

1 Running head: Can ecological traps be beneficial?

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3 **Good trap, bad trap: Under what conditions can an ecological trap benefit a population?**

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27

28 **Abstract**

29 Ecological traps are a challenge to conservation, potentially increasing extinction risk. However, not
30 all traps were made equal. We suggest that sites that usually constitute ecological traps may benefit
31 populations of r-selected species. As a model system we investigate the effects of man-made
32 ephemeral pools such as storm-water catchments on the population dynamics of an r-selected
33 amphibian species, and compare it to a k-selected species. Ephemeral pools may act as breeding sites
34 and habitat for adult individuals however they often desiccate too early for tadpole metamorphosis,
35 leading to offspring mortality. We use agent-based simulations over multi-generational timescales to
36 study a range of ecologically-reasonable parameters. We find that the contribution of traps to
37 population viability, thanks to rare years in which their hydro-period suffices for metamorphosis,
38 exceeds the detrimental effects in other years. Counterintuitively, eliminating such potential traps
39 from the environment may reduce the viability of meta-populations and increase extinction risk.

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41

42 **Introduction**

43 A species' past environment provides the evolutionary history that shapes the sensory and cognitive
44 processes controlling behavior. When the environment changes rapidly, a mismatch may arise
45 between the cues that individuals use to make decisions and the state of the environment (Sih et al.
46 2011). An evolutionary trap occurs when such a mismatch causes a previously reliable cue to no
47 longer result in an adaptive decision, leading to reduced survival or reproduction (Schlaepfer et al.
48 2002, 2005). An ecological trap is a specific type of evolutionary trap that concerns habitat selection.
49 Severe ecological traps form when animals prefer habitats where their fitness is lower than in other
50 available options as a result of a discrepancy between the cues that they use to assess habitat quality
51 and the true quality of the habitat (Robertson & Hutto 2006; Madliger 2012). However, it is not
52 necessary for individuals to *prefer* the lesser-quality habitat in order for a trap to be formed.
53 Sometimes it is enough that individuals do not distinguish between high and poor quality habitats (an
54 "equal-preference trap", Robertson & Hutto 2006; Robertson et al. 2013). In such cases, the lower
55 survival and/or reproductive success in the lesser-quality habitats will result in lower densities of
56 individuals, thereby attracting individuals from crowded source populations. This mechanism alone
57 can deplete both the source and the sink populations and may lead them towards extinction
58 (Gundersen et al. 2001; Hawlena et al. 2010). Both forms of ecological traps are of great concern for
59 conservation biologists since they are likely to increase local extinction risk (Battin 2004; Hale &
60 Swearer 2016) and to impede management solutions such as habitat restoration (Hale & Swearer
61 2017).

62 The impacts of ecological traps are not uniform and depend on various factors that may
63 greatly differ among species and even populations. These factors include: (i) the attractiveness of the
64 low-quality habitat (a continuum between severe and equal-preference traps); (ii) the impact of the
65 trap (i.e. the fitness costs of choosing the low-quality habitat, ranging from certain mortality to
66 reduced reproductive success, Hale et al. 2015); (iii) the density of the target population (with low
67 density populations being more sensitive to traps, Kokko & Sutherland 2001; Schlaepfer et al. 2002);
68 (iv) the probability of perceiving and encountering a low-quality habitat (Hale et al. 2015); (v)

69 behavioral traits of the target population such as the flow of social information within the population
70 (Schmidt et al. 2015); and (vi) species ecology and life history traits, such as reproduction dynamics
71 (Hale et al. 2015). In addition, temporal variability in environmental conditions is of vital importance
72 to the creation of ecological traps and the same site can sustain viable populations or allow successful
73 reproduction in 'good' years and act as an ecological trap for the same populations in subsequent 'bad'
74 years.

75 The creation and maintenance of artificial breeding sites or structures is a popular in situ
76 conservation strategy that has been applied successfully to mitigate the decline of wildlife populations
77 in a wide variety of species across taxa (e.g., Catry et al. 2009; D'Amico et al. 2014; McClure et al.
78 2017). Nevertheless, growing evidence suggests that there are cases where the provision of artificial
79 breeding sites can have negative effects on breeding populations, effectually creating an ecological
80 trap for the breeding individuals (DiMauro & Hunter 2002; Klein et al. 2007; Björklund et al. 2013;
81 McClure et al. 2017; Clevenot et al. 2018; Hale et al., 2018). Wildlife managers are therefore faced
82 with an increasing need to preemptively assess and predict the effects of providing artificial breeding
83 sites on wild populations, especially in species of conservation concern.

84 However, finding out that an artificial breeding site may act as an ecological trap does not
85 necessarily mean that this site should be abandoned or removed. In fact, theoretical work has
86 suggested that under the right set of conditions, traps can even have positive effects on population
87 growth. Positive effects may occur, for example, when traps are highly attractive but elicit only minor
88 (or slow) fitness costs. In these cases, traps may still serve as stepping stones within a meta-population
89 network, increasing landscape-scale connectivity and reducing overall predation risk (Hartman &
90 Ross 2014; Hale et al. 2015). We suggest that an r-selected breeding strategy may represent another
91 case in which ecological traps may still benefit populations. In r-selected species, population growth is
92 usually not limited by the number of breeding individuals, but rather by the number of juveniles that
93 manage to reach adulthood, frequently limited by competition for resources. Accordingly, the
94 population's limiting factor may be, in many cases, the number of available feeding or breeding sites
95 (Sara et al. 2005; Phillips et al. 2009). Therefore, in areas in which temporal variability in

96 environmental conditions means that some breeding sites may act as ecological traps, sustaining
97 population growth only during 'good' years, the benefits of these 'good' years to the long-term
98 population growth may outweigh the costs imposed by the 'bad' years.

