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

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## Abstract

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

Though musth behavior has long been observed and documented, the evolutionary advantages of musth remain poorly understood. Here we develop a game–theoretic model of male musth behavior which assumes musth duration as a parameter, and distributions of small, medium and large musth males are predicted in both time and space. The predicted results are similar to the musth timing behavior observed in the Amboseli National Park elephant population, and further results are generated with relevance to Samburu National Park. We discuss small male musth behavior, the effects of estrous female spatial heterogeneity on musth timing, conservation applications, and the assumptions underpinning the model.

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

## 1. Introduction

Musth is a state of heightened aggression that sexually mature male Asian and African elephants temporarily enter, and is particularly associated with mating behaviour (Poole, 1987, 1989a; Poole et al., 2011; Jainudeen et al., 1972). Though musth has long been known to occur in Asian elephants, musth was first observed in African Savannah elephants in 1981 in the Amboseli population in Kenya (Poole and Moss, 1981; Poole, 1982). Since then, researchers have extensively studied musth in the Amboseli population, finding that, while in musth, Amboseli males compete for females in estrus by engaging in agonistic interactions which are composed primarily of threats, but on rare occasions will escalate into potentially lethal fights (Poole, 1989a). Contests are usually won by the larger of the two musth males (Poole, 1989a; Briffa et al., 2013) (see also Chelliah and Sukumar (2013) for Asian elephants) and, because females may be in estrus at any time throughout the year, musth contests can be observed in both the wet and dry seasons (Poole, 1987, 1989a). Females in estrus prefer to be guarded by—and to allow matings with—musth males, and sometimes actively resist mating attempts by non-musth males (Poole, 1989b).

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

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

## 2. Model

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

We adopt the following additional assumptions:

### *2.1. Assumptions*

1. There are three size classes of males: small, medium and large.

2. Timing strategies for males of all size classes are vectors of probabilities. Let $\eta_j$, $\xi_j$ or $\mu_j$ be the probability that a large, medium or small male, respectively, will enter musth during time period $j$. Then the population strategies for large, medium and small males are $\vec{\eta} = \langle \eta_1, \eta_2, ..., \eta_N \rangle$, $\vec{\xi} = \langle \xi_1, \xi_2, ..., \xi_N \rangle$ and $\vec{\mu} = \langle \mu_1, \mu_2, ..., \mu_N \rangle$, respectively.

3. The expected number of time periods that a large, medium or small male will spend in musth is denoted by $T_L = \Sigma_{j=1}^{j=N} \eta_j$, $T_M = \Sigma_{j=1}^{j=N} \xi_j$ or $T_S = \Sigma_{j=1}^{j=N} \mu_j$, respectively.

4. Once in musth, each male has a spatial strategy, which can depend on the time period. Let $p_{ij}, q_{ij}$ or $w_{ij}$ be the probability that a large, medium or small male, respectively, competes in area $i$ in time period $j$. Then the spatial strategies for large, medium and small males are $\vec{p_j} = \langle p_{1j}, p_{2j}, ..., p_{Mj} \rangle$, $\vec{q_j} = \langle q_{1j}, q_{2j}, ..., q_{Mj} \rangle$ and $\vec{w_j} = \langle w_{1j}, w_{2j}, ..., w_{Mj} \rangle$, respectively.

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

6. If multiple males are in musth during the same time period and occupy the same area, then they will compete with each other for access to the available estrous females. This competition will always be won by the male in the largest size class. If multiple males are in the largest size class, each one has an equal probability of winning.

7. Males attempt to maximize the expected number of mating opportunities over the entire year.

8. There is no injury risk or other disincentive to enter musth. The only incentive for an individual to avoid entering musth or going to a given area while in musth is the opportunity cost of spending a portion of his (limited) musth duration in an undesirable place or time. This is a simplification of actual musth

incentives that we modify later (see Section 5.2).

