1   Ecosphere

2   Article

3   *PopEquus*: a predictive modeling tool to support management decisions for free-roaming horse

4   populations

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Abstract. – Feral horse (*Equus caballus*) population management is a challenging problem

around the world because populations often exhibit density-independent growth, can exert

negative ecological effects on ecosystems, and require great cost to be managed. However,

strong value-based connections between people and horses cause contention around management

decisions. To help make informed decisions, natural resource managers might benefit from more

detailed understanding of how horse management alternatives, including combinations of

removals and fertility control methods, could achieve objectives of sustainable, multiple-use

ecosystems while minimizing overall horse handling and fiscal costs. Here we describe a

modeling tool that simulates horse management alternatives and estimates tradeoffs in predicted

metrics related to population size, animal handling, and direct costs of management. The model

considers six management actions for populations (removals for adoption or long-term holding;

fertility control treatment with three vaccines, intrauterine devices, and mare sterilization), used

alone or in combination. We simulated 19 alternative management scenarios at 2-, 3-, and 4-year

management return intervals and identified efficiency frontiers among alternatives for tradeoffs

between predicted population size and six management metrics. Our analysis identified multiple

alternatives that could maintain populations within target population size ranges, but some

alternatives (e.g., removal and mare sterilization, removal and GonaCon treatment) performed

better at minimizing overall animal handling requirements and management costs. Cost savings

increased under alternatives with more effective, longer-lasting fertility control techniques over

longer management intervals compared to alternatives with less-effective, shorter-lasting fertility

control techniques. We built a user-friendly website application, *PopEquus*, that decision makers

and interested individuals can use to simulate management alternatives and evaluate tradeoffs

among management and cost metrics. Our results and website application provide quantitative

38   tradeoff tools for horse population management decisions and can help support value-based

39   management decisions for wild or feral horse populations and ecosystems at local and regional

40   scales around the world.

41

42   **Introduction**

43   An atypical problem in wildlife management occurs when the population size of a

44   species, N, is managed to be at a target population size, N_t, that is below where density-

45   dependent regulatory mechanisms limit population growth. Populations experiencing density-

46   independent growth lack significant mechanisms of population regulation (e.g., food limitation,

47   predation); high demographic vital rates (survival, reproduction) cause population dynamics with

48   strong, positive population growth (Lotka 1907) that can cause N to quickly exceed N_t through

49   time. The management target N_t can be achieved again by reducing N; however, the population

50   will require repeated, persistent management to achieve N_t on average into the future (Garrott

51   2018). If such populations are not managed persistently, populations can become large, have

52   negative ecological effects on ecosystems (Côté et al. 2004), become an increasingly unwieldy

53   and costly management problem (Garrott and Oli 2013), and potentially exhaust limited budgets

54   for natural resource management (Runge 2020). Regardless of management frequency, such

55   populations will always grow to exceed management targets unless population vital rates are

56   adjusted through management, such as through wildlife fertility control (Kirkpatrick and Turner

57   1985).

58   Feral horse (*Equus caballus*) population management exemplifies the challenge of

59   managing a species with strong positive population growth (National Research Council 2013).

60   Originally native to the Eurasian steppe (Olsen 2016), *Equus caballus* is a domesticated species

3

61   that have been introduced by humans to non-native areas on all global continents except

62   Antarctica (Schoenecker et al. 2021). Released horses have created feral populations (The

63   Wildlife Society 2020, Boyce et al. 2021) that grow rapidly due to high reproductive rates

64   (Ransom et al. 2016) because of a history of domestication (Price 1984); reproductive rates

65   remain high even when population densities are relatively high (Grange et al. 2009). Horse

66   populations may also outcompete native species for limited resources (Gooch et al. 2017, Hall et

67   al. 2018) and exert strong, negative ecological effects in arid ecosystems (Beever et al. 2018,

68   Davies and Boyd 2019, Eldridge et al. 2020, Rubin et al. 2021), particularly when horse

69   populations become excessively large (Coates et al. 2021). Given the size and plurality of

70   negative effects caused by horses, a typical goal in the field of conservation biology could be to

71   reduce horse populations through management so that negative ecological effects would be

72   reduced (Simberloff et al. 2005). Such reductions are common for horse populations in the

73   United States, for example, but may facilitate population growth by reducing populations below

74   where they are affected by food limitation and density dependence (National Research Council

75   2013). The management of horses is further complicated by the fact that horses are charismatic

76   and often beloved by human populations (Chamberlin 2006, Nimmo and Miller 2007, Scasta

77   2019) and are viewed as icons of national identity (Dawson and Hone 2012) and pioneer spirit

78   (U.S. Congress 1971), and some countries (e.g., United States) have legal protection for certain

79   designated free-roaming horse populations (e.g., Public Law 95-514). For these reasons, humans

80   populations often seek to maintain the persistence of horse populations at densities beneath

81   where they might experience density-dependent effects, so that horse populations have abundant

82   resources to permit horse health, ecosystems are healthy, and landscapes can accommodate other

83   multiple uses (Garrott 2018). However, this goal is challenged by high risks of horse populations

84   growing fast (National Research Council 2013), exerting negative ecological effects, and

85   requiring great cost to be managed (Garrott and Oli 2013).

86   Horse population management is often contentious (Symanski 1996, Nimmo and Miller

87   2007, de Steiguer 2011, Wagman and McCurdy 2011). Central to this contention lies a multiple-

88   objective decision problem (Hemming et al. 2022) with competing objectives of facilitating free-

89   roaming horse populations due to strong emotional connections that humans have toward horses

90   (Nimmo et al. 2007, Scasta et al. 2018) while also managing horse populations to promote

91   ecosystem health and allow other multiple uses on the landscape. Decision makers might benefit

92   from understanding tradeoffs between competing objectives that emerge among different

93   alternatives (Keeney and Raiffa 1993, Converse 2020, Hemming et al. 2022). There are many

94   alternative management actions that might be used to control horse populations (National

95   Research Council 2013), including gathering and removing animals (Bartholow 2007),

96   immunocontraceptive vaccines (e.g., GonaCon-Equine, ZonaStat-H; Kirkpatrick et al. 1992,

97   Turner et al. 2007, Baker et al. 2018), intrauterine devices (Gradil et al. 2021, Holyoak et al.

98   2021), sterilization (e.g., colpotomy; Prado and Schumacher 2017), and additional compound

99   alternatives involving two or more management actions (Danvir 2018, Garrott 2018).

100   Management alternatives can also be limited by legal constraints. In the United States, for

101   example, some feral horses whose ancestors lived in 1971 on lands in ten western states

102   administered by the Bureau of Land Management and the U.S. Forest Service are protected by

103   federal law as 'wild horses' (U.S. Congress 1971), and the US Congress forbids any federal

104   agency from using or planning for the use of lethal population control. Legal and culturally

105   acceptable management actions vary in their effectiveness to control horse population size and

106   minimize fiscal cost. With so many management actions available, varying population and cost

107   efficacy of management actions, and myriad ways to structure management, wildlife managers

108   seeking to make informed decisions could benefit from an analytical tool that makes predictions

109   and reveals tradeoffs among competing objectives that arise across different alternatives.

110   Matrix population models are useful tools that can describe how age- or stage-structured

111   populations function (Caswell 2001), predict how populations might change in response to

112   external influences (Morris and Doak 2002), and therefore provide clarity about the

113   consequences of management alternatives and tradeoffs among them. Management of wild

114   horses by the BLM has been partly informed by *WinEquus* (Jenkins 2002), a software program

115   that used an age-based population model for horses and estimates of initial population structure,

116   survival rates, and reproductive rates to stochastically project populations and simulate how two

117   management actions (removals and fertility reduction treatment) influence population size.

118   *WinEquus* was useful because it allowed users to explore how removals and fertility reduction

119   treatments of varying effectiveness could influence horse population size, and it was mainly used

120   to project whether or not proposed levels of ZonaStat-H treatment would cause a population to

121   decline precipitously (Bureau of Land Management 2010). However, fertility control methods

122   with different applications than vaccines have become available in recent years, and *WinEquus*

123   was limited in its ability to simulate more than one management action at a time and did not

124   account for financial cost. Thus, we developed a predictive model for horse populations that

125   considers multiple management alternatives, accounts for important metrics (e.g., population

126   size, cost), and can accommodate site-specific variation in demography or management

127   limitations (Garrott 1991).

128   Here we present a predictive modeling tool for horse population management that

129   estimates the consequences of six management actions (removals, three fertility reduction

130   vaccines [PZP-22, ZonaStat-H, and GonaCon-Equine], intrauterine devices, and mare

131   sterilization) – used alone or paired with another management action – on horse population size,

132   management cost, and metrics related to management. We built functions that simulated 19

133   alternatives for horse population management: six scenarios of single management alternatives

134   (i.e., elemental alternatives), nine compound alternatives with two management actions (e.g.,

135   removals + fertility treatment), three compound alternatives with three management actions, and

136   a null model scenario of no management. We used our simulation code to build an interactive

137   website application, *PopEquus*, which hosts the predictive model and allows managers, decision

138   makers, and other interested individuals to simulate management alternatives, compare outcomes

139   among alternatives, and understand tradeoffs in horse population management.

