and may even explain the existence of a third "sneaking" ART previously suggested in the males

519   of *A. troschelii* in this study population (Guillen-Parra et al., 2020) and for *A. sordidus* (Lobel et

520   al., 2019). Even though our study focuses on the analysis of a reproductive cycle in a population

521   of *A. troschelii* present in the Sea of Cortez, The similarities with results previously reported in *A.*

522   *troschelii* in Panama (Foster 1989) and the important homogeneity in space and time of marine

523   regions such as the southern Gulf of California and the Mexican Pacific Transition, could imply

524   that our results could be repeatable or common in *A. troschelii* populations distributed throughout

525   these biogeographic regions.

526   Similar behavior has been reported in the salamander *Hemidactylium scutatum* in which the

527   females can present one of three ARTs: solitary nesting with care of the progeny, group nesting of

528   females with care of the progeny and oviposition of eggs in the nests of other females (Harris et

529   al., 1995). Since these two nesting strategies have not been previously reported, we cannot conduct

530   a direct comparison with the data of other studies; however, Tyler (1995) found that *A. abdominalis*

531   males in larger groups (i.e. more than 15 individual) presented greater mating success than those

532   in smaller groups, since the definition of group provided by that author included solitary nests,

533   with small groups defined as those formed by one to seven individuals. It is possible that those

534   solitary individuals also had lower fitness than those in groups, but this pattern could not be

535   observed when defining groups of one individual.

536

537   **Conclusions**

538   The colonial nesting mating system of *A. troschelii* males provides asymmetrical benefits to

539   individuals. *A. troschelli* males non-randomly distribute their nests within the breeding colony.

540   Larger males establish nesting groups within the colony, while smaller males establish solitary

541   territories on the periphery of the colony. Females present a bias in their mating preferences

542   towards group-nesting males, which may be associated with these males having greater intrasexual

543   competitiveness, defensive ability, body condition, and experience or because their eggs will have

544 a lower probability of predation when in grouped nests. In this context, females may be assessing

545 the quality of males through the presence, intensity, and duration of nuptial coloration presented

546 by males. The reduction in male parental investment in paternal care behaviors is remarkable, and

547 it remains to be determined whether "time saved" allows males to have more nesting events

548 throughout the year. The observed nesting behaviors could represent two alternative mating tactics.

549 The solitary nesting tactic may allow paternity theft from males with group nesting tactics.

550

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Figure 1

Map of the breeding colony of Abudefduf *troschelii*.

The geo-referenced scaled location of male nests with a group and solitary nesting is shown. The total number of eggs each male receives is shown as squares to scale. We use the average size of the males in the population (0.95 m) to represent the size of the territory.

