1   *Short title*

2   **Experimental density-dependent immigration**

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5   *Full title*

6   **Immigration rates during population density reduction in a coral reef fish**

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18  **Abstract**

19  Although the importance of density-dependent dispersal has been recognized in theory, few

20  empirical studies have examined how immigration changes over a wide range of densities.

21  In a replicated experiment using a novel approach allowing within-site comparison, we

22  examined changes in immigration rate following the gradual removal of territorial

23  damselfish from a limited area within a much larger patch of continuous habitat. In all sites,

24  immigration occurred at intermediate densities but did not occur before the start of

25  removals and only rarely as density approached zero. In the combined data and in 5 of 7

26  sites, the number of immigrants was a hump-shaped function of density. This is the first

27  experimental evidence for hump-shaped, density-dependent immigration. This pattern may

28  be more widespread than previously recognized because studies over more limited density

29  ranges have identified positive density dependence at low densities and negative density

30  dependence at high densities. Positive density dependence at low density can arise from

31  limits to the number of potential immigrants and from behavioral preferences for settling

32  near conspecifics. Negative density dependence at high density can arise from competition

33  for resources, especially high quality territories. The potential for non-linear effects of local

34  density on immigration needs to be recognized for robust predictions of conservation

35  reserve function, harvest impacts, pest control, and the dynamics of fragmented

36  populations.

37  **Key-words:** Conspecific attraction, density dependence, harvest theory, metapopulation,

38  Pomacentridae, protected area, spillover

## Introduction

40   The connection between density and dispersal has important implications for ecology,

41   evolution, and behavior [1–5]. Over long distances, density-dependent dispersal can

42   influence range expansion and the extinction and colonization of patches [4,6]. When

43   dispersal involves localized movements within populations, density dependence can affect

44   other density-dependent processes such as reproduction, growth, and mortality. In addition,

45   it can affect source-sink dynamics, the function of conservation reserves and reintroduction

46   programs, and the control of pests and invasive species, for example, compensating for

47   localized mortality and increasing movements of animals from protected to harvested areas

48   [7–12].

49         Numerous empirical studies provide evidence for an association between emigration

50   rate and population density [13,14]. However, the broader relationship between local

51   density and dispersal is not well understood, in part because both theoretical and empirical

52   investigations have tended to focus on emigration. The effects of density on the equally

53   important movement and immigration stages of the dispersal process have been largely

54   ignored [5,13,15]. The substantial literature examining the influence of conspecifics on the

55   number of individual marine fish and invertebrate larvae that enter local populations from

56   the plankton [16–18] appears to be an exception. However, this literature has only limited

57   application to questions of density-dependent immigration because the number of

58   individuals arriving (called 'settlement' in this literature) often cannot be distinguished from

59   the number surviving to some early stage ('recruitment'), which itself is often density-

60   dependent [18].

61      Immigration may increase as density increases if Allee effects [19] occur or if

62      conspecific abundance provides an indication of habitat quality [20]. On the other hand,

63      immigration may decrease as density increases because higher densities result in lower *per*

64      *capita* resource availability or lower quality of locations available for settlement [21]. Since

65      the benefits of increasing density are more likely when densities are relatively low and the

66      costs of increasing density are more likely when densities are relatively high, a hump-

67      shaped relationship between immigration and density may be expected when density varies

68      over a broad range [22]. Alternatively, density might have no influence on immigration (*i.e.*

69      density independence) if animals are unable to assess density or resource availability, if

70      populations never approach carrying capacity, if Allee effects are unimportant, or if

71      immigration rate is limited by the availability of potential immigrants.

72      Empirical evidence to indicate whether immigration rate shows a hump-shaped

73      response to density is sparse. Only a few field studies have examined immigration rate over

74      a sufficient number and range of density levels to detect a hump-shaped pattern, if one were

75      present [22–30]. Some studies have presented immigration rate data only after dividing by

76      the number of residents, potentially obscuring lower immigration to sites with fewer

77      residents (discussed below). Finally, almost no studies have used a replicated, experimental

78      design to control for potentially confounding correlates of density and immigration such as

79      habitat quality, functional connectivity, and immigrant availability [22,24,27].

80      In the present study, we examine whether adults of two small, interspecifically

81      territorial coral reef damselfishes show density-related variation in local immigration in

82      response to the experimental manipulation of density from saturation to complete absence

83    of conspecifics. On 7 sites surrounded by suitable, occupied habitat, we repeatedly removed

84    a small, constant proportion of fish, continuing until no fish remained and immigration

85    ceased. Previously, using data from this experiment, we showed that the total number of

86    immigrants arriving over the entire experimental period was influenced by inter-site

87    differences in the availability of potential immigrants in adjacent areas and by the relative

88    habitat quality between the depletion and source areas but not by differences in landscape

89    connectivity [31]. Two control sites had almost no immigration during equivalent

90    observation periods. Here, we examine the number of immigrants arriving after each

91    removal event to ask how immigration rate within sites changes in response to the gradual

92    reduction of density.

93    **Methods**

94    STUDY SPECIES

95    Adult and subadult longfin *Stegastes diencaeus* and dusky damselfish *S. adustus* (formerly

96    *S. dorsopunicans*), hereafter 'damselfish', of both sexes defend small (about 1 m$^2$)

97    territories on dead coral substrate. These territories provide food (benthic algae), shelter

98    holes, and nest sites for males [31,32], and there are no non-territorial 'floaters'. Because

99    they are diurnal, active, conspicuous, and occur at high density, they are well suited for

100   studies of immigration. Their fringing reef habitat is a naturally fragmented landscape in

101   which continuous reef and patches of various sizes are separated by a matrix of sand and

102   rubble. Damselfish seldom move far from solid reef substrate, so sand and rubble patches

103   form partial barriers to movement within a reef [33]. Dispersal occurs at two life history

104   stages and spatial scales. After hatching from eggs guarded by males, larvae disperse in the

105   plankton, later settling on the reef as small juveniles. Thus, individuals are unlikely to be

106   closely related to their neighbors, and genetic differentiation is unlikely over relatively

107   large spatial scales [34]. Upon reaching adult size, mortality rate is low, and spontaneous

108   moves are rare [35]. Nevertheless, damselfish relocate quickly in response to vacancies in

109   higher quality habitat [35,36]. This local dispersal or 'home range relocation' of adult and

110   subadult individuals, almost certainly from within the same fringing reef and likely from

111   relatively close territories, is the focus of our study. It is similar to the within-patch

112   dispersal of many mammals and birds [30,37,38]. In our study area, adult territories are

113   contiguous on suitable substrate, with their number and spatial extent relatively stable over

114   the annual cycle as well as between years (K. Turgeon, *unpublished data*), as also noted for

115   other territorial damselfishes [39,40]. Stable densities and distributions suggest that these

116   populations are close to saturation on fringing reefs in Barbados.

117   REMOVAL EXPERIMENT

118   Our study design mimicked a situation in which localized predation or human exploitation

119   created an attractive sink for immigrants from surrounding source areas that were not

120   subject to the same mortality. To the best of our knowledge, this approach has not been

121   used in previous studies of density-dependent immigration. Although repeated removals

122   may reduce the number of potential immigrants, examining the density-immigration

123   relationship during gradual depletion provides a rare opportunity to examine immigration

124   over a broad range of densities while holding other ecological features constant, as well as

125   providing insight into the impacts of localized harvest and pest removal on dispersal.

126    We conducted the experiment on seven experimental and two control sites in the

127    spur and groove zones of five fringing reefs [experimental: Bachelor Hall (1), Heron Bay

128    (4), Sandy Lane (2); control: North Bellairs (1), South Bellairs (1), S1 Fig.] along the west

129    coast of Barbados (13°10'N, 59°38'W). Each site consisted of a rectangular depletion area

130    of about 150 m$^2$ within the much larger spur and groove zone of the fringing reef. We

131    defined a 10-m wide band around the depletion area as a source area for potential

132    immigrants, based on the distances of extraterritorial forays which could serve to detect

133    vacant territories [31,41,42]. We selected experimental sites so that the depletion areas

134    were similar in number of residents, total area, and area of hard substrate (S1 Table). Using

135    natural variation in the shapes of the reefs, we selected source areas to vary in abundance of

136    potential immigrants, quality of the habitat and landscape connectivity [S1 Table; see Fig.