99 Amphibians represent a good model taxon to test the possible beneficial effects of ecological
100 traps. Many amphibian species are r-selected species that rely in certain phases of their life-history on
101 ephemeral pools that may be patchily distributed, thus generating meta-population dynamics. In
102 addition, the world is currently facing a global decline of amphibians, with almost 40% of known
103 amphibian species threatened with extinction (Dawson et al. 2016; IUCN 2017), increasing our need
104 to efficiently manage small and declining amphibian populations. There are several known causes
105 underlining the great amphibian decline, which are made complex by their many interactions
106 (Kiesecker et al. 2001). Regardless, habitat loss and fragmentation are considered amongst the largest
107 threats to amphibian populations, either by directly contributing to their decline, or by interacting with
108 other factors such as climate change or disease transmission (Beebee & Griffiths 2005; Cushman
109 2006). Because in many cases, amphibian spatial dynamics resemble classic meta-population
110 dynamics (Marsh & Trenham 2001), habitat connectivity plays a key role in maintaining regional
111 viability of amphibian populations (Cushman 2006; Becker et al. 2007). Juvenile dispersal is critical
112 in amphibians for recolonization of suitable habitats following local extinctions and for maintenance
113 of regional populations, even in non-fragmented landscapes (Skelly et al. 1999; Cushman 2006), and
114 any disconnection between habitats that are used by the same species at different life stages is likely to
115 cause massive population declines (Becker et al. 2007).

116 In this context, temporary seasonal pools represent a management dilemma for wildlife
117 managers because they can act as ecological traps for amphibians (Clevenot et al. 2018). For example,
118 DiMauro & Hunter (2002) have compared the reproductive effort and success of amphibians breeding
119 in natural and artificial pools in managed forests in Maine, and found that in most years, artificial
120 pools acted as ecological traps for wood frogs (*Rana sylvatica*) because they dried sooner than natural
121 pools. Brand & Snodgrass (2009) measured amphibians breeding efforts and success in Baltimore
122 County, Maryland, and found the opposite trend – amphibians only survived in artificial stormwater

123 ponds, despite high concentration of pollutants in these pools, because the natural wetlands dried up
124 before larvae could complete development. These examples illustrate that regardless of their origin
125 (natural or artificial), temporary pools may not hold water long enough for larvae to complete
126 development, resulting in massive mortality of all larvae in a pool. Such pools can therefore act as
127 ecological traps, attracting amphibians to lay eggs in them despite the fact that their fitness benefit in
128 these patches can be zero. However, on unusually wet years, temporary pools may no longer act as
129 traps, producing a similar number of juveniles as the more reliable water sources. The dilemma
130 wildlife managers may therefore face concerns the proper way of managing these ephemeral pools.
131 Should such pools be drained and destroyed in order to remove dangerous ecological traps from
132 amphibian populations' environments? Alternatively, can the benefits arising from temporary pools in
133 rare wet years be enough to outweigh the costs?

134 We used agent-based simulations of population dynamics over multi-generational time scales
135 to investigate this dilemma under different scenarios, and to find out if, and under what conditions,
136 ecological traps can have positive effects on meta-populations.

137

138

139 Results

140 To explore population dynamics under different conditions, we conducted a series of agent-based
141 simulations. Each simulation follows the fate of a meta-population of the species of interest in an
142 artificial landscape over 200 years. The landscape is constructed as a grid of 100 demes, of which a
143 certain fraction are natural sites that always provide high-value habitat and allow reproduction, and
144 each of the others is either a potential ecological trap site which allows reproduction only in some
145 years, or a barren site which does not provide viable habitat. The simulations consider life history
146 parameters of the species of interest (table 1 in Methods) and parameters that characterize the
147 available habitats. They track the fate of each simulated individual, considering different dynamics for
148 juveniles, sub-adults, and adults, including reproduction, migration, and density-dependent mortality
149 (see Methods).

150 We provide results that demonstrate the predicted effects of potential ecological trap sites on two
151 species that differ in their life history parameters, and that can be simplistically viewed as an r-
152 selected species and a k-selected species. We use parameter values that are comparable in their
153 magnitude to those that characterize two species that breed in seasonal pools in Israel: European green
154 toad (*Bufo viridis*; locally endangered; (Elron, 2007)), and little grebe, a local water bird (*Tachybaptus*
155 *ruficollis*; See Methods). For each species, we explored a range of conditions, along two dimensions:
156 (1) The probability of a non-natural site to be a potential ecological trap ($P_{\text{trap}} = 0, 0.1, 0.2 \dots 1$), and
157 not a barren site, and (2) The rate at which potential traps do not function as traps, i.e. the rate at
158 which good years occur such that even the potential traps allow reproduction ($P_{\text{good}} = 0, 0.1, 0.2, \dots,$
159 1). For both species that we explored, as expected, we find that the population sizes (mean and
160 minimum) increase as the fraction of natural sites, which are always suitable for reproduction,
161 increases (*results not shown*). Hence, for all simulations we fixed the mean frequency of natural sites
162 at 15%, exploring for this setting the effect of other parameters.