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

### *2.2. Payoffs*

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

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

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

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

## 3. Methods

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

The expected value formulas defined above are useful because, at an ESS, any two viable space-time choices $(i,j),(l,k)$ should have an equal expected payoff (Maynard Smith, 1982). Mathematically, $E_*(i,j)$ must be equal to $E_*(l,k)$ for all viable choices of $(i,j),(l,k)$, where $*$ is either an $L$,$M$ or $S$. Because musth males are unaffected by the musth strategies of smaller male sizes, an ESS can be found by first numerically solving for the $\vec{\eta}$ and $\vec{p}$ strategies for which $E_L(i,j) = E_L(l,k)$, then finding the $\vec{\xi}$ and $\vec{q}$ strategies for which $E_M(i,j) = E_M(l,k)$ taking the $\vec{\eta}$ and $\vec{p}$ strategies from the large male population as environmental constants. Lastly, the ESS is completed by finding the $\vec{\mu}$ and $\vec{w}$ for which $E_S(i,j) = E_S(l,k)$ while using the $\vec{\eta}$, $\vec{p}$, $\vec{\xi}$ and $\vec{q}$ strategies from the large and medium male populations (for a further description of the numerical process and a proof that the above algorithm will yield an ESS, see Appendices **C** and **D**).

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

### *3.1. Parameter data*

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

category 2: 42 males ($\Gamma_S = 42$)
category 3: 36 males ($\Gamma_M = 36$)
category 4: 19 males
category 5: 2 males ($\Gamma_L = 19 + 2 = 21$)