137    S1 in [31] for examples].

138    In the depletion area at each experimental site, we marked all resident damselfish >

139    5 cm (total length) with visible implant elastomer (Northwest Marine Technology, Shaw

140    Island WA, USA) and mapped their territories. Experimental sites were observed at 2 or 3-

141    day intervals for two weeks prior to removal. Then, every 2 or 3 days, we removed a

142    constant number of randomly selected individuals, including both residents and the

143    immigrants that had replaced previously removed residents, equal to about 15% of the

144    original population (i.e., 7 - 10 individuals per event, depending on the number of

145    residents). In one case (site HB1), the sequence was delayed for several days by a

146    hurricane. The day after each removal, we mapped all occupied territories in the depletion

147    area, noting the presence of immigrants (untagged individuals). Approximately 30 hours

148    was considered sufficient to achieve a new equilibrium because about 90% of

149    recolonisations in both species occurred by the end of observations on the second day.

150    Previous studies also found that territory recolonisation in damselfishes often occurs within

151    one day [35,36,43]. Removals continued until no fish remained and immigration had ceased

152    for at least 6 days. (In 2 sites, a single, small individual could not be captured.) Complete

153    trials required approximately five weeks, depending on immigration rate. In the source

154    area, we counted all damselfish > 5 cm once but for logistical reasons were not able to

155    monitor changes in density or position at each removal event. Because of the intensity of

156    data collection, we were able to conduct only one trial at a time. Trials took place between

157    April and September 2005-2007.

158    ETHIC STATEMENT

159    Fish removal was needed to determine if movement occurs when the density is reduced.

160    Prior to the experiment, specimens were marked with an injection of a small amount of

161    inert elastomer under the scales (VIE tag - Northwest Marine Technologies). The tagging

162    procedures required less than 30 s to perform and mortality from this method of tagging is

163    extremely low. To reduce fish stress of these two highly territorial species, we marked them

164    underwater, without anaesthesia, near the site of capture so that they can return to their

165    territories quickly. During the removal experiment, fish were removed using cast nets

166    whenever possible. When cast nets were not successful, we used micro-spearfishing. After

167    capture, fish were immediately euthanized using an overdose of carbon dioxide prepared by

168    dissolving antacid powder (Eno, approx. 5g/L) in sea water. The effects of this localized

169    fish removal on the population and community are similar to the harvest effect produced by

170    fisheries and were expected to have modest effects on competition and predation. Our

171    research complied with the ABS/ASAB Guidelines for the Treatment of Animals in

172    Behavioral Research and Teaching and was approved by the McGill University Animal

173    Care Committee, Animal Use Protocol 5039. Field work did not involve endangered or

174    protected species. No specific permissions were required to harvest these two damselfish

175    species in Barbados.

176    DATA ANALYSIS

177    *Scaling immigration rate*

178    We carried out separate analyses of immigration rate using per site scaling (total number of

179    immigrants arriving on the site following each removal event), per new vacancy scaling

180    (number of immigrants/number of damselfish removed at each event), and *per capita*

181    scaling (number of immigrants/number of damselfish present following each removal

182    event). Per site scaling provides the most direct measure of immigrant movement and is

183    equivalent to per unit area scaling. We included per new vacancy scaling because territory

184    availability was the limiting resource and relating immigration to vacancies was therefore

185    likely to illuminate the processes involved [*e.g.,* [25]]. Because 92% of all immigrants (n =

186    122) settled on territories from which the owner had been removed during the immediately

187    preceding event rather than during previous removal events, we scaled to the number of

188    new vacancies rather than total vacancies. Even though removal of a constant number of

189    damselfish at each event means that per site and per new vacancy scaling would produce

190    similar patterns over most of the density range, important variation could occur at low

191    densities where the total number of remaining damselfish was less than the number to be

192    removed. *Per capita* scaling was included for completeness because demographic rates,

193    including emigration and immigration, are normally scaled to the population size in

194    analyses of density dependence [44]. However, it is important to recognize that relating

195    immigrants per damselfish to number of damselfish is an example of spurious correlation

196    (Y/X vs. X) that can produce a negative correlation even if immigration rate per site does

197    not change with density [45]. This is referred to as 'apparent' or 'pseudo-density

198    dependence' [18]. For per site scaling, we included data on immigration before the start of

199    removal as well as data after the number of residents had been reduced to zero. Per vacancy

200    scaling could not include data before any fish had been removed and *per capita* scaling

201    could not include data after density had been reduced to zero, because the values were

202    undefined.

203    *Statistical analyses*

204    To assess density dependence of immigration, we used curve-fitting analyses to compare

205    the fit of 6 alternative functions for each site and then examined the generality of the

206    pattern with Generalized Additive Mixed effect Models (GAMM) on the combined dataset.

207    Both analyses examined the relationship between the total number of damselfish still

208    present on each site after each removal event, including both residents and earlier

209    immigrants (independent variable), and the number of immigrants arriving at the site

210    between that removal and the subsequent count (dependent variable). For the independent

211    variable, number of damselfish was equivalent to density because area was constant within

212    sites. For the dependent variable, we scaled the number of immigrants in three ways to

213    facilitate interpretation as described above. We combined both species for this analysis

214    because territories were defended interspecifically, because there was too much variation in

215    relative numbers of the two species between sites and between removal events for separate

216    analyses by species, and because a preliminary analysis did not indicate an effect of species

217    on the response to density (K. Turgeon, *unpublished analysis*).

218        For each site, we compared the fit of six alternative functions corresponding to

219    density independence, linear negative or positive density dependence, exponential negative

220    or positive density dependence, saturating positive density dependence, and two functions

221    that can model a hump-shaped combination of negative and positive density dependence

222    (Table 1). Including alternative functions (linear and exponential for monotonic functions,

223    polynomial and Ricker for hump-shaped relationships) allowed greater flexibility in the fit.

224    The saturating positive density-dependent function addressed the potential for immigration

225    to be constant and then drop at lower density as the source became depleted. Parameters for

226    each function were estimated with maximum likelihood approach with the mle2 function

227    (normal probability distribution) available on the bbmle package version 1.0.4.1 [46]. To

228    compare the support of each function to explain observed immigration, we used the

229    Information Theoretic Approach [47]. We used Akaike's Information Criterion modified for

230    small sample sizes (AICc) to assess the fit of each function to observed data. Lower AICc

231    values indicated a better fit. We calculated the difference between AICc for each model $i$

232    and the lowest observed AICc (ΔAICc) and compiled normalized Akaike weights ($w_i$) the

233    probability that function $i$ is the best function, given the data and set of candidate functions

234    [48]. For each site, we also computed the "evidence ratio" to compare the relative

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235    likelihood of any two functions ($w_i/w_j$; [48]). To determine the best function overall, we

236    calculated the mean Akaike weights (mean $w_i$) for each function.

