

The impact of competition on elephant musth strategies: a game-theoretic model

J. Max Wyse

*Department of Mathematics
Florida State University
1017 Academic Way
Tallahassee, Florida 32306-4510, U.S.A*

Ian C.W. Hardy

*School of Biosciences,
Sutton Bonington Campus
University of Nottingham,
Loughborough, LE12 5RD, UK*

Lisa Yon

ORCID: 0000-0002-9765-3192

*School of Veterinary Medicine and Science,
Sutton Bonington Campus
University of Nottingham,
Loughborough, LE12 5RD, UK*

Mike Mesterton-Gibbons

*Department of Mathematics
Florida State University
1017 Academic Way
Tallahassee, Florida 32306-4510, U.S.A*

Email addresses: jmw11af@my.fsu.edu (J. Max Wyse), ian.hardy@nottingham.ac.uk (Ian C.W. Hardy), lisa.yon@nottingham.ac.uk (Lisa Yon), mesterto@math.fsu.edu (Mike Mesterton-Gibbons)

Manuscript accepted by the Journal of Theoretical Biology, January 17, 2017

Abstract

1 Mature male African Savannah elephants are known to periodically enter a tem-
2 porary state of heightened aggression called “musth,” often linked with increased
3 androgens, particularly testosterone. Sexually mature males are capable of entering
4 musth at any time of year, and will often travel long distances to find estrous females.
5 When two musth bulls or two non-musth bulls encounter one another, the agonistic
6 interaction is usually won by the larger male. However, When a smaller musth bull
7 encounters a larger non-musth bull, the smaller musth male can win. The relative
8 mating success of musth males is due partly to this fighting advantage, and partly
9 to estrous females’ general preference for musth males.

10 Though musth behavior has long been observed and documented, the evolu-
11 tionary advantages of musth remain poorly understood. Here we develop a game-
12 theoretic model of male musth behavior which assumes musth duration as a param-
13 eter, and distributions of small, medium and large musth males are predicted in
14 both time and space. The predicted results are similar to the musth timing behav-
15 ior observed in the Amboseli National Park elephant population, and further results
16 are generated with relevance to Samburu National Park. We discuss small male
17 musth behavior, the effects of estrous female spatial heterogeneity on musth timing,
18 conservation applications, and the assumptions underpinning the model.

Keywords:

evolutionarily stable strategy, African Savannah elephants (*Loxodonta africana*),
animal contests

1. Introduction

19 Musth is a state of heightened aggression that sexually mature male Asian and
20 African elephants temporarily enter, and is particularly associated with mating be-
21 haviour (Poole, 1987, 1989a; Poole et al., 2011; Jainudeen et al., 1972). Though
22 musth has long been known to occur in Asian elephants, musth was first observed in
23 African Savannah elephants in 1981 in the Amboseli population in Kenya (Poole and
24 Moss, 1981; Poole, 1982). Since then, researchers have extensively studied musth in
25 the Amboseli population, finding that, while in musth, Amboseli males compete for
26 females in estrus by engaging in agonistic interactions which are composed primarily
27 of threats, but on rare occasions will escalate into potentially lethal fights (Poole,
28 1989a). Contests are usually won by the larger of the two musth males (Poole, 1989a;
29 Briffa et al., 2013) (see also Chelliah and Sukumar (2013) for Asian elephants) and,

30 because females may be in estrus at any time throughout the year, musth contests
31 can be observed in both the wet and dry seasons (Poole, 1987, 1989a). Females
32 in estrus prefer to be guarded by—and to allow matings with—musth males, and
33 sometimes actively resist mating attempts by non-musth males (Poole, 1989b).

34 For a male of a given size, maximizing reproductive success involves balancing
35 multiple strategic considerations. The male could be more successful if it were in
36 musth during a period in which there is a larger number of females in estrus, but
37 would also benefit from avoiding competitions against larger males for access to those
38 females. A similar tradeoff exists once a male has entered musth and has to decide
39 where within the population’s spatial range to seek estrous females; certain regions
40 are more likely than others to contain estrous females (Croze and Moss, 2011), and
41 musth males will travel large distances searching for them (Croze and Moss, 2011;
42 Poole, 1989a; Barnes, 1982). Moreover, a male of a given size must choose which
43 region to visit while taking into account the expected number of available females
44 against the likelihood of encountering a larger male. Finally, a male that engages
45 in a musth competition may also face the possibility of injury or death in the event
46 that the competition escalates into a more violent confrontation. An optimal musth
47 strategy may therefore need to balance the immediate benefit associated with musth
48 against the possibility that future benefits will be forgone if the male suffers a musth-
49 related injury (Poole, 1989a; Slotow et al., 2000).

50 The large number of strategic considerations involved, and the different time
51 horizons over which they are relevant, has prompted elephant observers to suggest
52 that an unusually complex and long-term perspective is necessary to model musth
53 behavior (for an example, see Poole et al. (2011)), though no such model has thus far
54 been proposed. Here we develop a game-theoretic model that explores the effects of
55 likely key influences on musth strategies. The model suggests that male and female
56 population size, male size distribution and female estrus distribution are sufficient to
57 predict key aspects of musth behavior, though there may be further influences such
58 as injury risk and physiological constraints.

2. Model

59 Consider a population of male elephants that may choose to be located in any of
60 M different spatial areas at any time during a year, which is subdivided into N time
61 periods. In each of these periods, a male may choose whether to be in musth or not.
62 For $i = 1, \dots, M$ and $j = 1, \dots, N$, let V_{ij} represent the intrinsic value of an area i
63 during time period j in terms of mating opportunities (i.e., the expected number of
64 females that a male in area i could monopolize during time period j , given that he
65 defeats all musth competitors in the area).

66 We adopt the following additional assumptions:

67 2.1. Assumptions

- 67 1. There are three size classes of males: small, medium and large.
- 68
- 69 2. Timing strategies for males of all size classes are vectors of probabilities. Let
70 η_j , ξ_j or μ_j be the probability that a large, medium or small male, respec-
71 tively, will enter musth during time period j . Then the population strategies
72 for large, medium and small males are $\vec{\eta} = \langle \eta_1, \eta_2, \dots, \eta_N \rangle$, $\vec{\xi} = \langle \xi_1, \xi_2, \dots, \xi_N \rangle$
73 and $\vec{\mu} = \langle \mu_1, \mu_2, \dots, \mu_N \rangle$, respectively.
- 74
- 75 3. The expected number of time periods that a large, medium or small male will
76 spend in musth is denoted by $T_L = \sum_{j=1}^{j=N} \eta_j$, $T_M = \sum_{j=1}^{j=N} \xi_j$ or $T_S = \sum_{j=1}^{j=N} \mu_j$,
77 respectively.
- 78
- 79 4. Once in musth, each male has a spatial strategy, which can depend on the time
80 period. Let p_{ij} , q_{ij} or w_{ij} be the probability that a large, medium or small male,
81 respectively, competes in area i in time period j . Then the spatial strategies for
82 large, medium and small males are $\vec{p}_j = \langle p_{1j}, p_{2j}, \dots, p_{Mj} \rangle$, $\vec{q}_j = \langle q_{1j}, q_{2j}, \dots, q_{Mj} \rangle$
83 and $\vec{w}_j = \langle w_{1j}, w_{2j}, \dots, w_{Mj} \rangle$, respectively.
- 84
- 85 5. Males mate only while in musth. This is a simplification of natural mating
86 behavior (Hollister-Smith et al., 2007) (see Section 5.3).
- 87
- 88 6. If multiple males are in musth during the same time period and occupy the
89 same area, then they will compete with each other for access to the available
90 estrous females. This competition will always be won by the male in the largest
91 size class. If multiple males are in the largest size class, each one has an equal
92 probability of winning.
- 93
- 94 7. Males attempt to maximize the expected number of mating opportunities over
95 the entire year.
- 96
- 97 8. There is no injury risk or other disincentive to enter musth. The only incentive
98 for an individual to avoid entering musth or going to a given area while in
99 musth is the opportunity cost of spending a portion of his (limited) musth du-
100 ration in an undesirable place or time. This is a simplification of actual musth

101 incentives that we modify later (see Section 5.2).

102

103 9. Estrous females will mate with whichever musth male wins a competitive in-
 104 teraction; that is, female choice does not influence the mating success of male
 105 elephants. This is another simplification of natural mating behavior (Poole,
 106 1989b) (see Section 5.3).

107

108 2.2. Payoffs

109 With the above assumptions, payoff formulas can be derived for the large, medium
 110 and small males. Let $E_L(i, j)$ be the expected payoff that a large male would receive
 111 when in musth in area i during time period j , given that all the other large males
 112 in the population are using timing strategy $\vec{\eta}$ and spatial strategy \vec{p}_j . Similarly,
 113 let $E_M(i, j)$ and $E_S(i, j)$ represent the expected payoff a male (of either size) would
 114 receive for being in musth in area i during time period j , given that all other medium
 115 males are using timing strategy $\vec{\xi}$ and spatial strategy \vec{q}_j while all other small males
 116 are using $\vec{\mu}$ and \vec{w}_j . Lastly, Γ_L, Γ_M and Γ_S are the number of large, medium and small
 117 males in the total population, respectively. With these definitions, it can be shown
 118 that E_L, E_M and E_S have the following expressions (see Appendix A for details):

$$E_L(i, j) = \frac{V_{i,j}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - \eta_j p_{ij})^{\Gamma_L}) \quad (1)$$

$$E_M(i, j) = \frac{V_{i,j}}{\Gamma_M q_{ij} \xi_j} (1 - (1 - \xi_j q_{ij})^{\Gamma_M}) (1 - \eta_j p_{ij})^{\Gamma_L} \quad (2)$$

$$E_S(i, j) = \frac{V_{i,j}}{\Gamma_S w_{ij} \mu_j} (1 - (1 - \mu_j w_{ij})^{\Gamma_S}) (1 - \eta_j p_{ij})^{\Gamma_L} (1 - \xi_j q_{ij})^{\Gamma_M} \quad (3)$$

3. Methods

119 The payoff received by an individual in the above model is dependent on the
 120 frequency of strategies adopted within the population. In an evolutionary context,
 121 the process of natural selection would continually alter the frequency of strategies
 122 adopted within the population until the population arrives at an evolutionarily stable
 123 strategy (ESS); defined as a strategy which, when adopted by the population, cannot
 124 be invaded by any other strategy (Maynard Smith, 1982; McNamara et al., 1997).

125 The expected value formulas defined above are useful because, at an ESS, any
 126 two viable space-time choices $(i, j), (l, k)$ should have an equal expected payoff (May-
 127 nard Smith, 1982). Mathematically, $E_*(i, j)$ must be equal to $E_*(l, k)$ for all viable

128 choices of $(i, j), (l, k)$, where $*$ is either an L, M or S . Because musth males are
 129 unaffected by the musth strategies of smaller male sizes, an ESS can be found by
 130 first numerically solving for the $\vec{\eta}$ and \vec{p} strategies for which $E_L(i, j) = E_L(l, k)$,
 131 then finding the $\vec{\xi}$ and \vec{q} strategies for which $E_M(i, j) = E_M(l, k)$ taking the $\vec{\eta}$ and
 132 \vec{p} strategies from the large male population as environmental constants. Lastly, the
 133 ESS is completed by finding the $\vec{\mu}$ and \vec{w} for which $E_S(i, j) = E_S(l, k)$ while using the
 134 $\vec{\eta}, \vec{p}, \vec{\xi}$ and \vec{q} strategies from the large and medium male populations (for a further
 135 description of the numerical process and a proof that the above algorithm will yield
 136 an ESS, see Appendices **C** and **D**).

137 In the above model each size class has a spatial strategy $(p_j, q_j$ and $w_j)$ as well as
 138 a timing strategy $(\eta, \xi$ and $\mu)$. We define a spatial ESS for a given size class as the
 139 ESS for the spatial subgame that arises when the timing strategy for the size class
 140 (and the strategies of all other relevant size classes) is given. Similarly, we define
 141 a timing ESS for a size class as the ESS for the timing subgame that arises when
 142 the spatial strategies for the size class (and the strategies for all other relevant size
 143 classes) are given. Lastly, a large, medium, or small male ESS is the set of spatial
 144 and timing strategies used by the relevant size class at an ESS.

3.1. Parameter data

145 In a well-known field study of African elephants, Poole (1989a) separated adult
 146 males living in Amboseli National Park (ANP) into 6 different age categories: 1A
 147 (ages 10–14.9), 1B (ages 15–19.9), 2 (ages 20–24.9), 3 (ages 25–34.9), 4 (ages 35–49.9)
 148 and 5 (ages 50+). Groups 1A and 1B were never observed mating, and therefore are
 149 not considered relevant to the above model. Because male African elephants con-
 150 tinue to grow until late in life (Poole, 1989a; Poole et al., 2011; Briffa et al., 2013),
 151 we assumed that the older age categories contained larger males, and therefore we
 152 set Γ_S equal to the number of males in category 2; we set Γ_M equal to the number
 153 of males in category 3; and we set Γ_L equal to the combined number of males in
 154 categories 4 and 5. The relevant numbers are as follows:

- 155
 156 category 2: 42 males ($\Gamma_S = 42$)
 157 category 3: 36 males ($\Gamma_M = 36$)
 158 category 4: 19 males
 159 category 5: 2 males ($\Gamma_L = 19 + 2 = 21$)

160
 161 Poole (1989b) recorded (over a multiple-year time period) the number of observed
 162 estrous females in ANP by month, and obtained the following list (see also Figure
 163 1):

Month	J	F	M	A	M	J	J	A	S	O	N	D
Females	34	35	61	52	35	53	56	25	23	12	11	16

Table 1: The observed number of estrous females by month as reported by Poole (1989b)

164 Additionally, Poole et al. (2011) collected musth data and calculated median
165 durations for the separate age classes, finding a median duration of 2 days for 16–25
166 year old males, 13 days for 26–35 year old males and 69 days for 41–45 year old
167 males. The expected number of time periods (months) spent in musth for each size
168 class was found by dividing these averages by 30 (that is, the number of days per
169 month was assumed to be 30), and therefore the following musth duration parameters
170 were derived : $T_L = 2.3$ (69/30), $T_M = 0.433$ (13/30) and $T_S = 0.133$ (4/30). Note
171 that a value of 4/30 was used for the small males because of the inclusion of 16–19
172 year old males in the Poole et al. (2011) data set, which is not consistent with the
173 assumption that "small" males are between the ages of 20 and 24.9. The addition of
174 younger males into the age set likely lowered the median observed musth duration
175 (meaning that 2 days is likely a lower bound for T_S), while Poole (1989a) suggests
176 that males under the age of 25 are unlikely to have a median musth duration over a
177 week (meaning that 7 days is a likely upper bound for T_S). A musth duration of 4
178 days was chosen as a midpoint between these two bounds.

179 To test the above model, we set the number of time periods in each year to
180 $N = 12$, and we chose $M = 4$ for the number of areas. To obtain V_{ij} values, the
181 estrous females were assumed to be uniformly distributed in space, and therefore
182 V_{ij} is proportional to the number of females in estrus during time period j . For
183 example, there are 12 estrous females in October and 4 areas, thus we assume that
184 there are 3 estrous females in each area during October (the females are uniformly
185 distributed in space but not in time). Furthermore, by setting $T_L = 2.3$, $T_M = 0.433$
186 and $T_S = 0.133$ an ESS can be found numerically (as described in Appendix C).

187 For the purposes of discussion, the time periods are divided into a "wet sea-
188 son" (January through to July) and a "dry season" (August through to December),
189 which were chosen to correspond with periods of high estrous female availability and
190 low estrous female availability, respectively. This seasonal designation differs from
191 wet/dry season categorizations based on rainfall, as precipitation often predicts es-
192 trous female availability with a lag (Poole et al., 2011). Poole (1989a), for example,
193 refers to February through to July as the "wet season," while August through to
194 January are designated as the "dry season." Alternatively, Moss (2001) recognizes
195 two wet seasons, the "long rains" associated with March, April and May, and the
196 "short rains" associated with November and December.

