Demographic effects on fruit set in the dioecious shrub Canada buffaloberry (*Shepherdia canadensis)*

The effects of pollen limitation on reproductive success in plants have been well-documented using pollen supplementation experiments. However, the role of local demographics in determining pollen limitation, particularly in terms of the additive effects of pollen availability and competition are not well known. We measured fruit set in the dioecious shrub Canada buffaloberry (*Shepherdia canadensis*) to evaluate whether local demographics measured at three spatial scales (25, 50, and 100 m^2) affect fruit set in buffaloberry for a population of shrubs in central Alberta, Canada. We test whether density-dependence (population density), nearest pollen source (distance to nearest male shrub), pollen donor (male density), pollen competitor (female density), or the combined pollen donor and competitor hypotheses best explain natural variations in fruit set for a population of Canada buffaloberry. Support was highest for the combined pollen donor and competitor hypothesis at an intermediate spatial scale of 50 m^2. Average percent fruit set was 32.9% with fruit set increasing 3.3 units per one unit increase in male shrub density (pollen donors), while decreasing by 2.2 units per one unit increase in female density (pollen competitors). This illustrates that access to male shrubs within a 3.99 m radius affects pollen availability to female shrubs, while nearby females compete intra-specifically for pollen.

1 **Word Count (Abstract-Citations):** 4083

2 **Title:**

3 **Demographic effects on fruit set in the dioecious shrub Canada buffaloberry (*Shepherdia***

4 ***canadensis)***

5 **Authors:**

6 Kate M. Johnson & Scott E. Nielsen

7 **Affiliations:**

8 Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

9 Correspondence to: scottn@ualberta.ca, (780) 492-1656

10 Introduction

11 Fruit set is commonly limited by pollen availability, particularly in dioecious species due to the

12 isolation of male and female reproductive organs (Burd 1994; Knight 2005). As a result of having

13 half the number of seed bearers as monecious species, dioecious plants must produce more seeds

14 and disperse those seeds to as many areas as their hermaphroditic counterparts, but with twice the

15 population density (Heilbuth et al. 2001). Given such reproductive constraints, it is unsurprising

16 that evolution of dioecy has been rare among angiosperms with only 6% (14,620 of 240,000) of

17 all angiosperms being dioecious (Renner and Ricklefs 1995). Dioecious species tend to rely on

18 small, generalist pollinators (Armstrong & Irvine 1989). Charlesworth (1993) argued that this

19 association has developed because generalist pollinators are not able to determine the sex of a

20 particular flower and therefore associate it with its pollen or nectar reward, enabling the evolution

21 of female flowers by reducing the required investment in floral attractive structures. Borkent and

22 Harder (2007) confirmed this prediction by showing that the generalist pollinators of Canada

23 buffaloberry (*Shepherdia canadensis* L. Nutt) do not bias visits based on sex. However, generalist

24 pollinators may limit the reproductive success of dioecious species by reducing pollen quality due

25 to the deposit of foreign pollen by undiscriminating pollinators (Kunin 1993). The

26 competitiveness of dioecy may therefore be attributed to obligate outcrossing, which decreases

27 the accumulation of harmful mutations found in self-fertilizing plants (Slotte et al. 2013).

28 Fruit set has previously been shown to depend on (1) pollen quantity (Knight 2005), (2) pollen

29 quality (Kunin 1993) and (3) local resource competition (De Jong, van BatenBurg & van Dijk

30 2002). Here we deal specifically with the role of demographic factors in determining the quantity

31 of pollen available. Not surprisingly, an inverse relationship between fruit set and distance to

32 nearest conspecific male plant has been observed for many dioecious species (Kay et al. 1984; De

33   Jong, Batenburg & Klinkhamer 2005; Wang, et al. 2013,), as has a positive relationship between

34   local male density and fruit set (House 1992).