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

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

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

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

## 4. Results

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

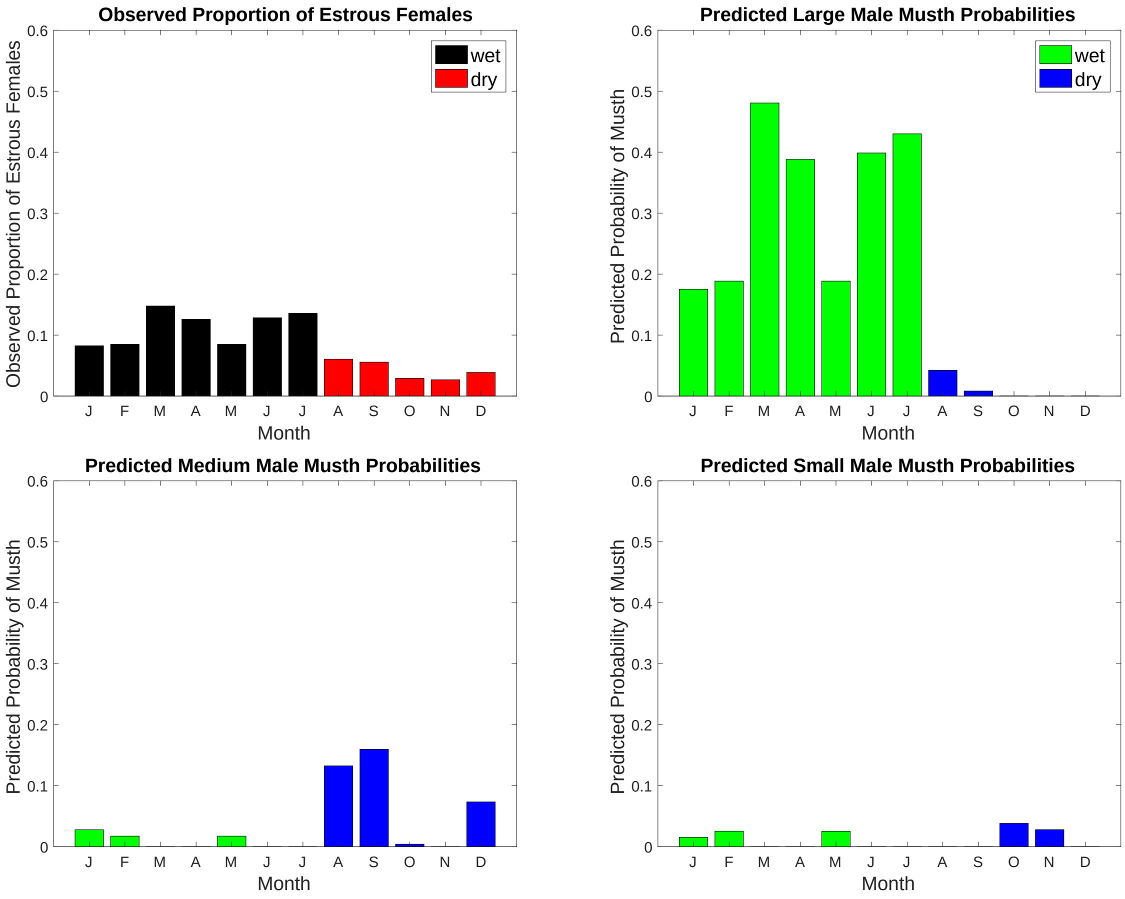


Figure 1: The observed proportion of estrous females by month as reported by Poole (1989b) (top left), the predicted equilibrium probabilities of being in musth by month for a large male (top right), medium male (bottom left) and small male (bottom right) with $\Gamma_L = 21$, $\Gamma_M = 36$ and $\Gamma_S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

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

### *4.1. The impact of population size*

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

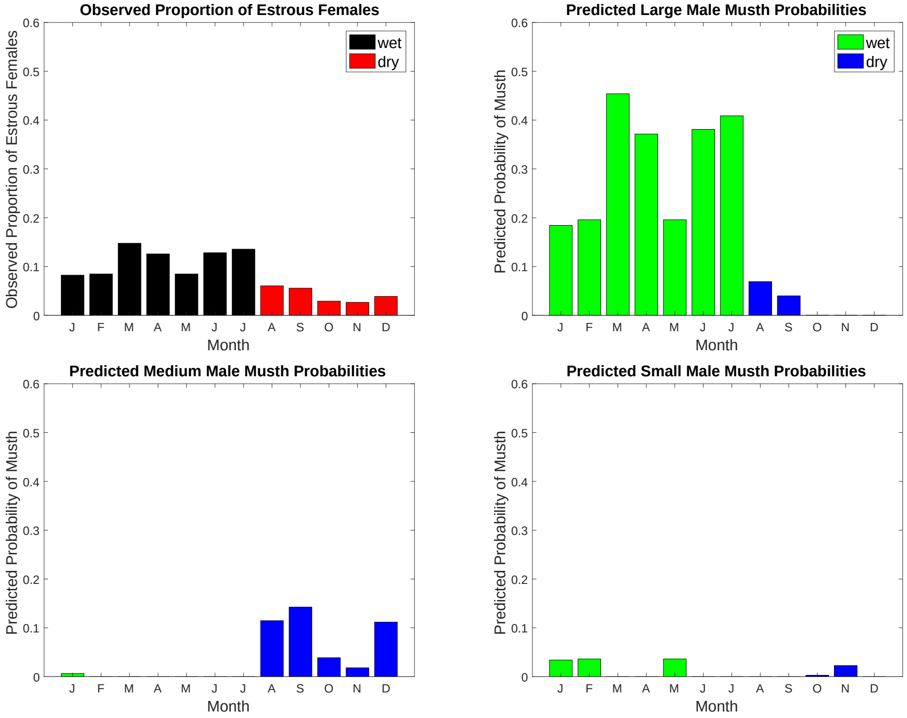


Figure 2: The observed proportion of estrous females by month as reported by Poole (1989b) (top left), the predicted equilibrium probabilities of being in musth by month for a large male (top right), medium male (bottom left) and small male (bottom right) using an increased large male population.

Some elephant populations suffer from heavy poaching activity, which disproportionately affects the large male population. Therefore, understanding how a reduction in the large male population will influence behavior in the general population is relevant from an ecological perspective. Two additional simulations with more extreme reductions in the large male population were run, and the results are displayed in Figure 3. The results of Figure 3 are further discussed in section 5.4.