140

141   **Materials and Methods**

142   *Study system*

143   The Bureau of Land Management (BLM]) and U.S. Forest Service (USFS) are tasked

144   with managing federal horse herds so that population size does not fall beneath or exceed pre-

145   determined target population size ranges, which are called Appropriate Management Levels

146   (AML; National Research Council 2013). Target population size ranges are designated by land

147   managers to promote sustainable, multiple-use federal lands with the goal of maintaining a

148   "thriving natural ecological balance" among horses, livestock, wildlife, and vegetation that

149   protects rangelands from deterioration and yields sufficient food and water to permit high

150   welfare of horses (U.S. Congress 1971, National Research Council 2013).

151   Federal management agencies in the United States monitor horse population size using

152   aerial survey methods on a regular basis through time (Lubow and Ransom 2009, Lubow and

153 Ransom 2016, Griffin et al. 2020). When horse populations exceed target population size ranges

154 on federal lands, management agencies have sought to reduce population size by removing

155 horses from the landscape (National Research Council 2013). Removals involve rounding up

156 horses during a 'gather' and removing individuals to decrease population size to be within AML.

157 Removed horses are taken to a holding facility and entered into a federal adoption program,

158 where private citizens can adopt horses for personal ownership (Adopt-A-Horse Program; Smith

159 2010). The challenge is that gathers and animal care in captivity are expensive, demand for horse

160 adoption has declined in recent decades, and many horses are never adopted, which leads to a

161 growing captive population at holding facilities and increased costs associated with removals as

162 a management action (ca. $50 million per year; Garrott and Oli 2013, Garrott 2018). Perhaps

163 most importantly, removals alone fail to change any underlying demographic process to prevent

164 the population from quickly returning to the over-populated state. While removals can reduce

165 population sizes to be within target population size ranges in the short-term, populations quickly

166 grow to exceed management targets without concomitant reductions in reproduction or survival,

167 while incurring significant costs in holding and requiring necessary future management.

168   For these reasons, managers have sought alternatives that reduce population vital rates

169 (Bechert et al. 2022). A demographic sensitivity analysis found that horse population dynamics

170 are more sensitive to adult survival than juvenile survival or reproduction (Garrott 1991), but

171 euthanizing healthy wild horses is illegal. Therefore, management efforts have focused on

172 reducing reproductive rates of populations (hereafter, fertility treatment). In particular,

173 immunocontraceptive vaccines (e.g., PZP vaccines; hereafter, vaccines) have been developed

174 that, when applied to female horses, reduce reproductive rates in subsequent years (Kane 2018).

175 Vaccines are viewed as a favorable management alternative by some because vaccine application

176   does not necessarily require gathering horses (e.g., remote delivery of vaccine by darting can be

177   used, although darting can be logistically difficult and is often viewed as practically impossible)

178   or moving individuals to holding facilities, which are both expensive procedures. However,

179   vaccines are <100% effective at reducing pregnancy, and currently available vaccines require re-

180   treatment to remain effective over time. Therefore, vaccine treatment alone cannot reduce

181   reproductive rates sufficiently to allow natural mortality to exceed recruitment and decrease

182   population size to be within target population size ranges within a desirable time period. More

183   recently, intrauterine devices (IUDs) have been developed as another fertility control method.

184   IUDs can be implanted in non-pregnant females and are 100% effective at preventing pregnancy

185   so long as they remain in the uterus (Gradil et al. 2021, Holyoak et al. 2021). However, most

186   types of IUDs tested over longer time periods (>1 year) are not retained perfectly, and

187   preliminary studies suggest that annual retention rates are between 80–90% (Daels and Hughes

188   1995, Gradil et al. 2019, Holyoak et al. 2021). Intrauterine device use is further limited because

189   treatment can only be given to non-pregnant females, which often comprise a small subset of the

190   female horse population at any time.

191   Perhaps the most effective form of fertility treatment would be sterilization of mares

192   (National Research Council 2013) because mare sterilization results in long-lasting 100%

193   effective fertility control of treated individuals with no retreatment required. Multiple surgical

194   methods have been used successfully for domestic horses (Bigolin et al. 2009, Rodgerson and

195   Loesch 2011, Hendrickson 2012, Prado and Schumacher 2017, Edwards et al. 2021). Mare

196   sterilization applied to free-roaming horse populations might be functionally similar to 'trap-

197   neuter-return' programs used to manage feral cat and dog populations throughout much of the

198   United States (Levy et al. 2003, Longcore et al. 2009).

199   Surgical castration of males (i.e., gelding or vasectomy; Scully et al. 2015, King et al.

200   2022) is commonly used for domestic horses and is another potential population management

201   tool to decrease reproduction by reducing fertilization rates. One study reported slight decreases

202   in female fertility in a feral horse herd that included some sterile males (Collins and Kasbohm

203   2017). Another study observed decreased reproductive rates of females for one year after

204   castrating 42% of males in a horse population, but reproduction returned to pre-treatment levels

205   in subsequent years (King et al. 2022). Because females can experience 6–10 reproductive cycles

206   per year and encounter multiple males during that time, researchers have concluded that male

207   sterilization is unlikely to be an effective tool to manage horse reproduction (unless an extremely

208   large portion [>90%] of a population is gelded; Garrott and Siniff 1992, King et al. 2022). For

209   this reason, we did not include gelding as a management alternative in our analysis.

210

211   *Management actions*

212   We worked with natural resource managers to identify management actions available and

213   of interest for horse management in the present and/or near future and to co-produce a model to

214   simulate those management actions. We identified six management actions of interest: removals,

215   three fertility reduction vaccines (GonaCon-Equine, PZP-22, and ZonaStat-H), intrauterine

216   devices, and mare sterilization.

217   **Removals –** Removals are a commonly used management strategy to directly decrease

218   the number of individuals in a population to AML (National Research Council 2013). To do a

219   removal, a 'gather' collects horses from a population (either by means of bait trapping or using

220   helicopters to herd individuals into corral traps; Scasta 2020), and individuals are removed from

221   the landscape to meet a target population size. The sex ratio or age structure of individuals being

222　　removed can be manipulated strategically to restructure the population in ways to help might

223　　minimize future population growth (e.g., removing more females than males, when possible;

224　　Bartholow 2007, National Research Council 2013). Removed horses are taken to a short-term

225　　holding facility, where they are vaccinated against communicable diseases, dewormed, freeze-

226　　branded, microchipped, and are held until they are offered to qualified citizens for adoption.

227　　While at the holding facility, females and males are kept in separate pens to prevent conflict

228　　among horses and new pregnancies. Un-adopted horses are eventually taken to off-range

229　　pastures where they live out their lives.

230　　　　**Fertility control vaccines** – Three forms of fertility control vaccine have recently been

231　　used to reduce fertility of free-roaming horse populations in the USA. GonaCon-Equine

232　　(hereafter, GonaCon) is a vaccine that reduces horse fertility by manipulating a critical hormone

233　　related to reproduction, the gonadotropin-releasing hormone (Kane 2018). GonaCon can be

234　　injected by hand or by dart and has perhaps the greatest potential for utility among the fertility-

235　　reducing vaccines, as it can be upwards of 90% effective at reducing fertility for several years

236　　after a booster dose is given (Baker et al. 2018). Porcine zona pellucida (PZP) vaccines are

237　　vaccines with a glycoprotein antigen from domestic pig (*Sus scrofa*) ovaries that, when given to

238　　a female horse, stimulates the immune system to produce antibodies to zona pellucida proteins

239　　on eggs, thereby blocking fertilization and decreasing ovary function over time (Kirkpatrick et

240　　al. 1992, Kane 2018). The most commonly used form of PZP is ZonaStat-H (hereafter,

241　　ZonaStat), a liquid vaccine that can be injected by hand or by dart. ZonaStat is 80–90% effective

242　　at preventing pregnancy for one year when a booster shot is given 30 days after initial treatment

243　　and 1–2 months before the breeding season (National Research Council 2013). However,

244　　ZonaStat utility is limited because it must be administered annually to maintain effectiveness,

245   although mares treated five or more times may have longer-lasting effects (Nuñez et al. 2017).

246   An alternative form of PZP is PZP-22, a pellet formulation of PZP with an extended release

247   period and longer effectiveness (National Research Council 2013). Field trials have found

248   varying effectiveness of PZP-22 (Turner et al. 2007, Kane 2018); however, recent results

249   indicate that PZP-22 applied with booster treatments may cause a 15–40% reproductive rate of

250   treated horses over a three-year period, relative to ca. 70% reproduction among untreated mares

251   (Rutberg et al. 2017). It is important to note that fertility control treatments may lead to increased

252   survival and longevity of treated females (Kirkpatrick and Turner 2007), likely because vaccine

253   treatment eliminated energetic demands and mortality risks associated with pregnancy, birth, and

254   lactation.