35   Buffaloberry is a shade intolerant (Humbert et al. 2007), nitrogen-fixing (Hendrickson & Burgess

36   1989; McCray-Batzli et al. 2004; Rhoades et al. 2008) dioecious shrub common to disturbed

37   boreal and temperate montane forests of western North America (Stringer & LaRoi 1970; LaRoi

38   & Hnatiuk 1980). Shrubs heights (widths are often similar) range between 0.9 to 3.9 m (Bormann

39   1988), although in Alberta they are rarely over 2 m. Fruit production in buffaloberry is inversely

40   related to canopy cover (Hamer 1996; Nielsen et al. 2004), with inter-annual variation in fruit

41   explained primarily by the previous year's midsummer rainfall suggesting that climate affects the

42   development of flower primordium (Krebs et al. 2009). Plants flower early in the spring, among

43   the earliest of plants in the region, shortly after the soil thaws and before the forest canopy leafs

44   out (Figure 1). Buffaloberry is pollinated nearly entirely by dipterans (97%), the majority of

45   which are in the Syrphidae and Empididae families (Borkent & Harder 2007), with

46   Hymenopterans and Hemipterans also known to pollinate buffaloberry (Lewis 1990). Male

47   buffaloberry flowers offer both pollen and nectar rewards to potential pollinators, while female

48   flowers only produce nectar (Mosquin 1971; Lewis 1990). Borkent and Harder (2007) found that

49   insect pollinators of buffaloberry visit each sex at equal rates, possibly due to an inability to

50   discriminate between flowers. Pollinators visit an average of 6 flowers per plant, spend >9

51   seconds at each flower, and have a 25.2% re-visitation rate (Borkent and Harder 2007). This

52   relationship suggests that the reproductive success of buffaloberry is pollen-limited due to a

53   deficiency in pollinator visits.

54   Here we use buffaloberry as a model species to examine how pollen donor (male) and pollen

55   competitors (female) affect fruit set in a dioecious species. We hypothesize that male-biased

56 population density should produce higher fruit set for any nearby female shrub due to increased

57 pollen availability (pollen donor hypothesis), while a female-biased population density should

58 increase competition for pollen and thus decrease fruit set for any given female plant (pollen

59 competitor hypothesis). Pollen donor and pollen competitor hypotheses are not mutually

60 exclusive. In fact, we expect both could be affecting fruit set in dioecious species and test this

61 additive effect as a competing hypothesis. We also test these hypotheses against a null model of

62 equal fruit set regardless of local demography, a simple density-dependent hypothesis based on

63 total population size ignoring local sex-biases, and distance to nearest male plant which could be

64 considered a simple pollen donor hypothesis as commonly measured in the literature. We

65 examine these hypotheses by measuring fruit set for a natural population of buffaloberry in

66 central Alberta, Canada.

67 **Materials and methods**

68 Sixty buffaloberry shrubs were randomly selected in Terwillegar Park in Edmonton, Alberta,

69 marked with a double-faced aluminum tag wired to one stem at the base of the shrub, and

70 monitored for flowering and fruit set between 8 May and 22 June 2012. Terwillegar Park is a 174

71 hectare natural area located along the North Saskatchewan River in the southwest part of

72 Edmonton (53.48071° N, 113.60785° W). The middle of the park is an open off-leash dog area

73 that is surrounded by natural vegetation with minimum management (City of Edmonton 2009).

74 All shrubs were located along forest edges or in semi-open deciduous forests of balsam popular

75 (*Populus balsamifera*) and trembling aspen (*Populus tremuloides*) and away from the off-leash

76 dog park. We used a natural experimental design to test pollen donor and pollen competition

77 hypotheses by examining variation in fruit set among shrubs within an open pollination system

78 following other studies of fruit set in dioecious plants (Armstrong & Irvine 1989; House 1992;

79 Wang et al. 2013). Although experimental hand pollination experiments (pollinator restriction

80   [bagging] would be unnecessary since it is a dioecious species) could be used to address pollen

81   limitations, we were interested here in examining how local demographic effects influenced fruit

82   set within the same population and year of fruiting.