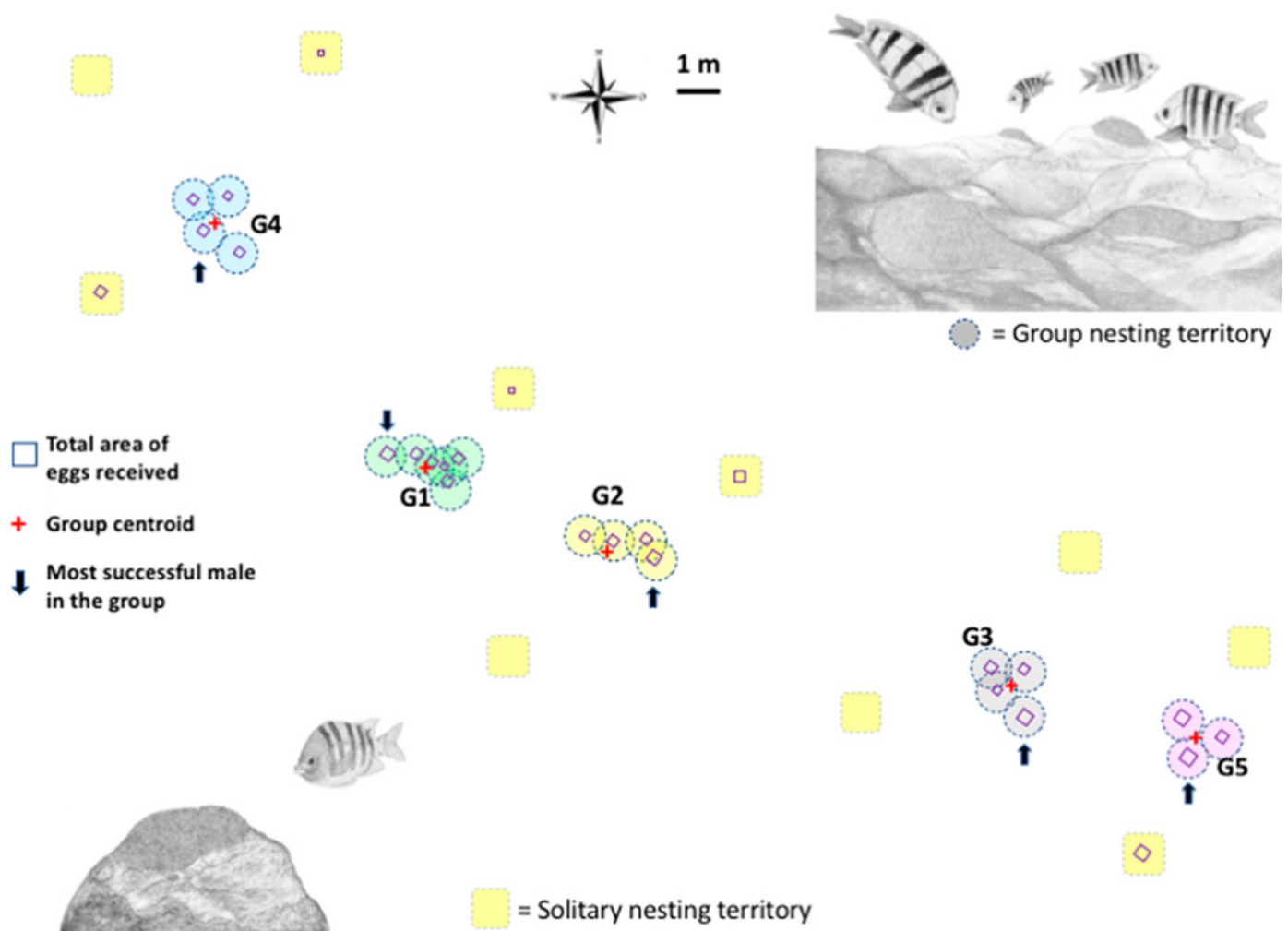



Figure 2

Images of the development of *A. troschelii* eggs per day. From the day of oviposition (day 1) to the day of hatching (days 4-5).