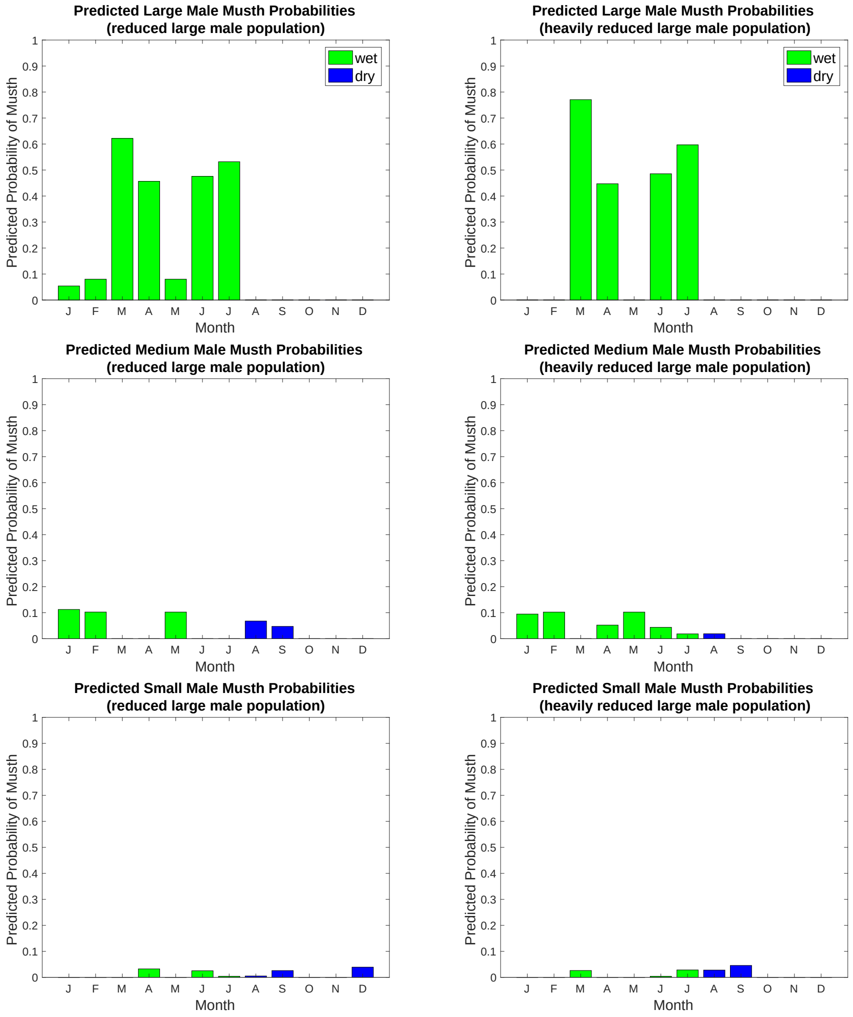


Figure 3: The predicted equilibrium probabilities of being in musth by month for a large male (top left), medium male (middle left) and small male (bottom left) using $\Gamma_L = 10, \Gamma_M = 36, \Gamma_S = 42$. The predicted equilibrium probabilities of being in musth by month for a large male (top 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*

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

| 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)