83   Due to the large number of potential flowers present on an individual shrub (many 1000s), a

84   subsample of flowers was counted to measure initial flower production and thereafter fruit set

85   (e.g. Bowers 2009; Khanizadeh 1989). Specifically, we systematically sampled from each of the

86   60 focal female shrubs four branch segments approximately 30 cm in length by randomly

87   selecting one branch from each the four cardinal directions. Sampled branch segment were

88   marked with a Sharpie® pen by encircling the branch stem 30 cm from the tip of the branch with

89   a 'permanent mark'. The number of flowers on each branch segment was counted twice. First

90   between 8 and 10 May and recounted again between 23 and 24 May to ensure full flower counts

91   since phenology of shrubs varied slightly and due to later than normal spring conditions. The

92   maximum number of flowers observed among either of the two counts was used as the total

93   number of flowers per sampled branch. Because fruit ripening begins here in early July, we

94   visited all shrubs between 22 and 28 of June as the color of fruit began to lighten in color to count

95   the number of fruit per marked branch. Fruit set for each shrub was defined as a percent of total

96   flowers with fruit based on the number of fruit to flowers counted on the different dates across all

97   four branch segments (initial analyses revealed no differences among branch orientations). Based

98   on general observations of fruit production in the prior five years, fruit abundance in Terwillegar

99   Park in 2012 appeared to be about average (Nielsen, personal observation).

100   We quantified population demography of local buffaloberry populations around each marked

101   female shrub at three spatial scales: 25 m^2 (2.82 m radius), 50 m^2 (3.99 m radius), and 100 m^2

102   (5.64 m radius). Distances to all neighboring shrubs (by sex) were measured using a Haglöf DME

103   201 Cruiser (Långsele, Sweden) with the transponder centered on the marked plant and the

104   electronic receiver held over the center of all other surrounding shrubs to measure distance to the

105   focal marked female shrub out to a maximum of a 5.64 m radius. In addition to sex-specific

106   densities, distance to nearest male shrub was measured as a simple test of the pollen donor

107   hypothesis (minimum distance) as this is commonly used in the literature. This included

108   measurements beyond 5.64 m (100 m^2) in the few cases where shrub density was low enough that

109   no males were present within the largest sampling scale used (5.64 m radius).

110   Six *a priori* candidate models were defined for each spatial scale (25 m^2, 50 m^2, and 100 m^2)

111   based on the following hypotheses (Table 1): (0) *null model* of equal (mean) fruit set among

112   plants (.); (1) *simple pollen donor or pollen source hypothesis* measured as distance to nearest

113   male shrub or source of pollen ($-\male_{dist}$); (2) *density-dependent hypothesis* measured as total

114   population density ($+D$); (3) *pollen donor hypothesis* measured as male shrub density ($+\male_D$); (4)

115   *pollen competitor hypothesis* measured as female shrub density ($-\female_D$); or (5) *pollen donor and*

116   *pollen competitor hypotheses* combined ($+\male_D -\female_D$). We used density of individual sexes, rather

117   than sex ratio to represent trade-offs between pollen donor and pollen competition hypotheses as

118   a few plots contained only one sex (inferences were similar when analyzing a smaller set of the

119   data using sex ratios as a predictor). We predicted the direction of the response in fruit set for

120   each hypothesis as indicated by the – or + symbols representing negative or positive effects on

121   fruit set respectively. Specific to our hypotheses, we expected fruit set to decrease with distance

122   to nearest male shrub ($-\male_{dist}$) since that is the source of pollen. Likewise fruit set was expected to

123   increase with population density ($+D$), and especially for male density ($+\male_D$), since again this

124   would be the source of pollen. Conversely, we expected fruit set to decrease with local increases

125   in female shrubs since they would be competing for pollen ($-\female_D$). Finally, we predicted an

126   additive effect of male and female shrub density ($+\male_D -\female_D$) on fruit set with male density

127 positively related to fruit set and female density negatively related to fruit set, but not necessarily

128 at the same rate.

129 To test support for these hypotheses, we modeled percent fruit set of buffaloberry based on our

130 hypothesized factors using a generalized linear model (GLM) using STATA 12.1 with a Gaussian

131 family and identity link (McCullagh & Nelder 1989). Collinearity (Pearson correlations > |0.7|)

132 was checked among variables within each model with no problems found. Models were ranked

133 for support using the small sample size corrected Akaike's Information Criterion (AIC_c) where

134 smaller AIC_c values indicate more support of the model given the data and models tested

135 (Burnham & Anderson 2004). Model parameters were estimated for the top AIC_c-selected model

136 and predictions graphed to assist with interpretation.