163 For our r-selected species, European toad, we find that the median population size (Figure 1a) and
164 the minimal population size across the whole simulation (Figure 1b) increase as the rate of good years
165 increases, and as the frequency of non-natural sites that are potential traps (instead of being barren
166 sites) increases. Studying both of these measures in parallel – median and minimal population sizes –
167 is important from a conservation standpoint, as each of them may be related in a different way to the
168 extent that a population is likely to persist in the long run. Median population sizes reflect more
169 prominently, for example, on the probability of adapting to new environmental challenges,
170 maintaining connectivity with other populations, and playing a meaningful role in the ecosystem,
171 while minimum population sizes may reflect more prominently on risk of extinction and sensitivity to
172 stochastic processes. We find that for toads, both measures increase monotonically across the full

173 parameter range, i.e. having any number of traps across the landscape increases, or does not change,
174 population sizes compared to the case in which all ecological traps are eliminated and replaced with
175 barren sites. Even in cases where the trap sites *never* allow reproduction, the population sizes (median
176 and minimal) never drop below their sizes in the no-trap scenario (no statistically-significant
177 difference, one-way Anova, $p > 0.05$). This implies that in the settings that we explore, an r-selected
178 species like the toad is never harmed by the existence of ecological traps instead of barren sites. At the
179 other extreme, as good years become more common, toads' populations, both in their mean and in
180 their minimum sizes, increase significantly, up to many times more their sizes in the absence of traps
181 (Figure 1). The traps thus increase the species' probability of persistence and fulfillment of functions
182 of ecological importance such as playing a part in the ecosystem's food web.

183
184 ((Figure 1 here))

185
186 The impact of ecological traps on a k-selected species, the common grebe, is different from their
187 influence on toads. Similar to toads, the traps allow increased population sizes of grebes if the
188 frequency of good years, in which the potential trap sites allow successful reproduction, is high (P_{good}
189 > 0.6 , for the chosen simulation parameters; Figures 2a, 2b). However, if potential trap sites usually
190 function as traps, and reproduction in them fails, the existence of potential traps instead of barren sites
191 decreases median and minimum population sizes (Figures 2a, 2b), and in some combinations of
192 parameters they lead to extinction (left corner in Figures 2a, 2b). The risk of extinction due to the
193 existence of traps is increased as their prevalence is higher, and as the frequency of good years is
194 lower.

195
196 ((Figure 2 here))

197
198 The factor which is often most pressing in conservation of endangered species is the extent to
199 which they are at risk of short-term extinction due to stochastic dynamics. Figure 3 presents for each
200 tested combination of parameters the fraction of simulation runs in which extinction did not occur. In
201 line with the findings presented in figures 1 and 2, the r-selected toad population in our simulations

202 never went extinct, regardless of the prevalence of potential traps and their severity, i.e. the frequency
203 of years in which they lead to failed reproduction. The k-selected grebe population, however, often
204 went extinct in the regime of parameters where good years were rare and prevalence of trap sites was
205 high.

206
207 ((Figure 3 here))

208
209 To gain insight about the population dynamics that take place in each of the two studied species,
210 Figure 4 presents for each species the overall population size as a function of time in a single
211 simulation run. Highlighted in green are good years, in which even potential traps allowed successful
212 reproduction. The population size of toads increases significantly following good years, followed by a
213 gradual decrease towards a low population steady-state which is reached, and maintained, when a
214 sequence of bad years occurs stochastically. In grebes, with the parameter values simulated in this run,
215 the population size decreases from its initial value almost continuously, with slight transient increases
216 in size following good years. These slight increases are insufficient to offset the population decline
217 that occurs in bad years, which are the majority, and eventually the population goes extinct.

218 Our simulation allows us to track the dynamics within each deme separately (results not shown)
219 and explain the population dynamics: in the toad simulation, thanks to their r-selected strategy of
220 producing a very large number of offspring, even very few individuals at each trap site allow the
221 population to capitalize on good years, increasing significantly following each such year. Migration
222 from natural sites, as well as from trap sites following good years, ensures that each trap site will
223 constantly be populated by adult toads awaiting an opportunity for reproduction. The loss of these
224 adult individuals from natural sites via migration is more than compensated-for by the successful
225 reproduction in the trap sites on good years, while the reproduction at the natural sites is not harmed
226 by this outgoing migration, because few adults in each such site are sufficient for the reproduction in
227 each year to realize the site's carrying capacity. Moreover, the presence of adults in trap sites, even
228 when they are not suitable for reproduction, decreases competition among adults in natural sites,

229 allowing an overall larger adult population size and the presence of a reservoir of adults in trap sites in
230 the years following a good year.

231 The grebe simulation, in contrast, demonstrates a different scenario: the species' carrying capacity
232 at each site is low so populations are small, and each female produces a small number of offspring.
233 Loss of individuals to trap sites leads to a significant decrease in the population's reproductive
234 potential at the natural sites, and the source-sink dynamics that ensue create an ongoing decrease in
235 the overall population and in the populations at natural sites. Accordingly, only few individuals are
236 found in trap sites when good years occur, and the population benefits only little from these years.
237 Because the species has few offspring, the benefit of reproduction at these sites for the overall
238 population, when it does occur, is limited. These small increases are not sufficient to compensate for
239 the loss of individuals and reproductive potential at natural sites that occur on bad years. These
240 dynamics lead the population to eventual extinction.

241

242

243

((Figure 4 here))

244

245 Both species that we explore may benefit from potential trap sites if these sites allow reproduction
246 frequently enough. However, if good years are uncommon these sites pose a threat to the continued
247 survival of k-selected species, as the source-sink dynamics that they create drain the natural sites from
248 adult individuals, decreasing the species' overall population and reproductive potential. In contrast, r-
249 selected species may benefit from trap sites' existence for a broad range of parameters, and at the
250 extreme – as demonstrated here – may benefit from them even if they never allow reproduction,
251 merely through their provisioning of viable habitat for adults.