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

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

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

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

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

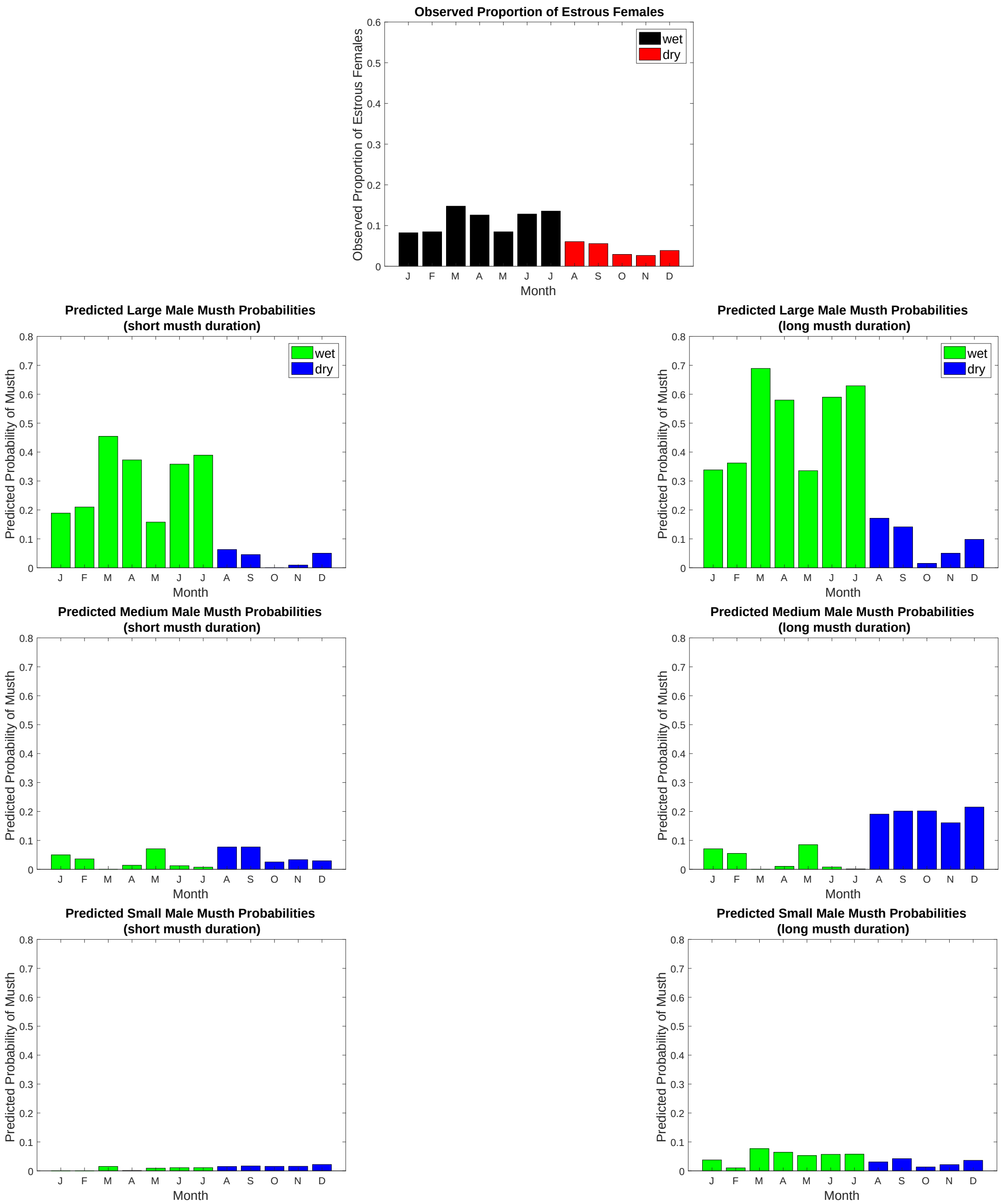
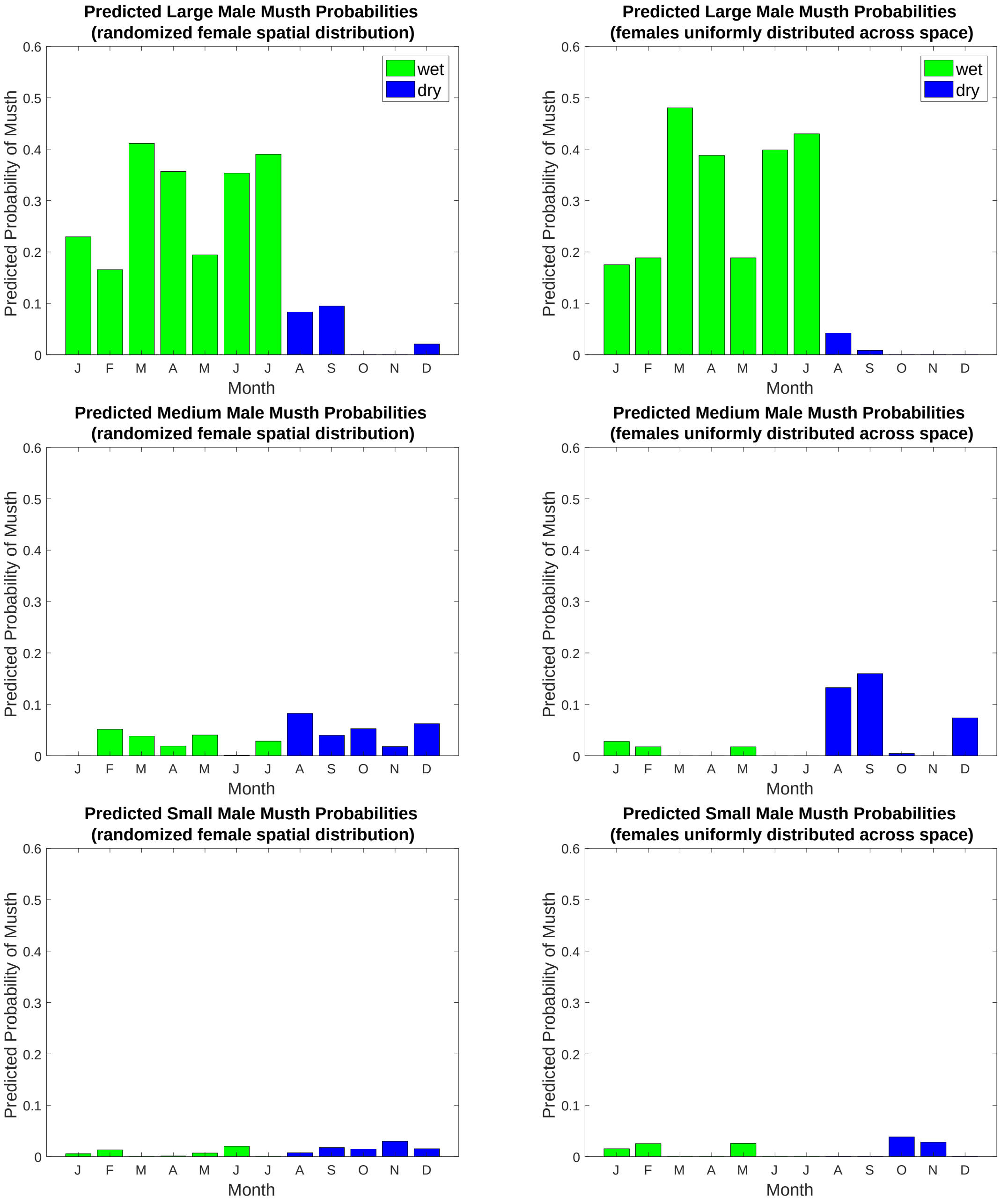