137 **Results**

138 The most supported candidate models explaining fruit set in buffaloberry were the pollen donor

139 and competitor hypothesis ($+\male_D -\female_D$) at both a 50 m^2 and 100 m^2 scales (Akaike weights, $w_i =$

140 0.470 and 0.263 respectively; Table 2) thus supporting both the pollen donor and pollen

141 competitor hypotheses. These models were followed by the simple pollen donor hypothesis ($-$

142 $\male_{dist}$) that was measured as the distance to the nearest male plant ($w_i = 0.104$; Table 2). All other

143 models had much less support ($\Delta AIC_c \geq 4.6$), including the null model (.) of equal fruit set among

144 shrubs regardless of local demography ($\Delta AIC_c = 7.3$) that was 39.2 times less supported

145 (evidence ratio of Akaike weights, w_i) than our top AIC_c. A simple density-dependence model

146 ($+D$) measuring local shrub density had less support than the null model, illustrating the

147 importance of sex-specific demography and thus opposite effects of sexes on fruit set.

148 Interestingly, the pollen competitor hypothesis ($-\female_D$) alone had the lowest support of all models

149 ($\Delta AIC_c = 9.4$; Table 2), despite being present as a variable in the top supported model which

150   included male density ($+\male_D - \female_D$). When considering the spatial scale at which fruit set was most

151   affected by surrounding shrubs, the 50 m² scale (3.99 m radius) was consistently more supported

152   than the other two spatial scales tested.

153   The top supported model representing the pollen donor and pollen competitor hypothesis ($+\male_D -$

154    $\female_D$ 50m²), measured average fruit set (model constant) among focal female shrubs at 32.9% (SE

155   = 2.9) with each additional increase in male shrub density resulting in an increase in percent fruit

156   set by 3.3 (SE = 0.9) units (Table 3). This supports the pollen donor hypothesis where access to

157   male shrubs affects pollen availability. Female shrub density, on the other hand, was inversely

158   related to percent fruit set with each one unit increase in female density resulting in a 2.1 (SE =

159   0.8) unit decrease in percent fruit set (Table 3) thus also supporting the pollen competitor

160   hypothesis where females compete intra-specifically for pollen. This negative effect on fruit set

161   was, however, evident only after considering pollen donor effects of male shrub density, since

162   there was little support for this effect alone ($w_i = 0.004$; Table 2). Fruit set was also marginally

163   more affected by the presence of males (pollen donor) than females (pollen competitor) with the

164   highest fruit set occurring when sex bias was skewed heavily towards males (Figure 2; see line in

165   graph representing the 1:1 sex ratio).

166   **Discussion**

167   Although a number of studies have demonstrated a negative effect of plant isolation on fruit set,

168   especially for dioecious plants (Kay et al 1984; House 1992; Steffan-Dewenter et al. 1999; De

169   Jong, Batenburg & Klinkhamer 2005; Wang et al. 2013), pollen limitation is not considered in

170   terms of the additive effects of pollen availability (pollen donor) and competition (surrounding

171   female shrubs). We found that density of male and female shrubs at both 50 m² and 100 m²

172   predicted fruit set in buffaloberry better than nearest male neighbor measures. However male

173   density alone was not a better predictor of fruit set than distance to nearest male. This contrasts

174   with studies of fruit set in other dioecious species in which local male density was more

175   significantly related to fruit set than distance to nearest male (House 1992). Our result may be

176   linked to the foraging habits of buffaloberry pollinators, which tend to visit an average of 6

177   flowers per plant, spend a relatively long time at each flower and revisit flowers frequently,

178   indicating that pollinators are not highly mobile and tend to forage within a small area (Borkent

179   & Harder 2007). As a result, proximity to the nearest pollen source is more important than a high

180   concentration of local pollen.

