Digging the pupfish out of its hole: Risk analyses to guide harvest of Devils Hole pupfish for captive breeding

The Devils Hole pupfish is restricted to one wild population in a single aquifer-fed thermal pool in the Desert National Wildlife Refuge Complex. Since 1995 the pupfish has been in a nearly steady decline, where it was perched on the brink of extinction at 35-68 fish in 2013. A major strategy for conserving the pupfish has been the establishment of additional captive or "refuge" populations, but all ended in failure. In 2013 a new captive propagation facility designed specifically to breed pupfish was opened. I examine how a captive population can be initiated by removing fish from the wild without unduly accelerating extinction risk for the pupfish in Devils Hole. I construct a count-based PVA model, parameterized from estimates of the intrinsic rate of increase and its variance using counts in spring and fall from 1995-2013, to produce the first risk assessment for the pupfish. Median time to extinction was 26 and 27 years from spring and fall counts, respectively, and the probability of extinction in 20 years was 26-33%. Removing individuals in the fall had less risk to the wild population than harvest in spring. For both spring and fall harvest, risk increased rapidly when levels exceeded six adult pupfish per year for three years. Extinction risk was unaffected by the apportionment of total harvest among years. A demographic model was used to examine how removal of different stage classes affects the dynamics of the wild population based on reproductive value (RV) and elasticity. Removing eggs had the least impact on the pupfish in Devils Hole; RV of an adult was roughly 25 times that of an egg. To evaluate when it might be prudent to remove all pupfish from Devils Hole for captive breeding, I used the count-based model to examine how extinction risk related to pupfish population size. Risk accelerated when initial populations were less than 30 individuals. Results are discussed in relation to the challenges facing pupfish recovery compared to management of other highly endangered

species.

2   **Digging the Pupfish Out of its Hole: Risk Analyses to Guide Harvest of Devils Hole Pupfish**

3   **for Captive Breeding**

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8 INTRODUCTION

9 The Devils Hole pupfish (*Cyprinodon diabolis*) may have the smallest geographic range of any

10 vertebrate in the wild. This species is restricted to a single population and occurs primarily in the

11 upper 10 meters of Devils Hole, an aquifer-fed thermal pool (~33.5°C) and limestone cavern with

12 a surface area of 50 m^2 that is located 17 m below the land surface in the Desert National Wildlife

13 Refuge Complex in Nye County, Nevada (Andersen & Deacon 2001; Baugh & Deacon 1983a).

14 Pupfish spawning takes place predominately on a shallow (~ 0.35 m), submerged ~2x4 m shelf

15 (Hausner et al. 2013; James 1969). It is the only fish in Devils Hole, where it has resided since

16 climate warming caused regional drying beginning ~20,000 years ago (Szabo et al. 1994).

17 The Devils Hole pupfish (DHP) has played an important role in the history of the

18 conservation movement. In 1952 Carl Hubbs, a pioneer of western ichthyology, convinced

19 President Harry Truman to designate Devils Hole as a disjunct part of Death Valley National

20 Monument to protect both its unique geological features and the pupfish (Riggs & Deacon 2004).

21 The DHP was among the initial species listed when the U.S. Endangered Species Preservation

22 Act was passed in 1967. A monitoring program was begun that used scuba divers to count fish

23 and initial counts found 100-250 individuals in the early 1970's (Riggs & Deacon 2004). Soon

24 after, the DHP was the subject of a historic four-year legal battle over water rights that

25 culminated in the U.S. Supreme Court (1976 Cappert v. United States). The decision caused a

26 cessation of groundwater mining from further dewatering the aquifer for development in the

27 Amargosa Valley and nearby Ash Meadows (Riggs & Deacon 2004), and the case had a major

28 influence on ground water rights in the region.

29 With the cessation of groundwater pumping, water levels rose in Devils Hole as did DHP

30 numbers (Andersen & Deacon 2001), which reached a maximum count of 541-548 individuals in

31 1980, 1990 and 1995 (Figure 1). Since 1995, however, the pupfish in Devils Hole has been in a

32 nearly steady decline, where it was perched on the brink of extinction at 35-68 fish in 2013.

33   Hypothesized causes of decline include food limitation due to changes in the Devils Hole algal

34   and invertebrate communities (K.P. Wilson, pers. comm., 3 June 2014), mutational meltdown

35   caused by centuries of reduced genetic variation (Martin et al. 2012), and climate warming

36   resulting in increased water temperatures and decreased dissolved oxygen (Hausner et al. 2013;

37   Hillyard et al. 2014). The population decline was amplified by the accidental deaths of at least 72

38   pupfish in Sept. 2004 in larval traps that were washed into Devils Hole during a flash flood

39   (Manning & Wullschleger 2004).

40   A major strategy for conserving the DHP, in addition to securing Devils Hole, has been

41   the establishment of captive or "refuge" populations (Baugh & Deacon 1988; Wilcox & Martin

42   2006). However, past attempts have not been successful. Between 1969 and 2012, multiple

43   attempts were made to propagate the DHP in captivity and establish refuges. Typically these

44   efforts removed 12-30 pupfish at a time from Devils Hole. They were transported to 14 different

45   locations ranging from managed efforts in established, commercial aquaria to constructed and

46   natural ponds or springs with less oversight. All ended in failure, with some populations lasting

47   for 1-2 decades and others for 1-2 years (Karam 2005; U.S.N.P.S. 2012; Wilcox & Martin 2006).

48   Reasons for failure, when known, were varied and included equipment or water supply failure,

49   predation by native and exotic species, vandalism, failure to reproduce, and hybridization.

50   Now in response to the recent population collapse and imminent threat of extinction, a

51   new captive propagation facility has been built and, unlike previous efforts, was designed

52   specifically to breed pupfish. It was built in nearby Ash Meadows, and received a total of 60

53   DHP eggs from August 2013 to January 2014. The Ash Meadows facility provides a new

54   opportunity for successful captive breeding, but it also presents a challenge. Without an obvious

55   track record of captive breeding success, can a captive population be initiated without unduly

56   accelerating the risk of extinction of the DHP in Devils Hole? Which life stages of the fish

57   should be collected to minimize impact on the wild population? On the other hand, if the

58 trajectory of decline for the DHP continues, will there be a moment when all individuals should

59 be removed from the wild in order to maximize the genetic diversity for captive breeding to

60 succeed? This occurred for the California condor (*Gymnogyps californianus*) in 1986 when

61 evidence indicated little hope of survival in the wild (Snyder & Snyder 1989). That controversial

62 and difficult decision was implemented after much debate within the U.S. Fish and Wildlife

63 Service over whether to proceed with removing the last wild condors, and after litigation by its

64 conservation partner, the National Audubon Society, to prevent it. Removing the last wild

65 individuals turned out to be the right decision, as it secured a gene pool for the subsequently

66 highly successful captive propagation program (Snyder & Snyder 2000), although reintroduction

67 to the wild remains problematic (Walters et al. 2010). Successful captive breeding was foreseen

68 for condors based on captive propagation undertaken with surrogate species, such as the Andean

69 condor (*Vultur gryphus*), and similar possibilities exist for the pupfish based on experiences with

70 the DHP and its congenerics (e.g., Baugh & Deacon 1983b; Deacon et al. 1995; Lema & Nevitt

71 2006).

72   Here I produce the first risk assessment for the Devils Hole Pupfish. I construct a count-

73 based population viability model to project the risk of extinction for the DHP parameterized from

74 recent biannual pupfish surveys. I then use the model to evaluate how the number of individuals

75 removed for captive breeding and the timing of harvest affects population viability of the DHP in

76 Devils Hole. Next I build a matrix population model to ask what the impact of removing pupfish

77 eggs, early life stage (larval) individuals, or adults will be on DHP population dynamics based on

78 patchy demographic data, expert opinion and data borrowing from closely-related species.