Figure 4: The observed proportion of estrous females by month as reported by Poole (1989b) (top), the predicted equilibrium probabilities of being in musth by month for a large, medium and small male with the shorter musth duration parameters (bottom three panels on left) and the predicted equilibrium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



Predicted Large Male Musth Probabilities (randomized female spatial distribution)

Predicted Large Male Musth Probabilities (females uniformly distributed across space)

Predicted Medium Male Musth Probabilities (randomized female spatial distribution)

Predicted Medium Male Musth Probabilities (females uniformly distributed across space)

Predicted Small Male Musth Probabilities (randomized female spatial distribution)

Predicted Small Male Musth Probabilities (females uniformly distributed across space)

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 $T_S = 0.133$.

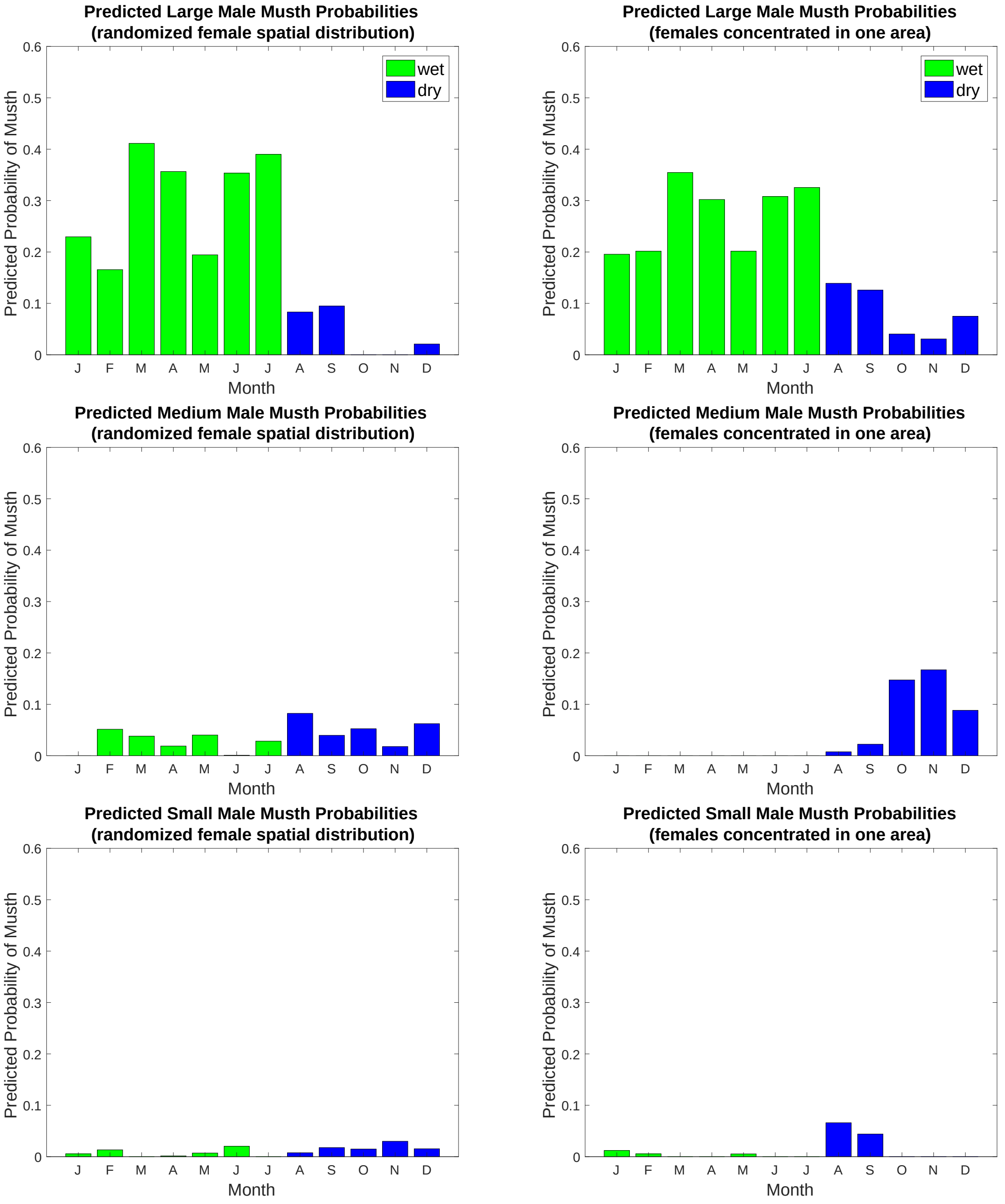


Figure 6: The predicted equilibrium probabilities of being in musth by month assuming a random spatial distribution of estrous females for a large male (top left), medium male (middle left) and small male (bottom left), and the predicted equilibrium probabilities of being in musth by month assuming all 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*