252

253 **Discussion**

254 Ecological traps represent an increasingly difficult challenge to conservation. The mismatch between
255 habitat quality and the way species perceive these habitats leads to a situation in which 'trapped'

256 species do not try to avoid these deleterious habitats (and in many cases they are even attracted to
257 them) with devastating consequences (Robertson & Hutto 2006; Robertson et al. 2013). It is therefore
258 quite clear that given a choice between protecting a 'good' habitat or an ecological trap (for a given
259 species, since traps are usually species-specific), wildlife managers should always opt to protect the
260 good habitats. Unfortunately, a dichotomy between good and bad habitats is a notion that does not
261 really exist in our complex world, and to paraphrase Tolstoy – all good habitats are alike; each bad
262 habitat is bad in its own way. In the real world, the choice that many wildlife managers face these
263 days is not between good and bad habitats, but rather between bad and worse habitats. Given such a
264 choice, we have shown that at least for r-selected species, protecting habitats that act as ecological
265 traps for the species may be preferable to eliminating the traps and replacing them with non-habitable
266 habitats.

267 The example we investigated in our model is a network of seasonal pools within a hostile
268 matrix in which some of the pools act as equal preference ecological traps – they are undistinguishable
269 from 'good' pool sites, but they may dry early in the season, resulting in mass mortality of all larvae
270 (or offspring in the hypothetical case of the k-selected species) in the pool and leading to a fitness gain
271 of zero for any individual choosing these sites. Our model shows that despite this catastrophic fitness
272 consequence, the long-term mean population size of a model r-selected species (the European green
273 toad) increases with increasing prevalence of trap habitats within the hostile matrix (i.e., the ratio of
274 trap habitats to barren habitats, Fig. 1). Not surprisingly, the mean toad population size also increases
275 as the probability for dry years decreases, since the traps only have negative consequences in dry
276 years. However, it is important to note that even when the probability for dry years is 100%, the
277 existence of the trap habitats always has a positive (even if sometimes small) effect on the toad
278 population size (Fig. 1). This is not the case for k-selected species. When the probability for dry years
279 is low, the mean population size of our model k-selected species (little grebe) indeed increases with
280 the prevalence of trap habitats within the hostile matrix, which means that preserving trap sites can
281 have a positive effect even on k-selected populations (Fig. 2). However, when the probability for dry
282 years is high, increasing the prevalence of trap habitats leads to extinction of the population (Fig. 3).

283 This means that the effects of trap habitats on k-selected species may go well beyond local extinction
284 dynamics and can cause the collapse of the entire meta-population. Similar equal-preference trap
285 dynamics have been reported in the wild for species of various taxa (e.g., reptiles - Hawlena et al.
286 (2010); Birds – Kloskowski 2012; Mammals – Balme et al. 2010).

287 The mechanistic underpinnings of our simulation's results can be elucidated from the example
288 scenario depicted in Figure 4. For the r-selected toads (Fig. 4a), each good year is followed by a spike
289 in population size, while a sequence of bad years results in a steep population decline. However, the
290 minimum population size is more or less in par with the population size in the absence of traps and
291 never goes below it. This population size is maintained by the small number of natural patches, in
292 which the toads can reliably reproduce. The very high recruitment rate of the toads allows them to
293 maintain a stable population in these patches, even after "losing" a large number of individuals each
294 year to mortality and dispersal to patches in which reproduction fails completely on dry years. The
295 much lower recruitment rate of the K-selected grebes means that the existence of the traps in the
296 environment further reduces the already small populations in the natural habitats due to increased
297 dispersal, and the infrequent good years are not sufficient to overturn this demographic decline. These
298 dynamics may lead the entire grebe population to extinction (Fig. 4b).

299 For r-selected species, potential trap sites can be valuable for the population for two additional
300 main reasons. First, even when juveniles cannot survive in trap sites, reducing the fitness of any
301 reproducing individual in these sites to zero, these habitats may still provide viable habitat for adults,
302 who can linger in them in the periods between good years. These sink habitats may also improve the
303 overall conditions in the source habitats by reducing competition within each habitat, decreasing
304 predation risk by attracting some of the predators away from the source sites and into the sinks, and
305 increasing the overall carrying capacity of the area (Hanski 1999). Second, the trap sites may act as
306 landscape-level stepping stones, facilitating dispersal among the different populations, re-enforcing
307 demes with existing local populations and recolonizing demes in which the local population had gone
308 extinct (Kanda et al. 2009).

309 Conservation work is all about prioritization (James et al. 2001; Balmford et al. 2003; Joseph
310 et al. 2008). We will never have enough resources to save all species and habitats, and therefore we
311 need to decide on which species and habitats to focus. These are crucial decisions and they must be
312 backed up by the best science available to us (Joseph et al. 2008). Ever since the concept of ecological
313 traps was developed (Dwernychuck & Boag 1972; Ratti & Reese 1988; Schlaepfer et al. 2002; Battin
314 2004), the most common approach to trap mitigation has been to invest efforts in eliminating the
315 traps. This can be done by removing the cues attracting species to the trap, improving the quality of
316 the habitat so it would no longer be a trap, or luring individuals to undervalued beneficial habitats
317 (Gilroy & Sutherland 2007; Robertson 2012). The steadily accumulating examples of the potentially
318 devastating effects of ecological traps clearly support this approach (e.g., Schlaepfer et al. 2002;
319 Robertson et al. 2013), and the results of our model for k-selected species add additional support for
320 this strategy. However, our results also highlight the fact that counterintuitively, under specific
321 conditions, eliminating potential traps from the environment may reduce the viability of meta-
322 populations and increase extinction risk. Temporal pools serve as a good example for such a case.
323 There isn't any doubt that a temporal pool that dries up early in the season may become an ecological
324 trap, especially for amphibians. If individuals do not distinguish between the cues given by such pools
325 and cues given by pools that would last the entire season, they will readily lay eggs in the temporary
326 pools, dooming all of their offspring and reducing the parents' fitness yield for that season to zero.
327 Given the current amphibian crisis and the declining trends of so many amphibian species (Dawson et
328 al. 2016), drying up these pools in advance and eliminating the ecological traps might seem like a
329 strategy that is both reasonable and feasible. However, it is important to remember that conservation
330 biology focuses on populations and not individuals, and thus individuals' failure to reproduce,
331 although unfortunate, may be preferable to the elimination of the trap, if its boost to the population
332 size and to its connectivity on rainy years outweighs the costs of lost reproductive efforts from the
333 population's perspective. Our work demonstrates that in a broad range of reasonable settings, drying
334 up temporary pools is a mistake that may further drive amphibian meta-populations towards
335 extinction.