237    **Table 1**. Alternative functions fit to the data relating immigration ($I_t$) to the number of

238    damselfish remaining on the site ($D_t$) following each removal event, where $a$ and $b$ are

239    estimated parameters. For per site scaling, $I_t$ equaled the total number of immigrants arriving

240    on the site between the removal and the subsequent count. For per new vacancy scaling, $I_t$

241    equaled the total number of immigrants arriving on the site between the removal and

242    subsequent count divided by the number of damselfish removed. For *per capita* scaling, $I_t$

243    equaled the total number of immigrants arriving on the site between the removal and the

244    subsequent count divided by the number of damselfish remaining immediately after the

245    removal.

| Function | Pattern |
|---|---|
| $I_t = b$ | 1) Density independent |
| $I_t = aD_t + b$ | 2) Linear negative or positive density dependence |
| $I_t = ae^{-bD_t}$ | 3) Exponential negative or positive density dependence |
| $I_t = a(1 - e^{-bD_t})$ | 4) Saturating positive density dependence |
| $I_t = -aD_t^2 + bD_t$ | 5) Quadratic polynomial (hump-shaped) |
| $I_t = aD_t e^{-bD_t}$ | 6) Ricker (hump-shaped) |

246     For the combined analysis, we used Generalized Additive Mixed effects Models

247     (GAMMs) because they combine the utilities of linear mixed models [49] and Generalized

248     Additive Models (GAM; [50] so that random factors, fixed factors and nonlinear predictor

249     variables can all be estimated in the same model. Rather than fitting curves as in the site

250     analysis, GAMMs model nonlinear relationships between density and immigration as a

251     smoothing function. Because of the potential temporal autocorrelation between successive

252     removal events and the risk of violating the assumption of residual independence in

253     interpreting *p*-values, we used an autoregressive correlation structure (corAR1) in the

254     GAMM. Site identity was used as a random factor, and the autocorrelation in error structure

255     was accounted for by nesting the removal event sequence within site. To make sites more

256     comparable, the independent variable was changed from number of damselfish at each

257     removal event to the proportion of the initial number. GAMMs for all three scales were fit

258     using the mgcv package v. 1.7-28 in R [51,52].

259     **Results**

260     Immigration occurred almost exclusively at intermediate densities. It never occurred during

261     the pre-removal period when densities were maximal, but started after the first removal in

262     three sites (SL1, SL2, BH1) and after the second removal in three others (HB3, HB2 and

263     HB4) but only after the sixth removal in HB1 (Fig. 1). After the first occurrence of

264     immigration in each site, immigration followed most subsequent removals until density

265     became very low. In 6 sites, there was no immigration after density was reduced to 0 or to a

266     single uncapturable individual. In 1 site (HB4), 2 individuals arrived after density was

267   reduced to zero the first time. However, most sites did have 1 - 4 immigrants when density

268   was first reduced to 1 or 2 individuals.

269         For per site scaling (*i.e.* the total number of immigrants arriving after each removal

270   event), the curve-fitting analysis of individual sites indicated that the best function was

271   hump-shaped density dependence in 5 sites (Ricker function in 3, polynomial in 2) and

272   density independence in 2 sites (Table 2, Fig. 1). In comparison to density independence,

273   the evidence ratio for density dependence was high (> 56) for 3 sites and moderate (2.6 –

274   3.0) in the other two. On average, the hump-shaped Ricker function provided the best fit as

275   indicated by the mean $w_i$ (Table 2), with a moderate evidence ratio compared to density

276   independence (2.3). The fitted functions indicated that, on average, immigration per site

277   continued to rise until density was less than half the starting density (peaks occurred

278   between 6% – 50% of the starting population, mean = 29%, Fig. 1). For the combined

279   dataset analysis, the GAMM supported a hump-shaped pattern (significance of the

280   smoothing term; p = 0.014; Fig. 1). As density decreased, mean immigration rose to a broad

281   peak between about 10 and 40% of the starting population, dropping to a very low level

282   only when density approached zero. These patterns were strongly influenced by but not

283   completely dependent on the very low immigration at zero density; when zero density data

284   were excluded from the analysis, the hump-shaped pattern remained very strong in the

285   GAMM analysis of the combined data and was most likely in 3 individual sites, but density

286   independence became slightly more likely than hump-shaped density dependence in 2 sites

287   for which a hump-shaped function fit best with zero density included (K. Turgeon,

288   unpublished analyses).

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289   Table 2. AICc scores (AICc) and Akaike weights ($w_i$) for each of the six empirical functions predicting the observed number of

290   immigrants arriving on the site following a removal event in relation to population size of damselfish following that removal

291   event (site scaling) on seven experimental sites. The mean Akaike weight (Mean $w_i$) for each function is given at the bottom of

292   each column. For each site and the mean of all sites, the function with the highest support is indicated by bold $w_i$. Sites are

293   ordered as in Fig. 1. See Figure 1 for site abbreviations and Table 1 for the functions.

| Site | Density-independent | | Linear | | Negative exponential | | Saturation | | Quadratic polynomial | | Ricker | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ |
| HB1 | 32.68 | 0.000 | 34.20 | 0.000 | 32.96 | 0.001 | 37.18 | 0.000 | 39.48 | 0.000 | 28.20 | **1.000** |
| HB3 | 54.76 | 0.001 | 54.37 | 0.001 | 55.35 | 0.001 | 57.87 | 0.000 | 60.53 | 0.000 | 41.29 | **0.996** |
| BH1 | 37.53 | 0.232 | 41.24 | 0.036 | 41.40 | 0.053 | 40.22 | 0.060 | 41.16 | 0.038 | 35.52 | **0.702** |
| SL2 | 52.23 | 0.011 | 55.90 | 0.002 | 55.90 | 0.002 | 51.82 | 0.014 | 44.16 | **0.647** | 45.54 | 0.324 |
| SL1 | 72.48 | 0.152 | 75.54 | 0.033 | 75.58 | 0.032 | 74.06 | 0.069 | 70.54 | **0.400** | 70.82 | 0.337 |

294     Table 2. Continued and concluded

| Site | Density-independent | | Linear | | Negative exponential | | Saturation | | Quadratic polynomial | | Ricker | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ | AICc | $w_i$ |
| HB2 | 35.22 | **0.487** | 37.38 | 0.165 | 37.94 | 0.125 | 40.02 | 0.044 | 41.14 | 0.025 | 37.52 | 0.154 |
| HB4 | 49.64 | **0.623** | 53.57 | 0.096 | 53.57 | 0.096 | 53.69 | 0.090 | 53.05 | 0.124 | 58.55 | 0.008 |
| Mean $w_i$ | | 0.215 | | 0.048 | | 0.041 | | 0.040 | | 0.176 | | **0.503** |

295    For per new vacancy scaling, the best function for individual sites was hump-shaped

296    (Ricker function) in all 5 sites that showed a hump-shaped response in per site scaling and

297    density-independent in the other 2 sites (S2 Table, S2 Fig. black dots and lines). Compared

298    to density independence, the evidence ratio for density dependence was high in 3 sites (>

299    10.9) but low at the other 2 (1.3 – 1.5). On average, the Ricker function provided the best

300    fit (Mean $w_i$; S2 Table) but was only slightly more likely than density independence

301    (evidence ratio = 1.6). The proportion of new vacancies occupied by immigrants following

302    individual removal events ranged from 0 to 1 but was almost always less than 0.3 (median

303    = 0.25, 95% CI = 0.20 – 0.31, N = 77; S2 Fig. black dots). For the combined dataset

304    analysis, the GAMM supported a hump-shaped relationship between the number of

305    immigrants per new vacancy and the proportion of the initial abundance (significance of the

306    smoothing term; $p = 0.016$; S2 Fig.).

307    For *per capita* scaling, the best-fitting function was density-dependent for all 7 sites

308    (S3 Table, S2 Fig. grey lines and dots). The best function was hump-shaped (Ricker) for

309    the 5 sites that showed hump-shaped relationships with per site and per new vacancy

310    scaling, negative exponential for 1 site that had been density independent with per site and

311    per new vacancy scaling and tied between hump-shaped (Ricker) and negative exponential

312    for the other. The evidence ratio for density dependence (Ricker and negative exponential)

313    compared to density independence was very high (> 100) for 5 sites and moderate and high

314    for the other 2 (2.1, 6.7). On average, the best fit was hump-shaped (Ricker; Mean $w_i$; S3

315    Table) with high evidence ratios in comparison to density independence (16.8) and the

316    negative exponential (6.1). For the combined dataset analysis, the GAMM supported a

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317    negative relationship between the number of immigrants *per capita* and the proportion of

318    the initial abundance (significance of the smoothing term; $p < 0.001$; S2 Fig.).