79 Finally, I return to the count-based population model to ask how extinction risk relates to DHP

80 population size to evaluate when it might be prudent to remove the remaining pupfish from

81 Devils Hole for captive breeding. In these applications of population models to project extinction

82 risk, commonly called population viability analysis or PVA (Beissinger & McCullough 2002), I

83 evaluate conservation decisions by comparing differences in projected outcomes among

84 management options incorporated into the models rather than basing recommendations solely on

85 the projected rates of extinction (Lotts et al. 2004; McCarthy et al. 2003; Ralls et al. 2002; Reed

86 et al. 2002).

87 **MATERIALS AND METHODS**

88 **Modeling Risk and Harvest Strategies for Captive Breeding Using DHP Counts**

89 Visual counts of pupfish from 1972 to 2013, made by SCUBA divers in the pool and by observers

90 on the shallow shelf, were obtained from Death Valley National Park personnel (Figure 1). See

91 Dzul et al. (2012) for survey details and sources of error. Counts of pupfish did not distinguish

92 between adults and detectable early life stage individuals, and were conducted on about a

93 monthly basis from 1972-1983. By 1985 counts were mainly done biannually, in the spring

94 (March-April) during the main breeding season of the pupfish and in the fall (Sept.-Oct.) during a

95 second but reduced pulse of breeding. Only one count per season was conducted in most years,

96 which precluded the use of N-mixture models of population estimation that require repeated

97 sampling (Royle & Dorazio 2008). In the absence of survey-level covariates of effort, I was

98 unable to use a single visit conditional likelihood approach to estimate abundance (Lele et al.

99 2012; Solymos et al. 2012). Thus, I choose to use the maximum count for each season in each

100 year as an estimate of the population size, creating two time series of counts. Treating counts

101 separately provided independently derived estimates of population trends and permitted seasonal

102 evaluation of harvest options.

103   I calculated the rate of population growth ($r = ln(N_{t+1} / N_t)$ from pairs of counts of

104 population size (N) from consecutive years (t). I then fit one density-independent and two

105 density-dependent models of population growth to the period when pupfish numbers grew (1972-

106 1995) and the period of population decline (1996-2013) following Morris and Doak (2002):

107 $$\ln(N_{t+1}/N_t) = r + \varepsilon_i \quad (1) \text{ Exponential (density-independent):}$$

$$\ln(N_{t+1}/N_t) = r\left[1 - \left(\frac{N_t}{K}\right) + \varepsilon_i\right]$$

108 (2) Logistic (density-dependent):

$$\ln(N_{t+1}/N_t) = r\left[1 - \left(\frac{N_t}{K}\right)^{\theta} + \varepsilon_i\right]$$

109 (3) Theta-logistic (density-dependent):

110 where r = growth rate, K = carrying capacity, θ adjusts how population growth changes with N,

111 and ε_i = is the variance or deviation in the natural logarithm of population growth ($\ln r$) centered

112 around zero. Akaike's Information Criterion (AIC) corrected for small sample size (AICc) was

113 used to quantify model fit (Burnham & Anderson 2002).

114   To model extinction risk in the wild, the pupfish population in Devils Hole was projected

115 forward in time for 100 years with separate models for spring and fall using each season's

116 estimates fitted values for average population growth rate, carrying capacity (when appropriate),

117 and annual deviations from mean growth rates (ε_i) estimated from 1996-2013 to yield the median

118 time (years) to extinction and probability of extinction. Starting population size was set to the

119 number of pupfish counted in 2013 for spring (35) and fall (68), and 10,000 iterations were run.

120 Fractional numbers of individuals were rounded down each year.

121   Using ε_i to model annual variation among counts has contrasting effects on the resulting

122 estimate of extinction risk. The ε_i term incorporates implicit effects captured in DHP count

123 fluctuations including: (1) demographic, environmental, and genetic stochasticity; (2)

124 catastrophes; and (3) sampling variation. Nevertheless, these processes were not explicitly

125 modelled. The inclusion of sampling variation in the estimate of ε_i will overestimate variation in

126 population growth and inflate extinction risk. However, in the absence of explicit incorporation

127 in the model of genetic processes (e.g., inbreeding depression), extinction risk may be

128 underestimated. As I am unable to determine the magnitude of each effect, estimates of

129 extinction risk are best interpreted when compared among different scenarios.

130   To evaluate the effects of different strategies for removing individuals to initiate a captive

131 breeding program on the wild population, I used the models that best described DHP population

132 dynamics for spring and fall from 1996-2013, and harvested (removed) different numbers of

133 individuals (0-14) at the start of each simulated year. Harvest was done for each of three years to

134 mimic building a new population for captive propagation. Median time to extinction and

135 probability of extinction were evaluated from 10,000 iterations.

136   I used the same model to examine how risk of extinction changes with DHP population

137 size to evaluate when to remove all pupfish individuals from Devils Hole based solely on changes

138 in wild population risk without considering genetic goals for the captive population. The

139 stochastic count-based PVA model was run for 10,000 iterations parameterized with the 1996-

140 2013 measures of population growth, incrementally changing the initial population size.

141 **Deterministic Matrix Demographic Model to Evaluate Age Classes to Remove**

142 A deterministic demographic model was developed to evaluate the effects of removing

143 individuals of different life stages on DHP population dynamics by calculating for each life stage

144 its reproductive value (i.e., expected future number of offspring produced) and elasticity

145 (sensitivity of population growth to changes in demographic parameters associated with each

146 stage). I sought opinions for constructing and parameterizing the model from 15 DHP and

147 fisheries experts that attended the DHP Risk Analysis Workshop (8 Nov. 2013). Demographic

148 data available for the DHP are so limited, and the uncertainties so large, that I could not justify

149 the choice of particular rates or scenarios. Instead, I generated 5000 matrices composed of

150 random combinations of potential average demographic rates for the pupfish chosen from

151   uniform distributions that sampled means between their possible minimum and maximum values

152   (Figure 2). This approach allowed exploration of the potential parameter space, resulting

153   distribution of reproductive value and elasticity for stage classes, and relationships among them.

154   A post-breeding projection was chosen to enable inclusion of eggs as a life stage because

155   they are potential targets for management. It was based on a life cycle diagram and projection

156   matrix with 3 stages (Figure 2): eggs, early life stage or ELS (from hatching at 4 mm to 11 mm in

157   length) and adults (>12 mm). A 7-day time step was used based on the time required for an egg

158   to hatch and become an ELS. I converted DHP demographic rates expressed in the literature on a

159   monthly basis to a daily rate (divided by 30) and then to a weekly rate (multiplied by 7).

160   The model required estimates for the proportion of individuals that: (a) survive over a

161   time step and remain *Adults* (P_3); (b) grow from *Eggs* and survive to become *ELS* (G_1); and (c)

162   that grow from *ELS* to become *Adults* (G_2), or that survive and remain as *ELS* (P_2). It also

163   required estimates for realized fecundity, which is the product of (d) the proportion of individuals

164   that survive and remain (P_3 for *Adults*) or that grow to a reproductive stage over the time step (G_2

165   for *ELS*), and (e) their fecundity (m_3). Because male fecundity was not known, rates were based

166   on females and sex ratio of eggs was assumed to be 50:50.