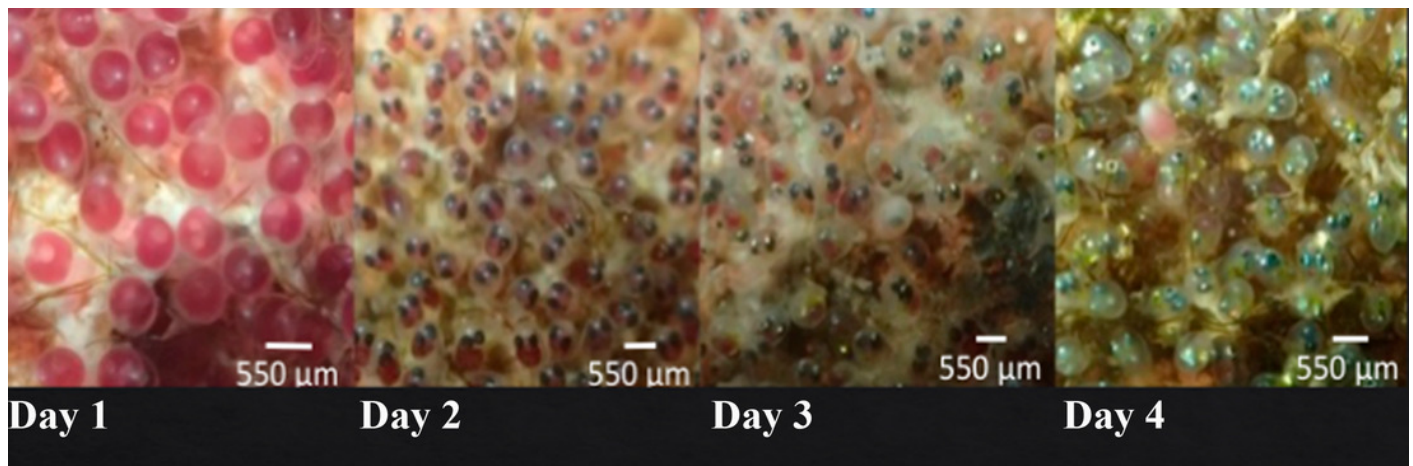



Figure 3

Effect of the nesting behavior on the total area occupied by oviposited eggs, hatching success and relative hatching success of males of *Abudefduf troschelii*.

*All of the parental care behaviors show significant differences after Bonferroni corrections associated with the spatial distribution patterns of their nests within the colony.