319    **Discussion**

320    Patterns of damselfish immigration in response to repeated small removals provided

321    evidence that immigration rate was non-linearly density-dependent with a maximum at

322    intermediate density. This relationship was supported by the GAMM analysis of the

323    combined data, by the presence of immigration at intermediate densities in contrast to the

324    near absence of immigration at the lowest and highest densities at all sites, and by support

325    for a hump-shaped relationship in 5 of 7 individual sites as well as the Akaike weights

326    averaged over all 7 sites. The statistical patterns for individual sites were similar with both

327    site and per new vacancy scaling. This was expected because the number of fish removed at

328    each event was constant for each site over most of the trial. However, although per new

329    vacancy scaling did not allow inclusion of the starting density before the first removal, it

330    did provide additional support by correcting for the limited number of new vacancies

331    generated by removal events at the lowest densities when the number of remaining

332    individuals was less than the prescribed number of individuals to be removed.

333    There was less support for density independence than for hump-shaped density

334    dependence. Density independence, the null hypothesis, was the best fitting model in 2

335    sites, and a good second alternative to hump-shaped functions in two others and in the

336    mean Akaike weights. Note that support for density independence was based not on

337    constant immigration over densities but on variable immigration that was not fit better by

338    any alternative pattern. Because there was only a single trial at each site, we cannot be sure

339   that there are true differences in the pattern of density dependence among sites. We found

340   no consistent relationships between site characteristics and strength of support for a hump-

341   shaped function (K. Turgeon, unpublished analyses). Although other studies have identified

342   spatial variation in immigration rates [24,29], we are not aware of any studies that have

343   examined differences among sites in the patterns of density dependence. Variable patterns

344   in territory availability arising from random selection of damselfish to be removed could

345   explain some of the variation in the fit of alternative functions. For example, removal

346   events in which more of the vacated territories were of high quality, closer to abundant

347   potential source populations, or adjacent to each other early in the sequence would have

348   been likely to favor higher immigration at high densities, thereby reducing support for a

349   hump-shaped pattern. Conversely, a high proportion of poor-quality territories made

350   available in the middle part of the sequence would reduce immigration where high

351   immigration was expected. Whether due to differences in factors influencing density

352   dependence or to the stochastic effects of removal patterns or both, among-site variation in

353   the pattern of density dependence highlights the importance of replication in such dispersal

354   studies, despite the logistical challenges of achieving it.

355         The support for negative density dependence with *per capita* scaling was likely a

356   mathematical artifact. In the two sites in which the density independent function provided

357   the best fit with per site scaling, there was a good fit to the negative exponential with *per*

358   *capita* scaling. Because a negative statistical trend is the expected result of relating Y/X to

359   X when Y shows no relationship to X, this is probably a spurious correlation, sometimes

360   referred to as pseudo-density dependence [18,45]. Apparently, the hump-shaped pattern

361     was sufficiently strong that it still provided the best fit with *per capita* scaling in the other 5

362     sites and in the average for all sites (S3 Table). However, the stronger negative trend

363     resulting from *per capita* scaling is apparent in all sites (S2 Fig.), resulted in increased

364     support for the negative exponential in 2 sites and the average for all sites (S3 Table), and is

365     reflected in the GAMM on the combined data, which indicated a simple negative

366     relationship. This pattern also may have been affected by limitations of the GAMM for

367     modeling the extremely sharp changes. [18], reviewing cases of larval fish recruitment to

368     coral reefs, noted that diverse patterns of positive, negative or neutral density dependence

369     with site scaling all became negative with *per capita* scaling. [30] also found that positively

370     density-dependent immigration of red-backed shrikes to their population became negative

371     with *per capita* scaling. Unlike other demographic variables, the numerator and

372     denominator of *per capita* immigration are derived from different populations,

373     necessitating that patterns be interpreted with caution.

374         Our study provides the first experimental evidence for a hump-shaped relationship

375     between immigration rate and local density. Only three observational studies have also

376     found hump-shaped relationships. Spiny lobsters (*Panulirus argus*) immigrating into

377     marine reserves when disturbed by sport fishing showed a hump-shaped relationship

378     between density in the reserves and immigration per site [28]. Hump-shaped relationships

379     in larval settlement, probably not confounded by post-settlement mortality, have also been

380     reported in barnacles *Semibalanus balanoides* [23] and humbug damselfish *Dascyllus*

381     *trimaculatus* [24].

382    A positive relationship between density and immigration similar to the one we

383    found between low and intermediate densities has been reported in several previous studies.

384    In studies covering a broad density range, density and immigration per site or per vacancy

385    were positively associated in three studies of birds [25,26,30] and in two studies of larval

386    crabs and fishes [22,27]. Studies with a more limited range of densities (often simply

387    presence/absence) also provide evidence for a positive effect of conspecifics in birds

388    (where it is referred to as 'conspecific attraction' and often studied using models and song

389    playback rather than established conspecifics, reviewed by [53], in marine invertebrate

390    larvae (where it is referred to as 'gregarious settlement' reviewed by [16], and in *Dascyllus*

391    damselfish larvae [54–56].

392    Removal experiments on a variety of territorial species suggest that a negative

393    relationship between density and immigration like that we found between intermediate and

394    high densities should be common, but there is relatively little support for this relationship in

395    studies covering a broad density range. Studies designed to test for the presence of a surplus

396    breeding population in territorial birds have often found rapid, complete or partial

397    replacement of removed territory holders [reviewed by [57]]. Similar patterns have been

398    found in some mammals  [*e.g*., [10]], reptiles [*e.g*., [58]], fishes, including territorial

399    damselfishes (*e.g*., [59,60]], and insects (*e.g*., [61]]. This suggests that immigration might

400    be proportional to the reduction in density, but direct evidence over a range of densities is

401    limited. An experiment using small juvenile humbug damselfish showed a nonlinear

402    negative relationship [24], although *per capita* scaling makes interpretation difficult. An

403    observational study on song sparrows *Melospiza melodia* immigrating to small islands

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404   reported a negative relationship in males but no relationship in females [29]. Two studies of

405   larval fish recruitment covering a broad range of densities found a negative effect of adult

406   density, but the study designs were unable to rule out post-settlement mortality as a factor

407   [62,63]. Among studies with a limited density range, we are aware of only one showing a

408   negative effect of density on larval fish settlement [64]. Thus, the negative trend we

409   observed over most of the density range is only the third example of such a pattern over a

410   broad density range. However, taken together, the literature suggests that both positive and

411   negative trends may occur, suggesting that hump-shaped relationships may be observed

412   more commonly if a sufficiently broad range of densities is studied.

413        The extremely low rate of immigration at very low densities in our study could be a

414   consequence of vacant habitat avoidance (the inverse of conspecific attraction), reduced

415   availability of potential immigrants, or both. If conspecific attraction exerts a powerful

416   influence on habitat selection, individuals might avoid otherwise suitable habitat lacking

417   conspecifics. Conspecific attraction can be favored by selection if the presence or

418   abundance of other individuals indicates higher habitat quality (habitat cueing) or if higher

419   density increases fitness (Allee effect) through improved predator avoidance, increased

420   access to mates, or other benefits [20,65]. Previous studies that found positive correlations

421   between density and immigration per site in nesting birds, spiny lobsters, as well as the

422   settlement and recruitment of marine larvae have attributed the patterns to this phenomenon

423   [22,25,26,28,66]. Allee effects might occur in damselfish because individuals with

424   neighbors are more able to resist intrusions by competing herbivorous parrotfish and

425   surgeonfish [60,67,68]. In addition, isolated damselfish have increased costs of mating and

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426    decreased choice because of the risks of longer excursions from their territory, especially if

427    they have to travel over open sand [41,69].