4. Results

197 The spatial ESS was to compete in each area with equal probability. The timing
 198 ESS is depicted in Figure 1:

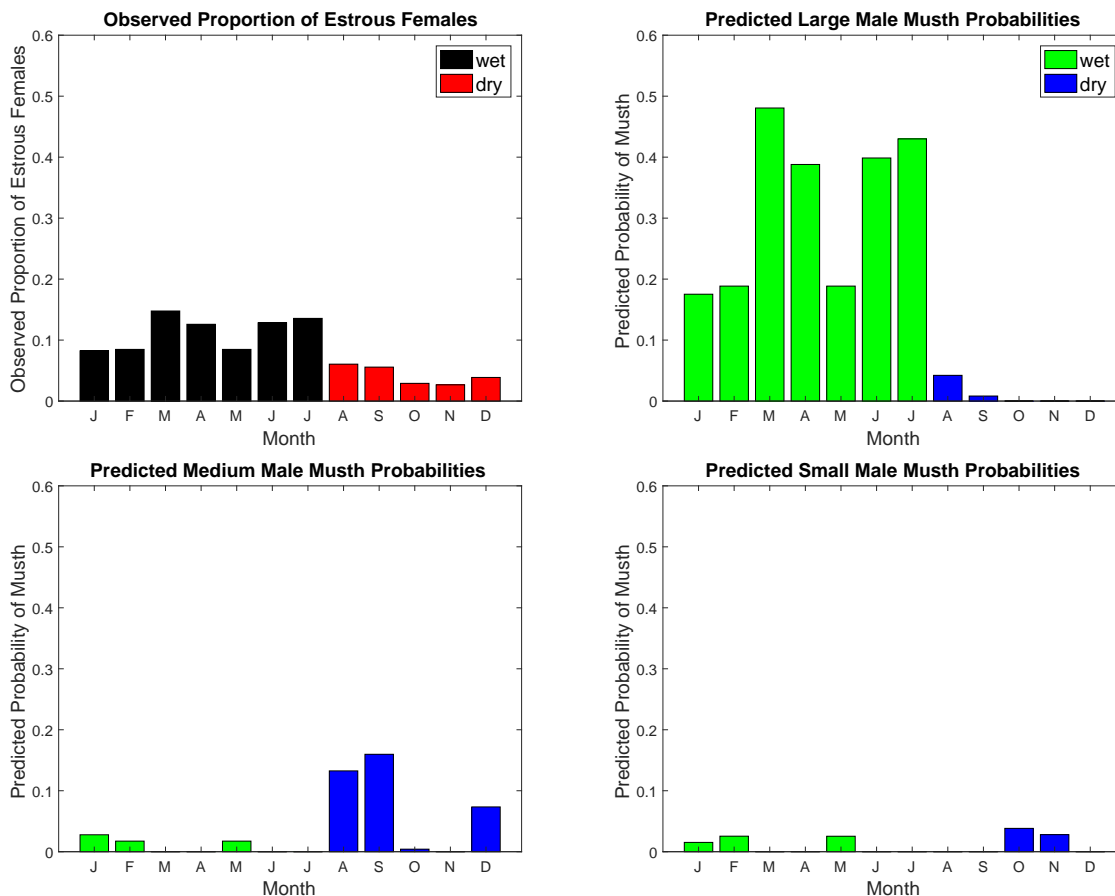


Figure 1: The observed proportion of estrous females by month as reported by Poole (1989b) (top left), the predicted equilibrium probabilities of being in musth by month for a large male (top right), medium male (bottom left) and small male (bottom right) with $\Gamma_L = 21$, $\Gamma_M = 36$ and $\Gamma_S = 42$.

199 As can be seen in Figure 1, predicted large-male timing strategies are broadly
 200 coincident with the observed distribution of estrous females, meaning that large
 201 musth males are most densely concentrated in wet season months (defined here as
 202 January through to July). Medium sized musth males, however, are concentrated
 203 in dry season months, and small males are most likely to be in musth during wet
 204 season months with the fewest number of estrous females (and therefore the lowest
 205 concentration of large males in musth during the wet season).

4.1. The impact of population size

206 To demonstrate how the strategies adopted by the different size classes are af-
 207 fected by population variance, an alternative simulation was run with parameter sets
 208 that differed from the first simulation only with respect to the number of large males
 209 in the population. The large male population was perturbed because, under the
 210 assumptions of the model, the behavior of larger males influences male behavior in
 211 smaller size classes but smaller males do not influence the behavior of males in larger
 212 size classes. For the alternative simulation, the population numbers for the different
 213 size classes were set with $\Gamma_L = 25, \Gamma_M = 36, \Gamma_S = 42$. A relatively small perturbation
 214 in the number of large males was used to exhibit the interaction between size and
 215 population number. That is, a small change in the number of males in a given size
 216 class will have a small impact on the behavior of males in the same size class, but a
 217 potentially larger impact on males of smaller sizes. An ESS was solved numerically
 218 and the results are displayed in Figure 2.

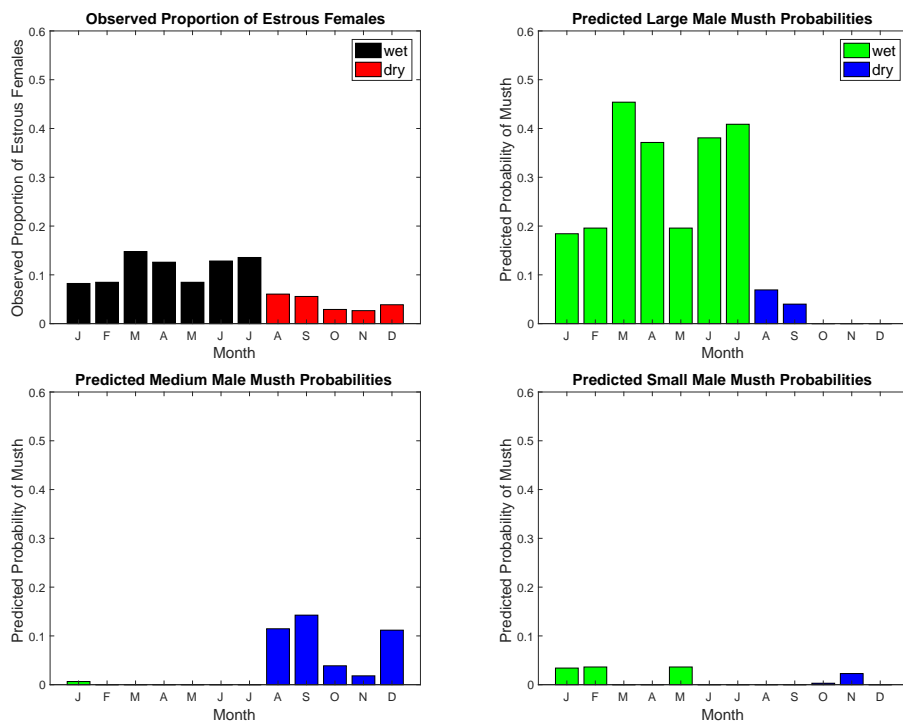


Figure 2: The observed proportion of estrous females by month as reported by Poole (1989b) (top left), the predicted equilibrium probabilities of being in musth by month for a large male (top right), medium male (bottom left) and small male (bottom right) using an increased large male population.

219 Some elephant populations suffer from heavy poaching activity, which disproportio-
 220 nately affects the large male population. Therefore, understanding how a reduc-
 221 tion in the large male population will influence behavior in the general population is
 222 relevant from an ecological perspective. Two additional simulations with more ex-
 223 treme reductions in the large male population were run, and the results are displayed
 224 in Figure 3. The results of Figure 3 are further discussed in section 5.4.

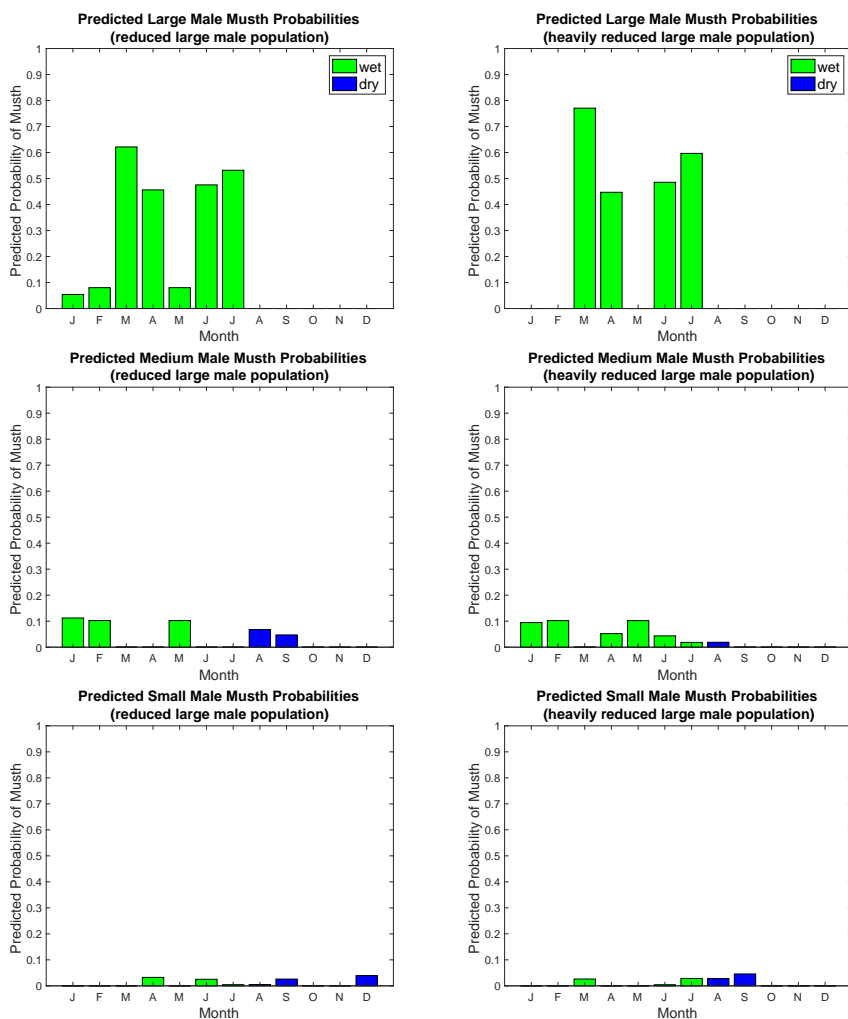


Figure 3: The predicted equilibrium probabilities of being in musth by month for a large male (top left), medium male (middle left) and small male (bottom left) using $\Gamma_L = 10, \Gamma_M = 36, \Gamma_S = 42$. The predicted equilibrium probabilities of being in musth by month for a large male (top right), medium male (middle right) and small male (bottom right) using $\Gamma_L = 5, \Gamma_M = 36, \Gamma_S = 42$. All other parameters are identical to those used in Figure 1.

4.2. *Musth strategy with a non-uniform distribution of estrous females*

225 In the above simulations it was assumed that estrous females were distributed
 226 uniformly across space, thus causing the musth ESS to be uniform in space as well,
 227 varying only in time. To explore the possible implications of adding spatial com-
 228 plexity to the distribution of estrous females, two simulations were run that utilize
 229 V_{ij} values based on Croze and Moss (2011), who have identified four major regions
 230 in Amboseli National Park and also noted which regions different family groups in-
 231 habit during different seasons. By assuming that the number of estrous females in a
 232 given area was proportional to the number of family groups in that area (and also
 233 proportional to the number of estrous females observed per month, as recorded by
 234 Poole (1989a)) the following V_{ij} values were derived (letting $M = 4$):

235

Areas	V_{i1}	V_{i2}	V_{i3}	V_{i4}	V_{i5}	V_{i6}	V_{i7}	V_{i8}	V_{i9}	V_{i10}	V_{i11}	V_{i12}
1	0.667	0.687	1.196	1.02	8.922	13.51	14.275	6.373	5.863	3.059	2.804	4.078
2	8	15.098	26.314	22.431	6.863	10.392	10.980	4.902	4.510	2.353	2.588	3.765
3	5.333	5.490	9.569	8.157	5.490	8.314	8.784	3.922	3.608	1.882	1.725	2.510
4	20	13.725	23.922	20.392	13.725	20.784	21.961	9.804	9.02	4.706	6.471	9.412

Table 2: The space–time distribution of estrous females derived from Croze and Moss (2011)

236 The assumption that the number of estrous females in a given area is proportional
 237 to the number of family groups in that area is a simplification. Several factors
 238 may contribute to the number of estrous females available at a given time, most
 239 notably, areas that have received more rainfall are likely to also have better vegetation
 240 availability, which in turn affects the physiological condition of local females and
 241 therefore the probability of estrus (Poole et al., 2011). Similarly, a female that enters
 242 estrus one year is unlikely to enter estrus again in the years that follow, meaning that
 243 the number of estrous females available in an area one year will also be a function of
 244 the number of females that had been in estrus during previous years (Moss, 2001).
 245 Nonetheless, the above V_{ij} values provide a useful comparison to the uniform spatial
 246 distribution.

247 Using the above V_{ij} values, a simulation was run with the population values
 248 $\Gamma_L = 21, \Gamma_M = 36, \Gamma_S = 42$ and musth duration parameters $T_L = 2.3, T_M = 0.433$
 249 and $T_S = 0.133$. Additionally, a second simulation was run using the modified V_{ij}
 250 values and the same population values, but with longer musth duration parameters
 251 chosen to approximate the upper limit of observed musth duration for each size class

252 (Poole, 1987). The modified musth duration parameters are $T_L = 4, T_M = 1.2$ and
253 $T_S = 0.5$. The results for both simulations are displayed in Figure 4.

254 The two simulations in Figure 4 show different basic patterns of behavior. With
255 the second simulation, the timing of musth in large, medium and small males was
256 predominantly in the wet, dry and wet seasons respectively, similar to the distribu-
257 tions seen in Figures 1 and 2. The results in the first simulation, however, predict
258 that the timing of musth for large, medium and small males is predominantly in the
259 wet, dry and dry seasons respectively. The difference in the behavior of the small
260 males is not large in absolute terms, but is large in relative terms owing to the small
261 amount of time small males are in musth. Another noticeable effect of allowing the
262 distribution of estrous females to vary in space as well as time was to make a larger
263 number of months viable as a part of the musth timing strategies used by the differ-
264 ent size classes. This is because small and medium sized males can avoid larger males
265 in space rather than in time, and because there are dense (spatial) concentrations
266 of estrous females that allow the use of dry season months to form part of a viable
267 large male musth timing strategy.

268 In order to gauge the sensitivity of the computed ESS to further variation in the
269 distribution of estrous females, a null simulation was run with the estrous females
270 available each time period distributed randomly across the four areas. The results of
271 the null simulation were then compared against the results from two other simulations
272 that used more extreme distributions. The first comparison is between the null
273 simulation and a simulation that assumes estrous females are distributed uniformly
274 across the four regions, and can be seen in Figure 5. The second comparison is
275 between the null simulation and a simulation in which all the available estrous females
276 are clustered in a single region each time period and can be seen in Figure 6.