336 While the concept of ecological traps has been around for almost half a century (Dwernychuck
337 & Boag 1972), it has only begun to attract major scientific attention relatively recently (Schlaepfer et
338 al. 2002; Battin 2004). For that reason, there was a fundamental need in the past couple of decades to
339 identify potential ecological traps to a large variety of species and raise awareness among ecologists
340 and conservationists to the consequences of traps and possible ways of mitigating them (Gilroy &
341 Sutherland 2007; Robertson 2012; Berger-Tal & Saltz 2016). However, we posit that we should now
342 move beyond the dichotomy of defining what is a trap and what isn't, and start characterizing traps in
343 quantifiable ways – How attractive is the trap? What are the negative impacts of the trap? How do the
344 attractiveness and impact of the trap interact with environmental conditions and the life history of the
345 species in question? These questions may be species-specific but understanding them may be crucial
346 to the management of these species and to their survival.

347

348

349 **Methods**

350 *Model species*

351 We model two species in our simulations, using parameter values that are comparable in their
352 magnitude to those that characterize two species that breed in seasonal pools in Israel: European green
353 toad (*Bufo viridis*; locally endangered; (Elron, 2007)), and little grebe, a local water bird
354 (*Tachybaptus ruficollis*). The green toad is directly relevant to the question at hand, as it breeds almost
355 exclusively in seasonal pools. It constitutes a straightforward example of a species that may be
356 influenced by the dynamics studied in this paper. The water bird differs, alongside its breeding
357 strategy, also in the extent to which it may be influenced by ecological traps in the form of short-lived
358 seasonal pools; it often breeds in aquatic habitats that hold water year-round, and, in reality and in
359 contrast to toad tadpoles, its young have some probability of survival even in pools that dry up early.
360 We chose it only to demonstrate the potential effects of ecological traps on a k-selected species, and
361 assume for the sake of this study's comparison that the young are reliant on their pond's hydroperiod
362 for successful fledging.

363

364 ((Table 1 here))

365

366 *The Model*

367 Each simulation tracks the fate of simulated agents – juvenile, sub-adult, and adult individuals of
368 the species of interest – over time. For each, it simulates reproduction, migration between sites across
369 the 100-site grid, and survival. For simplicity it is assumed that all eggs are fertilized, avoiding the
370 need to explicitly simulate pairing of individuals for mating. Each iteration of the simulation
371 represents the dynamics of these events over one year. Each simulation was run for 200 years, and all
372 summary statistics that are reported in the results were collected over years 100 to 200 of the
373 simulation, well after it had reached a dynamical steady state (see examples of the trajectory of
374 population size over time from year 0 onwards in figure 4). Each figure summarizes such results
375 across 50 runs in each tested combination of parameters. All simulations were initialized with 100
376 mature individuals per site.

377 At the start of each simulation run, each of the 100 potential sites along the grid is randomly
378 assigned to one of the following three categories at some probability: *natural sites*, at a probability of
379 0.15, *potential ecological traps*, at a certain probability in each simulation run, ranging from 0 in
380 some simulations to 0.85 in others, and *barren sites*, i.e. sites that are not habitable to the species of
381 interest. Sites that were not randomly assigned to one of the first two categories are determined to be
382 barren. A natural site is one in which reproduction is successful every year, while a potential
383 ecological trap is a site in which reproductive success differs between 'good' and 'bad' years; in the
384 context of seasonal pools, this would be prominently dependent on the amount of rains and their

385 distribution in time, with bad years being characterized by rapid desiccation of the pools, leading in
386 our simulations to 100% offspring mortality.

387 Variable sites, i.e. potential ecological traps, may be coupled with one another with respect to the
388 timing in which they act as traps, or independent of one another. In reality, whether the hydroperiod of
389 seasonal pools in a certain year is long or short is likely to be correlated across pools in a certain
390 region. This is due to the similarity in the rainfall they experience and its distribution in time. Such
391 coupling is more problematic, from a conservation perspective, than a situation in which good and bad
392 years are uncorrelated at different sites, because it means that on ‘bad’ years many sites act as traps
393 and can devastate a population of organisms, with reproduction failing across many breeding sites, a
394 correlation known as part of the Moran effect (e.g. (Hudson and Cattadori, 1999; Ranta et al., 1997)).
395 For realism and as a conservative approach to assessing the possible risks and benefits of potential
396 traps, we present in this study only results for the case in which good and bad years are correlated
397 across all potential trap sites.

398 Both natural and potential trap sites, in our simulations, provide habitat in which adult individuals
399 can subsist. Individuals in our simulation do not show any preference to a particular site type, i.e. trap
400 sites are equal-preference traps ((Robertson and Hutto, 2006)).

401 *Adult carrying capacity and mortality:* Both natural and potential trap sites are characterized by a
402 certain carrying capacity of adult individuals, and the probability of individuals’ mortality is density-
403 dependent following a sigmoidal function, which considers both the maximal carrying capacity and a
404 baseline adult mortality probability (see below). For simplicity, the probability of death for premature
405 (sub-adult) individuals, i.e. those at ages between 1 and 2 in our simulation, is independent of density,
406 and set by a mortality parameter that is significantly higher than that of adult individuals’ baseline
407 mortality rate.