428         An alternative explanation for very low immigration at the lowest densities is

429    depletion of the supply of potential immigrants. Successive removals in the depletion area

430    could reduce the pool of potential immigrants both by lowering the number of fish in the

431    surrounding source areas and by providing more choice of territories for those individuals

432    remaining. If immigrants moving to the depletion area were themselves quickly replaced by

433    others from more distant areas, immigrant depletion effect would be minor, but if

434    individuals were rarely replaced, the consequences could be substantial. Although we were

435    not able to census the potential source populations after each removal during the

436    experiment, we observed that many damselfish remained within 10-m of the borders of the

437    depletion area even after we had removed the last individual. It is possible that these

438    individuals remaining in the source areas were not part of the pool of potential immigrants

439    because their territory quality was already high enough that it could not be improved by

440    relocation. If depletion of potential immigrants had a predominant influence on

441    immigration rate, we would have expected a gradual reduction in immigration rate, with

442    immigration stopping at a range of densities depending on the supply. The observed pattern

443    of a gradual increase in immigration rate with a consistent, abrupt drop to zero only when

444    density was nearly zero suggests that other processes such as avoidance of vacant habitat

445    were involved. Uncertainty about the origin of immigrants is widespread in field studies of

446    density-dependent immigration as is uncertainty about settlement location in studies of

447    density-dependent emigration. This uncertainty creates a risk that studies of density-

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448    dependent dispersal may be confounded by correlations between source and settlement

449    densities as result of natural spatial and temporal variation and as a result of unrecognized

450    effects of experimental density manipulations on adjacent populations. Thus, improved

451    insights in future dispersal studies may be gained by monitoring both source and settlement

452    populations, despite the substantial logistical challenges of doing so.

453         While competition for a variety of resources could explain the negative relationship

454    between density and immigration that we observed over most of the density range,

455    competition for space seems the most likely in our system. In territorial species, space itself

456    can become limiting when all suitable habitat is occupied and territories cannot be

457    compressed below a minimal size [57,70–72]. Immigration then depends on the re-

458    occupation of the territory of a resident that dies, emigrates, or is physically displaced

459    [32,72,73]. In our study, the very low rate of immigration in control sites and the lack of

460    immigration during pre-removal observations on experimental sites follow this pattern. If

461    neighbors of individuals removed at high densities expand their territories into the

462    unoccupied space before it can be discovered by potential immigrants [74], then

463    opportunities for immigration may be limited until densities are low enough that such

464    expansion provides no additional benefit. Mutual defense in which individuals from several

465    territories simultaneously attack a potential immigrant [75] could reduce the probability of

466    both detecting and occupying a vacancy at high densities [76]. In addition, if vacant

467    territories are more likely to be occupied by nearby individuals [77], then removals early in

468    the removal sequence would be more likely to be taken by residents than by immigrants, as

469    operationally defined in our experiment.

470        Dispersal of post-settlement fish from protected areas to locations where harvesting

471        is allowed, often called 'spillover' in the marine fisheries and conservation literature,

472        reduces the protective effect of reserves. It therefore decreases the number of eggs and

473        larvae exported but at the same time provides resources for harvesters outside the reserve

474        [78]. Similar processes have been proposed for terrestrial systems [79]. While spillover can

475        occur through density-independent processes, it has been widely recognized that density-

476        dependent emigration from reserves could enhance spillover [11,80,81]. However, little

477        attention has been given to the potential density-dependence of immigrants settling in

478        harvested areas. Decreasing immigration with decreasing density at low density raises the

479        possibility that excessive harvest outside a reserve might inhibit movement from the

480        reserve. Indeed, conspecific attraction could even induce movement from harvested areas

481        into reserves [11].

482        In conclusion, this study provides evidence that density can strongly affect

483        immigration in complex ways, with both positive and negative correlations occurring at the

484        same site at different levels of density. While some of the possible mechanisms involved

485        may be limited to very local scales (*e.g.*, depletion of potential immigrants) or be restricted

486        to territorial species (*e.g.*, territorial expansion, mutual defense), others are likely to operate

487        at much larger scales and affect populations with other social systems and dispersal patterns

488        (*e.g.*, resource competition, conspecific attraction, and vacant habitat avoidance). For

489        theoretical explorations of metapopulation dynamics, reserve design and dispersal

490        evolution, our results reinforce recent calls for more recognition of density dependence at

491        all stages of the dispersal process [15], as pioneered by [82]. In addition, our results suggest

492    that simple formulations of dispersal probability as either a difference from or proportion of

493    carrying capacity [83] may be inadequate. It is important that empirical studies of dispersal

494    recognize the potential for density dependence in immigration as well as emigration, cover

495    a broad enough density range to detect such complex patterns, and carefully consider the

496    scaling of immigration rates. Localized harvest and pest control programs offer

497    opportunities to undertake such studies through gradual removal. Despite a long history of

498    using removal experiments to address a variety of questions ranging from habitat

499    preference and social organization to population regulation, interspecific competition, and

500    assemblage structure [57,58,61,84–86] and even emigration [87], ours appears to be the

501    first to use this method to examine immigration over a wide range of densities in the field.

## Acknowledgements

## References

510    1.    Clobert J, Wolff, Nichols JD, Danchin E, Dhondt AA. Introduction. In: Clobert J,

511          Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. Oxford University Press,

512          USA; 2001. pp. xvii–xxi.

513    2.    Clobert J, Baguette M, Benton TG, Bullock JM, editors. Dispersal ecology and

514          evolution [Internet]. Oxford: Oxford University Press; 2012. Available:

515          http://lib.myilibrary.com?id=395195

516    3.    Bullock JM, Kenward R, Hails R. Preface. In: Bullock JM, Kenward R, Hails R,

517          editors. Dispersal ecology: the 42nd symposium of the British Ecological Society held

518          at the University of Reading, 2-5 April 2001. Malden, MA: Blackwell Pub.; 2002. pp.

519          xv–xvii.

520    4.    Hanski IA, Gaggiotti OE, editors. Ecology, genetics and evolution of

521          metapopulations. Burlington MA USA: Academic Press; 2004.

522    5.    Bowler DE, Benton TG. Causes and consequences of animal dispersal strategies:

523          Relating individual behaviour to spatial dynamics. Biol Rev. 2005;80: 205–225.

524          doi:10.1017/S1464793104006645

525    6.    Travis JMJ, Mustin K, Benton TG, Dytham C. Accelerating invasion rates result from

526          the evolution of density-dependent dispersal. J Theor Biol. 2009;259: 151–158.

527          doi:10.1016/j.jtbi.2009.03.008

528    7.    Pulliam HR. Sources, sinks, and population regulation. Am Nat. 1988;132: 652–661.

529          doi:10.1086/284880

530    8.    Tuyttens FAM, Macdonald DW, Rogers LM, Cheeseman CL, Roddam AW.

531          Comparative study on the consequences of culling badgers (*Meles meles*) on

532          biometrics, population dynamics and movement. J Anim Ecol. 2000;69: 567–580.

533          doi:10.1046/j.1365-2656.2000.00419.x

534    9.    Rose KA, Cowan JH, Winemiller KO, Myers RA, Hilborn R. Compensatory density

535          dependence in fish populations: Importance, controversy, understanding and

536     prognosis. Fish and Fisheries. 2001;2: 293–327. doi:10.1046/j.1467-

537     2960.2001.00056.x

538  10.  Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW. The impact of sport-

539     hunting on the population dynamics of an African lion population in a protected area.

540     Biol Conserv. 2007;134: 548–558. doi:10.1016/j.biocon.2006.09.010

541  11.  Grüss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW. Consequences of adult

542     and juvenile movement for marine protected areas. Biol Conserv. 2011;144: 692–702.

543     doi:10.1016/j.biocon.2010.12.015

544  12.  Mihoub J-B, Robert A, Le Gouar P, Sarrazin F. Post-release dispersal in animal

545     translocations: Social attraction and the "vacuum effect." PLoS One. 2011;6.

546     doi:10.1371/journal.pone.0027453

547  13.  Lambin X, Aars J, Piertney SB. Dispersal, intraspecific competition, kin competition

548     and kin facilitation: A review of the empirical evidence. In: Clobert J, Danchin E,

549     Dhondt AA, Nichols JD, editors. Dispersal. Oxford: Oxford University Press; 2001.

550     pp. 111–122.

551  14.  Matthysen E. Density-dependent dispersal in birds and mammals. Ecography.