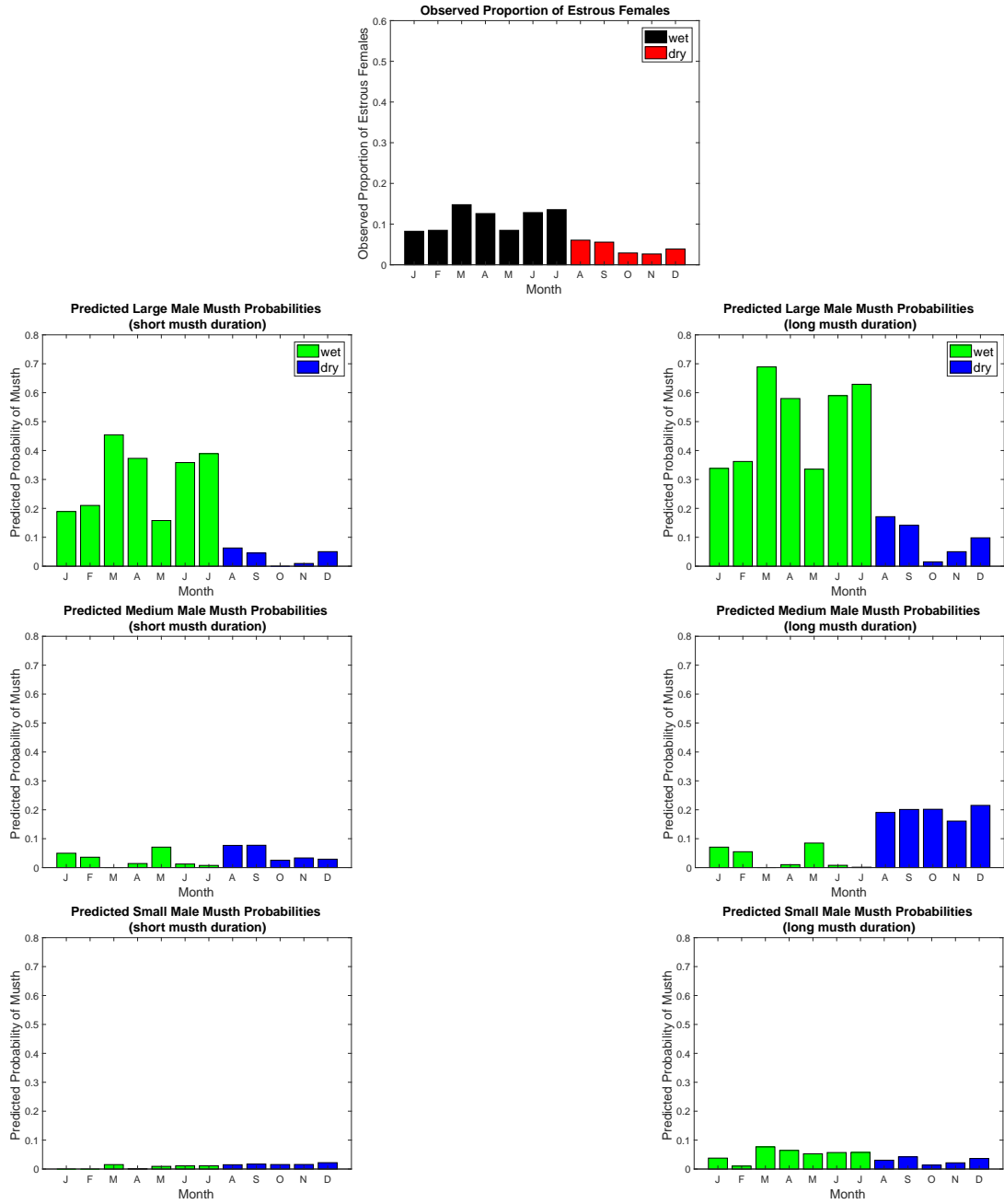


Figure 4: The observed proportion of estrous females by month as reported by Poole (1989b) (top), the predicted equilibrium probabilities of being in musth by month for a large, medium and small male with the shorter musth duration parameters (bottom three panels on left) and the predicted equilibrium probabilities of being in musth by month for a large, medium and small male with the longer musth duration parameters (bottom three panels on right). The model assumes spatial heterogeneity among estrous females.

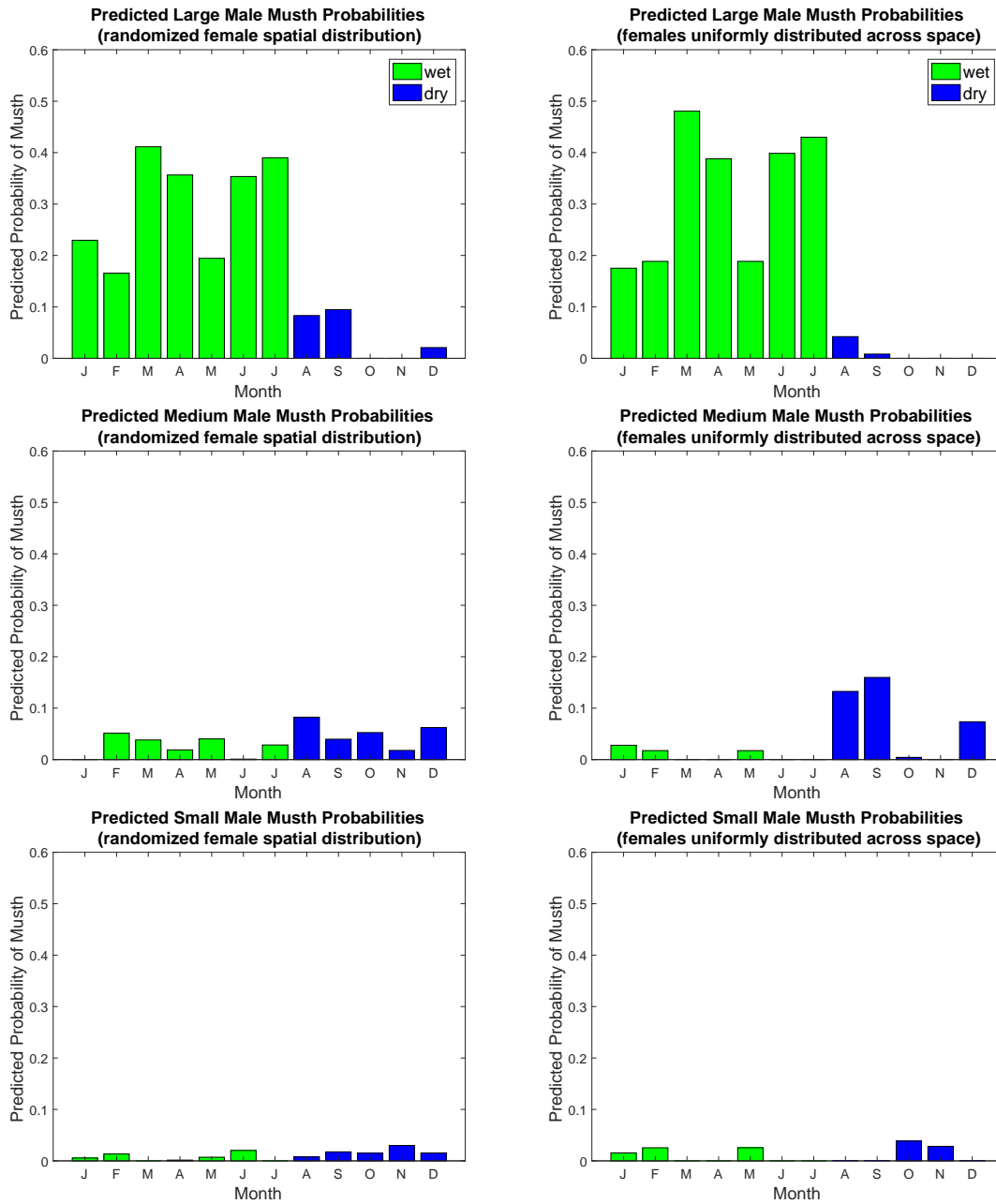


Figure 5: The predicted equilibrium probabilities of being in musth by month assuming a random spatial distribution of estrous females for a large male (top left), medium male (middle left) and small male (bottom left), and the predicted equilibrium probabilities of being in musth by month assuming a uniform distribution of estrous females (across 4 areas) for a large male (top right), medium male (middle right) and small male (bottom right). Calculated with $\Gamma_L = 21$, $\Gamma_M = 36$, $\Gamma_S = 42$, $T_L = 2.3$, $T_M = 0.433$ and $T_S = 0.133$.

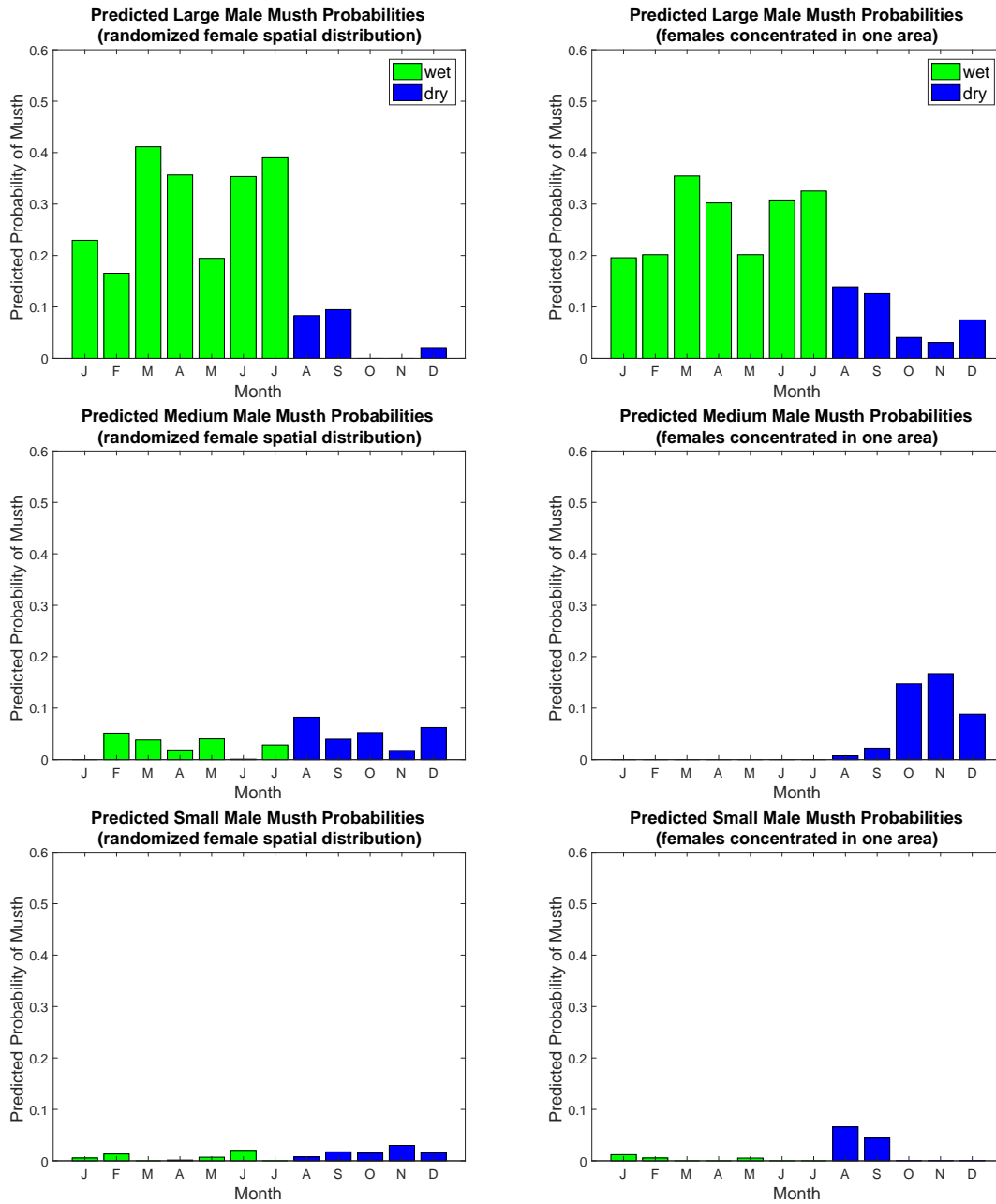


Figure 6: The predicted equilibrium probabilities of being in musth by month assuming a random spatial distribution of estrous females for a large male (top left), medium male (middle left) and small male (bottom left), and the predicted equilibrium probabilities of being in musth by month assuming all estrous females are concentrated in a single area for a large male (top right), medium male (middle right) and small male (bottom right). Calculated with $\Gamma_L = 21$, $\Gamma_M = 36$, $\Gamma_S = 42$, $T_L = 2.3$, $T_M = 0.433$ and $T_S = 0.133$.

4.3. *The Samburu population*

277 The behavioral data on which the above model is based were drawn largely from
278 the Amboseli population. To see how the model might be applied to other popu-
279 lations, male population data for the Samburu population in northern Kenya were
280 taken from Rasmussen et al. (2008). Additionally, Rasmussen (2001) separates Sam-
281 buru National Park into 9 areas (10km each lying along the Ewaso Ngrio river), and
282 reports the number of adult individuals observed in each area along with the percent-
283 age that were female. Rasmussen (2001) also reports 216 known breeding females at
284 the end of 1999, and assumes that on average 25 percent will enter estrous each year
285 based on gestation and post-birth refraction periods. Lastly, using observed birth
286 dates from 1998–2000 and gestation period length, Rasmussen (2001) estimates the
287 proportion of estrous females in each month. Assuming (as above) that the number
288 of estrous females in each area during a given time period is proportional to the
289 number of females observed in the area as well as the number of females expected to
290 be in estrus during that time period, V_{ij} values were derived. A simulation was run
291 with $\Gamma_L = 12$, $\Gamma_M = 24$, $\Gamma_S = 17$ and the number of areas $M = 9$. The musth dura-
292 tion parameters remain the same as those used in Figure 1 ($T_L = 2.3$, $T_M = 0.433$,
293 $T_S = 0.133$). The results are displayed in Figure 7.

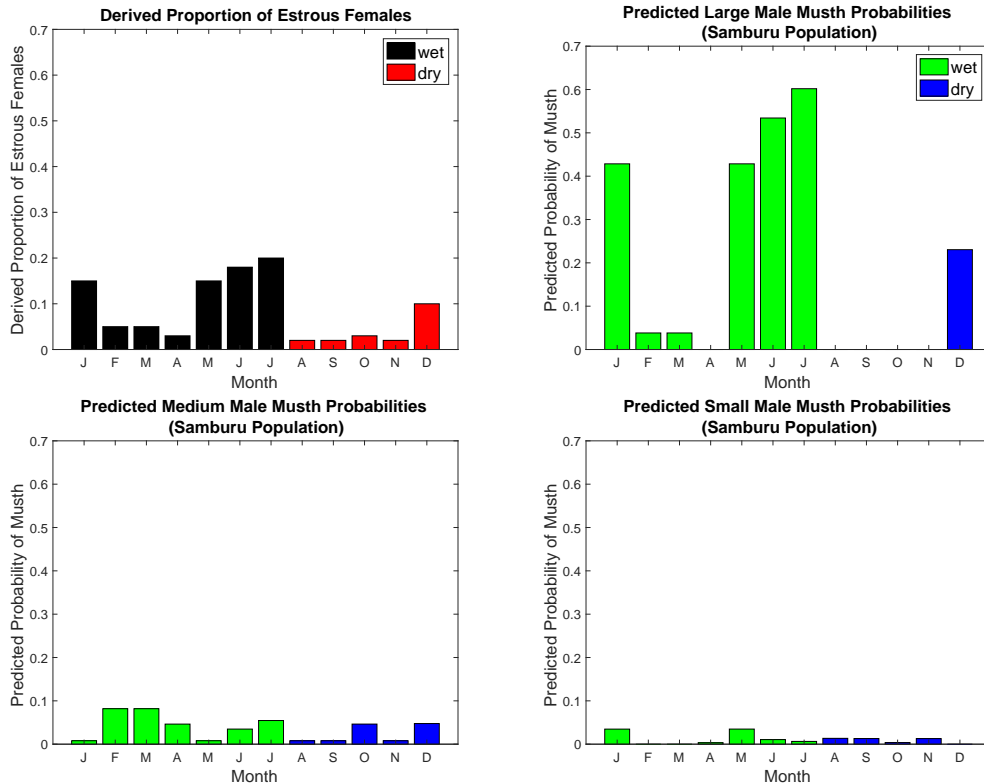


Figure 7: The proportion of estrous females by month derived by Rasmussen (2001) (top left), the predicted equilibrium probabilities of being in musth by month for large males (top right), medium males (bottom left) and small males (bottom right). Calculated with $\Gamma_L = 12, \Gamma_M = 24, \Gamma_S = 17, M = 9$ and the musth duration parameters from Figure 1. The model assumes spatial heterogeneity among estrous females.