167   As the overall probability of survival (S) for a stage class is $S = P + G$, I estimated the

168   proportion of individuals surviving and transitioning using the equation:

169
170   (6) $$G = \frac{S^t}{1 + S + S^2 + S^3 \dots S^{t-1}}$$
171

172   where t = number of time steps in a stage including the transition to the next stage. Estimating

173   G_2 in this manner reduced the number of demographic estimates the model required to four (P_3,

174   S_2, G_1, and m_3), but required an estimate of the number of time steps a newly arrived ELS (4 mm)

175   needed to grow to be an adult (>11 mm). James ([1969, p. 46](#)) estimated growth rates of caged

176   individuals of 4.7 mm per month for offspring in Devils Hole, which would require 1.6-2 months

177   (7-8 weeks) for growth from ELS to Adult. Hybrid DHP, which may grow faster than

178   nonhybrids, require 30-45 days to grow from hatching to adult (O. Feuerbacher, pers. comm.). I

179   let the number of weeks (time steps) that ELS require to reach adult size range from 4 to 7.

180   Monthly survival rates in the literature are based on best professional judgment, as a DHP

181   capture-recapture study has not been conducted in Devils Hole. Adult survival (P_3) in Dzul et

182   al.'s (2013) model was assigned values of 0.70, 0.80, and 0.86, while Chernoff (1985) used 0.91.

183   I explored values ranging from 0.7 to 0.9. Monthly survival (S_2) assigned by Dzul et al. (2013) to

184   juveniles (ELS in my model) was 0.047, 0.072 and 0.097, based primarily on simulation runs of

185   their model that resulted in the stable population growth observed during their one-year study. I

186   allowed ELS monthly survival to range between 0.05 and 0.15.

187   Fecundity (m_3) has not been measured for DHP in the wild. Females are thought to lay a

188   single egg with each spawn, which can occur at any time of year but peaks from mid-February to

189   mid-May with a secondary peak from July-Sept (Hausner et al. 2013; Lyons 2005). Fecundity is

190   unrelated to size in the DHP (Minckley & Deacon 1973; Mire & Millett 1994; Shrode & Gerking

191   1977). Minckley and Deacon (1973) stated that "an average female may have about 4-5 ova or

192   10-20% of her total complement in a mature condition during a peak reproductive season." This

193   suggests that a female might be capable of laying 20-50 eggs during her lifetime (minimum 4 x 5

194   = 20; maximum: 5 x 10 = 50) and that the eggs would be distributed differentially during the

195   year. Chernoff (1985), using data in James (1969) and Minckley and Deacon (1973), estimated

196   the average number of eggs spawned per female to be 24 and the average per female per month

197   during the breeding season from 1-5. In summary, females may lay 0-4 eggs per week.

198   Assuming a 50:50 sex ratio, I set reproductive rates to range from as low as 0.05 female eggs per

199   week to as many as 2 female eggs per week. In the absence of hatching success measures, I

200   assumed all eggs survived for one week and hatched, which may overemphasize their importance

201   to population dynamics.

202   **RESULTS**

203   **Estimation of Population Growth Measures**

204   Fits of density dependent and independent models of population growth (Table 1) reflect the shift

205   in pupfish dynamics over time (Figure 1). From 1972-1995, density dependent models provided

206   the best fit for both spring and fall counts (cumulative AIC weight of 0.99-1.0), with the logistic

207   model fitting best for both seasons (Table 1). Growth was positive before 1996 ($r = 0.82$; 95% CI

208   = 0.40-1.24), with a carrying capacity of 216 (95% CI: 194-237) for spring and 444 (95% CI:

209   390-498) for fall. From 1996-2013, density independent models best fit the DHP counts, with a

210   declining population growth (r) of -0.049 (95% CI = -0.24-0.15) and -0.088 (95% CI = -0.27-

211   0.09) for spring and fall counts, respectively. Associated values for annual environmental

212   variation were $\varepsilon = 0.117$ for spring and $\varepsilon = 0.096$ for fall.

213   **Count-based Risk Analysis for the DHP in Devils Hole**

214   Time to extinction for the DHP estimated separately from spring and fall counts followed the

215   expected logarithmic distribution, resulting in most simulated populations becoming extinct

216   within 50 years and a smaller number remaining extant for extended periods (Figure 3A).

217   Median and mean time to extinction were 26 and 27 years, and 17 and 22 years, respectively, for

218   spring and fall counts (Figure 3A). The chance of extinction within a decade was less than 5%,

219   but rose rapidly to 26-33% by 20 years, ~45% by 25 years, and 81-90% by 50 years (Figure 3B).

220   **Effect of Harvest for Captive Propagation on Extinction Risk in Devils Hole**

221   Risk to the wild population of removing pupfish from Devils Hole to initiate captive breeding

222   depended on the level and timing of harvest (Figure 4). Removing individuals in the fall had less

223   impact on risk to the wild population than the same level of harvest in spring, due to the larger

224   initial size of the pupfish population in fall. For both spring and fall harvest, risk increased

225   linearly with the number of individuals removed at rates of up to 6 pupfish per year for 3 years.

226   Above this level of harvest, extinction risk accelerated; the median time to extinction fell rapidly

227   (Figure 4A) and the probability of extinction increased at a greater rate (Figure 4C,D), especially

228   for spring harvest.

229   Surprisingly, extinction risk was relatively unaffected by the apportionment of the total

230   harvest among years (Figure 4B). Whether the total number of individuals was removed over

231   one, two or three years had little effect on the probability of extinction at year 20 years.

232   **Impact of Removing Different Age Classes on DHP Population Dynamics**

233   Analysis of reproductive value (RV) and elasticity both indicated that Adults were the stage class

234   with the greatest influence on population dynamics (Table 2). RV for ELS (Stage 2) was nearly

235   identical to RV of Eggs (Stage 1) and never exceeded 1.2 in the 5000 iterations of matrices

236   evaluated. RV for Adults, however, averaged 24.2 ± 0.3 and ranged from a minimum of 4.32 to a

237   maximum of 123 with a median value of 17.7 (Figure 5A). This pattern occurred partly because

238   so few ELS survived to become adults. Adult RV was strongly negatively related to ELS growth

239   and positively related to the stage duration (Figure 5B). Elasticity results also indicated that

240   changes in adult survival (P_3) had by far the greatest influence on population growth rates (Table

241   2).

242   **Extinction Risk versus DHP Population Size in Devils Hole**

243   As expected, the median time to extinction increased and probability of extinction in 10 years

244   decreased when simulations were begun with larger initial population sizes (Figure 6). Both

245 metrics of extinction risk changed linearly with initial population sizes between 30 and 50

246 individuals, but accelerated when initial populations were less than 30 individuals.

247 **DISCUSSION**

248 The Devils Hole Pupfish has been threatened with extinction since the Endangered Species Act

249 was enacted. A count-based PVA suggests this population faces a 28-32% chance of going

250 extinct in the wild over the next 20 years (Figure 3), but could disappear within 7 years. This

251 analysis undoubtedly underestimates extinction risk, as my model does not explicitly incorporate

252 the effects of inbreeding, demographic stochasticity, and catastrophes (Mangel & Tier 1994; Ralls

253 et al. 2002), depending instead on their intrinsic influences being accounted for in the estimates

254 of population growth and its variances derived from pupfish counts. Nevertheless, the projected

255 risk of extinction is moderately high; for comparison, IUCN red list criteria based on extinction

256 risk from a PVA associates "Critically Endangered" with forecasts of 50% extinction within 10

257 years and "Endangered" with forecasts of 20% extinction within 20 years (IUCN 2014). Even

258 when the population was growing or stable from 1972-1995, the average long-term carrying

259 capacity in Devils Hole was small (216 in spring and 444 in fall), as estimated from logistic

260 population growth (Table 1). Thus, despite the lack of long-term success with captive

261 propagation and refuge populations in the past, the need to establish a secure population outside

262 Devils Hole is greater than ever if this species is to persist.

263 **Risks to the Wild Population when Building the Captive Population**

264   Removing individuals from the wild to initiate captive breeding will reduce the time to

265 extinction of pupfish in Devils Hole (Figure 4). Risks can be mitigated by harvesting wild

266 pupfish in the fall, when the population tends to be larger, rather than in the spring, when less

267 recruitment has occurred. However, risk to the wild population accelerated when more than six

268 adults were harvested annually, although this effect is smaller in the fall. In any case, it may be

269 unwise to harvest adults for captive propagation if eggs or early life-stage individuals are

270 available and can be raised in captivity. Removing eggs has the least impact on the population

271 dynamics of DHP in Devils Hole (Figure 5, Table 2). The egg stage had the lowest reproductive

272 value and the lowest elasticity, although population dynamics was nearly as insensitive to

273 incremental, instantaneous changes in the rates of early life stage individuals.