255   **Intrauterine devices** – Safe and flexible intrauterine devices were first designed for and

256   implemented in horses in the 1990s; an O-ring design made with silastic elastomer polymer was

257   found to be effective at preventing pregnancy (Daels and Hughes 1995), but further investigation

258   found O-ring devices to often be expelled shortly after insertion (Holyoak et al. 2021). Recent

259   development of a Y-shaped silastic intrauterine device has fairly high retention within females

260   (ca. 86.6% retention per year) and is 100% effective at preventing pregnancy when intact

261   (Holyoak et al. 2021). Mares must not be pregnant to receive an IUD.

262   **Mare sterilization** – Mare sterilization would be the most-effective form of fertility

263   treatment because sterilization requires only a single treatment and is 100% effective at

264   preventing future pregnancy (National Research Council 2013). Even though the BLM has not

265   yet used mare sterilization as a management action for wild horses, we included mare

266   sterilization among our set of alternative management actions and scenarios because some form

267   of mare sterilization could possibly be used in the future.

268

269   *Model structure*

270   We simulated how horse population size is influenced by different management actions

271   using matrix population models (Caswell 2001). We built matrices of demographic vital rates

272   (survival, reproduction) and age-structured abundance in populations and used matrix

273   multiplication to project populations forward in time. We built an age-based, two-sex, post-

274   breeding census Leslie population model (Leslie 1945) for horse populations, wherein we

275   conceptualized horse demography as having 21 age classes for each sex: one age class for each

276   year of age from 0 (foals) to 19 years old, and a final stage with all individuals ≥20 years old

277   (Figure 1). During a given time-step, individuals in each age class had a probability of surviving

278   and transitioning to the next age class, until they reached age 20; all individuals ≥20 years old

279   were modeled as a single stage class with a probability of surviving and staying within that stage.

280   Females of age ≥2 years old had a probability of reproducing (foaling) and recruiting individuals

281   into the foal age class. Individuals that did not survive and transition during a time-step were

282   assumed to have died.

283   Because demographic rates of populations vary in space and time, we used studies of

284   wild horse populations in western North American ecosystems to build ten matrices describing

285   different plausible demographic conditions for horses. Three studies came from the Pryor

286   Mountains in Montana during different time periods (Garrott and Taylor 1990, Jenkins 2002,

287   Roelle et al. 2010), and two studies were from Nevada (Jenkins 2002); these multi-year studies

288   estimated demographic rates using mark-resight data. We built demographic matrices from these

289   studies that yielded mean population rates of change (λ) ranging from 1.066–1.178 and one

290   matrix with $\lambda < 1$ that described high-mortality demographic conditions that can occur during

291   uncommon extreme weather events (Table 1). However, a global review of horse population

292   dynamics suggested that λ can vary widely (range: 0.84–1.39; Ransom et al. 2016). Given the

293   great range of potential λ values, we built four additional matrices that approximated conditions

294   toward the upper range of potential λ values, which could yield λ of 1.14–1.32. In total, we built

295   ten demographic matrices that represented variable demographic conditions experienced by

296   horse populations in space and time.

297   To understand the consequences of management alternatives on horse population size, we

298   modeled a population of 500 individuals (including foals in a post-breeding census) that occurred

299   on a hypothetical management area of federally-owned land with a target population size range

300   of 200–300 horses. We chose to model an overpopulated context, because most horse

301   populations on BLM-managed lands currently exceed AML (e.g., 79% exceeded maximum sizes

302   in 2022; Bureau of Land Management 2020). To specify initial population structure for

303   simulations, we estimated the average percentage of a population in each age class using

304   population structure data from a study at Garfield Flat, Nevada, where no recent gathers or

305   management had occurred (data from Jenkins 2002). We multiplied the population estimate by

306   the population structure vector to specify initial population structure vector for projections.

307   While horse populations have occasionally been observed to decline in size between

308   consecutive years, no study has documented negative population rate of change of horses

309   consistent with declines over long-term, multi-year periods (i.e., mean λ < 1.00). For this reason,

310   our model assumed a baseline of increasing λ over multi-year time scales with a minimum and

311   maximum mean λ of 1.00 and 1.32. For each 0.01 value within and including λ = 1.00–1.32, we

312   created a vector of probability values associated with the ten demographic matrices, where each

313   matrix was assigned a weighted probability value and the sum of the product of each matrices' λ

314   value and its weighted probability generated a mean λ for each decimal value. For any given

315   user-specified λ between 1.00–1.32, we used the ten matrices and their weighted probability

316   values to project the population for 10 years using two functions: 1) a deterministic function

317   without random variation, and 2) a stochastic projection function that simulated random temporal

318   (i.e., environmental) and demographic variation. During deterministic projections, we projected

319   the population using matrix multiplication of each of the ten demographic matrices by the

320   population structure vector, and then used the probability weights for each matrix to calculate a

321   single, weighted-average outcome from among the ten projections. During stochastic projections,

322   we performed 100 replicate projections for each scenario. In each year within each replicate, we

323   randomly drew one of the ten demographic matrices using the matrix probability weights, which

324   prescribed the likelihood of a population experiencing each of the demographic matrices in a

325   given year (Table 1). We then projected the population one time-step in the future (year) by

326   multiplying the stochastically-drawn demographic matrix by the population structure vector

327   using the function 'multiresultm()' from the package 'popbio' (Stubben and Milligan 2007),

328   which uses a random binomial function to stochastically generate the number of births during

329   each time step. When simulating different scenarios, we held temporal stochasticity constant by

330   drawing the same order of demographic matrices among years within and among replicates

331   during stochastic projections. During stochastic projections, we assumed a population persistence

332   threshold where if the population decreased beneath 30 individuals the population was at

333   elevated risk of becoming locally extirpated due to demographic, environmental, or genetic

334   stochasticity; we measured the percentage of replicates that resulted in populations above the

335   persistence threshold.

336

337   *Management alternatives*

338   Based on the six management actions described above, we constructed 19 alternative

339   scenarios for horse management: six alternatives each with a single management action, nine

340   compound alternatives involving two management actions, three compound alternatives

341   involving three management actions, and a null-model scenario of no management for

342   comparative purposes (Table 2). We built a predictive function for each alternative that simulates

343   how the management action(s) influences horse population size and metrics related to animal

344   handling and cost objectives. We then performed a scenario analysis (described below) to

345   estimate the consequences of alternatives where we simulated each alternative under comparable

346   conditions.

347   **Simulation conditions** – We simulated each management scenario under similar

348   population and management conditions and measured the consequences of management

349   alternatives on important value-based metrics related to population management (described

350   below). We assumed a population size of 500 individuals from a post-breeding census (including

351   foals), a mean λ of 1.18 (Ransom et al. 2016), and a manager-specified target population size

352   range of 200–300 individuals. We simulated management scenarios by projecting the population

353   10 years into the future under scenarios involving gathers and management every three years

354   starting in the first year (i.e., years 1, 4, 7, and 10). During scenarios with two or three

355   management actions, management actions were performed on the same years if population

356   conditions were suitable for each action. We assumed that gathers would result in the collection

357   of 75% of the true total population size for management. We estimated per-horse cost of gathers

358   as varying depending on the number of horses gathered using cost approximations from the

359   Bureau of Land Management (Paul Griffin, personal communication), with larger gathers having

360   lower costs per horse (e.g., 1000 horses costs $668 per horse) than smaller gathers (e.g., 100

361   horses costs $1074 per horse).

362   **Removals** – We simulated removals where, during designated removal years when the

363   population size exceeded the maximum of the target population size range (300 individuals),

364   managers collect a large segment of a population during a gather and individuals are selectively

365   removed to reduce the population size to a target population size of the minimum of the target

366   population size range (200 individuals). We assumed that: 1) managers would selectively remove

367   more females than males from among the gathered horses, when possible, so that individuals

368   released back to the population have a male-biased structure (6 males : 4 females; Bartholow

369   2007, National Research Council 2013); 2) the maximum number of individuals that can be

370   removed from a population and taken to a holding facility in a single year is 1500; 3) removed

371   individuals are taken to a short-term holding facility where they become a captive population that

372   is available for public adoption for one year; and 4) any horses that are not adopted after one year

373   in captivity are taken to a long-term holding facility to live out their lives. We projected the

374   population in holding for the rest of the 10-year projection interval and an additional 25 years,

375   which approximates the maximum longevity of horses in captivity. While female and male

376   horses are kept separate in holding facilities to prevent reproduction, some females are pregnant

377   upon being removed and give birth during their first year in captivity. To project horse

378   populations in holding facilities, we assumed that: 1) female reproduction during the first year in

379   captivity is a 25% reduction of the birth rate experienced by females in the wild population the

380   year the horses were removed; 2) 69% of removed horses and any offspring produced during the

381   year in short-term holding are removed from the captive population as a result of adoption, sale

382   with limitation, or transfer to government agencies (this is an average of 2019–2021;

17

383   https://www.blm.gov/programs/wild-horse-and-burro/about-the-program/program-data); 3)

384   females do not reproduce in long-term holding facilities; and 4) all captive individuals

385   experience an annual survival rate of 0.95 (Government Accountability Office 2008). Costs

386   associated with removals as a management strategy include short-term holding of animals in

387   captivity ($7.60 per horse daily; Paul Griffin, personal communication), long-term holding of

388   animals in captivity ($2.02 per horse daily; Paul Griffin, personal communication), and an

389   average net administration cost to adopt out a horse ($1700; Paul Griffin, personal

390   communication).