294 The results depicted in Figure 7 are notable in that the medium sized males are
 295 often in musth during the wet season. This is due to the relatively small number
 296 of larger males ($\Gamma_L = 12$) and to the larger number of areas inhabited by estrous
 297 females ($M = 9$).

4.4. Observed and predicted musth timing behavior

298 To empirically evaluate the above model, the predicted musth timing probabili-
 299 ties were compared to musth timing data from Poole (1982). Poole (1982) recorded
 300 both estimated age and observed musth timing behavior in 23 male African Ele-
 301 phants sampled from a larger population over two years (1980–1981). Each male
 302 was classified as either "large" or "medium" (no small males were sampled) using

303 the age classes described in the parameter data section, then were marked as ei-
 304 ther "in musth" or "not in musth" for each month. The resulting observed musth
 305 distribution for 1980 is shown in Figure 8.

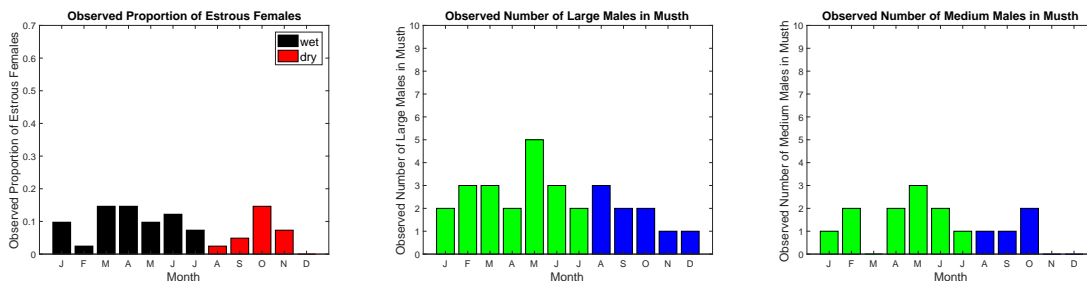


Figure 8: The observed number of estrous females per month, and the observed number of large and medium males in musth per month in 1980.

306 The observed musth behavior differs from the predicted musth behavior shown
 307 in Figure 1. However, the results in Figure 1 were computed using male popula-
 308 tion values from Poole (1989a), which used data collected over a longer time frame
 309 (January 1976 to June 1986). Furthermore, Figure 1 also assumed a uniform spa-
 310 tial distribution of estrous females. To improve the predictive power of the model,
 311 the uniform spatial distribution of estrous females was replaced by the spatial dis-
 312 tribution used in Figure 4. Most importantly, however, the question remains as to
 313 whether the aggregated estrous female data from Poole (1989b) should be used, or
 314 if year-specific estrous female data would be more appropriate. The argument for
 315 using aggregated data is that the model assumes male musth timing is contingent
 316 on the *expected* rather than observed estrous female timing, so that using an average
 317 of female timing behavior over a longer interval may be preferable (see Poole et al.
 318 (2011) for a discussion of the "inherent stochasticity" of the factors influencing male
 319 elephant behavior). Alternatively, males may estimate the expected estrous female
 320 distribution for a given year using year-specific environmental heuristics, such as
 321 relying on rainfall or the availability of vegetation. To the extent that such year-
 322 specific heuristics are used, year-specific estrous female data may be a more reliable
 323 estimate of the expected estrous female distribution. Results from simulations using
 324 both aggregated estrous female timing data and estrous female data specific to 1980
 325 are depicted in Figure 9.

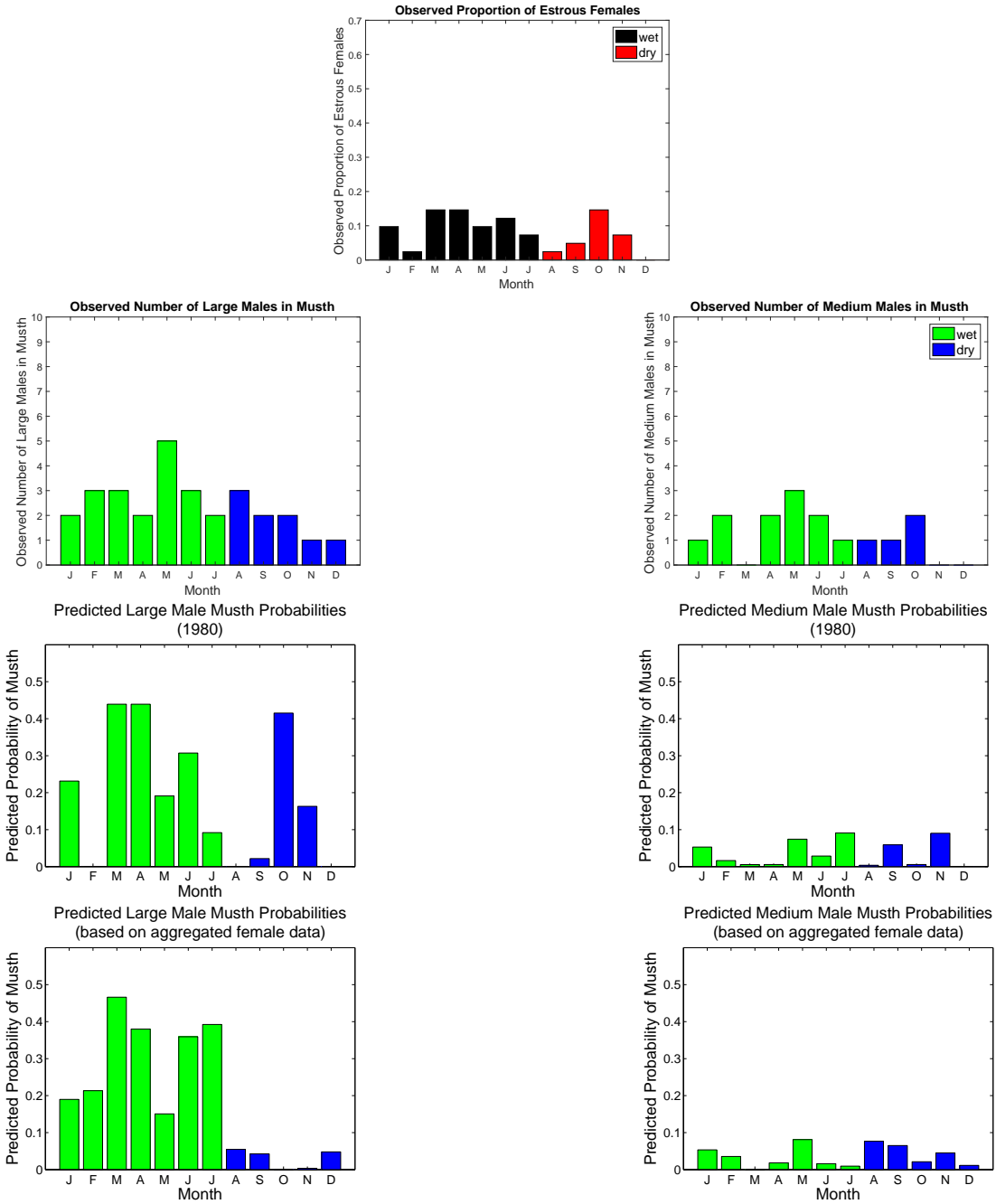


Figure 9: The observed number of estrous females each month in 1980 (top), the observed and predicted number of large musth males each month in 1980 (bottom three rows, left). The observed and predicted number of medium musth males each month in 1980 (bottom three rows, right). Calculated with $T_L = 2.3$, $T_M = .433$, $\Gamma_L = 19$, $\Gamma_M = 25$ and using estrous female data from Poole (1987). Estrous female data can be seen in Figure 11.

326 Additionally, similar simulations were carried out using data from 1981, as shown
 327 in Figure 10. Note that no estrous female observational data were available for
 328 November and December, and therefore the simulations assumed a value of 0 observed
 329 estrous females because no estrous females were observed during surveys carried out
 330 from July to October.

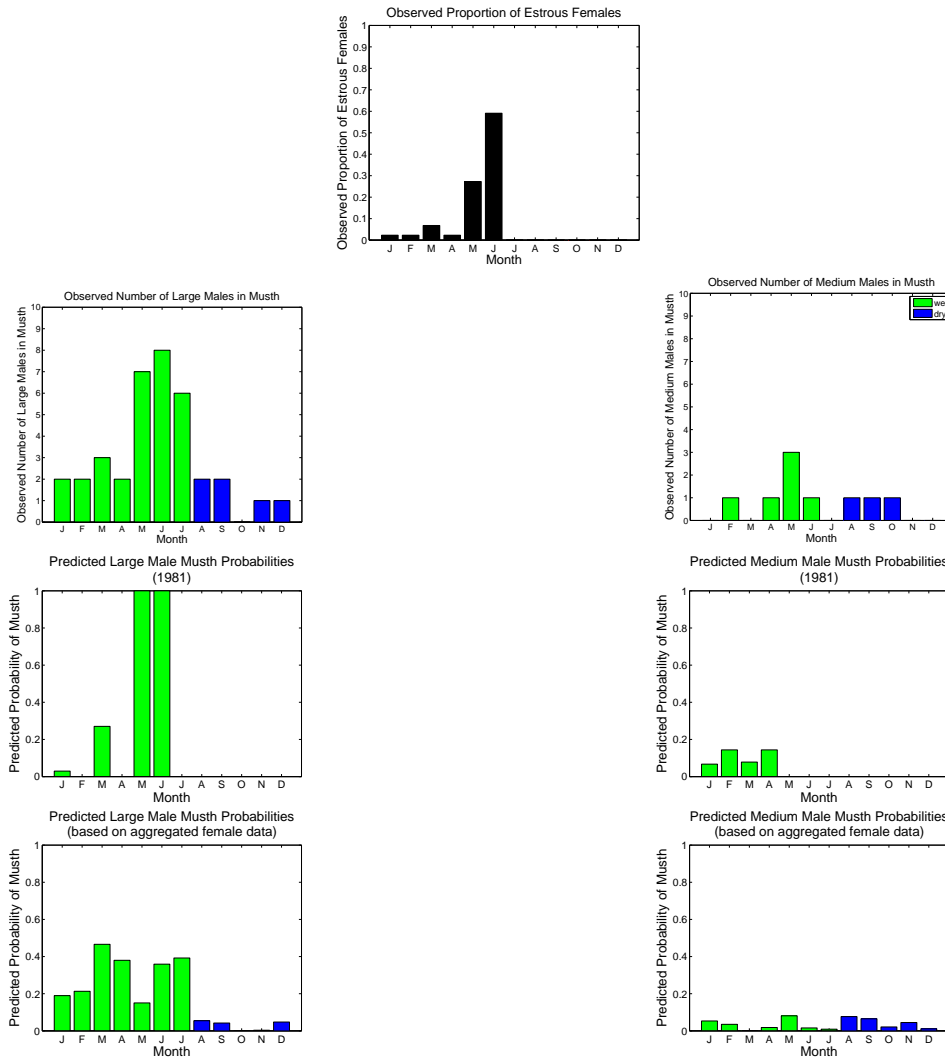


Figure 10: The observed number of estrous females each month in 1981 (top), the observed and predicted number of large males in musth each month in 1981 (bottom three rows, left). The observed and predicted number of medium males in musth each month in 1981 (bottom three rows, right). Calculated with $T_L = 2.3$, $T_M = .433$, $\Gamma_L = 19$, $\Gamma_M = 25$, and using estrous female data from Poole (1987). Estrous female data can be seen in Figure 11.

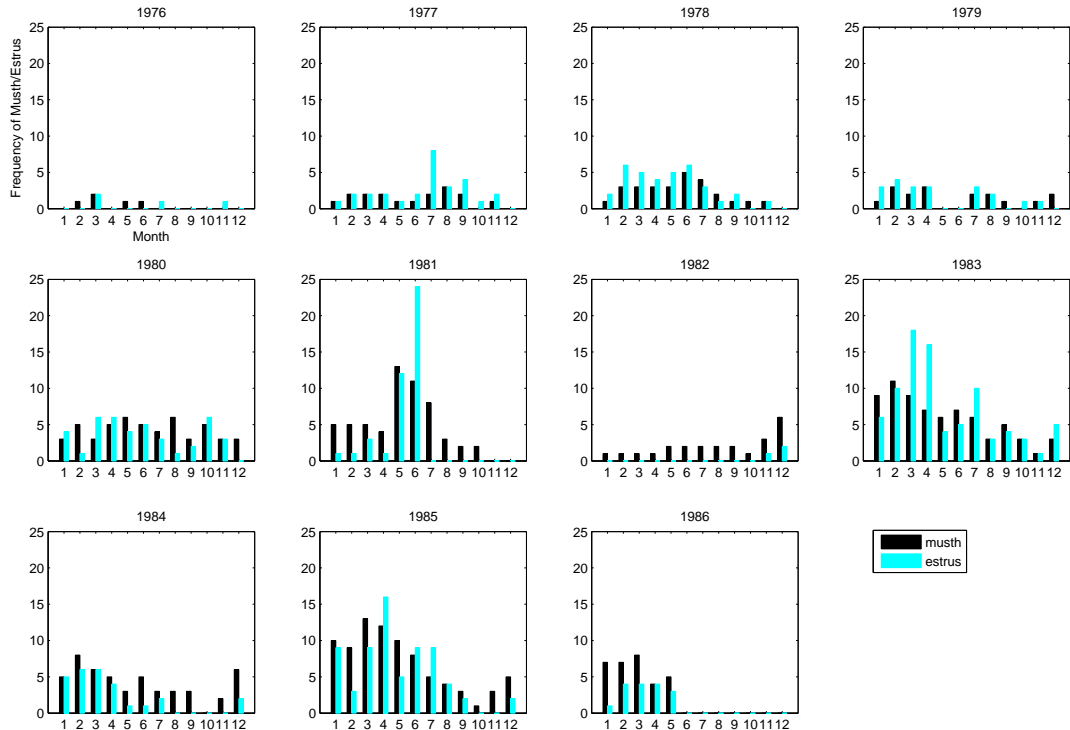


Figure 11: The number of estrous females observed by month versus the number of musth males observed by month. Based on Figure from Poole (1987).

331 To further compare the predicted musth timing probabilities shown in Figures
 332 9 and 10 with the observed number of musth males in each size class, p-values for
 333 each month in each simulation and size class were computed. Because each monthly
 334 probability in each simulation and size class represents a separate hypothesis, a
 335 simple significance test is not appropriate given the large number of resulting p-
 336 values. The Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995) was
 337 therefore applied to the set of p-values associated with each size class per simulation
 338 using a false discovery rate of $\alpha = 0.05$ and a significance threshold of $q^* = 0.05$.
 339 Note that the computed large and medium male ESS uses total population values
 340 ($\Gamma_L = 19$, $\Gamma_M = 25$, Γ_S does not affect the medium or large male ESS and is not
 341 reported), while the computed p-values are based only on the 23 sampled males.
 342 The number of months for which the predicted musth probability can be rejected are

343 displayed below:

	Months Rejected	Months Accepted
Large (1980)	3	9
Large (1980, Aggregated)	1	11
Medium (1980)	3	9
Medium (1980, Aggregated)	0	12
Large (1981)	10	2
Large (1981, Aggregated)	1	11
Medium (1981)	5	7
Medium (1981, Aggregated)	0	12

Table 3: The number of monthly probabilities rejected and accepted for each simulation

344 The simulations that use aggregated data to estimate the expected distribution of
 345 estrous females appear to perform better than the simulations that use year-specific
 346 data. The aggregated data simulations for both 1980 and 1981 have only one month
 347 that can be rejected for the large males and no months rejected for the medium
 348 males. Additionally, the model predictions also appear to fit the 1981 data better
 349 than the 1980 data, which can be observed by increasing the false discovery rate to
 350 $\alpha = 0.2$. If the larger α value is used on the aggregated data simulations, the number
 351 of rejections increases for 1980 though not for 1981, as can be seen below:

	Months Rejected	Months Accepted
Large (1980, Aggregated)	4	8
Medium (1980, Aggregated)	6	6
Large (1981, Aggregated)	1	11
Medium (1981, Aggregated)	0	12

Table 4: The number of monthly probabilities rejected and accepted for the aggregated data simulations, using the false discovery rate $\alpha = 0.2$

352 There are, however, some important caveats for the above simulations. Firstly,
 353 the spatial distribution of estrous females is based on the observed distribution of all
 354 females as reported in Croze and Moss (2011), which both assumes that the number
 355 of estrous females in an area is proportional to the number of females in an area, and
 356 does not capture any yearly variation in the spatial distribution of estrous females
 357 that may have existed in 1980 or 1981. Furthermore, the age categories from Poole
 358 (1989a) may not be ideal approximations for size designations. Using the age-size
 359 designations derived from Croze and Moss (2011) and Poole (1989a), there are no

360 small males among the 23 individuals from Poole (1982). Yet in the same group of
361 males Poole (1982) noted three distinct subgroups of males.