274   Results from the two population models can be connected by translating reproductive

275 value of the egg stage from the demographic matrix model to a number of adults that can be

276 removed in the count-based models. The mean RV of an adult pupfish is roughly 25 times

277 greater than that of a pupfish egg in Devils Hole (Table 2). From this perspective, removing 25

278 eggs for captive breeding is equivalent to removing a single adult in terms of its influence on

279 population dynamics (Caswell 2001).

280   The success of removing pupfish eggs or adults to build the captive population and

281 support the wild population depends upon subsequent husbandry and (re)introduction. This

282 requires success in each of a series of steps (Armstrong & Seddon 2008; Snyder et al. 1996): (1)

283 survival, growth and reproduction in captivity; (2) maintenance in captivity of genetic diversity

284 and a viable gene pool; and (3) successful preconditioning and release to the wild, either to

285 establish a new refuge in a secure location or to bolster the pupfish in Devils Hole, ideally after

286 conditions that caused the population to decline have been identified and ameliorated. While the

287 first step in the process has been successfully accomplished, as eggs taken from Devils Hole have

288 been hatched in captivity, serious obstacles remain before releases of pupfish can occur.

289 Unfortunately, the longer that pupfish remain in captivity before being returned to the wild, the

290 greater the likelihood of selection for domestication and loss of behaviors needed to survive in

291 the wild (Ford et al. 2008; Frankham 2008; Kelley et al. 2006; Snyder et al. 1996). Avoidance of

292 domestication will be a key priority in managing the captive population (Lee H. Simons, pers.

293 comm., 3 June 2014).

When to Designate the "Condor Moment" and Remove All Pupfish from Devils Hole

294

295   Designating the "California Condor moment" for the DHP – when removing the

296   remaining pupfish from Devils Hole would be the best course of action – is a management option

297   conservation biologists have rarely considered. Similar situations have been faced in a few other

298   extreme cases, such as the Hawaiian Crow (*Corvus hawaiiensis*) which was rescued from

299   extinction but cannot be reintroduced to the wild due to the persistence of the toxoplasmosis

300   responsible for its decline (Work et al. 2000), and the black-footed ferret (*Mustela nigripes)*

301   which was captured for captive breeding after a few individuals were rediscovered in the 1980's

302   (Clark 1990; Jachowski et al. 2011). I evaluated when to designate the condor moment by

303   searching for nonlinearity in the relationship between risk of extinction and population size

304   (Figure 6). Extinction risk accelerated when population size fell below 30 individuals. However,

305   the risk analysis presented here only partly addresses the issue of when to intervene by removing

306   all individuals from the wild to save the DHP. The degree that genetic diversity of the wild

307   population is represented in the captive population is a major concern that the model does not

308   address.

309   There are many similarities between the situation currently facing the DHP and the

310   decline of the California Condor in the mid-1980s (Meretsky et al. 2000; Snyder & Snyder 2000;

311   Snyder & Snyder 1989). Both species experienced a rapid population decline occurring over

312   decades as a result of poorly understood causes that were difficult to reverse. Neither species had

313   a history of successful captive breeding, although experiences with the target or a surrogate

314   species indicated the potential for success. Neither species was sufficiently represented in

315   captivity to conserve genetic diversity. Concerns were voiced for condors that capturing the

316   remaining individuals for captive breeding would reduce the need to conserve of habitats needed

317   for their reintroduction, and similar issues relating to water rights affect the pupfish. Finally, a

318 long history of management controversies and struggles to conserve each species has made them

319 conservation icons.

320   Some key differences, however, between pupfish and condor life history and management

321 could make it easier to recover the DHP. First, the "faster" life history of the DHP (early

322 maturation, reproduction and short life span) promotes rapid population growth and recovery

323 compared to the "slower" life history" of the condor (delayed age of first breeding, low level of

324 reproduction and long life span). Yet, it also dictates that immediate reproductive success in

325 captivity must occur, given the one year lifespan of the pupfish. Second, reintroduction of

326 captive-reared DHP to the wild should be much easier than it has been for the condor.

327 Reintroduction of condors has been on-going for two decades without achieving a self-supporting

328 population due to poisoning from ingestion of lead fragments in their food, excessive tameness of

329 released birds, parents feeding microtrash to nestlings, and other causes of mortality (Meretsky et

330 al. 2000; Walters et al. 2010). DHP habitat is protected and threats to the species should be easier

331 to control, at least in theory.

332   As a result of the potential for fast population growth in captivity, it is not be too late to

333 rescue the Devils Hole pupfish from extinction. Needed now to ensure success is a diagnosis of

334 the causes of decline in Devils Hole in order to recover the wild population, an evaluation of the

335 extent that the DHP harbors a significant genetic load and whether this requires a genetic

336 restoration strategy (Martin et al. 2012), an analysis of the risks (e.g., introduction of diseases or

337 parasites) and benefits (e.g., genetic and demographic rescue) of connectivity between the captive

338 population and Devils Hole, and an evaluation of locations for new refugia to introduce the

339 pupfish and better analysis of why refugia failed in the past. Of key importance will be

340 maintaining the wild pupfish population in Devils Hole, while launching the new captive

341 breeding facility.

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345   Sean Maher, J. Michael Reed, Lee Simons, Noel F. R. Snyder, Ian Watson, Kevin Wilson, and the

346   Beissinger lab.

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466   **Figure 1**. Maximum spring and fall counts of the Devils Hole pupfish.

467   **Figure 2.** Devils Hole pupfish postbreeding life cycle, projection matrix, and range of weekly

468   demographic rates used in creating matrices for analysis.

469   **Figure 3**. Risk projections for Devils Hole pupfish based on estimates from Spring and Fall

470   counts (A) time to extinction; and (B) probability of extinction.

471   **Figure 4**. Pupfish extinction risk in Devils Hole as in relation to (A) harvest season (spring or

472   fall), (B) apportionment of the total number of individuals harvested among 1, 2 or 3 years; and

473   harvest level (0-14 fish per year for 3 years)

474   **Figure 5**. A. Distribution of the Reproductive Value (RV) for Adults (stage 3) scaled relative to

475   Eggs (stage 1). B. Scatterplots of Adult RV (scaled) versus demographic rates used a input for

476   the matrix model, color coded by ELS stage duration or the number of weeks required to reach

477   adult size (4 = blue, 5 = purple, 6 = black and 7 = green).

478   **Figure 6.** Extinction risk (circles = median time to extinction; squares = probability of extinction

479   in 10 years) versus population size at the start of the simulation for spring (blue) and fall (red).

Figure 1

Maximum spring and fall counts of the Devils Hole pupfish.

Figure 1 . Maximum spring and fall counts of the Devils Hole pupfish.