181   Local male density was most predictive of fruit set when considered in terms of the additive

182   effect of increased pollen donors and decreased pollen competitors. Our support for the pollen

183   competitor hypothesis contrasts with the findings of Wang et al. (2013) who found no significant

184   effect of female competition on fruit set in the dioecious tree *Rhamnus davurica*. We show that

185   female density is not a good predictor of fruit set unless considered in conjunction with male

186   density, indicating that future assessments of pollen limitation should consider these factors in

187   terms of their additive or possibly even their multiplicative effects. Competition for pollen at high

188   female densities limits the quantity pollen available to any given female. Because buffaloberry

189   pollinators visit both sexes at equal rates (Borkent and Harder 2007), pollinators are more likely

190   to have visited a female previously and be carrying less pollen in a population with high female

191   density. In addition to facilitating higher fruit set, females occurring within male-biased

192   populations may experience increased long-term fitness. Females with access to a wider choice of

193   mates could produce a surplus of embryos, which would enable selective abortion of lower

194   quality seeds (Melser & Klinkhamer 2001). The reproductive advantages attributed to females

195   occurring within male-biased populations may be necessary to compensate for the greater

196   reproductive costs incurred by females that attract seed dispersers with fleshy fruits. Indeed male-

197   biased sex ratios are common in other long-lived dioecious species with biotic seed dispersal and

198   fleshy fruit (Field, Pickup & Barrett 2012).

199   All demographic factors were most predictive of fruit set at a 50 m^2 scale, indicating that

200   pollinators most actively transfer pollen between plants that are within a 3.99 m radius of each

201   other. Similar studies of dioecious species have documented a threshold of isolation below which

202   fruit set is not limited by insufficient pollinator visits (Kay et al. 1984; De Jong, Batenburg &

203   Klinkhamer 2005). It is likely that the high flight costs of generalist pollinators confine pollinator

204   activities to a small area and discourage travel between patches (Klinkhammer et al. 2001). The

205   high number of flowers visited per plant and rate of re-visits (25.2%, Borkent & Harder 2007)

206   indicates pollinator reluctance to leave a patch once they have begun foraging.

207   The lack of support for the density dependent hypothesis indicates that as well as not biasing

208   visits based on sex, pollinators also do not prefer patches with a higher density of plants. We

209   conclude that the Dipteran pollinators of buffaloberry are opportunistic, and given similar rates of

210   pollinator visitation to males and females, and low and high density patches, females located

211   within male biased populations are least likely to be pollen-limited and will therefore experience

212   higher fruit set.

213   **Conclusion**

214   A male-biased population of buffaloberry surrounding a female shrub (within 3.99 m radius; 50

215   m^2) exhibits higher fruit set, supporting both the pollen donor and pollen competitor hypotheses.

216   Although fruit set in buffaloberry was influenced by both male (positively) and female

217   (negatively) shrub density, local male density had a stronger effect on fruit set. This study

218   demonstrates that local demographics affect fruit set through the additive effects of pollen donors

219   and competitors. More research is needed to understand factors affecting flower production and

220   pollinators of buffaloberry.

221   **Acknowledgements**

222   We thank Andrew Braid and Tyler Bateman for their assistance during fieldwork.

223   **References**

224   Agren J (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb.

225   *Lythrum salicaria*. Ecol 77:1779-1790

226   Armstrong JE, Irvine AK (1989) Flowering, sex ratios, pollen-ovule ratios, fruit set, and

227   reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different

228   rain forest communities. Am J Bot 76:74-85

229   Bawa KS (1980) Evolution of dioecy in flowering plants. Annu Rev of Ecol Evol Syst 11:15-39

230   Borkent CJ, Harder LD (2007) Flies (Diptera) as pollinators of two dioecious plants: behavior

231   and implications for plant mating. Can Entomol 129:235-246

232   Bormann, BT (1988) A masterful scheme: Symbiotic nitrogen-fixing

233   plants of the Pacific Northwest. Univ Washington Arboretum

234   Bulletin 51:10-14.

235   Bowers JE (2009) Branch length mediates flower production and inflorescence architecture of

236   *Fouquieria splendends* (ocotillio). Plant Ecol 186:87-95

237   Burd M (1994) Bateman's Principle and Plant Reproduction: The Role of Pollen Limitation in

238   Fruit and Seed Set. Bot Rev 60:83-139

239   Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model

240   selection. Sociol Method Res 33:261-304

241 Charlesworth D (1993) Why are unisexual flowers associated with wind pollination and

242   unspecialized pollinators. Am Nat 141:481-490

243 City of Edmonton (2009) Terwillegar Park concept plan study.

244   http://www.edmonton.ca/city_government/projects_redevelopment/terwillegar-park-