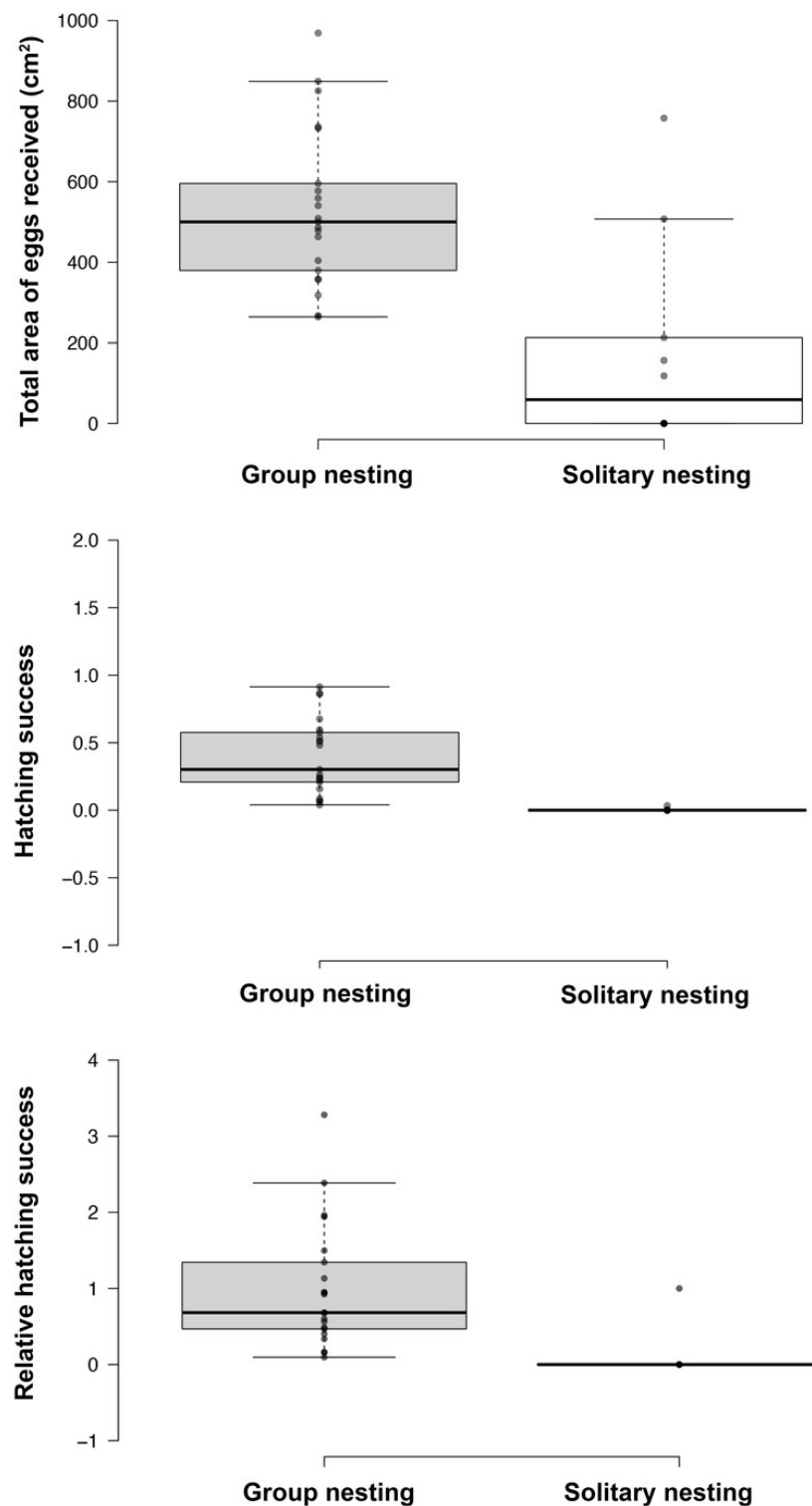



Figure 4

Investment in parental care behaviors between group nesting and solitary nesting males.

* Asterisk shows significant differences between the male nesting strategies for each behavior.