391   **Fertility control vaccines** – We modeled fertility control vaccination as a management

392   action where, during vaccine treatment years, gathers are performed to collect horses and

393   administer vaccine to all females ≥1 year old that are to be released back onto the range.

394   Vaccine-treated individuals were then subject to different reproductive and survival rates,

395   depending on how many vaccine doses they received and the number of years since the last dose.

396   Because fertility control using vaccine increases survival and longevity of females (Kirkpatrick

397   and Turner 2007), we increased survival rates of all fertility-control treated females by

398   multiplying the age-specific survival rate of untreated females by 1.02 to accommodate for likely

399   increases in survival due to reduced future pregnancy (*sensu* Kirkpatrick and Turner 2007).

400   We modeled effects of GonaCon treatment on reproductive rates using results from

401   published field trials in Theodore Roosevelt National Park, North Dakota, USA (Baker et al.

402   2018). GonaCon has relatively weak effects when individuals are only given one dose (e.g., ca.

403   37% and 29% reductions in fertility after one and two years, respectively), but substantially

404   stronger effects when individuals are treated with a booster shot (i.e., a second shot; 100%, 85%,

405   and 50% reductions in fertility during 1, 2–4, and 5–7 years after booster shot; Baker et al. 2018,

406   Paul Griffin, personal communication). We assumed all GonaCon-treated individuals would be

407   held for 30 days to receive a booster. Costs associated with GonaCon treatment included:

408   gathering horses, giving primer and booster shots ($50 each) to eligible females, and holding

409   treated females for a booster ($7.60 per day [Paul Griffin, personal communication] for 30 days).

410   We modeled efficacy of PZP-22 using results from Rutberg et al. (2017). Because PZP-

411   22 batches can vary in effectiveness, we modeled a stochastic effect where batch effectiveness

412   was a randomly drawn value between the minimum and maximum effectiveness of receiving one

413   dose, two doses, or three doses observed through time in field studies. We assumed minimum

414   and maximum percent reductions in fertility from PZP-22 treatments were 33–72% one-year

415   after a primer dose and 20–40% two-years after receiving a primer; 68–85% one-, 70–75% two-,

416   and 60–72% three-years after receiving a booster; and 78–95% one-, 80–85% two-, and 70–82%

417   three-years after receiving an additional booster. Effectiveness rates for the hypothetical third

418   dose of PZP are suppositions based on expert elicitation (Paul Griffin, Bureau of Land

419   Management). A single treatment of PZP-22 includes two injections: intramuscular injection of

420   three polymer pellets that are intended to degrade over different time intervals, and also injection

421   of one dose of ZonaStat-H (Kane 2018). Costs associated with PZP-22 treatment included:

422   gathering horses, giving a dose of the PZP pellets that confer longer immunogenic effects ($400)

423   and a dose of ZonaStat-H vaccine ($30) to eligible females, and holding treated females for 7

424   days before they are returned to the range ($7.60 per day for 7 days; Paul Griffin, personal

425   communication). Additional booster doses involved re-treatment with ZonaStat-H.

426   We modeled effects of ZonaStat-H treatment on reproductive rates using results from

427   published fields trials (Turner Jr et al. 1997, Kirkpatrick and Turner 2008, Nuñez et al. 2017).

428   We assumed that ZonaStat-H treatment would involve all treated females being held in short-

429   term captivity to receive a booster shot 30 days after they received a primer dose to increase

430   effectiveness (i.e., two doses). We modeled ZonaStat-H effects as: 95% and 19% reductions on

431   reproduction one and two years, respectively, after receiving two doses (Turner Jr et al. 1997,

432   Kirkpatrick and Turner 2008); 95% and 19% reductions one and two years, respectively, after

433   receiving a third dose (Turner Jr et al. 1997, Kirkpatrick and Turner 2008); 95%, 72%, 58%, and

434   30% reductions one, two, three, and four years, respectively, after receiving a fourth dose (Nuñez

435   et al. 2017); and a persistent 95% reduction after receiving a fifth dose (Nuñez et al. 2017). Costs

436   associated with ZonaStat-H treatment included: gathering horses, giving primer and booster

437   shots ($30 each) to eligible females, and holding treated females for a booster ($7.60 per day for

438   30 days).

439   **Intrauterine devices** – Because our model assumes a post-breeding census with

440   management occurring after the birthing season, management may occur when females are most

441   likely to not be pregnant and therefore are available to receive an IUD. We modeled IUD

442   treatment assuming that, during treatment years, populations are rounded up in a gather, gathered

443   females are screened by a veterinarian for pregnancy using ultrasonography, and all non-

444   pregnant females ≥1 year old are given an IUD and returned to the range. We estimated the

445   proportion of non-pregnant females using one minus the fertility rate for each female age class

446   specified by the randomly-selected demographic matrix during each year of projections. Non-

447   pregnant females implanted with an IUD implanted at the beginning of a year cannot become

448   pregnant during the following year, and IUDs have an annual retention probability of 0.86

449   (extrapolated from Holyoak et al. 2021). Survival rates of IUD-treated females were increased,

450   as with during vaccine treatment. Costs associated with IUD implantation included: gathering

451   horses, using veterinary ultrasound to scan all females to determine pregnancy status ($30 per

452   female), materials ($60 per device for each non-pregnant female), veterinarian costs ($50 per

453   device implanted), and holding costs associated with treatment ($5 per day for 14 days per

454   treated female).

455   **Mare sterilization** – We modeled mare sterilization assuming that during treatment

456   years, populations are rounded up in a gather and all females ≥1 year old are sterilized. Because

457   a portion of the gathered female population will be pregnant during a treatment year, we assumed

458   that all pregnant females would carry out their current pregnancy in the immediate year, but that

459   all females would be unable to reproduce in all future years. Survival rates of sterilized females

460   were increased, as with during other fertility control treatments. We assumed costs associated

461   with mare sterilization as: gathering horses, performing the procedure ($300 per individual), and

462   holding costs associated with seven days of post-treatment monitoring ($5 per day).

463   **Functions for compound alternatives** – We built nine functions that each simulated

464   how two management actions (i.e., compound alternatives) can be used jointly to manage horse

465   populations. Five functions used removals along with a fertility treatment (one of three different

466   vaccines, IUDs, or mare sterilization). During treatment years with removals and fertility control,

467   the functions simulated gathers and removals from the population first, then fertility treatment of

468   the remaining gathered females second. If fertility treated individuals were present during a

469   removal, untreated females would be preferentially selected for removal. Removals sought to

470   reduce the population size to the target size, if possible, and fertility control treatment was

471   applied to remaining mares that would be released back to the range. We built four functions

472   simulating how IUDs could be used jointly with another form of fertility treatment (GonaCon,

473   PZP-22, ZonaStat, or mare sterilization). When treating IUDs with vaccine or mare sterilization,

21

474   all non-pregnant females were implanted with IUDs first, and then the remaining pregnant

475   females were treated with vaccine or sterilization.

476   We also built three functions that simulated how three management actions could be used

477   jointly for management: 'Removals with IUDs and GonaCon', 'Removals with IUDs and PZP-

478   22', and 'Removals with IUDs and ZonaStat-H'. All three functions involved managing with

479   removals first (when the population met removal conditions) and then treating any remaining

480   females with IUDs (non-pregnant females) or vaccine (pregnant females). A full list of the

481   predictive functions is included in Table 2.

482

483   *Metrics*

484   Management alternatives trade-off in creating outcomes related to population size, the

485   amount of animal handling performed, and fiscal costs (Folt et al. 2023b). We quantified seven

486   metrics during simulations and used them to evaluate performance of alternatives: mean

487   population size, number of horses gathered, number of horses removed, number of horses

488   treated, cost (USD) of management in the field ('on-range'), cost (USD) in holding facilities

489   ('off-range'), and total cost of management (sum of on-range and off-range costs). Mean

490   population size can be viewed as an index of potential ecological impacts to ecosystem health

491   and horse health. When management causes populations to be within target population size

492   ranges, ecological effects of horses are small enough to permit high ecosystem health (i.e.,

493   healthy, multi-use landscapes) and horses have sufficient resources (i.e., food and water) to

494   permit high horse health (National Environmental Policy Act 1970, Bureau of Land Management

495   2010). When horse populations exceed target ranges, horse overpopulation might have negative

496   effects on ecosystem health (i.e., ecological costs). At even higher horse population sizes, there

497   may be increased risk of negative density-dependent effects on horse welfare due to resource

498   limitation. The number of horses gathered, removed, and treated are indices of the magnitude of

499   animal handling; management alternatives that are effective in reducing population size and

500   minimizing the amount of animal handling necessary may be preferred by some members of the

501   public, who often prefer the level of horse handling to be minimized (Folt et al. 2023b, Carlisle

502   and Adams in press). Management costs on-range, off-range, and overall are indices of fiscal

503   costs of management. So long as the primary management goals for natural resources are met

504   (e.g., achieving a thriving natural ecological balance through AML), most stakeholders and

505   decision makers would prefer to minimize management costs to save limited financial resources.