362 Members of group 1, which was made up of the oldest males, came into musth
363 before associating with females, and stayed in musth for the entirety of time spent
364 associating with females. Group 2, made up of males old enough to be considered
365 "large" by the age categories from Croze and Moss (2011), entered musth after
366 associating with females for several weeks and often dropped out of musth before
367 they left the females. Group 3 males, which included males from both the "large" and
368 "medium" age categories, often associated with females for a month before entering
369 musth, were rarely in musth for more than a few days, could be forced out of musth
370 by other males and entered and exited musth multiple times while associating with
371 females. These three groups exhibit behaviors similar to the large, medium and
372 small size classes described in the model, suggesting that the age thresholds should
373 be increased so that some of the medium sized males would be classified as small,
374 and some of the large males would be classified as medium sized.

375 The most important caveat, however, is that the numbers of expected estrous
376 females (the V_{ij} values) used in the above simulations are assumed to be the same as
377 the numbers of observed estrous females. Furthermore, the correlation between the
378 observed number of musth males and the observed number of estrous females does
379 not always hold, even for the large males which are the most likely to have musth
380 periods that coincide with peak estrous female availability (Poole, 1987). This could
381 be because large males have good information regarding estrous female availability,
382 but choose musth timing strategies based (at least in part) on factors not considered
383 in the model; however, it is also consistent with the hypothesis that musth males hold
384 imperfect information regarding female availability and therefore sometimes "guess
385 incorrectly."

386 The model presented here predicts that large males will more frequently be in
387 musth during periods with relatively large numbers of estrous females. Not surpris-
388 ingly, the model performs better when large male musth periods are more strongly
389 correlated with the number of available estrous females, as seen in Figure 12.

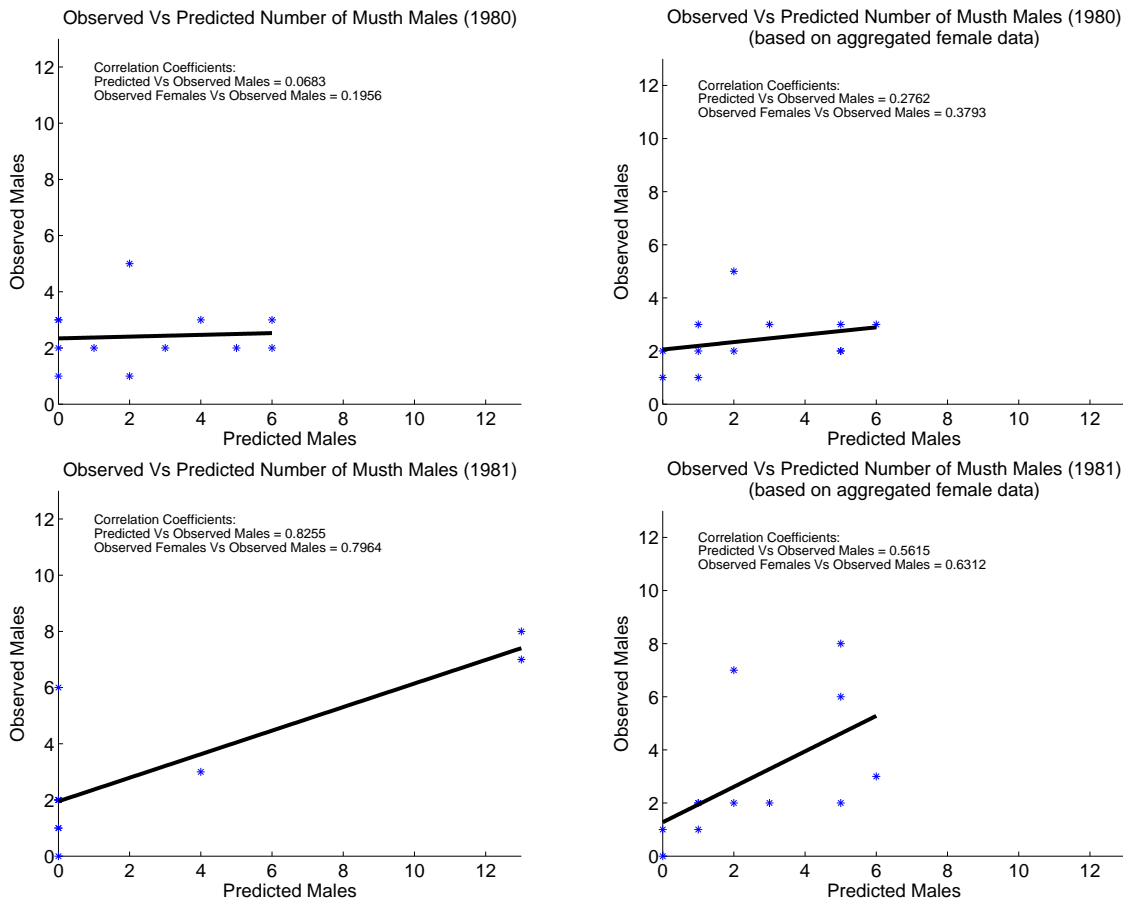


Figure 12: The observed number of large males in musth each month versus the predicted number of large males in musth each month for 1980 (year-specific data, top left) 1980 (Aggregated data, top right), 1981 (year-specific data, bottom left) and 1981 (Aggregated data, bottom right). Additionally, The Pearson product-moment correlation coefficient between the number of observed large musth males each month and the number of predicted large musth males each month is depicted in the upper left corner of each panel, along with the correlation coefficient between the number of observed estrous females each month and the number of observed large musth males each month. Both coefficients were computed for both 1980 and 1981, using both year-specific and aggregated estrous female data.

390 4.5. Injury Risk

391 The above model assumes that musth is costless, which is clearly a simplification.
 392 One possible cost of musth is the risk of injury or death associated with musth
 393 behavior. To examine the effect of injury risk on ESS outcomes, an injury risk model
 394 was developed based on the simple model discussed above (for details see Appendix

395 **B**). The injury risk model assumes that the probability of injury is dependent on the
396 size difference of the competing males. λ is the probability that a musth male will
397 be injured while competing against a musth male of equal size, β is the probability
398 a musth male will be injured competing against a musth male that is one size class
399 larger, while ω is the probability that a musth male will be injured competing against
400 a male that is two size classes larger. Furthermore, while large male musth duration is
401 taken as a parameter, the medium and small males may adjust their expected musth
402 duration as a strategic variable while seeking to maximize their expected lifetime
403 payoffs. Three examples of an ESS from the injury risk model are shown in Figure
404 13. The results are discussed further in Section 5.2.

405 The injury risk model predicts the effects of age and size in determining musth
406 strategy in male elephants and, importantly, distinguishes between the two. The
407 simple model assumes that size is the relevant variable for determining the outcome
408 of musth competitions, while age is used as a proxy for size in determining the number
409 of large, medium and small males. The causes of musth duration are not modeled, but
410 age is again used as a proxy for expected musth duration. Alternatively, the injury
411 risk model offers a plausible relationship between age, size and musth duration in
412 the form of a trade-off between current benefits (which are larger for larger males
413 because they are more able to win musth competitions) and future benefits (which
414 are smaller for older males because older males have fewer musth seasons ahead of
415 them).

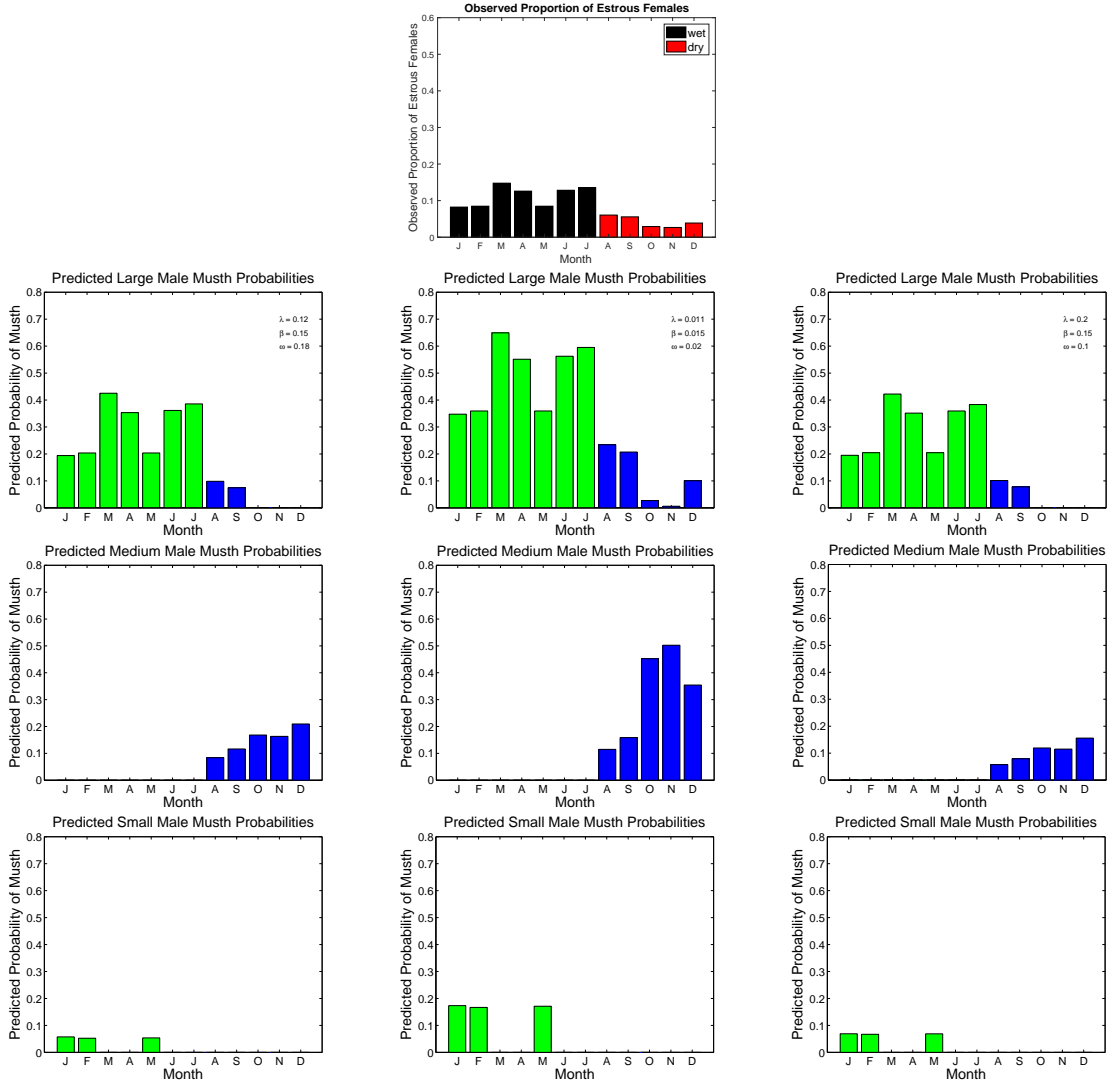


Figure 13: The observed proportion of estrous females by month as reported by Poole (1989b) (top). The predicted equilibrium probabilities of being in musth by month for large, medium and small males assuming $T_L = 2.3$, $\lambda = 0.12$, $\beta = 0.15$, $\omega = 0.18$ (probability of injury increases as opponent gets bigger) and predicting $T_M = 0.742$ and $T_S = 0.164$ (1st column). The predicted equilibrium probabilities of being in musth by month for large, medium and small males assuming $T_L = 4$, $\lambda = 0.011$, $\beta = 0.015$, $\omega = 0.02$ (probability of injury increases as opponent gets bigger) and predicting $T_M = 1.583$ and $T_S = 0.512$ (2nd column). The predicted equilibrium probabilities of being in musth by month for large, medium and small males assuming $T_L = 2.3$, $\lambda = 0.2$, $\beta = 0.15$, $\omega = 0.1$ (probability of injury increases as the opponent's size approaches the size of the focal male) and predicting $T_M = 0.527$ and $T_S = 0.205$ (3rd column).

5. Discussion

5.1. *Small male inconsistency*

416 While the musth timing of medium and large males is generally consistent from
417 one year to the next, small males are less predictable and may enter and exit musth
418 multiple times in a single year (Poole, 1987, 1989a). Game-theoretic modeling offers
419 two possible, and mutually compatible, explanations for this behavior. The first is
420 that, at equilibrium, the best months for a small male to be in musth are not clustered
421 together in time, this is in contrast to the equilibrium timing for medium and large
422 males. The second possible explanation is that variation in important parameter
423 values (such as population sizes) may cause larger changes to the equilibrium strategy
424 for small males than for other size classes.

425 The latter phenomenon can be seen by inspecting Figures 1 and 2, and also
426 by considering the effect of changing musth duration on the small males shown in
427 Figure 4. Figures 1 and 2 depict simulations with populations of 21 and 25 large
428 males, respectively. The two simulations show similar strategies adopted by the
429 large male populations at the ESS, but show bigger differences in the equilibrium
430 strategies adopted by the small and medium sized male populations. Similarly, the
431 effect of changing the musth-duration parameters shown in Figure 4 is largest for the
432 small males. In Figure 4, the simulation with shorter musth-duration parameters
433 has the musth timing of small males concentrated during the dry season; in the
434 simulation with longer musth-duration parameters, however, the small males are
435 more concentrated in the wet season.

436 Similarly, Figures 5 and 6 compare a null model simulation with randomized V_{ij}
437 values to the extreme cases of a uniform spatial distribution of estrous females and
438 a distribution in which all the estrous females are concentrated in a single area. The
439 comparisons reaffirm the observation that, for a given change in the environmental
440 parameters, the change in strategy for larger males will be less pronounced than for
441 smaller males.

442 Similar results can be observed with other environmental changes. The reason
443 that small male equilibrium strategies are usually the most influenced by parameter
444 changes is because they are affected by every size class, whereas large and medium
445 sized males are not affected by the size classes below them. Because natural con-
446 ditions may vary over time, the ESS for smaller males will not be as consistent as
447 that of large and medium sized males. Therefore, observed small male musth behav-
448 ior, which presumably tends toward equilibrium behavior over time through either
449 facultative adjustment or natural selection, is less predictable as well.

5.2. *Costless musth*

450 In creating the initial model, several simplifying assumptions were made regard-
451 ing musth behavior that do not always hold in the wild. Although making these
452 assumptions has allowed the development of a model which appears to yield insight
453 into musth strategy, it is worthwhile to explore their legitimacy as well as the impact
454 that relaxing some of the assumptions could have on predicted musth behavior.