245   concept-plan-study.aspx. Accessed January 13, 2013

246 De Jong T, Batenburg JC, Klinkhamer PGL (2005) Distance-dependent pollen limitation of seed

247   set in some insect-pollinated dioecious plants. Acta Oecol 28:331-335

248 De Jong T, van Batenburg FHD, van Dijk J (2002) Seed sex ratio in dioecious plants depends on

249   relative dispersal of pollen and seeds: an example using a chessboard simulation model. J

250   Evol Biol 15:373-379

251 Field DL, Pickup M, Barrett SCH (2012) Comparative analyses of sex-ratio variation in

252   dioecious flowering plants. Evol 67:661-672

253 Hamer D (1996) Buffaloberry (*Shepherdia Canadensis)* fruit production in fire-successional bear

254   sites. J Range Manage 49:520-529

255 Heilbuth JC, Ilves KL, Otto PS (2001) The consequences of dioecy for seed dispersal: modeling

256   the seed shadow handicap. Evol 55: 880-888

257 Hendrickson OQ, Burgess D (1989) Nitrogen-fixing plants in a cut-over lodgepole pine stand of

258   southern British-Columbia. Can J For Res 19:936-939

259 Humbert L, Gagnon D, Kneeshaw D, Messier C (2007) A shade tolerance index for common

260   understory species of northeastern North America. Ecol Indic 7:195-207

261 Kay QON, Lack AJ, Bamber FC, Davies CR (1984) Differences between sexes in floral

262   morphology, nectar production and insect visits in a dioecious species, *Silene dioica*. New

263   Phytol 98:515 to 528

264 Khanizadeh S, Buszard D, Fanous MA, Zarkadas CG (1989) Effect of crop load on seasonal

265   variation in chemical composition and spring frost hardiness of apple flower buds. Can J

266   Plant Sci 69:1277-1284

267 Klinkhamer GL, de Jong TJ, Bruyn GJ (1989) Plant size and pollinator visitation in *Cynoglossum*

268   *Officinale*. Oikos 54:201-204

269 Klinkhammer GL, de Jong TJ, Linnebank LA (2001) Small-scale spatial patterns determine

270   ecological relationships: an experimental example using nectar production rates. Ecol Lett

271   4:559-567

272 Knight TM, Steets JA, Vamosi JC, Mazer SJ, Burd M, Campbell DR, Dudash MR, Johnston MO,

273   Mitchell RJ, Ashman T (2005) Pollen limitation of plant reproduction: pattern and process.

274   Annu Rev of Ecol Evol Syst 36:467-497

275 Krebs CJ, Boonstra R, Cowcill K, Kenney AJ (2009) Climatic determinants of berry crops in the

276   boreal forest of the southwestern Yukon. Bot 87:401-408

277 Kunin WE (1993) Sex and the single mustard: population density and pollinator behavior effects

278   on seed set. Ecol 74:2145-2160

279 LaRoi G, Hnatiuk RJ (1980) The *Pinus contorta* forests of Banff and Jasper National Parks: a

280   study in comparative synecology and syntaxanomy. Ecol Monogr 50:1-29

281 Lewis G (1990) Sex ratio, sexual dimorphism and population dynamics in the dioecious shrub

282   *Shepherdia canadensis.* Dissertation, University of Calgary

283 McCray-Batzli J, Zimpfer JF, Huguet V, Smyth CA, Fernandez M, Dawson JO (2004)

284   Distribution and abundance of infective, soilborne *Frankia* and host symbionts *Shepherdia*,

285   *Alnus*, and *Myrica* in a sand dune ecosystem. Can J Bot 82:700-709

286 McCullagh P, Nelder J (1989) *Generalized Linear Models*, Second Edition. Boca Raton:

287   Chapman and Hall/CRC.

288   Melser C, Klinkhamer PGL (2001) Selective seed abortion increases offspring survival in

289   *Cynoglossum officinale* (Boraginaceae). Am J Bot 88:1033-1040

290   Mosquin T (1971) Competition for pollinators as a stimulus for the evolution of flowering time.

291   Oikos 22:398-402

292   Nielsen SE, Munro RHM, Bainbridge E, Boyce MS, Stenhouse GB (2004) Grizzly bears and

293   forestry II: distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada.