506

Estimating tradeoffs

508   We first sought to understand tradeoffs by simulating 19 alternatives (Table 2) under

509   scenarios where management with gathers, handling, and treatment was performed in the first

510   year and every third year thereafter during a 10-year projection interval. We summarized outputs

511   for each alternative with mean and 95% confidence intervals (CI) estimates for each metric.

512   Management with gathers, handling, and treatment performed at different frequencies

513   might better achieve different objectives in horse management (Folt et al. 2023b). To understand

514   tradeoffs among metrics predicted by management alternatives conducted at different

515   frequencies, we simulated two additional scenarios for each alternative and compared outcomes

516   from when management is performed every three years ('scenario 1') to when management

517   frequency is increased (every two years; 'scenario 2') or decreased (every four years; 'scenario

518   3') over a 10-year interval. For a given outcome of one metric, alternatives may vary

519   substantially in the outcome of another objective, such that one alternative may outperform (i.e.,

520   dominate) others at minimizing metrics. We illustrated outcomes for each alternative scenario

521   (55 total, including a 'no management' scenario) using point graphs and identified Pareto

522   efficiency frontiers (Keeney and Raiffa 1993) describing the most efficient scenarios for

523   minimizing individual metrics (e.g., cost) along variation of outcomes for predicted mean

524   population size (Runge et al. 2020) among all alternatives. A Pareto efficiency frontier represents

525   the best possible outcomes for the two metrics among the multiple management alternatives

526   considered. Alternatives on the Pareto efficiency frontier are 'Pareto optimal', because it is not

527   possible to identify another alternative that increases performance in one metric without

528   decreasing performance in another metric (Lyons 2020). We identified Pareto efficiency frontiers

529   among all alternatives for between overall mean population size and six metrics: 1) number of

530   horses gathered, 2) number of horses removed, 3) number of horses treated, 4) management cost

531   in the field ('on-range'), 5) management cost in holding facilities ('off-range'), and 6) total

532   management cost. Three of the alternatives that we simulated involved mare sterilization as a

533   management action ('Mare sterilization', 'Removal and mare sterilization', 'IUDs and mare

534   sterilization'; Table 2). However, there is some public resistance to certain surgical methods for

535   mare sterilization of horses in field settings (Bechert et al. 2022). For this reason, we identified a

536   second Pareto efficiency frontier that identified the most efficient scenarios for minimizing

537   metrics among alternatives that did not involve mare sterilization.

538   The effectiveness of alternatives for minimizing metrics might also vary by the temporal

539   scale of management, where effectiveness of alternatives at minimizing metrics changes over

540   longer time periods. To this end, we simulated four alternatives ('Removals', 'Removals and

541   GonaCon', 'Removals, IUDs, and GonaCon', 'Removals and mare sterilization') with

542   management every three years over a 20-year projection interval and compared results between

543   the 10- and 20-year projection intervals to understand how the duration of management with

544   gathers and treatment influences important metrics in horse management.

545

546   *Code*

547   We built all simulation functions and performed scenario analyses in the statistical

548   program R (R Core Team 2021) using the package 'popbio' (Stubben and Milligan 2007). We

549   also built a website application using the package 'shiny' (Chang et al. 2021) that allows

550   individuals to call the simulation functions and perform custom simulations to estimate

551   consequences of management alternatives on horse populations; we describe the 'shiny'

552   application below. Code from our analysis and software for the website application are provided

553   in U.S. Geological Survey (USGS) software releases (Folt et al. 2023a, Folt et al. 2023c).

554

555   **Results**

556   *Scenario analysis*

557   Population projection of 500 horses under 19 management alternatives over 10 years

558   generated divergent outcomes in population size and metrics related to management effort and

559   cost (Table 2). Predictions from the 'No management' alternative resulted in a five-fold increase

560   in population size over a ten-year period (Table 2). Among single-action alternatives with

561   management every three years, the 'Mare sterilization' and 'GonaCon' scenarios yielded smaller

562   final population size relative to other fertility control alternatives, but no alternative with fertility

563   treatment alone reduced population size to within target population size ranges within 10 years.

564   Rather, 'Removals' was the only single-element alternative that reduced population size to

565   within target population size ranges during the projection (Figure 2); it did so by removing, on

566   average, 530 (445–617; 95% CI) individuals from the population over 10 years. However,

567   predicted total cost of the 'Removals' scenario ($4.73 million; $3.81–5.51, 95% CI) was

568   substantially higher than other single-action alternatives (Table 2), largely due to costs of horses

569   being held in captivity for up to 25 years after management is performed on the range. Among

570   the eleven compound alternatives, alternatives involving removals and one or two forms of

571   fertility control all yielded average population size within target population size ranges over the

572   projection interval, while alternatives involving two forms of fertility control without removals

573   generated populations that exceeded target population size ranges (Table 2). The three scenarios

574   with the lowest mean population size were 'Removals and GonaCon' [238 (192–327, 95% CI)],

575   'Removals and mare sterilization' [258 (180–310, 95% CI)], and 'Removals with IUDs and

576   GonaCon' [224 (182–323, 95% CI)]; however, 'Removals and mare sterilization' required the

577   fewest horses to be gathered, removed, and treated and had the lowest overall management cost

578   among those three scenarios, and the population size did not differ strongly from the other two

579   scenarios (Table 2).

580   Simulation of 18 management alternatives with animal capture, handling, and treatment

581   at two-, three-, and four-year management return intervals and 'No management' allowed us to

582   visualize tradeoffs among alternatives varying in both management actions and frequency

583   (Figure 2, Appendix S1). Removals-only scenarios (e.g., 'Removals' every 4 years) required the

584   fewest number of horses to be gathered (838; 783–1046, 95% CI) and treated (0; 0–0, 95% CI)

585   and were relatively inexpensive for management on-range ($0.72 million; $0.67–0.90 million,

586   95% CI). However, removal-only scenarios were relatively expensive off-range (e.g.,

587   'Removals' every 4 years cost $3.52 million off-range [$2.99–3.92 million, 95% CI] and was the

588   fourth-most costly scenario off-range) due to costs associated with horses in long-term holding

26

589   facilities; those scenarios did not include fertility control treatment that could have reduced

590   reproduction in the population. Two scenarios ('Removals and GonaCon' and 'Removals and

591   mare sterilization' every 2 years) each required the fewest number of horses to be removed (312;

592   312–312, 95% CI), required only a single removal in the first year, and as a consequence were

593   relatively inexpensive off-range (e.g., 'Removals and GonaCon' every 2 years was the least-

594   costly off-range scenario [$2.34 million; $2.14–2.53 million, 95% CI]). The management

595   scenario that produced the smallest mean population size within target population size ranges

596   and was least-costly overall (the sum of costs both on-range and off-range) was 'Removal and

597   mare sterilization' every 2 years, which caused average population size to be 248 (184–505, 95%

598   CI) horses and cost $3.65 million ($3.37–3.83 million, 95% CI) in total (Figure 2).

599   Simulated outcomes of alternatives with management every three years at 10-year and

600   20-year projection intervals demonstrated that variation in predicted outcomes among

601   alternatives after ten years propagated over longer projection intervals. Predicted increases in the

602   number of horses gathered, removed, and treated and management costs between 10- and 20-

603   year projection intervals were smaller for 'Removals and mare sterilization' than other

604   alternatives that achieved population size within target ranges (Figure 3).

605

606   *Website application*

607   We built an online website application, *PopEquus*, that hosts the simulation functions and

608   allows users to perform custom simulations to estimate the effects of alternative management

609   strategies on wild horse populations in western rangeland ecosystems managed by federal

610   agencies (https://rconnect.usgs.gov/popequus/). Two simulation tools are available within the

611   application: one page with a relatively basic interface that can simulate and compare among six

612   single-action alternatives and a 'no management' scenario ('Basic Tool'), and a second page that

613   can simulate and compare more numerous and complex alternatives, including alternatives with

614   more than one management action ('Advanced Tool'). Users can specify input values for

615   different variables related to the population, select management alternatives, and then simulate

616   how populations and metrics would be influenced by alternatives. Output metrics are visualized

617   with graphs, a table, and text. We also included an introductory page that frames challenges

618   associated with horse management, a user manual page with explanatory details for how to use

619   the simulation tools, a page that explains the mechanics of the population projections and

620   assumptions during simulations, and a page with exercises that demonstrate how users might use

621   the Advanced Tool to perform simulations to support various decision problems (Appendix S2).

622   For both tools, the user can download reports summarizing simulation inputs and outputs.

623   *PopEquus* provides a flexible tool to estimate the consequences of management alternatives and

624   tradeoffs that emerge among them.