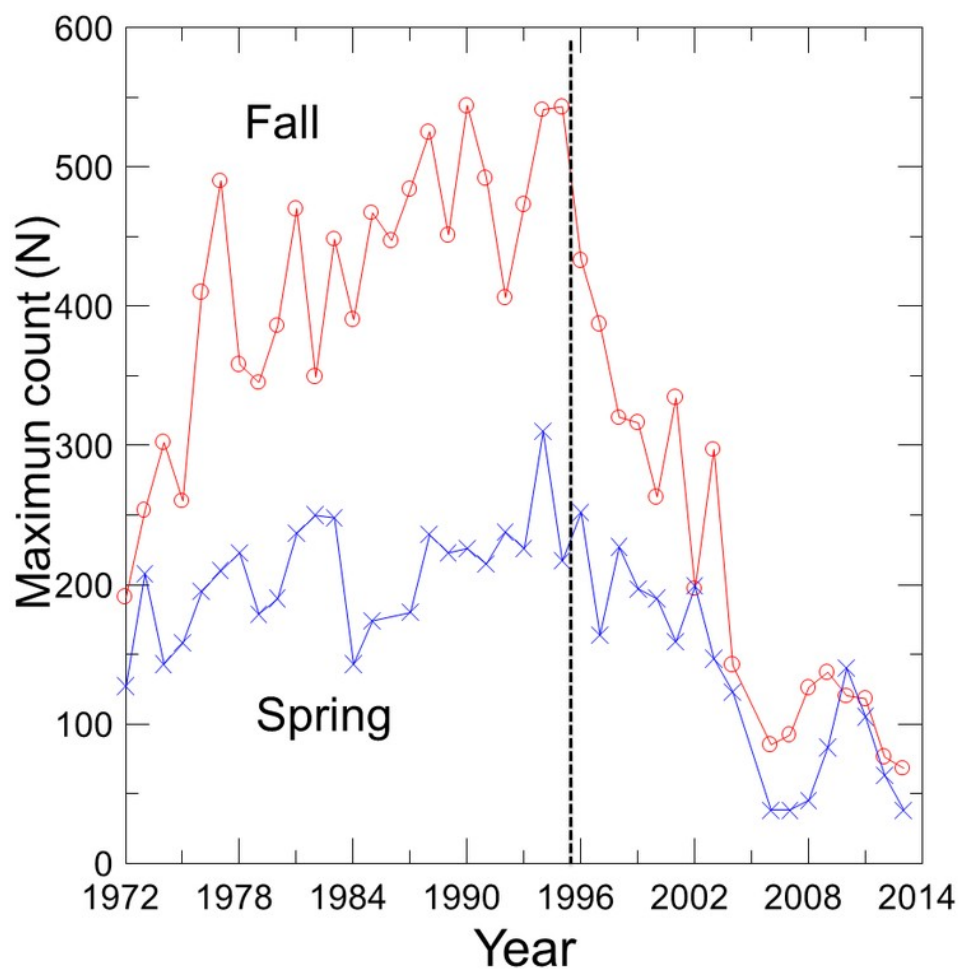



Figure 2

Devils Hole pupfish postbreeding life cycle, projection matrix, and

Figure 2. Devils Hole pupfish postbreeding life cycle, projection matrix, and range of weekly demographic rates used in creating matrices for analysis.

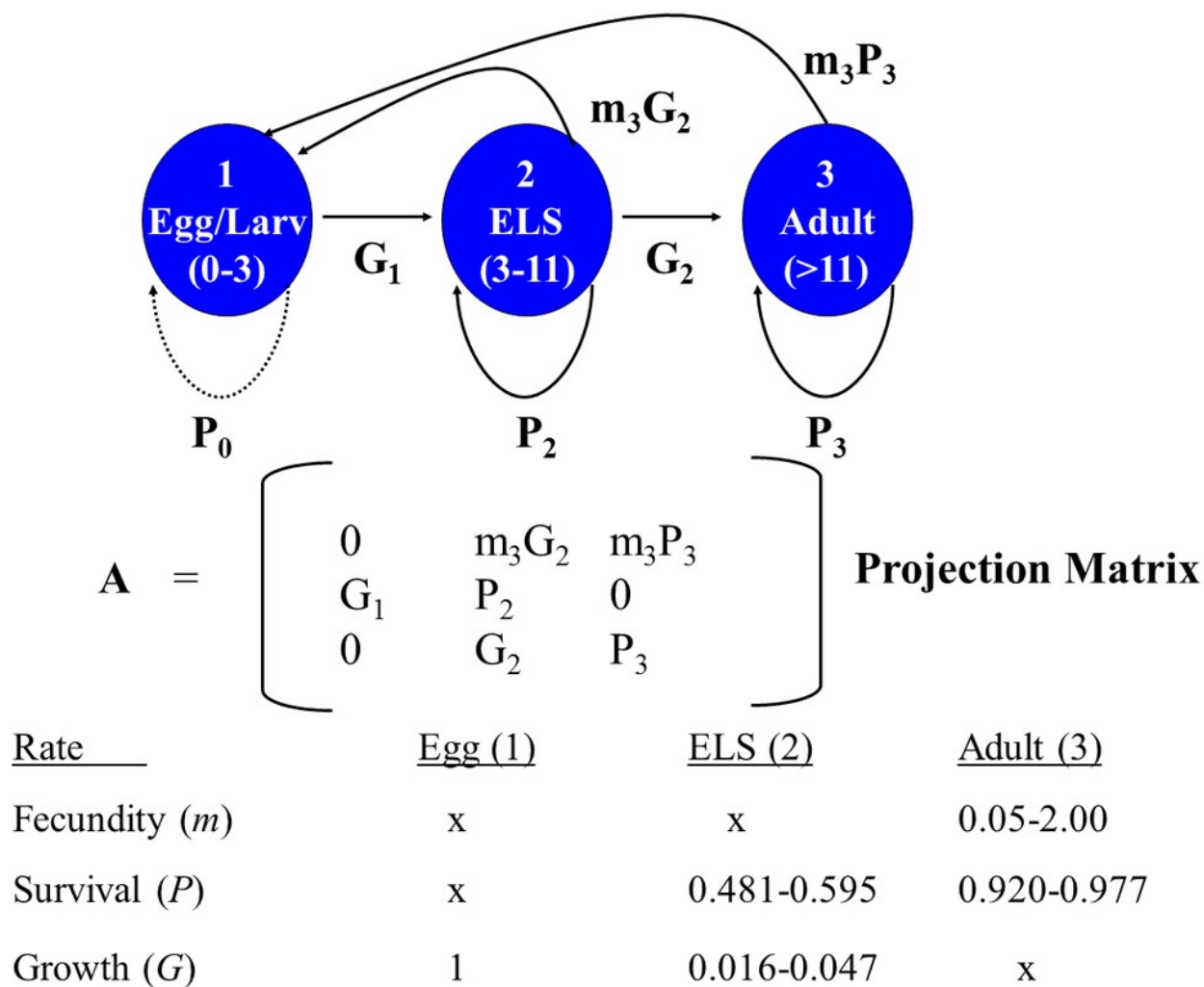



Figure 3

Risk projections for Devils Hole pupfish

Figure 3. Risk projections for Devils Hole pupfish based on estimates from Spring and Fall counts (A) time to extinction; and (B) probability of extinction.

A.

Year of extinction	Spring	Fall
Minimum	7	7
Maximum	100	100
Mean	31.6	30.2
Mode	17	22
Median	26	27
SD	18.6	14.5

B.