552     2005;28: 403–416. doi:10.1111/j.0906-7590.2005.04073.x

553  15.  Travis JMJ, Mustin K, Barton KA, Benton TG, Clobert J, Delgado MM, et al.

554     Modelling dispersal: An eco-evolutionary framework incorporating emigration,

555     movement, settlement behaviour and the multiple costs involved. Methods Ecol Evol.

556     2012;3: 628–641. doi:10.1111/j.2041-210X.2012.00193.x

557  16.  Burke R. Pheromones and the gregarious settlement of marine invertebrate larvae.

558     Bull Mar Sci. 1986;39: 323–331.

559    17. Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA. Recruitment and

560          the local dynamics of open marine populations. Annu Rev Ecol Syst. 1996;27: 477–

561          500. doi:10.1146/annurev.ecolsys.27.1.477

562    18. Hixon M, Webster M. Density dependence in reef fish populations. In: Sale P, editor.

563          Coral reef fishes: Dynamics and diversity in a complex ecosystem. San Diego:

564          Academic Press; 2002. pp. 303–325.

565    19. Stephens PA, Sutherland WJ, Freckleton RP. What is the Allee effect? Oikos.

566          1999;87: 185–190. doi:10.2307/3547011

567    20. Stamps JA. Habitat selection by dispersers: Integrating proximate and ultimate

568          approaches. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal.

569          Oxford: Oxford University Press; 2001. pp. 230–242.

570    21. Fretwell SD, Lucas HL. On territorial behavior and other factors influencing habitat

571          distribution in birds. Acta Biotheoretica. 1969;19: 16–36.

572    22. Donahue MJ. Allee effects and conspecific cueing jointly lead to conspecific

573          attraction. Oecologia. 2006;149: 33–43. doi:10.1007/s00442-006-0419-y

574    23. Chabot R, Bourget E. Influence of substratum heterogeneity and settled barnacle

575          density on the settlement of cypris larvae. Mar Biol. 1988;97: 45–56.

576          doi:10.1007/BF00391244

577    24. Schmitt RJ, Holbrook SJ. Local-scale patterns of larval settlement in a planktivorous

578          damselfish - Do they predict recruitment? Mar Freshw Res. 1996;47: 449–463.

579          doi:10.1071/MF9960449

580    25.  Doligez B, Part T, Danchin E, Clobert J, Gustafsson L. Availability and use of public

581         information and conspecific density for settlement decisions in the collared flycatcher.

582         J Anim Ecol. 2004;73: 75–87. doi:10.1111/j.1365-2656.2004.00782.x

583    26.  Serrano D, Forero MG, Donazar JA, Tella JL. Dispersal and social attraction affect

584         colony selection and dynamics of lesser kestrels. Ecology. 2004;85: 3438–3447.

585         doi:10.1890/04-0463

586    27.  Anderson TW, Carr MH, Hixon MA. Patterns and mechanisms of variable settlement

587         and recruitment of a coral reef damselfish, *Chromis cyanea*. Mar Ecol-Prog Ser.

588         2007;350: 109–116. doi:10.3354/meps07135

589    28.  Eggleston DB, Parsons DM. Disturbance-induced "spill-in" of Caribbean spiny

590         lobster to marine reserves. Mar Ecol-Prog Ser. 2008;371: 213–220.

591         doi:10.3354/meps07699

592    29.  Wilson AG, Arcese P. Influential factors for natal dispersal in an avian island

593         metapopulation. J Avian Biol. 2008;39: 341–347. doi:10.1111/j.2008.0908-

594         8857.04239.x

595    30.  Schaub M, Jakober H, Stauber W. Strong contribution of immigration to local

596         population regulation: evidence from a migratory passerine. Ecology. 2013;94: 1828–

597         1838. doi:10.1890/12-1395.1

598    31.  Turgeon K, Kramer DL. Compensatory immigration depends on adjacent population

599         size and habitat quality but not on landscape connectivity. J Anim Ecol. 2012;81:

600         1161–1170. doi:10.1111/j.1365-2656.2012.01990.x

601    32.  Robertson DR. Competitive ability and the potential for lotteries among territorial reef

602         fishes. Oecologia. 1995;103: 180–190. doi:10.1007/BF00329078

603    33.  Turgeon K, Robillard A, Gregoire J, Duclos V, Kramer DL. Functional connectivity

604         from a reef fish perspective: Behavioral tactics for moving in a fragmented landscape.

605         Ecology. 2010;91: 3332–3342. doi:10.1890/09-2015.1

606    34.  Kritzer JP, Sale PF. Chapter 2 - The metapopulation ecology of coral reef fishes. In:

607         Sale JPKF, editor. Marine Metapopulations. Burlington: Academic Press; 2006. pp.

608         31–67. Available:

609         http://www.sciencedirect.com/science/article/pii/B9780120887811500054

610    35.  McDougall PT, Kramer DL. Short-term behavioral consequences of territory

611         relocation in a Caribbean damselfish, *Stegastes diencaeus*. Behav Ecol. 2007;18: 53–

612         61. doi:10.1093/beheco/ar1055

613    36.  Cheney KL, Côté IM. Habitat choice in adult longfin damselfish: Territory

614         characteristics and relocation times. J Exp Mar Biol Ecol. 2003;287: 1–12.

615         doi:10.1016/S0022-0981(02)00500-2

616    37.  Waser PM, Busch JD, McCormick CR, DeWoody JA. Parentage analysis detects

617         cryptic precapture dispersal in a philopatric rodent. Mol Ecol. 2006;15: 1929–1937.

618         doi:10.1111/j.1365-294X.2006.02893.x

619    38.  Loe LE, Mysterud A, Veiberg V, Langvatn R. Negative density-dependent emigration

620         of males in an increasing red deer population. Proc R Soc B-Biol Sci. 2009;276:

621         2581–2587. doi:10.1098/rspb.2009.0224

622    39.  Sale PF. Recruitment, loss and coexistence in a guild of territorial coral-reef fishes.

623         Oecologia. 1979;42: 159–177. doi:10.1007/BF00344855

31

624    40.   Robertson DR, Schober UM, Brawn JD. Comparative variation in spawning output
625          and juvenile recruitment of some Caribbean reef fishes. Mar Ecol-Prog Ser. 1993;94:
626          105–113. doi:10.3354/meps094105

627    41.   Itzkowitz M. Group organization of a territorial damselfish, *Eupomacentrus*
628          *planifrons*. Behaviour. 1978;65: 125–137. doi:10.1163/156853978X00233

629    42.   Bartels PJ. Extra-territorial movements of a perennially territorial damselfish,
630          *Eupomacentrus dorsopunicans* Poey. Behaviour. 1984;91: 312–322.
631          doi:10.1163/156853984X00137

632    43.   Wellington GM, Victor BC. Variation in components of reproductive success in an
633          undersaturated population of coral-reef damselfish - a field perspective. Am Nat.
634          1988;131: 588–601. doi:10.1086/284808

635    44.   Herrando-Perez S, Delean S, Brook BW, Bradshaw CJA. Density dependence: An
636          ecological Tower of Babel. Oecologia. 2012;170: 585–603. doi:10.1007/s00442-012-
637          2347-3

638    45.   Brett MT. When is a correlation between non-independent variables "spurious"?
639          Oikos. 2004;105: 647–656. doi:10.1111/j.0030-1299.2004.12777.x

640    46.   Bolker B, R Development Core Team. bbmle: Tools for general maximum likelihood
641          estimation [Internet]. 2012. Available: http://CRAN.R-project.org/package=bbmle

642    47.   Burnham KP, Anderson DR. Model selection and multimodel inference: A practical
643          information-theoretic approach. 2nd ed. New York: Springer; 2002.

644    48.   Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel
645          inference in behavioral ecology: Some background, observations, and comparisons.
646          Behav Ecol Sociobiol. 2011;65: 23–35. doi:10.1007/s00265-010-1029-6

647    49.    Pinheiro JC, Bates DM. Mixed-Effects Models in S and S-PLUS. New York, USA:

648           Springer; 2000.

649    50.    Hastie TJ, Tibshirani RJ. Generalized Additive Models. London: Chapman & Hall;

650           1990.