625

626   **Discussion**

627   The management of feral horse populations is a global issue that is challenged by

628   passionate stakeholders, multiple competing objectives, and complex social-ecological system

629   dynamics (Nimmo and Miller 2007, Beever et al. 2018, Scasta et al. 2018, Scasta 2019, Folt et

630   al. 2023b). Decision makers around the world can benefit from better understanding tradeoffs

631   that exist within horse population management (Converse 2020), and our results illustrate

632   important tradeoffs among competing objectives in horse management. *PopEquus* provides

633   decision makers with a tool to identify cost-effective population management alternatives that

634   might manage populations to be within target population size ranges while also minimizing the

635   amount of management performed to achieve desired outcomes. Specifically, among simulated

636   alternatives that reduced population size to within target ranges, management with periodic

637   removals and mare sterilization minimized the number of horses that were handled, removed,

638   and treated and minimized the overall cost of management. This result suggests that mare

639   sterilization could be a useful alternative for achieving multiple objectives. We also

640   demonstrated that shorter intervals between management and/or more effective, longer-lasting

641   fertility control methods required fewer horses to be gathered, removed, and treated and

642   decreased management costs compared to longer intervals between management or less effective

643   fertility-control approaches. For this reason, decision makers might benefit from allocating more

644   resources toward shorter management intervals and/or more effective management in the short-

645   term to minimize management effort and costs in the long-term. Taken together, our results

646   provide policy makers with information about what management actions could be used and how

647   they can be structured to manage horse populations in ways that maximize ecosystem health and

648   horse welfare while minimizing fiscal costs of management.

649   Our results indicated that mare sterilization might be a highly effective form of fertility

650   control for reducing horse population growth; however, some horse advocacy groups in the

651   United States have opposed surgical mare sterilization for free-roaming horse populations

652   (Bechert et al. 2022). Other than alternatives with mare sterilization, two alternatives involving

653   removals with GonaCon treatment or removals with both IUDs and GonaCon treatment also

654   performed strongly at reducing population size and minimizing management metrics compared

655   to other alternatives. Future research might seek to develop and test additional methods for long-

656   lasting fertility control that can be effective with a single handling occasion (Bureau of Land

657   Management 2021). While our model identifies alternatives that are effective at reducing or

658   maximizing different metrics, the model cannot account for all factors that might be important

659   during management decisions, such as multiple uses of lands, local land use planning

660   considerations, threatened and endangered species' needs, or other important factors. Therefore,

661   the results from simulations, while useful, are unlikely to be the sole basis for site-specific land

662   management decisions.

663   We compared alternatives under the context of a horse population that exceeded its

664   maximum target population size in year 0 by 66% – a common situation for BLM-managed

665   populations in the last ten years which tend to exceed AML (Garrott and Oli 2013, Bureau of

666   Land Management 2020). Our results suggested that, when populations exceed maximum target

667   population sizes, removals are a largely necessary management action to achieve population size

668   within target ranges (Garrott 2018) and avoid ecosystem degradation. Most North American

669   horse populations occur in expansive rangeland ecosystems where management actions

670   involving animal capture and fertility control treatment are logistically difficult (e.g., difficult

671   access, unapproachable horses, large populations but with low population density, low capture

672   rates during gathers) and limited or no top-down predators effects on horse populations

673   (Andreasen et al. 2021). With very limited mortality due to predators, fertility control treatment

674   alone (e.g., by darting) might need to be applied repeatedly in populations for many consecutive

675   years to reduce reproduction sufficiently, so that losses to the population by natural mortality

676   exceed gains by reproduction and the population would stabilize in size (e.g., Appendix S2:

677   Figure S9; National Park Service 2008). Given limited financial and logistical resources (e.g.,

678   off-range holding space) available to perform management, decision makers are often only able

679   to perform management with gathers, removals, and fertility control treatment every 3–5 years,

680   such that populations are likely to continue to grow above management-defined population

681   maxima (Garrott 2018). Excluding alternatives with removals, the fertility-control-only

682   alternative with the lowest mean population size after 10 years was 'IUDs and mare

683   sterilization'; however, the 95% confidence intervals for mean population size failed to overlap

684   the starting population size (500 horses), so even this alternative did not come close to reducing

685   the population to be within the target population size range over 10 years. Therefore, our results

686   suggest that, to achieve population size objectives, at least one removal is needed to reduce

687   populations to within AML, followed by fertility control with frequent application to a large

688   proportion of the female population (e.g., mare sterilization or GonaCon treatment at a two- or

689   three-year return interval) to maintain population stability. If fertility control treatment is less

690   effective, used less frequently, or is less long-lasting, then periodic removals are needed to

691   account for the surplus of births minus deaths to maintain population stability within target

692   population size ranges (Garrott 2018).

693   We modeled a relatively broad suite of alternatives, including 'No management'. We

694   included 'no management' as a baseline comparison of no action but note that horse population

695   management at identified AML population sizes is legally-mandated for populations under the

696   jurisdiction of the BLM and USFS (16 U.S. Code Section 1333). We focused our scenario

697   analysis by making several assumptions based on input from wildlife managers, including

698   assumptions that vaccine treatment would involve gathers, vaccine treatment would be

699   performed by hand, fertility control treatment would be used to treat all females ≥ 1 year old, all

700   age-eligible females would be treated, and for vaccines a booster shot would be given to all

701   treated individuals after holding until an optimal booster treatment time. However, the website

702   application, *PopEquus*, is a flexible tool that is highly customizable, can simulate specified local

703   population conditions, limitations, and management actions, and can therefore support diverse

704   management decisions (Garrott 1991). *PopEquus* can simulate populations that differ in

705   population size and sex ratios, logistical constraints on management (e.g., populations that are

706   more or less difficult to capture by gathers or treat by darting), management timeframes (2–20

707   years), and management actions (e.g., adjustable removal settings, booster treatments, vaccine

708   treatment method by darting, costs, etc.). While the primary purpose of *PopEquus* is to support

709   management decisions for individual horse populations (e.g., a single Herd Management Area

710   managed by the BLM or a single Horse Territory managed by the USFS), when settings are

711   adjusted appropriately and a few assumptions are made, the tool also can simulate management

712   of extremely large populations that might occur over large spatial scales or comprise multiple

713   smaller populations (e.g., a BLM horse complex). For example, one can simulate a large regional

714   population (e.g., 10,000 horses) with adjustments to certain variables to reflect limitations in the

715   number of horses that can be gathered, removed, and treated each year when a relatively large

716   number of horses must be managed (Appendix S2: Figure S15). In general, we developed

717   *PopEquus* to support decisions related to wild horse management in the United States, but it

718   could also be used or adapted to understand tradeoffs in horse management worldwide, including

719   native horse reintroductions and feral horse management. Because feral and wild burro

720   populations also require management in many places but differ from horses in demographic rates

721   and population structure, future work might revise the modeling framework to include additional

722   simulation capabilities for burros as well.

723   Our analytical framework estimates the consequences of alternatives on metrics related to

724   ecological costs of horses and horse health (i.e., whether populations are within or exceed

725   management targets that are thought to yield healthy horses and ecosystems), animal handling,

726   and fiscal costs of management. Some have suggested that horse management decisions could

727 benefit from better understanding stakeholder values and objectives through greater stakeholder

728 engagement, potentially through some form of participatory decision making (National Research

729 Council 2013, Beever et al. 2018, Folt et al. 2023b), so that decisions are informed by an

730 inclusive and transparent consideration of stakeholder values. For example, structured decision

731 making (Runge et al. 2020) might help achieve a careful, inclusive, value-focused analysis of a

732 decision problem that might better uncover and explore the full suite of values relevant to

733 different elements of horse management decisions. Such an exercise could use our simulation

734 tool to estimate the consequences of alternatives on value-focused objectives. However, solving

735 multiple-objective decision problems ultimately requires incorporating decision-maker

736 preferences among objectives to identify a solution that strikes a balance among competing

737 objectives (Williams and Kendall 2017). Future efforts might also revise our model to improve

738 system dynamics, incorporate emerging approaches to fertility control treatment or gathers,

739 account for additional values of decision makers or stakeholders, and incorporate legal

740 requirements or preferences of decision makers as a more explicit decision analysis.

741 Consistent with predictions about horse population growth (Eberhardt et al. 1982, Garrott

742 and Oli 2013, National Research Council 2013), horse populations on federally managed lands in

743 the western United States have increased dramatically over the last decade (Garrott 2018,

744 Schoenecker et al. 2021) and there are now more than 82,000 wild horses and burros on BLM-

745 managed lands (Bureau of Land Management 2022). Our scenario analyses and simulation tool

746 can provide informative technical support for decision makers and managers who are mandated

747 to achieve and maintain population sizes within AML, but who also want to minimize cost and

748 animal capture, handling, and care requirements. If the tools provided here are used to identify

749 effective management alternatives at scale, decision makers might be able to 'change the course'

750   of free-roaming horse population growth (Garrott and Oli 2013) and better protect rangelands

751   from the deterioration associated with excessively large horse populations, maintain high-quality

752   habitat conditions for on-range horse welfare, preserve taxpayer resources, and promote a

753   sustainable ecological balance among horses, natural plant and animal communities, and

754   multiple other important land uses pursuant with BLM and USFS mandates.