455 Two related assumptions are that musth is costless, and that each male has
456 only a limited amount of time to spend in musth, which is assigned as a parame-
457 ter. Together, these two assumptions allow the model to sidestep the issue of what
458 determines musth duration. Rather than being costless, musth incurs significant
459 physiological expense (Poole, 1989a; Poole et al., 2011) which may constrain musth
460 duration either because males go into musth every year for the longest time that
461 is physiologically possible, or because repeatedly incurring high physiological costs
462 could shorten a given elephant’s lifespan (or slow down his physical growth) and
463 therefore be sub-optimal from a life–history perspective. Additionally, though con-
464 tests during musth take the form of agonistic interactions which are composed pri-
465 marily of threats, these interactions do sometimes escalate into fights, and the risk
466 of serious injury or death from musth related events could be another cost of musth
467 (Moss, 2001; Poole et al., 2011).

468 Lastly, though non-musth males sometimes attempt to mate, musth males are
469 most aggressive towards other musth males when mate-guarding estrous females
470 (Poole, 1989a). It may therefore be strategically beneficial for a given male to stay
471 out of musth so as to avoid attention from musth males, but still attempt to mate
472 with available estrous females. Females often actively resist mating attempts from
473 smaller non-musth males, and Poole (1982) suggests that the failure of small non-
474 musth males to successfully mate with females is due more to the female’s ability
475 to elude them than from musth male guarding. These non-musth mating attempts,
476 however, do sometimes succeed (Poole, 1989a), and therefore the difference in musth
477 duration between large and small males could be determined by the relative difficulty
478 of pursuing a female versus defeating male musth competitors.

479 Consider four possible answers to the question of what determines musth dura-
480 tion:

481

482 1.) Male elephants always enter musth for as long as they are physically capable
483 of so doing.

484

485 2.) Male elephants enter musth in such a way as to maximize a trade–off be-
486 tween current benefits (greater access to estrous females gained by entering musth

487 now) versus expected future benefits (access to estrous females in the future), which
488 are decreased due to a resulting shorter lifespan (or slowed growth in physical size)
489 caused by the physiological costs of musth.

490

491 3.) Male elephants enter musth in such a way as to maximize a trade-off between
492 current benefits (greater access to estrous females gained by going into musth now)
493 versus expected future benefits (access to estrous females in the future) which are
494 decreased by the risk of serious injury or death that could happen in a musth related
495 fight.

496

497 4.) Male elephants enter and exit musth based on whichever state is most likely
498 to lead to a successful mating attempt. That is, a sexually active male that is un-
499 likely to be the largest musth male at a given time will stay out of musth and instead
500 make non-musth mating attempts, but the same male will enter musth if he has a
501 reasonable probability of being the largest musth male in an area.

502

503 Which, if any, of the above are correct and which, if any, are consistent with the
504 results of the model?

505 There is evidence—from introducing young male elephants into a national park in
506 the absence of any older bulls, and later reintroducing older bulls—to suggest that the
507 duration of musth in small and medium males may be inhibited when the presence of
508 large males serves as an implicit threat (Slotow et al., 2000). Similarly, males held in
509 captivity, where socially induced musth suppression is unlikely, will sometimes enter
510 musth at an earlier age than observed in the wild (Poole and Granli, 1989) and large
511 musth males have been observed harassing smaller musth males until they drop out
512 of musth (Poole, 1989a). This evidence collectively suggests that, at least for small
513 and medium sized males, the optimal musth strategy is not simply to be in musth
514 for as long as is physiologically possible (as in the first explanation listed above), but
515 instead is determined by a trade-off between costs and benefits (Poole et al., 2011).

516 The second and third possible explanations are similar in that they both require
517 evaluation from a life-history perspective. Poole (1989a) reports that those medium
518 males which time musth to coincide with the dry season stay in musth for longer
519 than those medium males that are in musth during the wet season. This behavior
520 may be unexpected from a physiological cost perspective, as costs are likely to be
521 easier to offset during the wet season due to the greater abundance of food; but is
522 not surprising if competing against a larger male is more dangerous than competing
523 against a similarly sized male, as larger males are more likely to be in musth during
524 the wet season. Alternatively, male elephants that are unwell or in poor physiological

525 condition will skip or shorten their musth periods (Poole, 1989a), suggesting that
526 physiological costs can be a binding constraint.

527 Thirty-one escalated contests were observed at Amboseli National Park over a 14
528 year period (Poole, 1989a); of these, 20 were between musth males, 3 were between
529 sexually active non-musth males and 8 were between a musth male and a sexually
530 active non-musth male. This indicates an injury risk associated with musth, but it
531 remains unclear how it may affect the ESS.

532 Fights between musth males usually occur between individuals of similar size
533 (Poole, 1989a), possibly due to an increased probability of a fight escalating if neither
534 male is clearly dominant. This suggests that the probability of injury should be
535 greatest when competing against a similarly sized opponent, and therefore that λ
536 should be the highest risk parameter. Alternatively, it could be that most fights
537 occur between males of a similar size because most musth interactions, at least for
538 the large and medium size classes, occur between males of similar size (as males in
539 the same size class have similar musth strategies, and smaller male musth strategies
540 often involve minimizing contact with larger musth males). Furthermore, large musth
541 males have been observed harassing smaller musth males (Poole, 1989a), which could
542 carry a risk of injury to the smaller male and may be more likely to occur when the
543 size difference between competitors is large, though small males can mitigate this
544 risk by dropping out of musth after encountering a larger musth male. Figure 13
545 depicts two simulations where the probability of injury increases when the focal male
546 is significantly smaller than the opposing male (columns 1 and 2), and also depicts
547 a third simulation where the probability of injury increases when the opposing male
548 is of similar size to the focal male (column 3).

549 A life-history perspective could also be used to examine physiological costs, al-
550 though such a model is not presented here. Females are more likely to enter estrus
551 during (or following) months with more rain (Poole, 1987; Poole et al., 2011), pre-
552 sumably due to increased access to vegetation. One could reasonably expect that a
553 male can likewise more easily offset the physiological cost of musth during months
554 with (or following) heavy rainfall. A male would thus benefit from entering musth
555 in rainy months both due to more abundant vegetation and because of the greater
556 access to estrous females (for an interesting discussion of male searching strategies
557 with physiological costs as a limiting constraint, see Barnes (1982)). Because large
558 males are unaffected by the actions of smaller males, inserting physiological costs
559 into the above model should not greatly alter the incentives for large males. Instead,
560 physiological costs provide another reason for the large males to enter musth during
561 the wet season, and therefore if the above model were modified to include physiolog-
562 ical costs, the likely result would be to reinforce the tendency of the largest males to

563 enter musth during the rainy/high female time periods.

564 Once the large males have adopted a musth timing strategy focused on the wet
565 season, the behavior of the medium and small males is also likely to be similar to the
566 basic behavior predicted above. Medium males would be likely (barring unusually
567 low numbers of large males or implausibly high physiological costs) to avoid the larger
568 males by entering musth more frequently during the drier time periods, and small
569 males would thus probably enter musth during the wet season, competing against
570 the large males instead of the more numerous medium males.

571 A reasonable conclusion, therefore, is that for a given musth duration, the predic-
572 tions of a model that incorporates physiological cost concerns is unlikely to contradict
573 the basic characteristics of the wet-dry-wet temporal musth distribution that is pre-
574 dicted without considering physiological costs. The possibility that physiological
575 costs are the primary concern limiting the musth duration of sexually active males is
576 therefore potentially consistent with the above observed and predicted musth distri-
577 butions, though further examination is necessary to determine if such concerns can
578 adequately account for differences in musth duration.

579 The final possible explanation, that sexually active males choose between a musth
580 strategy and an alternative non-musth strategy, would also require a further model-
581 ing effort to explore, and we do not undertake that here. There is, however, some
582 evidence that such a trade-off is an important constraint on musth duration. First,
583 when adult males are not sexually active, they spend time foraging in what Poole
584 (1982) refers to as "bull areas" or "retirement zones," which generally have more
585 woody vegetation than the foraging areas frequented by cow/calf groups. When a
586 large male becomes sexually active, he enters musth before associating with females,
587 then leaves the bull area and begins searching for estrous females in the cow/calf
588 regions, only exiting musth after returning to the bull area (Poole, 1982). Smaller
589 males, however, spend a smaller proportion of time in musth when around females,
590 and the smaller the male, the smaller the musth proportion becomes. This suggests
591 that smaller sexually active males may find musth to be a less viable mating strat-
592 egy relative to non-musth mating attempts. Furthermore, Poole (1982) cites data
593 suggesting that a low-ranking male is in fact more likely to obtain a copulation as
594 a non-musth non-guarder than as a musth male in situations where the available
595 estrous females are already monopolized by a high ranking male. This is because the
596 dominant musth male is more likely to allow the low-ranking male to get close to a
597 estrous female when the low-ranking male is not in musth.

5.3. *Other assumptions*

598 In addition to the duration related assumptions, four other potentially problem-
599 atic simplifications were made: There is no female choice, all males in an area must
600 compete with each other, non-musth males do not mate and all males of the same
601 size class use the same probabilistic strategy.

602 In fact, females solicit guarding behavior from musth males, produce low fre-
603 quency calls to attract males during estrus and will sometimes flee from smaller non-
604 musth males that attempt to mate with them (Poole, 1989b). Females do, therefore,
605 influence mate selection, but the modeling simplification is nonetheless reasonable.
606 Firstly, musth is an honest signal of good condition (Poole, 1989b), so although
607 female elephants will avoid smaller non-musth males they are less likely to avoid
608 musth males, which the model assumes are the only males that mate. Secondly, the
609 fact that females produce low frequency mating calls to attract males strengthens
610 the assumption that all musth males in an area compete with each other. Lastly,
611 females do solicit guarding behavior from large males, especially larger musth males,
612 but the likely result is to decrease the probability that a smaller musth male could
613 successfully mate without challenging any nearby larger musth male, which fits with
614 the modeled incentives of musth timing and spatial distribution.

615 The third assumption that males only mate while in musth is strictly false but,
616 like the other simplifications, is justifiable. Although males do sometimes mate while
617 not in musth, the majority of conceptions are sired by musth males. Hollister-Smith
618 et al. (2007) found that 74 percent of tested conceptions were sired by males that
619 were known to be in musth. Further, although the presence or absence of larger
620 sexually active non-musth males could, in principle, influence the musth decisions of
621 smaller males, a male would still be advantaged by timing his musth period so that
622 fewer larger males would be in musth at the same time, otherwise entering musth
623 would be of little value. The possibility of non-musth mating, therefore, may have
624 importance in determining musth duration in small males, but for a given musth
625 duration, such mating possibilities are unlikely to have a large effect on the observed
626 musth distribution.

627 Finally, the fourth assumption that all males in a given size class use a single
628 probabilistic strategy is also false, but does not stop the model from capturing the
629 role of competition in forming musth strategies. A given male's musth timing strat-
630 egy, rather than being probabilistic, can be remarkably consistent from one year to
631 the next, especially for larger males (Poole, 1989a). Furthermore, differences in per-
632 sonality, size for age and learned behavior may also influence aspects of the musth
633 strategy adopted by a given male (e.g. age of first musth) (Lee et al., 2013). However,
634 the model proposed here can still capture important aspects of musth behaviour.

635 Over the course of a given male’s lifetime, his observed musth timing can move
636 into different time periods as the male grows older and larger (Poole, 1989a). This
637 is seen in the above model in the different strategies adopted by the small, medium
638 and large males. Furthermore, game-theoretic models that suppose a population uti-
639 lizing a single probabilistic strategy and models that suppose a population utilizing
640 a variety of deterministic strategies in different proportions often result in equivalent
641 equilibrium behavior (Maynard Smith, 1982). A deterministic model of musth be-
642 havior similar to the one proposed here has not been created, though such a model
643 may be worthwhile in future work to check the robustness of the results presented
644 in this paper.

5.4. Conservation applications

645 The model presented here was developed to better understand the relationships
646 between competition, space, time and musth in natural populations. It may also
647 have practical applications because it could be used to understand how changes in
648 a population of elephants, such as a loss of several large males due to poaching,
649 could impact the musth behavior of the remaining elephants. The impact of such
650 population changes can be problematic for both elephants and for other animals,
651 including humans, that may share the territory. Slotow et al. (2000), for example,
652 describe a situation in which young elephants were introduced into Pilanesburg,
653 South Africa without any larger elephants present. The younger males adopted
654 unusually long musth durations and exhibited violent behavior while in musth, which
655 resulted in the deaths of more than 40 white rhinoceroses.

656 Figure 3 depicts the results of two simulations of populations with greatly reduced
657 numbers of large males. It should be noted that, because musth duration is treated
658 as a parameter, the simulations are unable to capture any change in musth duration
659 that medium or small sized males might exhibit. However, the model can predict
660 the nature of certain changes to the ESS. For example, the simulation with $\Gamma_L = 10$
661 predicts a medium male ESS with a higher musth probability during wet season
662 periods, particularly time periods with relatively few large males. Similarly, the
663 simulation with $\Gamma_L = 5$ predicts an ESS with the medium males in musth almost
664 exclusively during the wet season, with the greatest concentration of medium males
665 in time periods with large numbers of estrous females. In general, as the number of
666 large males decreases, the presence of medium males in musth during time periods
667 normally associated with large males increases.

668 Other scenarios could also be explored with regard to changes in land availability
669 or quality, for example due to expansion of agriculture or human habitation. Lastly,
670 the model, when paired with additional knowledge of the region or population, could

671 be used to better understand how elephant populations may react to extended periods
 672 of drought or to attempts at mitigating drought, such as the use of artificial water
 673 sources.

6. Acknowledgments

674 We thank the two anonymous referees and the associate editor of Journal of
 675 Theoretical Biology for their helpful comments. This work was partially supported
 676 by a grant from the Simons Foundation (#274041 to Mike Mesterton-Gibbons).