651    51.    Wood SN. Stable and efficient multiple smoothing parameter estimation for

652           generalized additive models. J Am Stat Assoc. 2004;99: 673–686.

653           doi:10.1198/016214504000000980

654    52.    Wood S. Mixed GAM computation vehicle with GCV/AIC/REML smoothness

655           estimation. R Package: mgcv, Version: 17-28. 2014;

656    53.    Ahlering MA, Arlt D, Betts MG, Fletcher RJ, Nocera JJ, Ward MP. Research needs

657           and recommendations for the use of conspecific-attraction methods in the

658           conservation of migratory songbirds. Condor. 2010;112: 252–264.

659           doi:10.1525/cond.2010.090239

660    54.    Sweatman H. The influence of adults of some coral-reef fishes on larval recruitment.

661           Ecol Monogr. 1985;55: 469–485. doi:10.2307/2937132

662    55.    Jones G. Some interactions between residents and recruits in 2 coral-reef fishes. J Exp

663           Mar Biol Ecol. 1987;114: 169–182.

664    56.    Booth D. Larval settlement patterns and preferences by domino damselfish *Dascyllus*

665           *albisella* Gill. J Exp Mar Biol Ecol. 1992;155: 85–104. doi:10.1016/0022-

666           0981(92)90029-A

667    57.    Newton I. Experiments on the limitation of bird numbers by territorial behavior. Biol

668           Rev Cambridge Philosophic Soc. 1992;67: 129–173. doi:10.1111/j.1469-

669           185X.1992.tb01017.x

670    58.  Baird TA, Baird TD, Shine R. Aggressive transition between alternative male social

671          tactics in a long-lived Australian dragon (*Physignathus lesueurii*) living at high

672          density. PLoS One. 2012;7. doi:10.1371/journal.pone.0041819

673    59.  Robertson D, Polunin N, Leighton K. Behavioral ecology of 3 Indian-Ocean

674          surgeonfishes (*Acanthurus lineatus, Acanthurus leucosternon and Zebrasoma scopas*)

675          - Their feeding strategies, and social and mating systems. Environ Biol Fishes.

676          1979;4: 125–170. doi:10.1007/BF00005448

677    60.  Meadows DW. Centre-edge differences in behaviour, territory size and fitness in

678          clusters of territorial damselfish: Patterns, causes, and consequences. Behaviour.

679          2001;138: 1085–1116. doi:10.1163/156853901753287154

680    61.  Davies NB. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The

681          resident always wins. Animal Behaviour. 1978;26: 138–147. doi:10.1016/0003-

682          3472(78)90013-1

683    62.  Stimson J. Density dependent recruitment in the reef fish *Chaetodon miliaris*. Environ

684          Biol Fishes. 1990;29: 1–13. doi:10.1007/BF00000563

685    63.  Forrester GE. Strong density-dependent survival and recruitment regulate the

686          abundance of a coral reef fish. Oecologia. 1995;103: 275–282.

687          doi:10.1007/BF00328615

688    64.  Wilson J, Osenberg CW. Experimental and observational patterns of density-

689          dependent settlement and survival in the marine fish *Gobiosoma*. Oecologia.

690          2002;130: 205–215. doi:10.1007/s004420100784

691  65.  Danchin E, Heg D, Doligez B. Public information and breeding habitat selection. In:

692       Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. New York: Oxford

693       University Press; 2001. pp. 243–258.

694  66.  Wormald CL, Steele MA, Forrester GE. High population density enhances recruitment

695       and survival of a harvested coral reef fish. Ecol Appl. 2013;23: 365–373.

696  67.  Robertson DR, Sweatman HPA, Fletcher EA, Cleland MG. Schooling as a mechanism

697       for circumventing territoriality of competitors. Ecology. 1976;57: 1208–1220.

698       doi:10.2307/1935045

699  68.  Foster SA. Territoriality of the dusky damselfish - influence on algal biomass and on

700       the relative impacts of impacts of grazing by fishes and *Diadema*. Oikos. 1987;50:

701       153–160. doi:10.2307/3565995

702  69.  Karino K, Nakazono A. Reproductive behavior of the territorial herbivore *Stegastes*

703       *nigricans* (Pisces, Pomacentridae) in relation to colony formation. J Ethol. 1993;11:

704       99–110. doi:10.1007/BF02350043

705  70.  Grant JWA, Kramer DL. Territory size as a predictor of the upper limit to population-

706       density. Can J Fish Aquat Sci. 1990;47: 1724–1737. doi:10.1139/f90-197

707  71.  Heg D, Ens BJ, Van der Jeugd HP, Bruinzeel LW. Local dominance and territorial

708       settlement of nonbreeding oystercatchers. Behaviour. 2000;137: 473–530.

709       doi:10.1163/156853900502187

710  72.  Komdeur J, Edelaar P. Male Seychelles warblers use territory budding to maximize

711       lifetime fitness in a saturated environment. Behav Ecol. 2001;12: 706–715.

712       doi:10.1093/beheco/12.6.706

713    73.    Krebs JR. Territory and breeding density in the great tit, *Parus major* L. Ecology.

714           1971;52: 2–22.

715    74.    Adams ES. Approaches to the study of territory size and shape. Annu Rev Ecol Syst.

716           2001;32: 277–303. doi:10.1146/annurev.ecolsys.32.081501.114034

717    75.    Detto T, Jennions MD, Backwell PRY. When and why do territorial coalitions occur?

718           Experimental evidence from a fiddler crab. Am Nat. 2010;175: E119–E125.

719           doi:10.1086/651588

720    76.    Hestbeck JB. Population regulation of cyclic mammals - the social fence hypothesis.

721           Oikos. 1982;39: 157–163. doi:10.2307/3544480

722    77.    Efford M, Warburton B, Spencer N. Home-range changes by brushtail possums in

723           response to control. Wildl Res. 2000;27: 117–127. doi:10.1071/WR99005

724    78.    Russ GR. Yet another review of marine reserves as reef fishery management tools. In:

725           Peter F. Sale, editor. Coral Reef Fishes. San Diego: Academic Press; 2002. pp. 421–

726           443. Available:

727           http://www.sciencedirect.com/science/article/pii/B9780126151855500244

728    79.    Novaro AJ, Redford KH, Bodmer RE. Effect of hunting in source-sink systems in the

729           neotropics. Conserv Biol. 2000;14: 713–721. doi:10.1046/j.1523-1739.2000.98452.x

730    80.    Kramer DL, Chapman MR. Implications of fish home range size and relocation for

731           marine reserve function. Environ Biol Fishes. 1999;55: 65–79.

732           doi:10.1023/A:1007481206399

733    81.    Abesamis RA, Russ GR. Density-dependent spillover from a marine reserve: Long-

734           term evidence. Ecol Appl. 2005;15: 1798–1812. doi:10.1890/05-0174

735  82.  Saether BE, Engen S, Lande R. Finite metapopulation models with density-dependent

736      migration and stochastic local dynamics. Proc R Soc Lond Ser B-Biol Sci. 1999;266:

737      113–118.

738  83.  Lloyd-Smith JO. Modeling density dependence in heterogeneous landscapes:

739      Dispersal as a case study. J Theor Biol. 2010;265: 160–166.

740      doi:10.1016/j.jtbi.2010.03.032

741  84.  Foster SA. Group foraging by a coral-reef fish - a mechanism for gaining access to

742      defended resources. Anim Behav. 1985;33: 782–792. doi:10.1016/S0003-

743      3472(85)80011-7

744  85.  Robertson DR, Gaines SD. Interference competition structures habitat use in a local

745      assemblage of coral-reef surgeonfishes. Ecology. 1986;67: 1372–1383.