408 The probability of mortality of an adult individual per year is described by:

409
$$P_{\overline{a}}^{adult_mortality} = P_a + (1 - P_a) / \left(1 + \exp\left(-0.002 \times (n - 0.75 \times C_a)\right) \right)$$
, where P_a describes the probability of
410 mortality of an adult individual per year in the absence of competition, n denotes the population with
411 which the individual is competing, and C_a represents the carrying capacity of adult individuals per
412 site, which for simplicity was set to be constant across sites.

413 In the simulation, the probability of mortality of adults was calculated for each individual in each
414 site separately, considering as the competing individuals only those individuals whose probabilities
415 had been calculated already at that site on that generation. Thus, the first individual whose probability
416 of mortality was calculated at a certain site on a certain generation experiences no competition, and
417 the last individual whose mortality probability is calculated experiences the greatest competition. The
418 order in which individuals were chosen for this calculation was randomized on every year. This
419 scheme may be seen to reflect a situation in which the first adults to arrive at a breeding site
420 experience the least competition (on territory, for example), or to reflect a situation in which some
421 individuals suffer from competition more than others due to differences in body size and ability to
422 monopolize resources. This scheme was chosen to avoid a computational artifact, whereby years with
423 high population size would be characterized by high competition and very high mortality, reducing the
424 population severely, and being followed by years of extremely low competition; such dynamics would
425 constitute an artifact, because in reality competition-related mortality is gradual over the year or over

426 the breeding season, allowing a gradual approach of the population size to the carrying capacity
427 without harsh year-to-year fluctuations that are driven by competition.

428 *Juvenile carrying capacity and survival:* The number of surviving juveniles is also density-dependent,
429 and depends on the overall site carrying capacity, which is for simplicity the same for all sites. It
430 follows a curve of diminishing returns: For small numbers of juveniles, the number of surviving
431 individuals is nearly linearly correlated with the number of eggs laid, but this relation changes as the
432 number of eggs increases, with the number of surviving individuals characterized by an asymptote at
433 the per-site juvenile carrying capacity. The curve is described by the expression:

434
$$S = C_j \times \left(1 - \exp\left(-N_{eggs} \times P_j / C_j\right) \right)$$
, where S describes the number of juveniles that survive their first year
435 (in amphibians, metamorphosis), C_j describes the per-site juvenile carrying capacity, N_{eggs} describes
436 the overall yearly number of eggs laid at the site, and P_j describes the probability of survival of a
437 juvenile in the absence of competition.

438 *Migration:* In each year, each adult individual migrates at a certain probability which is a simulation
439 parameter, and is equal across individuals and throughout the simulation run. The destination of
440 migration is chosen randomly among the natural sites and the trap sites, as a function of the distance
441 from the site of origin of the migrant. The probability of migrating from one site to another decreases
442 exponentially (with $\gamma = 1$) with the distance between them. Migration does not incur a direct
443 fitness cost. Individuals' fitness is influenced by migration via its dependence on the nature of the
444 destination site (natural site or potential trap) and its existent population. This scheme allows a focus
445 on the influence of potential traps on the population via their influence on reproduction dynamics and
446 their potential to function both as a sink (in 'bad' years) and as a source (in 'good' years).

447 *Migration and population dynamics:* For many species and trap types, the implemented migration
448 scheme may be a conservative estimate of the potential positive contribution of trap sites to a
449 population's dynamics: often migration is in the form of semi-random dispersal, and is not goal-
450 directed from the onset. In many landscapes, if an individual reaches a barren site – one that is neither
451 a natural nor a trap site – it will likely die. Trap sites may thus provide viable habitat which serves as a
452 non-lethal destination of migration. If this is the case, trap sites, beyond their functioning as
453 demographic sinks or sources, may contribute to the robustness of a species population both via an
454 increase in the meta-population connectivity and via decrease in dispersal-related mortality.