294   Forest Ecol Manag 199:67-82.

295   Renner SS, Ricklefs RE (1995) Dioecy and its correlates in flowering plants. Am J Bot 82:596-

296   606

297   Rhoades C, Binkley D, Oskarsson H, Stottlemyer R (2008) Soil nitrogen accretion along a

298   floodplain terrace chronosequence in northwest Alaska: Influence of the nitrogen-fixing

299   shrub *Shepherdia canadensis*. Ecoscience 15:223-230.

300   Slotte T et al. (2013) The Capsella rubella genome and the genomic consequences of rapid

301   mating system evolution. Nature Genet: DOI:10.1038/ng.2669

302   Smith JL, Doran JW (1996) Measurement and use of pH and electrical conductivity for soil

303   quality analysis. In: Doran JW, Jones AJ (eds) Methods for assessing soil quality, Soil Sci

304   Soc Am Spec Publ 49. SSSA, Madison, pp 169-185

305   Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities

306   and seed set. Oecologia 121:432-440

307   Stringer P, LaRoi GH (1970) The Douglas-fir forests of Banff and Jasper National Parks, Canada.

308   Can J Bot 48:1703-1726

Zammit CA, Zedler PH (1992) Size structure and seed production in even-aged populations
of Ceanothus greggi in mixed chaparral. J Ecol 81:499-511

309 **Tables**

310 Table 1: List of candidate models (hypotheses) predicting fruit set in buffaloberry based on

311 demographic factors and scale of measurement.

ID	Hypothesis	Scale	Model
0	Null (mean fruit set)	*N.A.*	.
1	Pollen source (nearest male)	*N.A.*	$-\male_{dist}$
2a	Density dependence	25	$+D_{25}$
2b	Density dependence	50	$+D_{50}$
2c	Density dependence	100	$+D_{100}$
3a	Pollen donor	25	$+\male_{D25}$
3b	Pollen donor	50	$+\male_{D50}$
3c	Pollen donor	100	$+\male_{D100}$
4a	Pollen competitor	25	$-\female_{D25}$
4b	Pollen competitor	50	$-\female_{D50}$
4c	Pollen competitor	100	$-\female_{D100}$
5a	Pollen donor & competitor	25	$+\male_{D25}-\female_{D25}$
5b	Pollen donor & competitor	50	$+\male_{D50}-\female_{D50}$
5c	Pollen donor & competitor	100	$+\male_{D100}-\female_{D100}$

312   Table 2: Ranking of support among candidate models using Akaike's Information Criteria

313   adjusted for small sample size (AIC_c). Hypothesis, model ID, scale, model structure, parameter