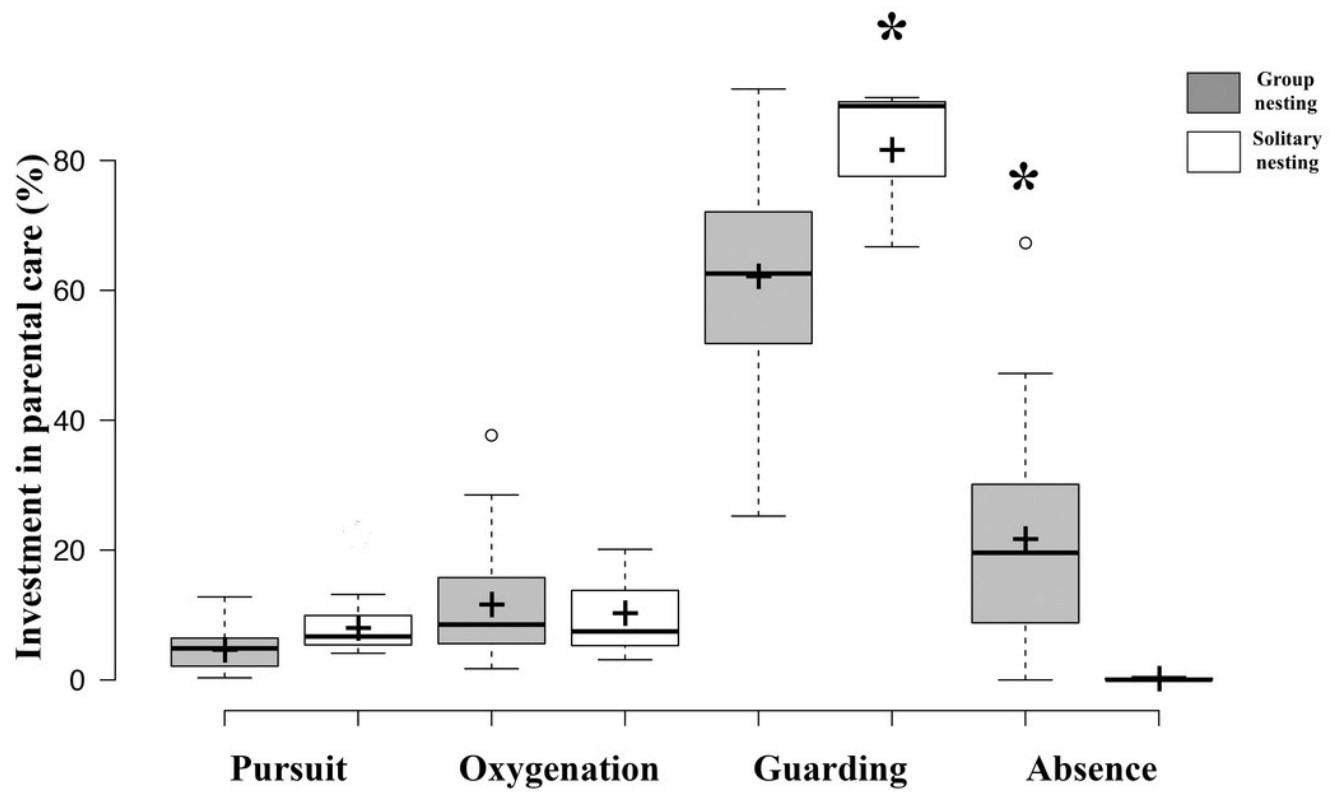
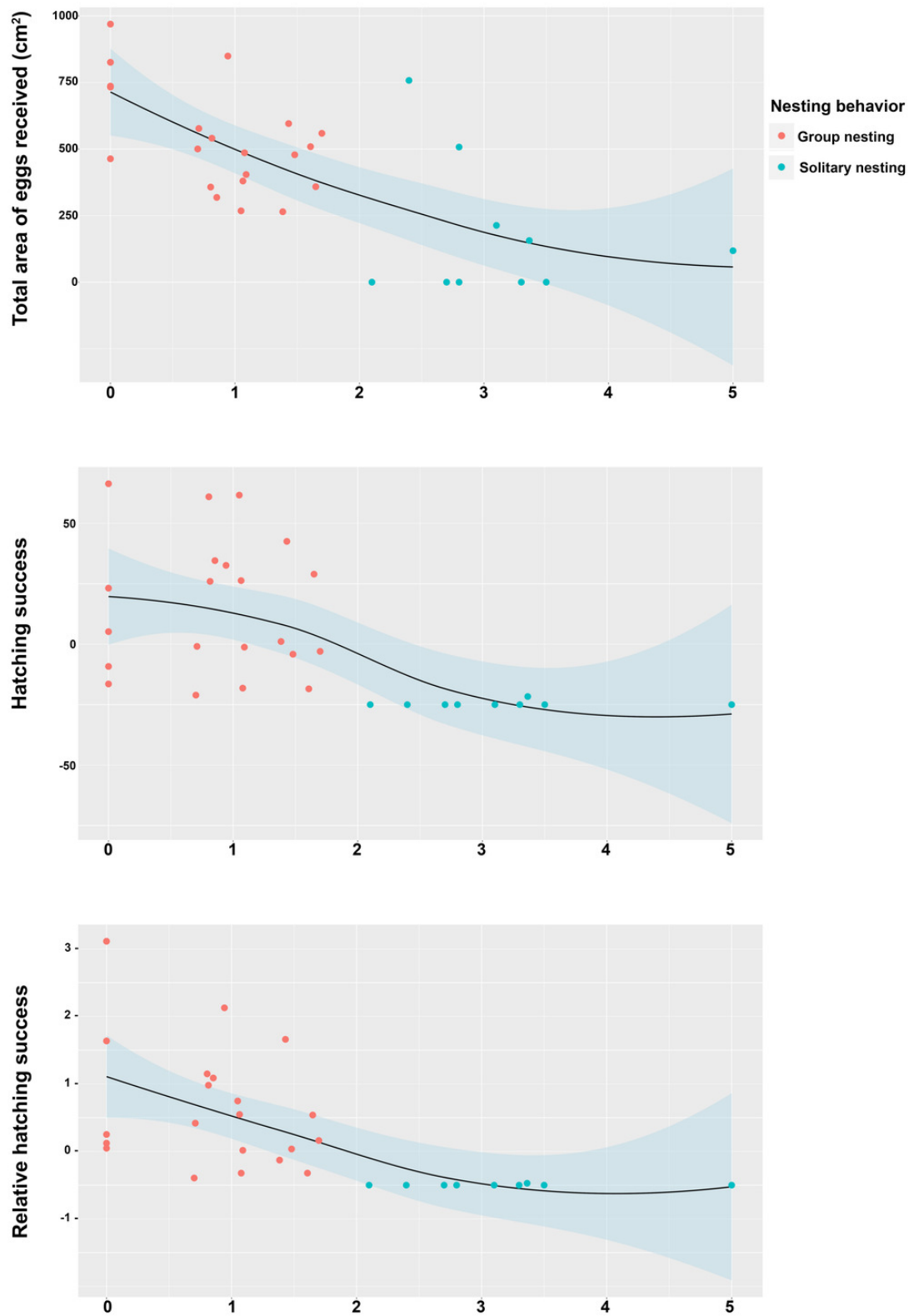