455

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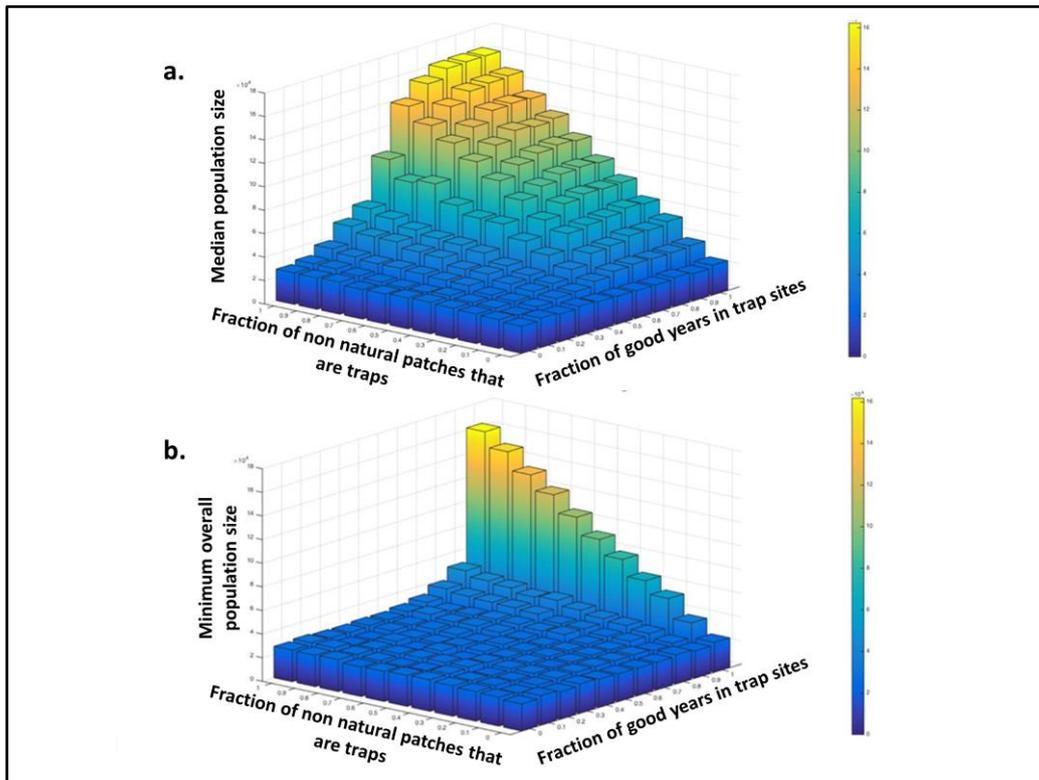
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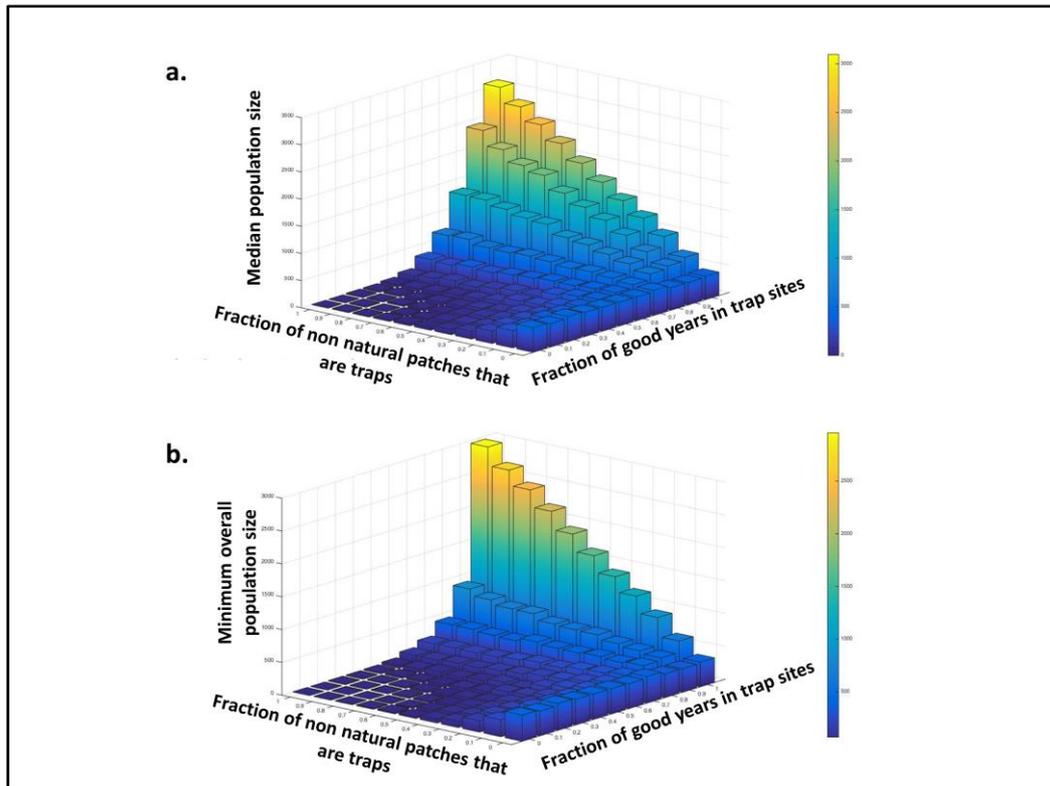
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574 **Figure 1: Existence of ecological trap sites increases both median and minimum population sizes of toads**
575 **for all combinations of parameters. (a)** The mean across simulations of the median overall population size of
576 toads. **(b)** The mean across simulations of the minimum overall population size of toads. Each bar represents
577 simulation results for a different parameter combination: the fraction of years on which trap sites allow toad
578 reproduction (x-axis), and the fraction, among the non-natural patches, of trap sites as opposed to barren
579 sites (y-axis). The values depicted are calculated for generations 100 to 200 across 50 simulation runs.