755

756   **Acknowledgments**

763

764   **Author Contributions**

765   Brian Folt and Kathryn A. Schoenecker designed the study. Brian Folt, L. Stefan Ekernas, and

766   David R. Edmunds performed statistical analysis, and Brian Folt and Mark Hannon built the

767   website application. Brian Folt wrote the first draft of the paper, and Kathryn A. Schoenecker

768   and David R. Edmunds contributed critical feedback to manuscript drafts. All authors gave final

769   approval for publication.

770

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1015   Table 1. Studies of free-roaming horses (*Equus caballus*) used to build age-based Leslie matrix models describing horse demographics

1016   in western North America. Each matrix yielded a distinct deterministic population rate of change, λ, that spanned a range of possible λ

1017   values for horses (Ransom et al. 2016). During each year of stochastic population projections, one matrix was randomly drawn, given

1018   the probability p, to yield an overall mean λ of 1.18 among years. Other matrix probability vectors can be used to simulate additional

1019   mean values for λ that vary from 1.00–1.32 using the *PopEquus* simulation tool (Folt et al. 2023a).

Number	State	Site	Year	λ	Probability	Reference
1	Montana	Pryor Mountains	1976–1986	1.148	0.08	Garrott and Taylor (1990)
2	Montana	Pryor Mountains	1977	0.533†	0.00	Garrott and Taylor (1990)
3	Montana	Pryor Mountains	1996–2000	1.089	0.01	Jenkins (2002)|
4	Montana	Pryor Mountains	1993–2007	1.066	0.00	Roelle et al. (2010)
5	Nevada	Garfield Flat	1993–1999	1.178	0.42	Jenkins (2002)|
6	Nevada	Granite Range	1979–1983	1.138	0.06	Berger (1986)
7				1.196	0.27	Ransom et al. (2016)
8				1.231	0.10	Ransom et al. (2016)
9				1.143	0.06	Ransom et al. (2016)
10				1.317	0.00	Ransom et al. (2016)

†Low survival from an extreme winter; lower limit of population growth

1020

1021 Table 2. Simulated outcome metrics [mean (95% confidence intervals)] for free-roaming horse (*Equus caballus*) populations under 19

1022 management alternatives. Populations were simulated using a predictive function for each alternative assuming a starting population

1023 size of 500 individuals, Appropriate Management Levels [AML] of 200–300 individuals, ten-year projection interval with an average

1024 annual population rate of change of 1.18, and a three-year return interval between animal handling events (gathers, removals, fertility

1025 control treatments). Management costs (millions of USD) were calculated over ten years on public land ('on range'), 35 years when

1026 horses were removed and taken to holding facilities off range ('off range'), and 35 years for the total cost.

Management alternatives	Alternative number	Final population size	Mean population size	Number of horses gathered	Number of horses removed	Number of horse treatments	On-range cost (USD; millions)	Off-range cost (USD; millions)	Total cost (USD; millions)
No management	1	2537 (2206-2898)	1253 (505-2632)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Removals	2	271 (208-341)	289 (194-505)	972 (803-1160)	530 (445-617)	0 (0-0)	0.84 (0.69-1)	3.89 (3.13-4.52)	4.73 (3.81-5.51)
GonaCon	3	924 (811-1048)	705 (505-951)	2634 (2463-2849)	0 (0-0)	960 (885-1025)	2.2 (2.07-2.34)	0 (0-0)	2.2 (2.07-2.34)
PZP-22	4	1710 (1461-1974)	990 (505-1788)	3599 (3195-4026)	0 (0-0)	1223 (1130-1399)	2.94 (2.68-3.25)	0 (0-0)	2.94 (2.68-3.25)
ZonaStat-H	5	1794 (1610-1960)	984 (505-1855)	3583 (3282-3829)	0 (0-0)	1178 (1098-1247)	2.78 (2.57-2.95)	0 (0-0)	2.78 (2.57-2.95)
Intrauterine devices (IUDs)	6	1795 (1533-2100)	1013 (505-1866)	3693 (3307-4071)	0 (0-0)	484 (412-605)	2.8 (2.55-3.02)	0 (0-0)	2.8 (2.55-3.02)
Mare sterilization	7	692 (615-767)	638 (505-745)	2392 (2236-2535)	0 (0-0)	384 (350-413)	2.02 (1.92-2.1)	0 (0-0)	2.02 (1.92-2.1)
Removals and GonaCon	8	238 (192-327)	279 (186-505)	1283 (1202-1355)	401 (312-454)	237 (185-272)	1.19 (1.14-1.25)	2.97 (2.31-3.43)	4.16 (3.46-4.67)
Removals and PZP-22	9	278 (196-340)	290 (192-505)	1340 (1271-1426)	478 (417-569)	207 (162-242)	1.24 (1.19-1.31)	3.46 (3.07-4.03)	4.71 (4.27-5.33)
Removals and ZonaStat-H	10	291 (234-356)	292 (193-505)	1354 (1270-1443)	493 (415-578)	209 (170-252)	1.23 (1.17-1.3)	3.59 (3.04-4.21)	4.82 (4.21-5.43)
Removals and IUDs	11	268 (203-344)	284 (192-505)	1326 (1267-1428)	477 (423-572)	62 (39-86)	1.2 (1.15-1.27)	3.52 (3.04-4.18)	4.72 (4.23-5.42)
Removals and mare sterilization	12	258 (180-310)	277 (189-505)	1254 (1171-1342)	342 (312-441)	127 (87-151)	1.17 (1.11-1.23)	2.56 (2.2-3.26)	3.73 (3.36-4.49)
IUDs and GonaCon	13	1038 (894-1198)	746 (505-1087)	2770 (2537-3008)	0 (0-0)	789 (711-871)	2.23 (2.08-2.39)	0 (0-0)	2.23 (2.08-2.39)
IUDs and PZP-22	14	1780 (1341-2317)	984 (505-2013)	3498 (2980-4074)	0 (0-0)	1055 (832-1302)	2.78 (2.44-3.17)	0 (0-0)	2.78 (2.44-3.17)
IUDs and ZonaStat-H	15	1500 (1242-1719)	892 (505-1580)	3271 (2869-3522)	0 (0-0)	939 (823-1035)	2.51 (2.29-2.67)	0 (0-0)	2.51 (2.29-2.67)
IUDs and mare sterilization	16	685 (597-794)	604 (505-722)	2296 (2131-2473)	0 (0-0)	413 (371-449)	1.94 (1.83-2.05)	0 (0-0)	1.94 (1.83-2.05)

Removals with IUDs and GonaCon	17	224 (182-323)	279 (186-505)	1299 (1208-1371)	428 (312-488)	177 (137-212)	1.18 (1.1-1.24)	3.17 (2.26-3.62)	4.35 (3.4-4.86)
Removals with IUDs and PZP-22	18	275 (193-369)	295 (193-505)	1355 (1279-1489)	513 (422-622)	171 (133-229)	1.25 (1.19-1.36)	3.78 (3.15-4.47)	5.03 (4.35-5.79)
Removals with IUDs and ZonaStat-H	19	261 (217-329)	283 (192-505)	1319 (1254-1412)	464 (420-526)	172 (149-199)	1.19 (1.14-1.26)	3.39 (3.06-3.93)	4.58 (4.22-5.17)

1028   Figure 1. An age-based, two-sex, population projection model for free-roaming horses (*Equus*

1029   *caballus*). (A) A conceptual diagram illustrating how abundance (*N*), survival (*φ*), and fecundity

1030   (*F*) vary by age stages (subscripts: 0, 1, 2, …., ≥20 years old); circles denote age-class

1031   abundance, arrows indicate survival and reproductive rates, and '…' indicate abundance and

1032   demographic rates for ages 3–19. (B) An illustration of how parameters from the conceptual

1033   model (*N*, *φ*, *F*) were articulated with a matrix of demographic rates (left) and a vector of initial

1034   population size (right) for population projection. Dotted lines ('…') indicate when rows and

1035   columns were collapsed for illustrative purposes. The top 21 rows of the vector and matrix

1036   describe parameters for females and the bottom 21 rows are for males. For fecundity terms, the

1037   proportion of offspring that were female and male were indicated by the symbols ♀ and ♂,

1038   respectively. Stochastically-drawn demographic rates at time *t* were multiplied by the vector of

1039   population size to project the population size vector forward to time *t*+1. Rectangles are

1040   management alternatives; arrows are effects of management alternatives on demographic rates,

1041   population size, and management metrics (round-cornered rectangles). (C). Population size at

1042   time *t*+1 (N_{t+1}) is a product of the demographic rate matrix (*A*) and abundance at time *t* (N_t).