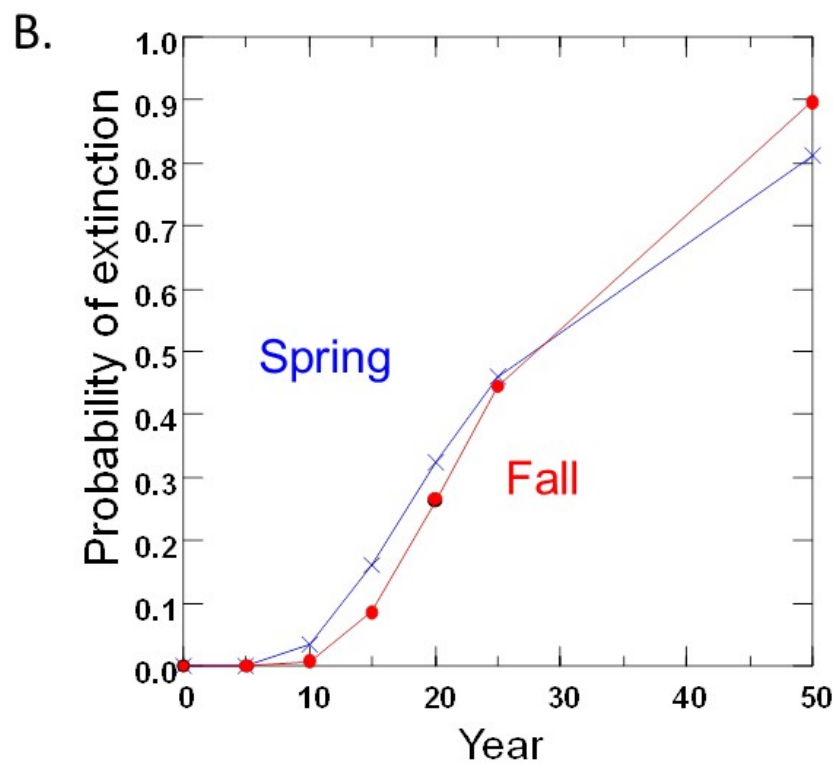
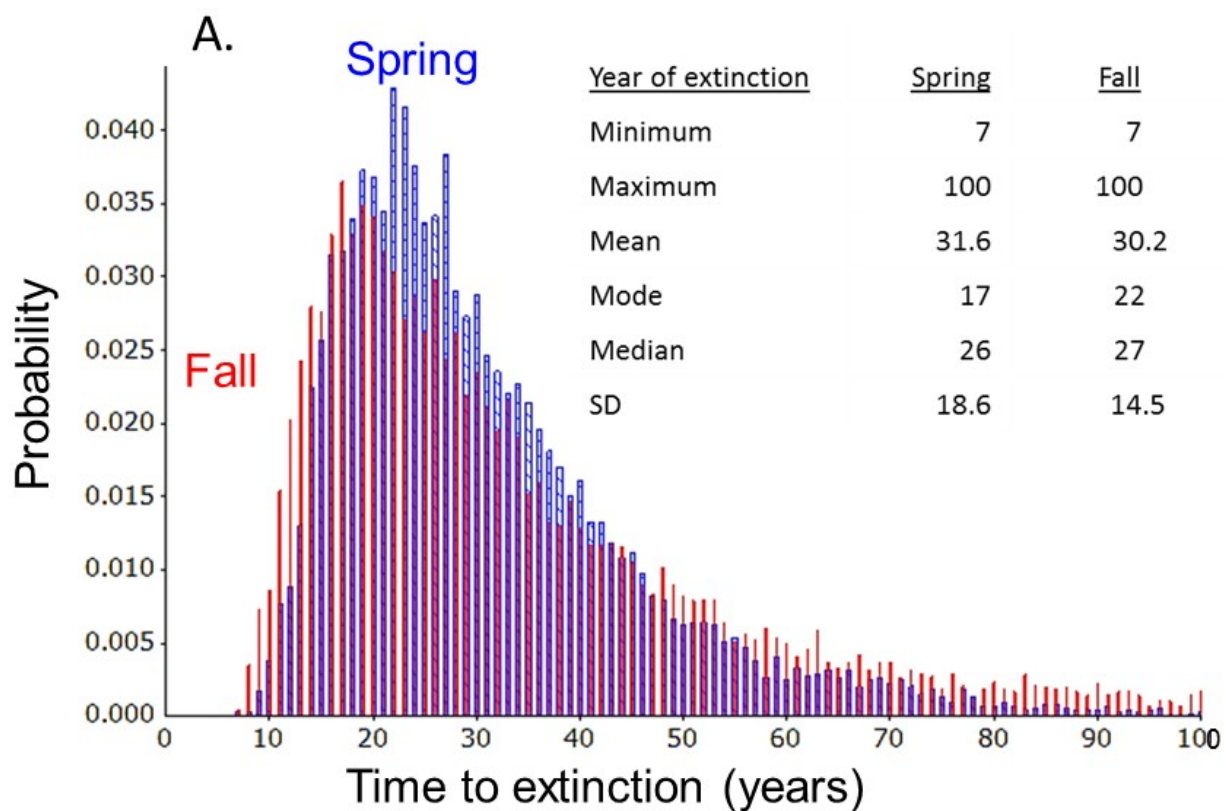



Figure 4

Pupfish extinction risk in Devils Hole in relation to:

Figure 4. Pupfish extinction risk in Devils Hole in relation to (A) harvest season (spring or fall), (B) apportionment of the total number of individuals harvested among 1, 2 or 3 years; and harvest level (0-14 fish per year for 3 years).