A. Finding $E_L(i, j)$ (simple model)

677 Consider the expected payoff an invading large male would receive from being in
 678 musth during time period j and in area i . If γ large males will be competing in the
 679 area during that period, then from Assumption 6 the payoff function is:

$$680 \quad \frac{V_{ij}}{\gamma}$$

681
 682
 683 The value of γ , however, is dependent on the probabilistic strategies of the large
 684 male population. To find the expected value of the payoff function, let there be γ_L
 685 large males in musth during time period j (including the invading male), the prob-
 686 ability that $\gamma - 1$ large musth males (each using the population spatial strategy p_j)
 687 are also in area i is then given by:

$$688 \quad \binom{\gamma_L-1}{\gamma-1} (p_{ij})^{\gamma-1} (1-p_{ij})^{\gamma_L-\gamma}.$$

689
 690 Thus the expected payoff a large musth male would receive in area i is:

$$691 \quad \sum_{\gamma=1}^{\gamma_L} \frac{V_{ij}}{\gamma} \binom{\gamma_L-1}{\gamma-1} (p_{ij})^{\gamma-1} (1-p_{ij})^{\gamma_L-\gamma} =$$

$$692 \quad \sum_{\gamma=1}^{\gamma_L} \frac{V_{ij}}{\gamma_L} \binom{\gamma_L}{\gamma} (p_{ij})^{\gamma-1} (1-p_{ij})^{\gamma_L-\gamma} =$$

$$693 \quad \sum_{\gamma=1}^{\gamma_L} \frac{V_{ij}}{\gamma_L p_{ij}} \binom{\gamma_L}{\gamma} (p_{ij})^{\gamma} (1-p_{ij})^{\gamma_L-\gamma} =$$

$$694 \quad \frac{V_{ij}}{\gamma_L p_{ij}} \sum_{\gamma=1}^{\gamma_L} \binom{\gamma_L}{\gamma} (p_{ij})^{\gamma} (1-p_{ij})^{\gamma_L-\gamma}.$$

695
 696
 697
 698
 699
 700
 701 The above summation is identical to the probability mass function for γ_L Bernoulli
 702 trials, except that the summation starts at $j = 1$ rather than $j = 0$. Therefore the

703 sum must be equal to 1 minus the $j = 0$ term, and the expected value becomes:

$$704 \quad \frac{V_{ij}}{\gamma_L p_{ij}} (1 - (1 - p_{ij})^{\gamma_L}).$$

705
706
707 The above formula was derived assuming that there were γ_L large males in musth
708 during period j . As, again, γ_L is probabilistic, the expected value of the above for-
709 mula must be found with respect to γ_L . To find the expected value, note that the
710 focal male will be in musth during time period j , and let there be Γ_L large males in
711 the total population. The probability that $\gamma_L - 1$ other large males will also be in
712 musth is given by:

$$713 \quad \binom{\Gamma_L - 1}{\gamma_L - 1} (\eta_j)^{\gamma_L - 1} (1 - \eta_j)^{\Gamma_L - \gamma_L}.$$

714
715
716 Therefore, the expected payoff to an invading large strategist going into musth
717 during time period j and visiting area i is:

$$718 \quad \sum_{\gamma_L=1}^{\Gamma_L} \frac{V_{ij}}{\gamma_L p_{ij}} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L - 1}{\gamma_L - 1} (\eta_j)^{\gamma_L - 1} (1 - \eta_j)^{\Gamma_L - \gamma_L} =$$

$$719 \quad \sum_{\gamma_L=1}^{\Gamma_L} \frac{V_{ij}}{\Gamma_L p_{ij}} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L - 1} (1 - \eta_j)^{\Gamma_L - \gamma_L} =$$

$$720 \quad \sum_{\gamma_L=1}^{\Gamma_L} \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} =$$

$$721 \quad \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} \sum_{\gamma_L=1}^{\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} - (1 - p_{ij})^{\gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L}$$

$$722 \quad = \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} \sum_{\gamma_L=1}^{\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} - (\eta_j - \eta_j p_{ij})^{\gamma_L} \binom{\Gamma_L}{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L}$$

723
724
725
726
727
728 Now, consider the two terms in the summation above, the first is:

$$729 \quad \sum_{\gamma_L=1}^{\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L}$$

730
731
732 Note that once again this is the probability mass function for Γ_L Bernoulli trials,
733 without the $\gamma_L = 0$ term. Therefore this summation is equal to one minus the term
734 evaluated at $\gamma_L = 0$:

$$735 \quad \sum_{\gamma_L=1}^{\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} = 1 - (1 - \eta_j)^{\Gamma_L}$$

736
737
738
739 Now consider the second term in the summation:

740

$$\sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j - \eta_j p_{ij})^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L}.$$

742

743 Evaluation of the next term employs the Binomial theorem, which states:

744

$$\sum_{i=0}^n \binom{n}{i} x^i y^{n-i} = (x + y)^n$$

746

747 If i is replaced by γ_L , n with Γ_L , x with $(\eta_j - \eta_j p_{ij})$ and y with $(1 - \eta_j)$, then the
748 binomial theorem without the $i = \gamma_L = 0$ term is obtained. Therefore:

749

$$\sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j - \eta_j p_{ij})^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} =$$

751

$$[\eta_j - \eta_j p_{ij} + (1 - \eta_j)]^{\Gamma_L} - (1 - \eta_j)^{\Gamma_L} =$$

753

$$(1 - p_{ij} \eta_j)^{\Gamma_L} - (1 - \eta_j)^{\Gamma_L}.$$

755

756 Combining these expressions gives:

757

$$758 E_L(i, j) = \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - \eta_j)^{\Gamma_L} - [(1 - p_{ij} \eta_j)^{\Gamma_L} - (1 - \eta_j)^{\Gamma_L}])$$

$$759 = \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - p_{ij} \eta_j)^{\Gamma_L}),$$

760 yielding (1). Applying the above reasoning to small and medium males as well yields
761 (2)–(3).

762 Using the above payoff formula, a large male ESS can be found by numerically
763 solving $E_L(i, j) = E_L(l, k)$ for all viable choices (i, j) and (l, k) subject to the con-
764 straint $T_L = \sum_j \eta_j$ where T_L is a given parameter (for details of the numerical process,
765 see Appendix C)..

B. Finding probability of survival (injury risk model)

766 To develop this model into a life-history model that incorporates injury risk, we
767 adopt the following assumptions:

768

769 1.) There are 3 size classes of males: small, medium and large. A given male
770 starts small, becomes medium sized after one year, becomes large after two years,
771 and dies after the third year. In reality, adult males typically live much longer, but
772 these 'years' can be thought of as representing longer periods of the male's adult life.

773 It should be noted, however, that inducing cautious behavior over a short time hori-
774 zon requires larger risk parameters than for a longer time horizon, and therefore λ , β
775 and ω (see assumption 10) should be considered over-estimates of injury risk facing
776 an adult male elephant. Nonetheless, the shorter time frame should be sufficient for
777 observing the qualitative effects that injury risk can have on musth seasonality and
778 spatial distribution.

779
780 2.) There are N time periods in a year and therefore $3N$ time periods in a male's
781 lifetime. Additionally, there are M spatial areas that a musth male could occupy,
782 each with some intrinsic mate value $V_{ij} = V_{i(j+N)}$ reflecting the number of estrous
783 females.

784
785 3.) Males of all size classes have timing strategies denoted by a vector of proba-
786 bilities. For example, a large male using timing strategy $\vec{\eta} = \langle \eta_{2N+1}, \eta_{2N+2}, \dots, \eta_{3N} \rangle$
787 will enter musth during time period j ($2N + 1 \leq j \leq 3N$) with probability η_j . The
788 population timing strategy for small, medium and large males are denoted $\vec{\mu}$, $\vec{\xi}$ and
789 $\vec{\eta}$, respectively.

790
791 4.) The expected number of time periods a large male will spend in musth is
792 dependent only on physiological constraints and is denoted T , and $T = \sum_{j=2N+1}^{3N} \eta_j$.
793 For small and medium males, the expected number of time periods spent in musth is
794 bounded above by T , but it can vary strategically depending on the trade off between
795 injury risk and reward.

796
797 5.) Once in musth, each male has a spatial strategy, which can vary depending
798 on the time period. For example, a large male in musth during time period j uses
799 spatial strategy $\vec{p}_j = \langle p_{1j}, p_{2j}, \dots, p_{Mj} \rangle$ where the male competes in area i with prob-
800 ability p_{ij} . The spatial strategies for small and medium sized males are denoted by
801 \vec{w}_j , and \vec{q}_j respectively.

802
803 6.) Males only mate while in musth. This is a simplification of natural mating
804 behavior (Hollister-Smith et al., 2007) (see Section 5.3).

805
806 7.) If multiple males are in musth during the same time period and occupy the
807 same area, then they will compete with each other for access to the available estrous
808 females. This competition will always be won by the male in the largest size class.
809 If multiple males are in the largest size class, each one has an equal probability of
810 winning.(This accords with observed contest data, see Briffa et al. (2013))

811

812 8.) Large males attempt to maximize the expected number of mating opportu-
813 nities in year 3 (more specifically, $\vec{\eta}$ is chosen to maximize the combined number of
814 mating opportunities over periods $2N + 1$ to $3N$), ignoring injury risk.

815

816 9.) Small and medium males attempt to maximize the sum of current and future
817 mating opportunities, which is dependent on injury risk.

818

819 10.) The risk of a given male being injured in a musth competition is dependent
820 entirely on the size disparity between the given male and the opposing male. If both
821 males are the same size, then the probability of injury is λ . If the opposing male is
822 one size class larger, the probability of injury is β while a disadvantage of two size
823 classes gives a probability of injury of ω . If the focal male is larger than the opposing
824 male, the probability of injury to the focal male is 0.

825

826 11.) If a male is injured or killed, he is removed from the population.

827

828 12.) Males are only removed from the population by musth related injury or by
829 old age (at the end of year 3).

830

831 13.) At the end of every year Γ_S small males are added to the adult male popu-
832 lation.

833

834 14.) Estrous females will mate with whichever musth male wins a competitive
835 interaction; that is, female choice does not influence the mating success of male ele-
836 phants. This is another simplification of natural mating behavior (Poole, 1989b) (see
837 Section 5.3).

838

839 Because large males are assumed to be unaffected by injury risk, consider the
840 medium sized males. The probability that a given medium male is not injured by
841 another medium sized male in a particular time period, given that he has entered
842 musth and visited a particular area, must be calculated. If it is known that he will
843 face γ medium sized opponents, then his chances of surviving would be:

844

$$845 (1 - \lambda)^\gamma$$

846

847 (recall that λ is the probability that a male is injured while competing against a
848 male of the same size).

849 However, γ is not given, so the above value must be multiplied by the probability
 850 that there are in fact γ competitors, then summed over all possible values of γ . Let
 851 the number of medium males in musth during time period j be denoted γ_M , the
 852 probability of the focal male surviving the time period after choosing area i is given
 853 by:

$$854 \sum_{\gamma=0}^{\gamma_M-1} (1-\lambda)^\gamma \binom{\gamma_M-1}{\gamma} q_{ij}^\gamma (1-q_{ij})^{\gamma_M-1-\gamma} =$$

$$855 (1-\lambda q_{ij})^{\gamma_M-1}.$$

856
 857
 858
 859 The above equivalence can be found by applying the binomial theorem, as in
 860 Appendix A. This probability of survival, however, is conditional on there being γ_M
 861 males in musth during time period j (counting the focal male). This probability
 862 must therefore be multiplied by the probability that there are in fact γ_M males in
 863 musth during time period j . Summing over all possible values of γ_M then determines
 864 the probability of survival for the focal male. This gives:

$$865 \sum_{\gamma_M=1}^{\Gamma_M} (1-\lambda q_{ij})^{\gamma_M-1} \binom{\Gamma_M-1}{\gamma_M-1} (\xi_j)^{\gamma_M-1} (1-\xi_j)^{\Gamma_M-1-(\gamma_M-1)} =$$

$$866 (1-\lambda \xi_j q_{ij})^{\Gamma_M-1}.$$

867
 868
 869
 870 Once again the above equivalence is found by applying the binomial theorem.
 871 Of course, a medium male must also consider the risk associated with competing
 872 against large males. If a similar derivation against large opponents is applied, it is
 873 found that a medium sized focal male's probability of surviving time period j in area
 874 i (considering both opponent size classes) is:

$$875 (1-\lambda \xi_j q_{ij})^{\Gamma_M-1} (1-\beta \eta_j p_{ij})^{\Gamma_L}$$

876
 877
 878 Where β is the probability that a focal male will be killed given that he is com-
 879 peting against a musth male that is one size class above the focal male. For small
 880 males the survival probability is given by:

$$881 (1-\lambda \mu_j w_{ij})^{\Gamma_S-1} (1-\beta \xi_j q_{ij})^{\Gamma_M} (1-\omega \eta_j p_{ij})^{\Gamma_L}$$

882
 883
 884 Where ω is the probability a focal male will be killed given that he is competing
 885 against a musth male that is two size classes larger.

886 To incorporate these probabilities into the payoff functions, expected future ben-

887 efits must be added to the payoff expressions. For medium sized males, the expected
 888 value of going to an area i during time period j is now given by:

$$889 \quad E_M(i, j) = \frac{V_{i,j}}{\Gamma_M q_{ij} \xi_j} (1 - (1 - \xi_j q_{ij})^{\Gamma_M}) (1 - \eta_j p_{ij})^{\Gamma_L} + (1 - \lambda \xi_j q_{ij})^{\Gamma_M - 1} (1 - \beta \eta_j p_{ij})^{\Gamma_L} E_{next}.$$

892 Where E_{next} is the expected value associated with being alive in the next round
 893 (i.e. $E_{next} = E_M(i, j + 1)$). If the male is in the final time period for the medium
 894 size class (period $2N$), then $E_{next} = TE_L$, where E_L is the payoff rate associated
 895 with being in musth as a large male (this will be a constant when the large males
 896 are at an ESS). At a spatial ESS $E_M(i, j)$ should equal $E_M(l, j)$ for all viable spatial
 897 decisions i, l . Furthermore, during each period a given medium male must either
 898 enter musth or skip musth. If he skips musth, the sum of his current and expected
 899 future benefits will be E_{next} , if he enters musth, the sum will be $E_M(i, j)$. At a timing
 900 ESS, these payoffs must be equal, thus a space-time ESS can be found by setting
 901 $E_M(i, j) = E_{next} = TE_L = P_L$ for all viable choices (i, j) . Similarly, A space-time
 902 ESS can be found for the small males by setting $E_S(i, j) = P_L$ for all viable (i, j) .

903 Before an ESS can be found, however, it must be considered that the number
 904 of competitors that will be alive at any point in time will be in part dependent on
 905 the musth strategies adopted by the general population. Let the probability that a
 906 male survives time period j be denoted S_j . If $N < j < 2N + 1$ (the male is medium
 907 sized), this gives:

$$908 \quad S_j = 1 - \xi_j + \sum_{i=1}^{i=M} \xi_j q_{ij} (1 - \lambda \xi_j q_{ij})^{\Gamma_M - 1} (1 - \beta \eta_j p_{ij})^{\Gamma_L}$$

911 If $0 < j < N + 1$ (the male is small), this gives:

$$912 \quad S_j = 1 - \mu_j + \sum_{i=1}^{i=M} \mu_j w_{ij} (1 - \lambda \mu_j w_{ij})^{\Gamma_S - 1} (1 - \beta \xi_j q_{ij})^{\Gamma_M} (1 - \omega \eta_j p_{ij})^{\Gamma_L}$$

915 To find the expected number of males alive in each time period, assume that
 916 each year Γ_S small males are added to the population, while the surviving small
 917 males become medium sized, the medium males become large and the large males
 918 die. If Γ_j denotes the expected number of males alive in an age cohort during the
 919 j th time period of the cohort's life history, then $\Gamma_{j+1} = \Gamma_j S_j$ and $\Gamma_1 = \Gamma_S$. Now
 920 the expected value functions can be modified to include the new population numbers:

$$921 \quad \Gamma_L = \Gamma_{2N+1}$$

923

$$924 \quad E_L(i, j) = \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - p_{ij} \eta_j)^{\Gamma_L}), 2N < j < 3N + 1.$$

$$925 \quad E_M(i, j) = \frac{V_{ij}}{\Gamma_j q_{ij} \xi_j} (1 - (1 - \xi_j q_{ij})^{\Gamma_j}) (1 - \eta_{j+2N} p_{i(j+2N)})^{\Gamma_L} + (1 - \lambda \xi_j q_{ij})^{\Gamma_j - 1} (1 -$$

$$926 \quad \beta \eta_{j+2N} p_{i(j+2N)})^{\Gamma_L} P_L, N < j < 2N + 1$$

$$927 \quad E_S(i, j) = \frac{V_{ij}}{\Gamma_j w_{ij} \mu_j} (1 - (1 - \mu_j w_{ij})^{\Gamma_j}) (1 - \eta_{j+2N} p_{i(j+2N)})^{\Gamma_L} (1 - \xi_{j+2N} q_{i(j+2N)})^{\Gamma_{j+2N}}$$

$$928 \quad + (1 - \lambda \mu_j w_{ij})^{\Gamma_j - 1} (1 - \beta \xi_{j+2N} q_{i(j+2N)})^{\Gamma_{j+2N}} (1 - \omega \eta_{j+2N} p_{i(j+2N)})^{\Gamma_L} P_L$$

929 With this final set of payoff functions a lifetime history ESS can be found by
 930 setting $E_S(i, j) = E_M(l, k) = T E_L$ under the constraints $T = \sum_{j=2N+1}^{j=3N} \eta_j$ and $\Gamma_{j+1} =$
 931 $\Gamma_j S_j$.

932 C. The numerical process

933 Using expected payoff formulas from Appendix A we can find a space-time ESS
 934 numerically using the following algorithm:

- 935 1.) Begin by considering only the large males.
- 936 2.) Select an initial population timing strategy $\vec{\eta}$, then select an initial population
 937 spatial strategy \vec{p}_j for each of the phases.
- 938 3.) Select the area A_{h1} with the highest expected payoff out of all the areas during
 939 phase 1.
- 940 4.) Set $p_{h1} = p_{h1} + \epsilon$.
- 941 5.) Select the area A_{l1} with the lowest expected payoff out of all the areas during
 942 phase 1 (not including areas A_{i1} for which $p_{i1} = 0$).
- 943 6.) Set $p_{l1} = p_{l1} - \epsilon$.
- 944 7.) Repeat steps 3-6 until $E_L(h, 1) = E_L(l, 1)$, (or until $p_{h1} = 1$).
- 945 8.) Repeat steps 3-7 for each of the remaining phases.