Figure 5

Relationship between the position of the individual territory of the males to the center of the territory of the most successful male of the group with respect to the estimators of reproductive success.

(A) total area occupied by eggs, (B) hatching success, (C) Relative hatching success

Comparison among the patterns of parental care between the nesting behavior presented by males of *A. troschelii*.

Model GLMM$_{TA}$				
Parameter	**Estimate**	**S.E.**	**Z value**	**P**
Strategy	-246.010	88.480	-2.780	0.0054
Male size	51.784	20.833	2.486	0.0129
Guarding	-2.596	2.147	-1.209	0.2265
Model GLMM$_{HS}$				
Parameter	**Estimate**	**S.E.**	**Z value**	**P**
Strategy	-0.3758	0.1050	-3.550	0.00038
Absence	-0.0097	0.0044	-2.171	0.02996
Guarding	-0.0101	0.0039	-2.550	0.0107
Model GLMM$_{RHS}$				
Parameter	**Estimate**	**S.E.**	**Z value**	**P**
Strategy	-0.6881	0.3402	-2.012	0.0442
Guarding	-0.0153	0.0079	-1.926	0.0541

Male size, patterns of parental care and estimators of fitness between the nesting behavior presented by males of *A. troschelii*.

Significant differences among nesting strategies are shown

Male trait	Group nesting (mean ± S.D.)	Solitary nesting (mean ±S.D.)	GLMM p-value
Size of male (TL in cm)	13.60 ± 1.88	12.7 ± 1.07	P = 0.212
Parental care behaviors	**Group nesting (mean ± S.D.)**	**Solitary nesting (mean ±S.D.)**	**GLMM p-value**
Average guarding (%)	65.46 ± 21.37	80.69 ± 30.85	P = 0.0004
Absence (%)	29.81 ± 16.89	19.30 ± 30.8	P = 0.00195
Chasing (%)	0.04 ± 0.02	13.79 ± 6.05	P = 0.299
Oxygenation of progenies (%)	13.084 ± 9.9	12.25 ± 9.57	P = 0.358
Estimator of fitness	**Group nesting (mean, range)**	**Solitary nesting (mean, range)**	**GLMM p-value**
Total area of received eggs (mm^2)	532 (265-969)	350 (118-758)	P = 0.0054
Hatching success	0.4 (0.039-0.913)	0.007 (0-0.033)	P = 0.00038
Relative fitness	1.236 (0.12-4.06)	0.006 (0.0-0.031)	P = 0.0442
Predation (% of area lost)	60 (9-96)	99 (97-100)	P < 0.0001