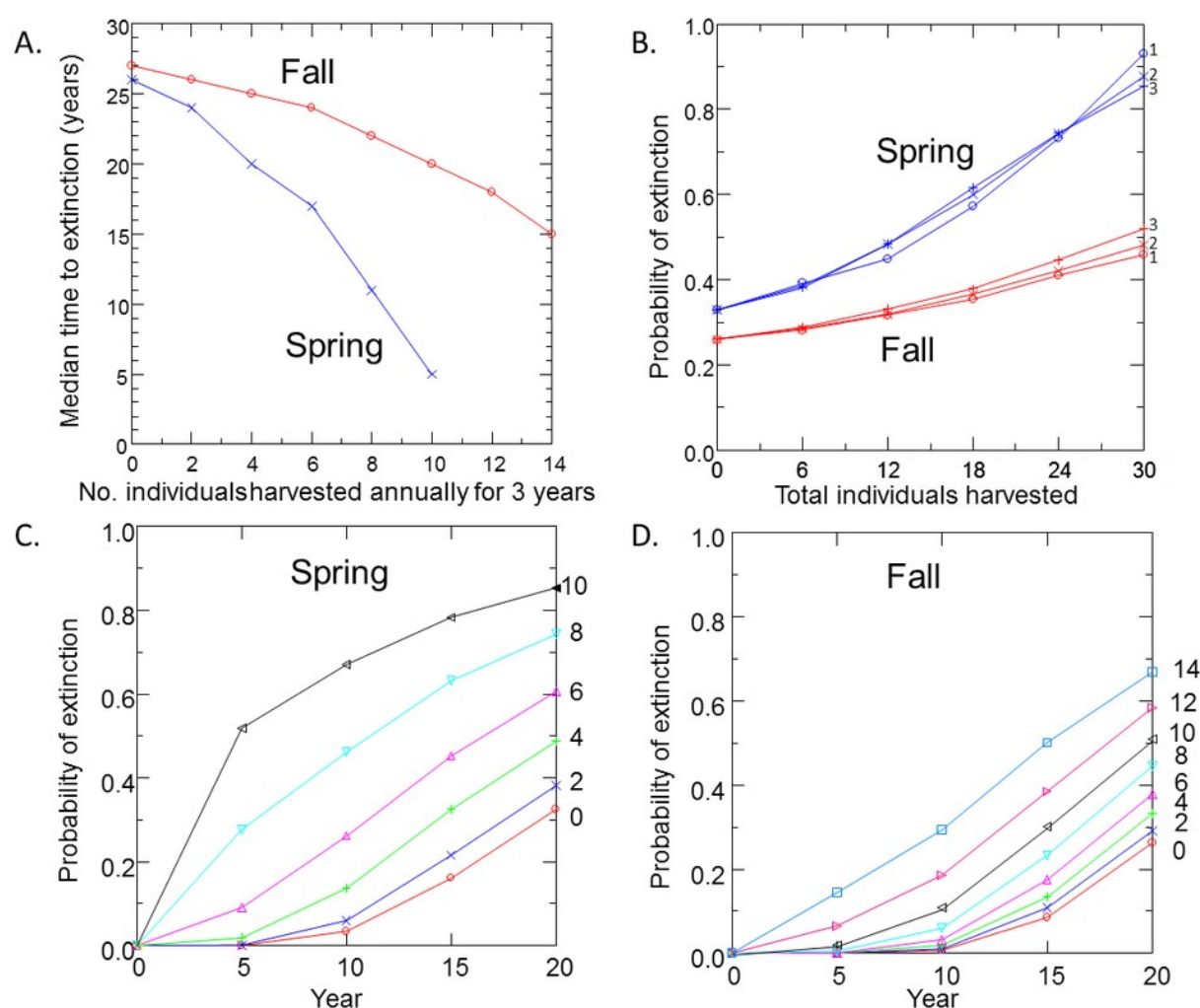



Figure 5

Reproductive Value (RV)

Figure 5. A. Distribution of the Reproductive Value (RV) for Adults (stage 3) scaled relative to Eggs (stage 1). B. Scatterplots of Adult RV (scaled) versus demographic rates used a input for the matrix model, color coded by ELS stage duration or the number of weeks required to reach adult size (4 = blue, 5 = purple, 6 = black and 7 = green).

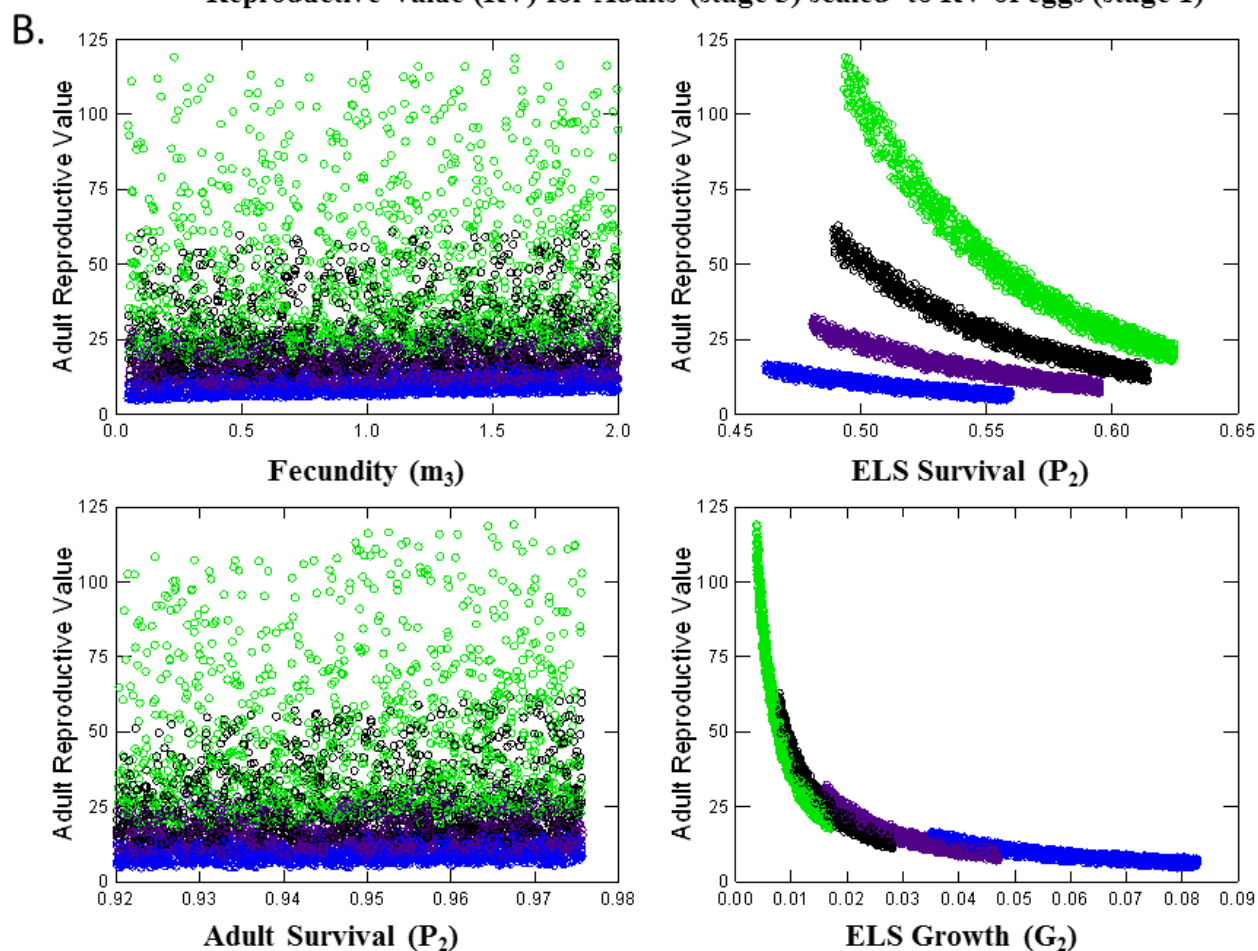
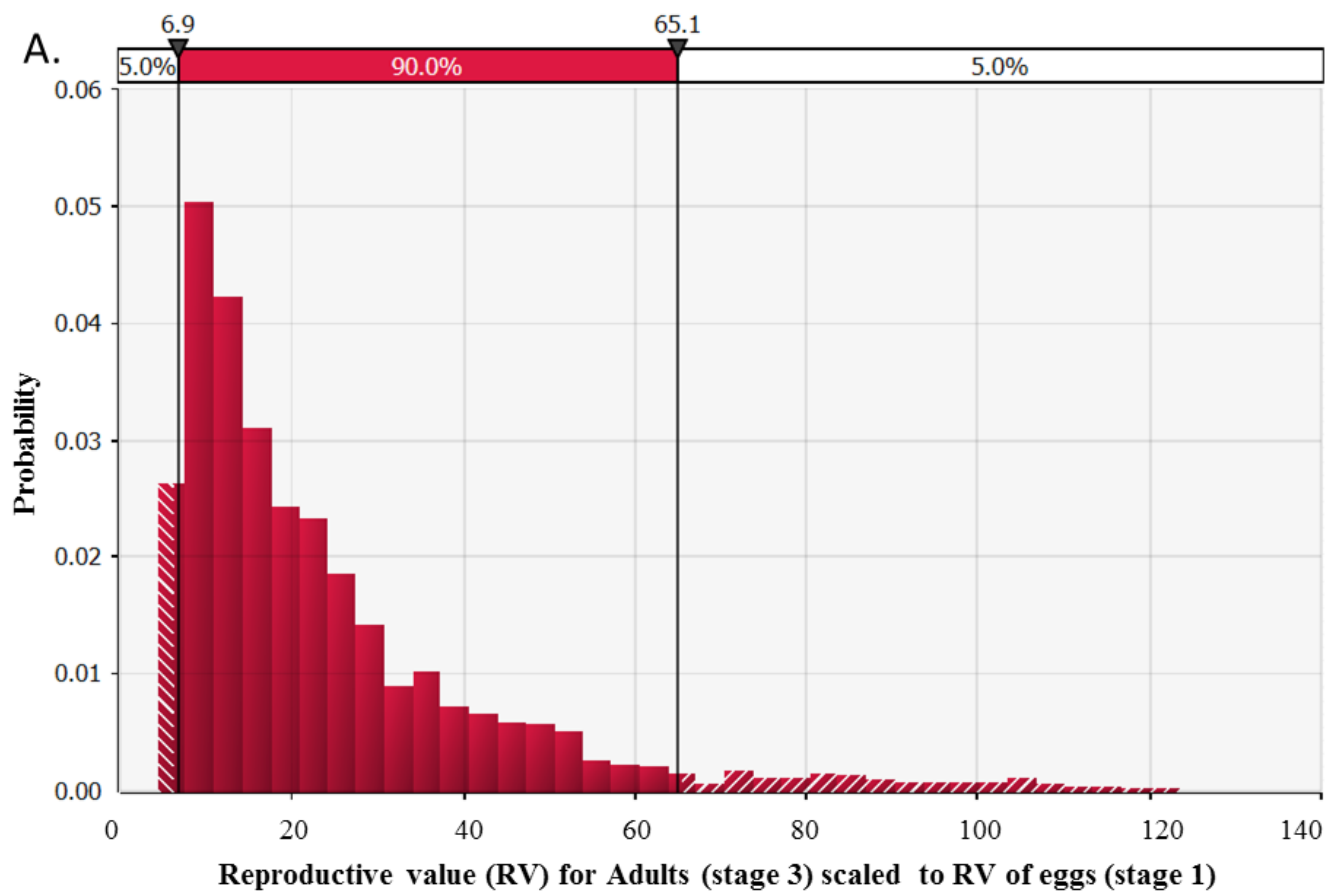
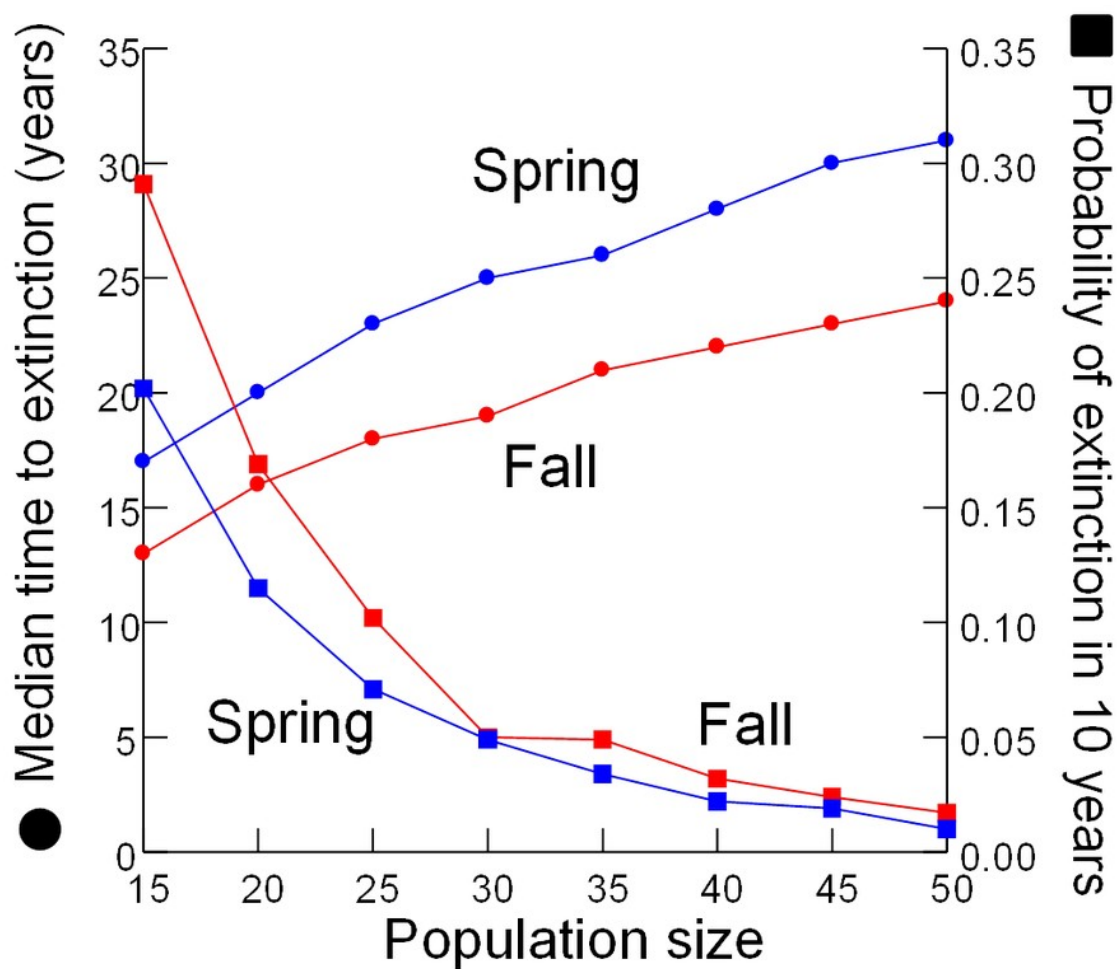