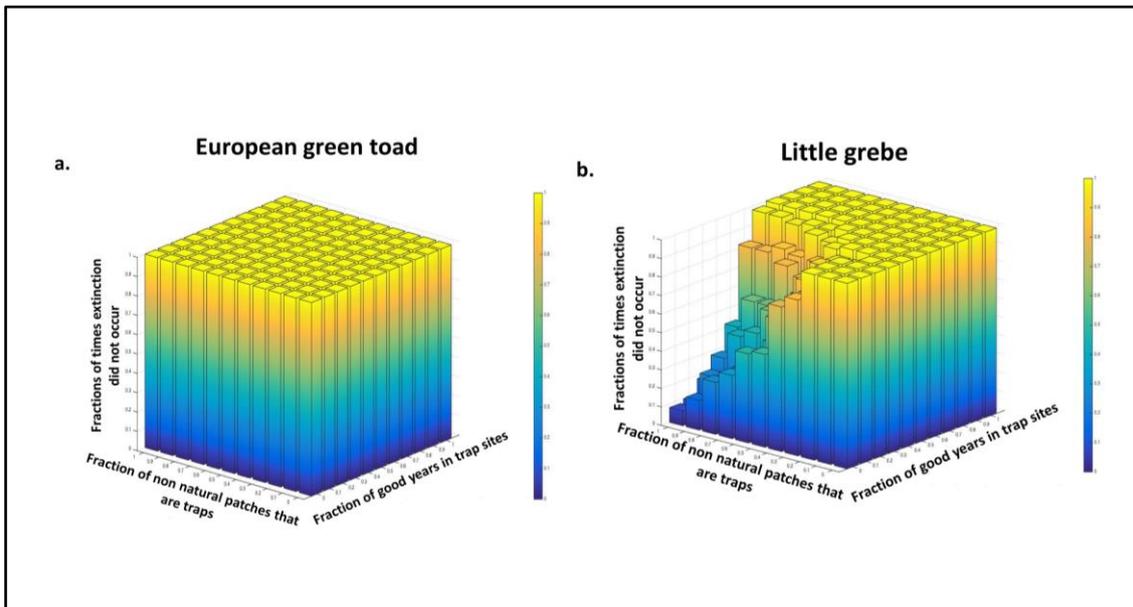


581

582 **Figure 2: Existence of ecological trap sites decreases median and mean sizes of grebe populations across a**
 583 **broad range of parameters, often driving them to extinction. (a)** The mean across simulations of the median
 584 overall population size of grebes. **(b)** The mean across simulations of the minimum overall population size of
 585 grebes. Each bar represents simulation results for a different parameter combination: the fraction of years on
 586 which trap sites allow toad reproduction (x-axis), and the fraction, among the non-natural patches, of trap
 587 sites as opposed to barren sites (y-axis). The values depicted are calculated for generations 100 to 200 across
 588 50 simulation runs.

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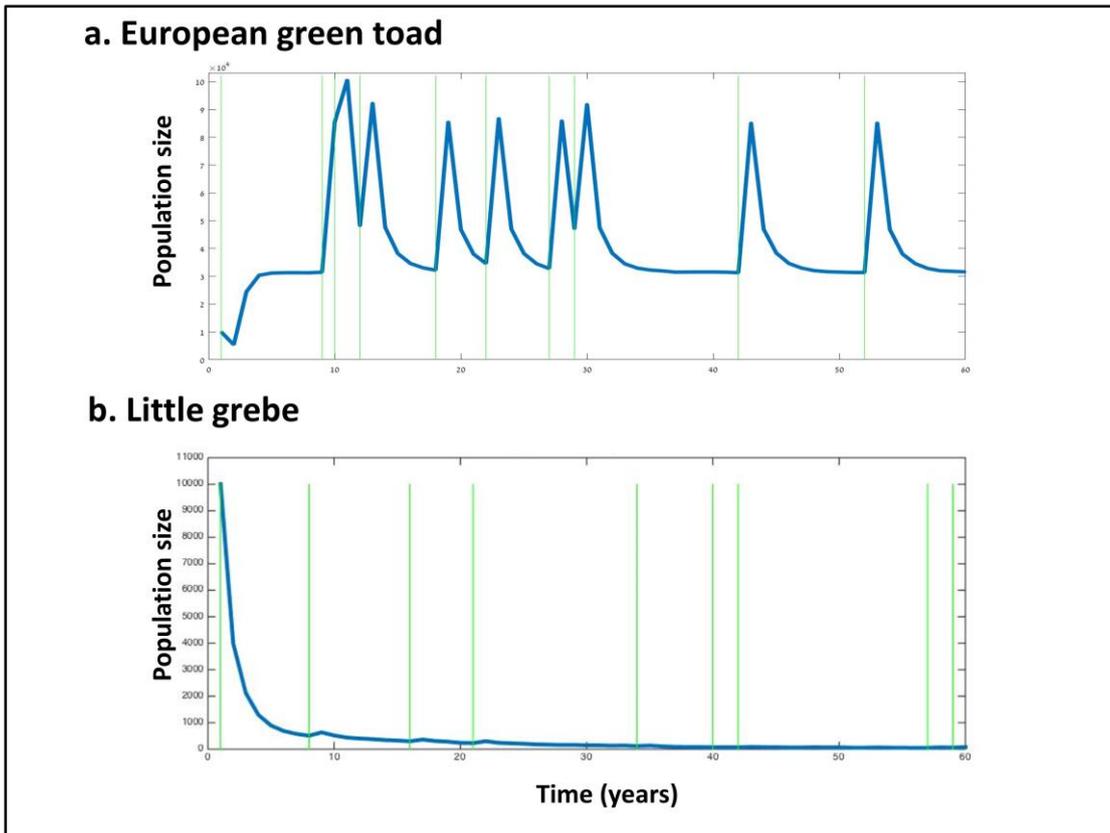


591

592 **Figure 3: Across the full range of parameters, existence of ecological trap sites does not lead to extinction of**
 593 **toads, but does lead to extinction of grebes in multiple combinations of parameter values.** The fraction of
 594 simulations, across 50 simulation runs in each condition, in which the global population of (a) toads and (b)
 595 grebes went extinct.

596

597



599

600 **Figure 4: Demographic trajectories over time demonstrate the effect of traps on toads and on grebes.** The
 601 trajectory of population size over time in a single simulation, in which half of the non-natural sites are
 602 ecological traps, and in which good years, allowing reproduction in ecological trap sites, occur at a probability
 603 of 0.2. **(a)** The toad population increases dramatically in size following each good year, in which breeding in
 604 ecological trap sites is successful. The population size gradually decreases during bad years in the ecological
 605 trap sites, but the minimal population size it reaches is never significantly different from the population size in
 606 the scenario in which all non-natural sites are completely barren. **(b)** The grebe population decreases almost
 607 monotonously, due to the ecological traps' function as a demographic sink in bad years. Good years are
 608 followed by slight increases in population size, but these are insufficient to offset the effect of bad years.

609

610

611 Table 1: The parameters studied and their values for each species.

	Green toad	Little grebe
#eggs per female	8000	4
No-competition $P(\text{survival})$ per offspring	0.5	0.75
Juvenile carrying capacity per site	2000	40
Adult carrying capacity per site	500	15
$P(\text{death, premature individual, per year})$	0.4	0.25
$P(\text{death adult individual per year})$	0.2	0.15
$P(\text{migration})$	0.1	0.2

612