946 Once step 8 is complete, the large male population will be at a spatial ESS dur-
 947 ing each phase. This spatial ESS, however, will be dependent on the timing strategy
 948 $\vec{\eta}$. Therefore, to continue with the algorithm we must consider the expected yearly
 949 payoff for a large male utilizing timing strategy $\vec{\eta}$:

$$950 \quad \text{yearly payoff} = \eta_1 E_1 + \eta_2 E_2 + \dots + \eta_N E_N$$

951

952

953

954

955

956

957 Here E_j is the expected payoff associated with playing a spatial game during
 958 time phase j . This can be represented by the expected value associated with any
 959 of the areas that have non-zero probabilities, because the elephant population is at
 960 a spatial ESS and therefore all of the (viable) spatial choices must have the same
 961 expected value. Additionally, we also have the conditions:

962

$$963 \quad 0 \leq \eta_j \leq 1, \text{ and}$$

$$964 \quad \sum_{j=1}^{j=N} \eta_j \tau = T_L \Rightarrow \sum_{j=1}^{j=N} \eta_j = \frac{T_L}{\tau}$$

965

966 Where T_L is a parameter representing the average amount of time a large male
 967 will be in musth every year, and τ is the amount of time in each phase. If we let
 968 $\tau = 1$, then this condition becomes:

969

$$970 \quad \sum_{j=1}^{j=N} \eta_j = T_L.$$

971

972 In order for $\vec{\eta}$ to be a timing ESS, we must have that an invading large male can-
 973 not have a higher yearly payoff with a different timing strategy when the population
 974 is using $\vec{\eta}$. This requires that $E_a = E_b, \forall a, b$ (except possibly when η_a or $\eta_b = 1$ or
 975 0). Continuing with the algorithm, we have:

- 976
- 977 9.) Select the time phase h which has the highest payoff E_h (excluding phases j
 978 such that $\eta_j = 1$).
 - 979 10.) Set $\eta_h = \eta_h + \epsilon$.
 - 980 11.) Select the time phase l which has the lowest payoff E_l (excluding phases j
 981 for which $\eta_j = 0$).
 - 982 12.) Set $\eta_l = \eta_l - \epsilon$.
 - 983 13.) Repeat steps 3-7 for time phase h and time phase l .
 - 984 14.) Repeat steps 9-13 until $E_h = E_l$.
 - 985 15.) Once step 14 is complete, the population of large males will be at a space-
 986 time ESS. Repeat steps 1-14 for medium sized males (replacing η with ξ , p with q ,
 987 T_L with T_M and $E_L(i, j)$ with $E_M(i, j)$).
 - 988 16.) Once step 15 is complete, the population of large and medium sized males
 989 will be at a space-time ESS. Repeat steps 1-14 for small males (replacing η with μ ,
 990 p with w , T_L with T_S and $E_L(i, j)$ with $E_S(i, j)$).

D. Proof that the computed strategy is an ESS

991 Let $V_{ij} > 0, \Gamma_L > 2, 0 \leq v_{ij} \leq 1$ and $0 \leq u_{ij} \leq 1$. Consider the following lemma:

992

993 Let $E_{L^*}(i, j) = \frac{V_{ij}}{(\Gamma_L - 1)v_{ij}} (1 - (1 - v_{ij})^{\Gamma_L - 1}) (1 - u_{ij}) +$
 994 $u_{ij} \sum_{\gamma=1}^{\Gamma_L - 1} \frac{V_{ij}}{\gamma + 1} \binom{\Gamma_L - 2}{\gamma - 1} (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma_L - 1 - \gamma}.$
 995

996 This quantity is a monotonically decreasing function of u_{ij} .

997 Proof of lemma:

998 $E_{L^*}(i, j)$ is a monotonically decreasing function of u_{ij} if and only if

1000
$$\frac{V_{ij}}{(\Gamma - 1)v_{ij}} (1 - (1 - v_{ij})^{\Gamma - 1}) > \sum_{\gamma=1}^{\Gamma_L - 1} \frac{V_{ij}}{\gamma + 1} \binom{\Gamma_L - 2}{\gamma - 1} (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma_L - 1 - \gamma}.$$

 1001
 1002

1003 From Appendix **A** we have:

1004
$$\frac{V_{ij}}{(\Gamma - 1)v_{ij}} (1 - (1 - v_{ij})^{\Gamma - 1}) = \sum_{\gamma=1}^{\Gamma - 1} \frac{V_{ij}}{\gamma} \binom{\Gamma - 2}{\gamma - 1} (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma - 1 - \gamma}.$$

 1005
 1006

1007 Taking the summation on the RHS and subtracting the second summation in
 1008 E_{L^*} , we obtain:

1009
$$\sum_{\gamma=1}^{\Gamma - 1} \frac{V_{ij}}{\gamma} \binom{\Gamma - 2}{\gamma - 1} (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma - 1 - \gamma} - \sum_{\gamma=1}^{\Gamma_L - 1} \frac{V_{ij}}{\gamma + 1} \binom{\Gamma - 2}{\gamma - 1} (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma - 1 - \gamma}$$

 1010
 1011

1012 which must be positive. Therefore $E_{L^*}(i, j)$ is a monotonically decreasing func-
 1013 tion of u_{ij} .

1014
 1015 Theorem: The expected value formulas derived in Appendix **A** can be used to
 1016 find a weak ESS by solving $E_*(i, j) = E_*(l, k)$ for all viable $(i, j), (l, k)$.

1017
 1018 Proof: Consider the case where $*$ is equal to L (thus we are finding an ESS for
 1019 the large male population).

1020
 1021 Let the number of individuals in the large male population be Γ_L and let $\sigma =$
 1022 $\langle S_1, S_2, \dots, S_{\Gamma_L} \rangle$ be the population state where S_n is the strategy adopted by individ-
 1023 ual n .

1024
 1025 Each strategy S_n can be represented as a matrix whose entries s_{ij} represent the
 1026 the probability of being in musth in area i during time period j , and are subject to
 1027 the constraints $T_L = \sum_{i=1}^M \sum_{j=1}^N s_{ij}$ and $\sum_{i=1}^M s_{ij} \leq 1$ where M and N represent the
 1028 number of areas and time periods respectively. Note that $s_{ij} = p_{ij}\eta_j$ where p_{ij} and

1029 η_j are defined at the beginning of this paper.

1030
1031 Let $\sigma'_n = \langle S_1, S_2, \dots, S_{n-1}, S_{n+1}, \dots, S_{\Gamma_L} \rangle$ be the modified population state.

1032
1033 Let $E(S, \sigma'_n)$ be the expected yearly payoff that individual n receives when play-
1034 ing strategy S against the modified population state σ'_n .

1035
1036 We say that a strategy V is a weak ESS if, when we let $\sigma'_n = \langle V, V, \dots, V \rangle$, we have:

1037
1038 $E(V, \sigma'_n) \geq E(U, \sigma'_n) \forall U \neq V$, and

1039
1040 if $E(V, \sigma'_n) = E(U, \sigma'_n)$ then $E(V, \sigma'_m) > E(U, \sigma'_m)$

1041
1042 where $\sigma'_m = \langle V, V, \dots, U, \dots, V \rangle$. That is, V and U are only equally viable strate-
1043 gies from player n 's perspective if individual n is the only player using strategy U .
1044 If a second individual m adopts strategy U , then U will have a lower payoff than V
1045 for both players m and n .

1046
1047 Let $\sigma = \langle V, V, \dots, V \rangle$ and let V be chosen so that $E_L(i, j) = E_L(l, k) \forall (i, j), (l, k)$
1048 such that $v_{ij} \neq 0 \neq v_{lk}$ and so that if $v_{ab} = 0$ then $E_L(a, b) < E_L(i, j)$.

1049
1050 We must show that V satisfies the above weak ESS conditions.

1051
1052 Let individual n adopt strategy U . For individual n , we still have that $E_L(i, j) =$
1053 $E_L(l, k)$ for all viable $(i, j), (l, k)$, because the E_L formula only requires that the males
1054 opposing the focal male use V . If strategy U places a non-zero probability u_{ab} on a
1055 non-viable choice (a, b) then:

1056
1057
$$E(V, \sigma'_n) - E(U, \sigma'_n) = \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} v_{ij} E_L(i, j) - \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} u_{ij} E_L(i, j) > 0.$$

1058
1059 Where the above inequality holds because $E_L(a, b) < E_L(l, k)$ and $v_{ab} = 0$ while
1060 $u_{ab} \neq 0$. This implies $E(V, \sigma'_n) > E(U, \sigma'_n)$ and completes the proof. If, however,
1061 $u_{ab} = 0$ for all non-viable choices (a, b) , then the payoffs are equal. We have:

1062
1063
$$E(V, \sigma'_n) = E(U, \sigma'_n).$$

1064
1065 Consider the modified population state $\sigma'_m = \langle V, V, \dots, U, \dots, V \rangle$.

1066

1067 In order for V to be a weak ESS, we must have $E(V, \sigma'_m) > E(U, \sigma'_m)$, or equiva-
 1068 lently $E(V, \sigma'_m) - E(U, \sigma'_m) > 0$.

1069

1070 In order to compute $E(V, \sigma'_m)$, we must first redefine $E_L(i, j)$ to account for the
 1071 fact that one opposing male is using a different strategy than the others. Call this
 1072 new function $E_{L^*}(i, j)$.

1073

1074 We have that $E_{L^*}(i, j) = \frac{V_{ij}}{(\Gamma_L - 1)v_{ij}} (1 - (1 - v_{ij})^{\Gamma_L - 1}) (1 - u_{ij}) +$
 1075 $u_{ij} \sum_{\gamma=1}^{\Gamma_L - 1} \frac{V_{ij}}{\gamma + 1} (\Gamma_L - 2) (v_{ij})^{\gamma - 1} (1 - v_{ij})^{\Gamma_L - 1 - \gamma}$.

1076

1077 The first term of E_{L^*} is obtained by finding the payoff that individual m is
 1078 expected to receive for competing in area i during time period j , given that individual
 1079 n does not compete in area i during time period j , (this is given by the formula
 1080 $E_L(i, j)$ with $\Gamma_L = \Gamma_L - 1$) times the probability that individual n does not compete
 1081 in area i during time period j . The second term of E_{L^*} is obtained by finding the
 1082 expected payoff to individual m for competing in area i during time period j , given
 1083 that individual n competes in area i during time period j , times the probability that
 1084 individual n competes in area i during time period j . Note that if $u_{ij} = v_{ij}$ then
 1085 $E_{L^*}(i, j) = E_L(i, j)$.

1086 Recall that V was chosen so that $E_L(i, j)$ was a constant for all viable (i, j) . Let
 1087 that constant be π .

1088

1089 Consider $E(V, \sigma'_m) - E(U, \sigma'_m)$. We have:

1090

1091 $E(V, \sigma'_m) - E(U, \sigma'_m) = \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} v_{ij} E_{L^*}(i, j) - \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} u_{ij} E_{L^*}(i, j)$
 1092 $= \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} (v_{ij} - u_{ij}) E_{L^*}(i, j)$.

1094

1095 V is a weak ESS if this sum is positive. When $u_{ij} > v_{ij}$, the term in the sum-
 1096 mation is negative but $E_{L^*} < \pi$. When $u_{ij} < v_{ij}$ the term is positive and $E_{L^*} > \pi$.
 1097 Thus, we can strictly underestimate this sum by replacing E_{L^*} with π , so that we
 1098 have:

1099

1100 $\sum_{j=1}^{j=M} \sum_{i=1}^{i=N} (v_{ij} - u_{ij}) E_{L^*}(i, j) > \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} (v_{ij} - u_{ij}) \pi = \pi \sum_{j=1}^{j=M} \sum_{i=1}^{i=N} (v_{ij} - u_{ij}) =$
 1101 0 .

1102

1103 Thus, we have that $E(V, \sigma'_m) - E(U, \sigma'_m) > 0$ as long as $V \neq U$, and therefore V

1104 is a weak ESS.

1105

1106 A similar proof is possible if L is replaced with an M or S .

E. References

Barnes, R.F.W., 1982. Mate Searching Behaviour of Elephant Bulls in a Semi-Arid Environment. *Animal Behaviour* 30, 1217–1223.

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Theoretical Biology* 57, 289–300.

Briffa, M., Hardy, I.C.W., Gammell, M.P., Jennings, D.J., Clarke, D.D., Goubalt, M., 2013. Analysis of animal contest data, in: Hardy, I.C.W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge. chapter 4, pp. 47–85.

Chelliah, K., Sukumar, R., 2013. The role of tusks, musth and body size in male–male competition among Asian elephants, *Elephas maximus*. *Animal Behaviour* 86, 1207–1214.

Croze, H., Moss, C.J., 2011. Patterns of Occupancy in Time and Space, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), *The Amboseli Elephants*. The University of Chicago Press, Chicago and London. chapter 7, pp. 89–105.

Hollister-Smith, J.A., Poole, J.H., Archie, E.A., Vance, E.A., Georgiadis, N.J., Moss, C.J., Alberts, S., 2007. Age, musth and paternity success in wild male African elephants, *Loxodonta africana*. *Animal Behaviour* 74, 287–296.

Jainudeen, M.R., Katongole, C.B., Short, R.V., 1972. Plasma Testosterone Levels in Relation to Musth and Sexual Activity in the Male Asiatic Elephant, *Elephas maximus*. *J. Reprod. Fert.* 29, 99–103.

Lee, P.C., Bussiere, L.F., Webber, E., Poole, J.H., Moss, C.J., 2013. Enduring consequences of early experiences: 40 year effects on survival and success among African elephants *Loxodonta africana*. *Biol Lett.* 9, 20130011.

Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

- McNamara, J.M., Webb, J.N., Collins, E.J., Szekely, T., Houston, A., 1997. A General Technique for Computing Evolutionarily Stable Strategies Based on Errors in Decision-making. *J. theor. Biol.* 189, 211–225.
- Moss, C.J., 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology* 255, 145–156.
- Poole, J.H., 1982. Musth And Male–Male Competition In The African Elephant. Ph.D. thesis. University of Cambridge.
- Poole, J.H., 1987. Rutting Behavior In African Elephants: The Phenomenon of Musth. *Behaviour* 102, 283–316.
- Poole, J.H., 1989a. Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour* 37, 140–152.
- Poole, J.H., 1989b. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour* 37, 842–849.
- Poole, J.H., Granli, P., 1989. Mind and Movement: Meeting the Interests of Elephants. *Animal Behaviour* 37, 842–849.
- Poole, J.H., Lee, P.C., Njiraini, N., Moss, C.J., 2011. Longevity, Competition, and Musth: A Long-Term Perspective on Male Reproductive Strategies, in: Moss, C.J., Croze, H., Lee, P.C. (Eds.), *The Amboseli Elephants*. The University of Chicago Press, Chicago and London. chapter 18, pp. 272–286.
- Poole, J.H., Moss, C.J., 1981. Musth in the African elephant, *Loxodonta africana*. *Nature* 292, 830–831.
- Rasmussen, H., Okello, J., Wittemyer, G., Siegismund, H., Arctander, P., Vollrath, F., Douglas-Hamilton, I., 2008. Age- and tactic-related paternity success in male African elephants. *Behavioral Ecology* 19, 9–15.
- Rasmussen, H.B., 2001. Aspects of Male Mating Strategies in the African Elephant (*Loxodonta africana*). Master’s thesis. University of Aarhus.
- Slotow, R., Dyk, G.V., Poole, J., Page, B., Klocke, A., 2000. Older bull elephants control young males. *Nature* 408, 425–426.