Figure 6

Extinction risk vs. population size

(circles = median time to extinction; squares = probability of extinction in 10 years) versus

population size at the start of the simulation for spring (blue) and fall (red).

Model selection and model estimates for DHP counts by time period.

Model selection and model estimates for DHP counts by time period. Bolded models are the best, based on their AICc score for the years and seasons evaluated. AICc weight (wt) indicates the strength of a model relative to other models in that set of years and season.

Table 1. Model selection and model estimates for DHP counts by time period. Bolded models are the best, based on their AICc score for the years and seasons evaluated. AICc weight (wt) indicates the strength of a model relative to other models in that set of years and season.

Years	Season	Model	ΔAICc	AICc wt	r	K	θ
1972-1995	Spring	**Logistic**	**0.0**	**0.84**	**0.820**	**215.9**	
		Theta-logistic	3.3	0.16	0.691	216.7	1.2
		Exponential	10.5	0.00	0.029		
	Fall	**Logistic**	**0.0**	**0.78**	**0.574**	**444.0**	
		Theta-logistic	2.6	0.22	0.328	452.0	2.1
		Exponential	9.5	0.01	0.034		
1996-2013	Spring	**Exponential**	**0.0**	**0.59**	**-0.049**		
		Logistic	1.0	0.36	0.201	110.0	
		Theta-logistic	4.8	0.05	0.676	95.8	0.3
	Fall	**Exponential**	**0.0**	**0.64**	**-0.088**		
		Logistic	1.4	0.32	0.136	140.0	
		Theta-logistic	5.4	0.04	0.565	134.0	0.3

Reproductive values (+ 1 SE) scaled relative to Eggs (stage 1) and elasticity from analyses of 5000 potential demographic matrices of the Devils Hole pupfish.

See Figure 2 for life cycle diagram, matrix construction and rates.

Table 2. Reproductive values ($\pm$ 1 SE) scaled relative to Eggs (stage 1) and elasticity from analyses of 5000 potential demographic matrices of the Devils Hole pupfish. See Figure 2 for life cycle diagram, matrix construction and rates.

		Elasticity		
	Reproductive value	Fecundity	Growth	Survival
Life Stage	(RV)	(*Gm* or *Pm*)	(*G*)	(*P*)
Egg (1)	1.00	0	0.049	0
ELS (2)	1.01$\pm$0.01	0.004	0.056	0.045
Adult (3)	**24.4 $\pm$ 0.29**	0.045	0	**0.800**