1043   Figure 2. The tradeoff between predicted mean population size and the total cost of management

1044   among 55 management alternatives for a free-roaming horse (*Equus caballus*) population with a

1045   starting population size of 500 horses. Points are model-predicted mean estimates with 95%

1046   confidence intervals (horizontal and vertical black lines) for alternatives; blue vertical dashed

1047   lines indicate the minimum (200 individuals; left) and maximum (300 individuals; right) target

1048   population size range for the population (i.e., Appropriate Management Levels). The 55

1049   alternatives include 18 alternatives that were each simulated as three different 'scenarios' with

1050   prescribed animal capture or treatment at different intervals: 3-year intervals (scenario 1; 'sc. 1'),

1051   2-year intervals (scenario 2; 'sc. 2'), and 4-year intervals (scenario 3; 'sc. 3'). Colored lines are

1052   Pareto efficiency frontiers that identify the most cost-efficient alternatives for any outcome in

1053   population size (i.e., Pareto optimal alternatives). The red line indicates the Pareto optimal

1054   alternatives among the entire set of 55 simulated scenarios; the orange line indicates the Pareto

1055   optimal alternatives when alternatives with mare sterilization were excluded. Sub-optimal,

1056   dominated alternatives are above or right of Pareto frontiers.

1057   Figure 3. Mean estimates (and 95% confidence intervals [CI]) for six metrics of free-roaming

1058   horse (*Equus caballus*) population management produced by four alternatives (removals;

1059   removals and GonaCon-Equine [GonaCon] treatment; removals with intrauterine [IUD] devices

1060   and GonaCon treatment; removals and mare sterilization treatment) simulated over 10- and 20-

1061   year population projection intervals. Horse gather, removal and fertility control activities were

1062   performed in the first year and every third year thereafter (3-year interval) until the end of the

1063   projection interval. Metrics are the: (A) number of horses gathered, (B) number of horses

1064   removed, (C) number of horses treated, (D) cost of gathers and fertility control treatments ('on-

1065   range cost'), (E) cost of animal handling, care, and adoption efforts ('off-range cost'), and (F)

1066   overall cost ('total cost'). Cost estimates are in millions of US dollars. 95% CI were calculated

1067   from 50 simulation replicates at both projection intervals.

Ecosphere

A

Females

$N_0 \xrightarrow{\varphi_0} N_1 \xrightarrow{\varphi_1} N_2 \xrightarrow{\varphi_2} N_3 \cdots \xrightarrow{\varphi_{\geq 20}} N_{\geq 20}$

$♀F_2 \quad ♀F_3 \quad ♀F_{\geq 20}$

$♂F_2 \quad ♂F_3 \quad ♂F_{\geq 20}$

Males

$N_0 \xrightarrow{\varphi_0} N_1 \xrightarrow{\varphi_1} N_2 \xrightarrow{\varphi_2} N_3 \cdots \xrightarrow{\varphi_{\geq 20}} N_{\geq 20}$

B

Number treated

Population size metrics

Cost metrics

Number removed

Fertility treatment

$$
\begin{bmatrix}
0 & 0 & ♀F_2 & ♀F_3 & \cdots & ♀F_{\geq 20} & 0 & 0 & 0 & 0 & \cdots & 0 \\
\varphi_0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 \\
0 & \varphi_1 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 \\
0 & 0 & \varphi_2 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
0 & 0 & 0 & 0 & \cdots & \varphi_{\geq 20} & 0 & 0 & 0 & 0 & \cdots & 0 \\
0 & 0 & ♂F_2 & ♂F_3 & \cdots & ♂F_{\geq 20} & 0 & 0 & 0 & 0 & \cdots & 0 \\
0 & 0 & 0 & 0 & \cdots & 0 & \varphi_0 & 0 & 0 & 0 & \cdots & 0 \\
0 & 0 & 0 & 0 & \cdots & 0 & 0 & \varphi_1 & 0 & 0 & \cdots & 0 \\
0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \varphi_2 & 0 & \cdots & 0 \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
0 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & \varphi_{\geq 20}
\end{bmatrix}
\times
\begin{bmatrix}
N_0 \\ N_1 \\ N_2 \\ N_3 \\ \cdots \\ N_{\geq 20} \\ N_0 \\ N_1 \\ N_2 \\ N_3 \\ \cdots \\ N_{\geq 20}
\end{bmatrix}
$$

Removals

Management alternatives

Number gathered
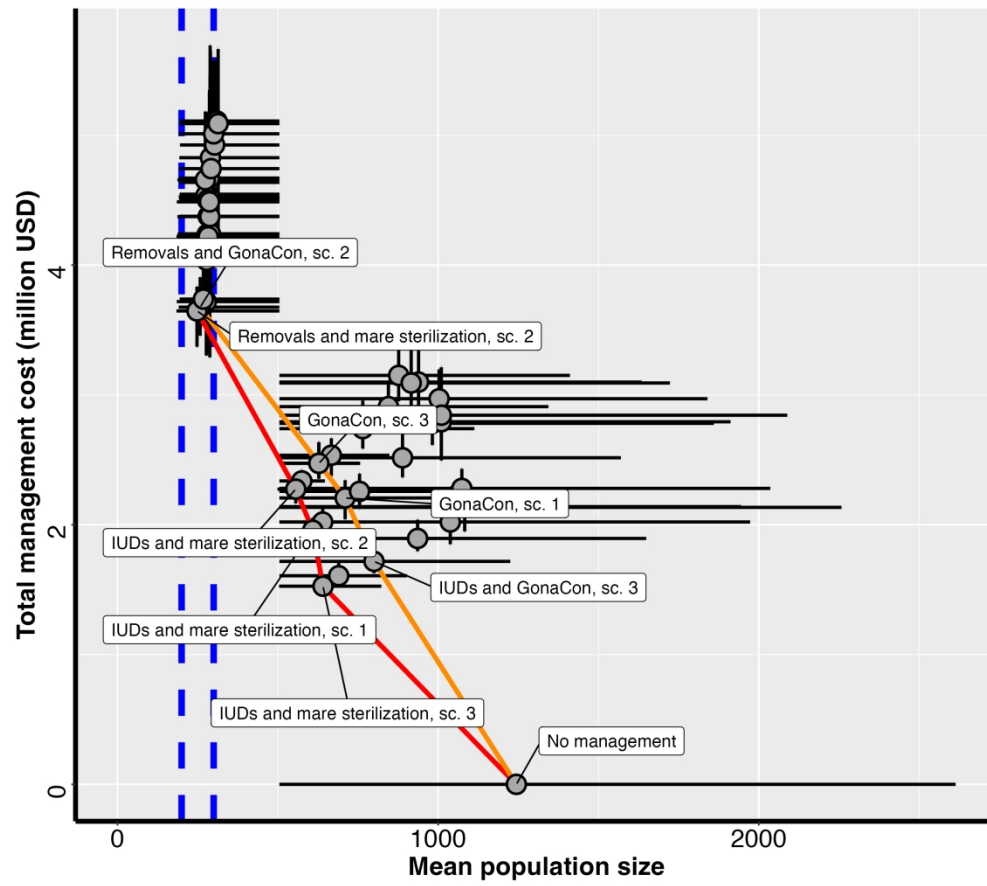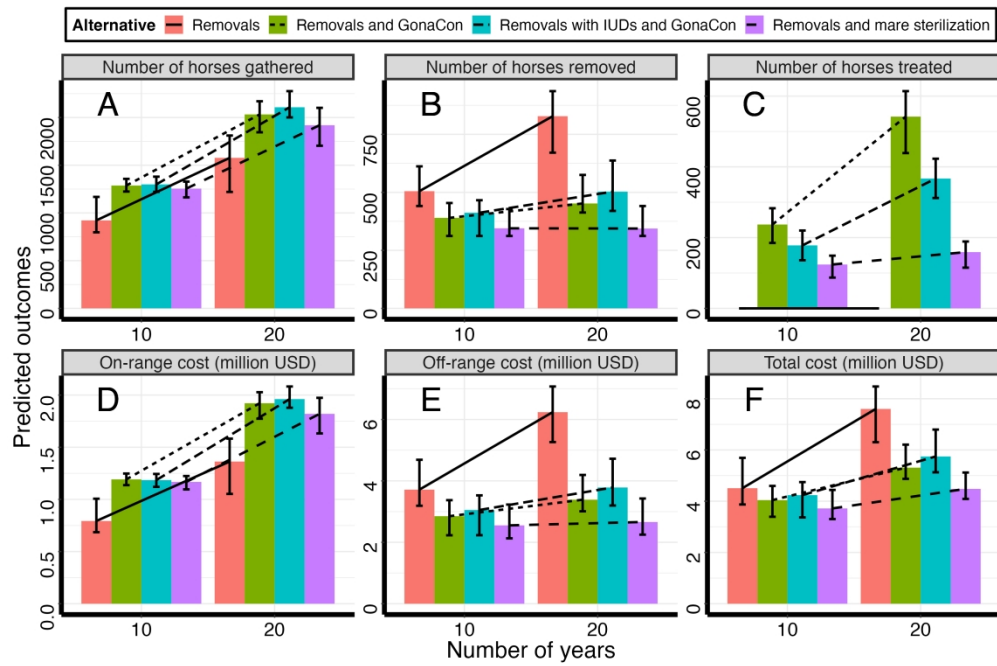
C

$$N_{t+1} = A \times Nt$$

Figure 2

581x516mm (118 x 118 DPI)

Figure 3

774x516mm (118 x 118 DPI)