746      doi:10.2307/1938693

747  86.  Larsen KW, Boutin S. Exploring territory quality in the North American red squirrel

748      through removal experiments. Can J Zool. 1995;73: 1115–1122. doi:10.1139/z95-133

749  87.  Boutin S, Gilbert BS, Krebs CJ, Sinclair ARE, Smith JNM. The role of dispersal in

750      the population-dynamics of snowshoe hares. Can J Zool. 1985;63: 106–115.

751

**Figure caption**

**Figure 1**. Relationship between the number of immigrants arriving on a site after a removal

event and the number of damselfish remaining following each removal event (site scaling) for

each individual site and for all sites combined (upper left panel). Individual sites are ordered by

strength of support for a hump-shaped (Ricker or polynomial) function and identified by

abbreviations (Bachelor Hall Reef: BH1; Heron Bay Reef: HB1, HB2, HB3, HB4; Sandy Lane

Reef: SL1, SL2). Lines represent the best fitting empirical function based on maximum

likelihood estimates (MLE) of parameter values. For all sites combined, the abscissa indicates

the proportion of the initial number of fish on the site before removal. Each point represents the

mean $\pm$ 1 SE of all points falling within bins of 0.1, with density = 0 shown separately. Sample

sizes per bin vary depending on replacement rates. The short inside tick marks on the abscissa

represent observed proportion values. The black line in the upper left panel represents the

significant smoothing term function from a GAMM model and the dashed lines represent the

Bayesian credible interval as calculated by the mgcv package v. 1.7-28 in R.
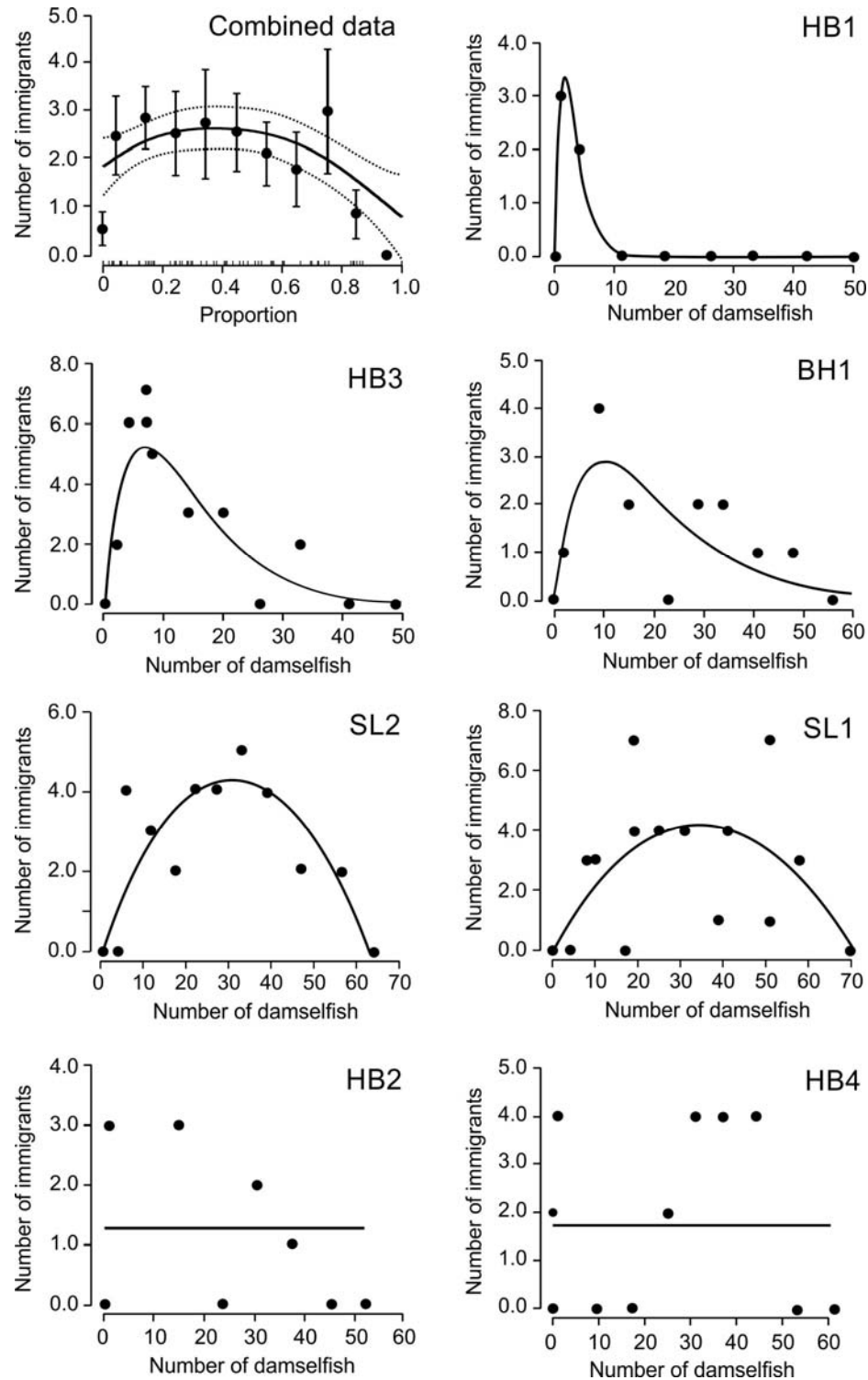
Figure 1.

## Supporting Information captions

### S1 Figure: Location of experimental and control sites

Location and names of fringing reefs along the west coast of Barbados, West Indies. Reefs are shown as dark green and the area covered by the Barbados Marine Reserve as light blue. On the left, two reefs illustrate the positions of reef zones, with the spur and groove zone used in this study shown in light green.

### S1 Table: Habitat variables of the seven sites

Habitat variables of seven sites in which the density of two damselfish species (*Stegastes diencaeus* and *S. adustus*) was manipulated. See Figure 1 for site abbreviations.

### S2 Table: Model support (AICc scores) for per new vacancy scaling

Per new vacancy scaling. AICc scores (AICc) and Akaike weights ($w_i$) for each of the six empirical functions predicting observed immigration rate per new vacancy (number of immigrants/number of damselfish removed in a removal event) in relation to population size following each removal event (not including saturation because new vacancies = 0) on seven experimental sites. Sites are ordered as in Figure 1. The mean Akaike weight (Mean $w_i$) for each function is given at the bottom of each column. For each site and the mean of all sites, the function with the highest support is indicated by bold $w_i$. See Figure 1 for site abbreviations and Table 1 for the functions.

### S3 Table: Model support (AICc scores) for *per capita* scaling

*Per capita* scaling. AICc scores (AICc) and Akaike weights ($w_i$) for each of the six empirical functions predicting observed *per capita* immigration rate (number of immigrants/number of remaining damselfish) in relation to population size following each removal event (excluding population size = 0) on seven experimental sites. The mean Akaike weight (Mean $w_i$) for

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each function is given at the bottom of each column. For each site and the mean of all sites, the function with the highest support is indicated by bold $w_i$. Sites are ordered as in Figure 1. See Figure 1 for site abbreviations and Table 1 for the functions.

**S2 Figure: Relationships between immigration and the number of damselfish for new vacancy and *per capita* scaling**

Relationships between immigration (per new vacancy scaling: black dots and lines, left ordinate; *per capita* scaling: grey dots and lines, right ordinate) and the number of damselfish remaining following each removal event for each individual site and for all sites combined (upper left panel). Individual sites are ordered by strength of support for a hump-shaped (Ricker) function and abbreviated as in Fig. 1. Lines represent the best fitting empirical function based on maximum likelihood estimates (MLE) of parameter values. For all sites combined, the abscissa indicates the proportion of the initial number of fish on the site before removal. Each point represents the mean $\pm$ 1 SE of all points falling within bins of 0.1, with density $= 0$ shown separately. Sample sizes per bin vary depending on replacement rates. The short inside tick marks on the abscissa represent observed proportion values. The solid lines in the upper left panel represent the significant smoothing term functions from GAMM models and the dashed lines represent the Bayesian credible intervals.