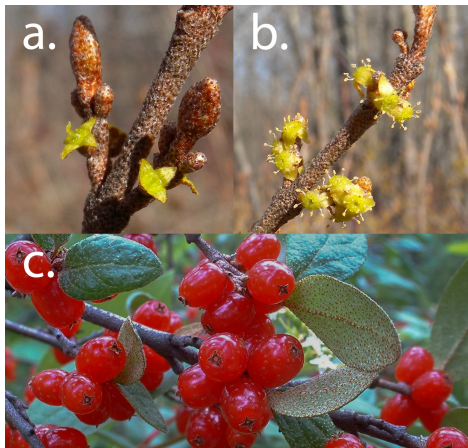
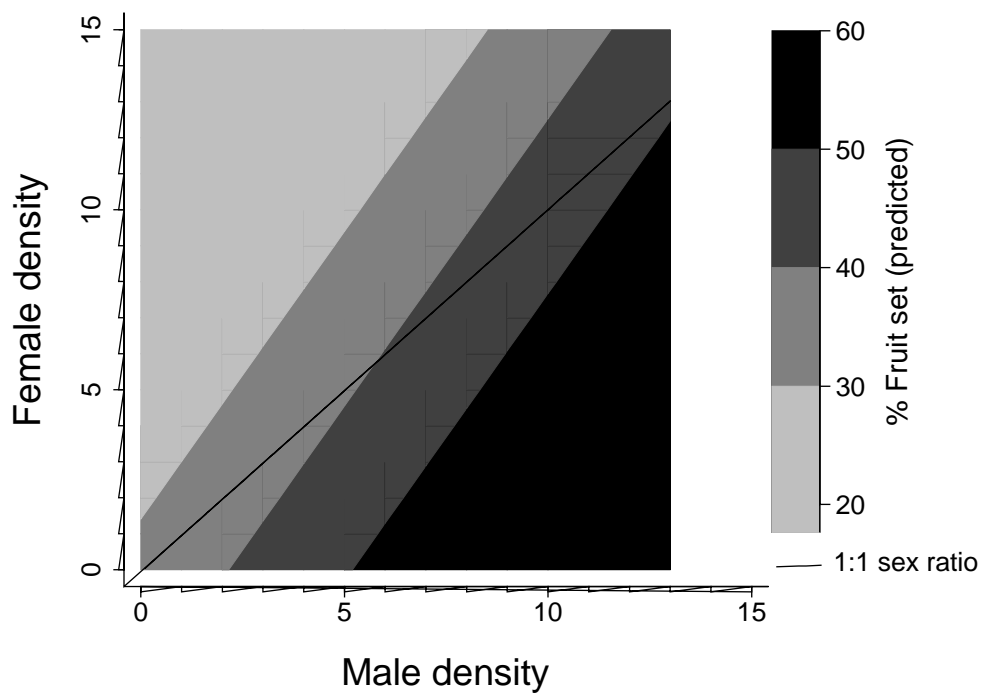
314   number (K), change in AIC_c and Akaike weights (w_i) are also provided.

ID	Hypothesis	Scale	Model	K	AIC_c	ΔAIC_c	w_i
5b	Pollen donor & competitor	50	$+\male_D -\female_D$	3	503.9	0.0	0.470
5c	Pollen donor & competitor	100	$+\male_D -\female_D$	3	505.1	1.2	0.263
1	Pollen source (nearest)	N.A.	$-\male_{dist}$	2	506.9	3.0	0.104
3b	Pollen donor	50	$+\male_D$	2	508.6	4.6	0.046
5a	Pollen donor & competitor	25	$+\male_D -\female_D$	3	508.8	4.9	0.040
3a	Pollen donor	25	$+\male_D$	2	510.4	6.5	0.018
3c	Pollen donor	100	$+\male_D$	2	510.6	6.7	0.016
0	Null (mean fruit set)	N.A.	.	1	511.2	7.3	0.012
2b	Density dependence	50	$+D$	2	512.6	8.7	0.006
2a	Density dependence	25	$+D$	2	512.8	8.9	0.005
2c	Density dependence	100	$+D$	2	512.9	9.0	0.005
4b	Pollen competitor	50	$-\female_D$	2	513.3	9.4	0.004
4a	Pollen competitor	25	$-\female_D$	2	513.3	9.4	0.004
4c	Pollen competitor	100	$-\female_D$	2	513.3	9.4	0.004

315 Table 3: Model parameters for variables included in the most supported candidate model

316 describing fruit set in buffaloberry representing the pollen donor and pollen competitor

317 hypothesis (50 m^2 scale).

Variable	Coef.	SE	95% Conf. Interval	
			Lower	Upper
$\male_{D_{50}}$	3.29	0.94	1.44	5.14
$\female_{D_{50}}$	-2.06	0.78	-3.60	-0.52
constant	32.90	2.91	27.20	38.61

323   Figure 2: Percent fruit set predicted for buffaloberry based on female and male shrub density. A

324   line representing equal sex ratio (1:1) is provided for reference.