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

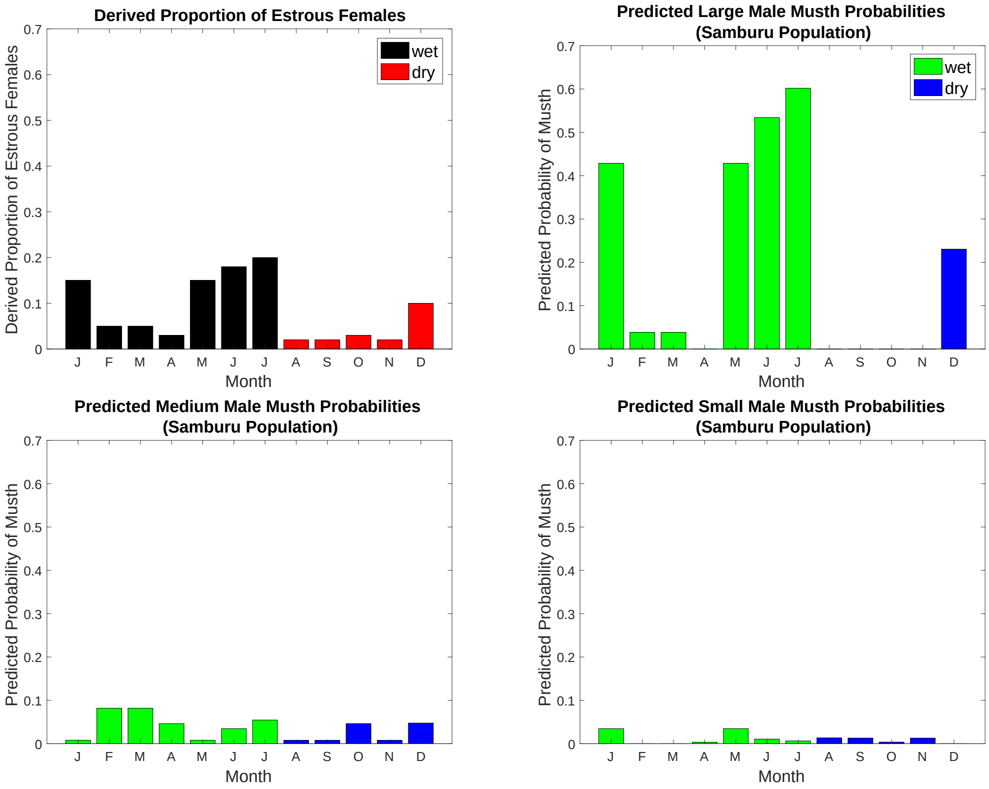


Figure 7: The proportion of estrous females by month derived by Rasmussen (2001) (top left), the predicted equilibrium probabilities of being in musth by month for large males (top right), medium males (bottom left) and small males (bottom right). Calculated with $\Gamma_L = 12, \Gamma_M = 24, \Gamma_S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

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

### *4.4. Observed and predicted musth timing behavior*

To empirically evaluate the above model, the predicted musth timing probabilities were compared to musth timing data from Poole (1982). Poole (1982) recorded both estimated age and observed musth timing behavior in 23 male African Elephants sampled from a larger population over two years (1980–1981). Each male was classified as either ”large” or ”medium” (no small males were sampled) using the age classes described in the parameter data section, then were marked as either "in musth" or "not in musth" for each month. The resulting observed musth distribution for 1980 is shown in Figure 8.

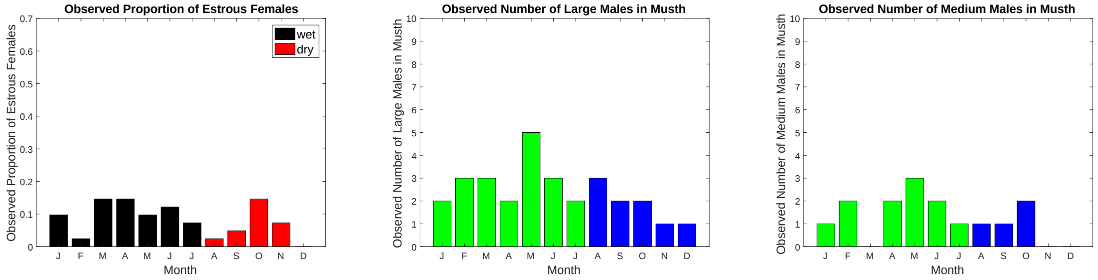


Figure 8: The observed number of estrous females per month, and the observed number of large and medium males in musth per month in 1980.

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

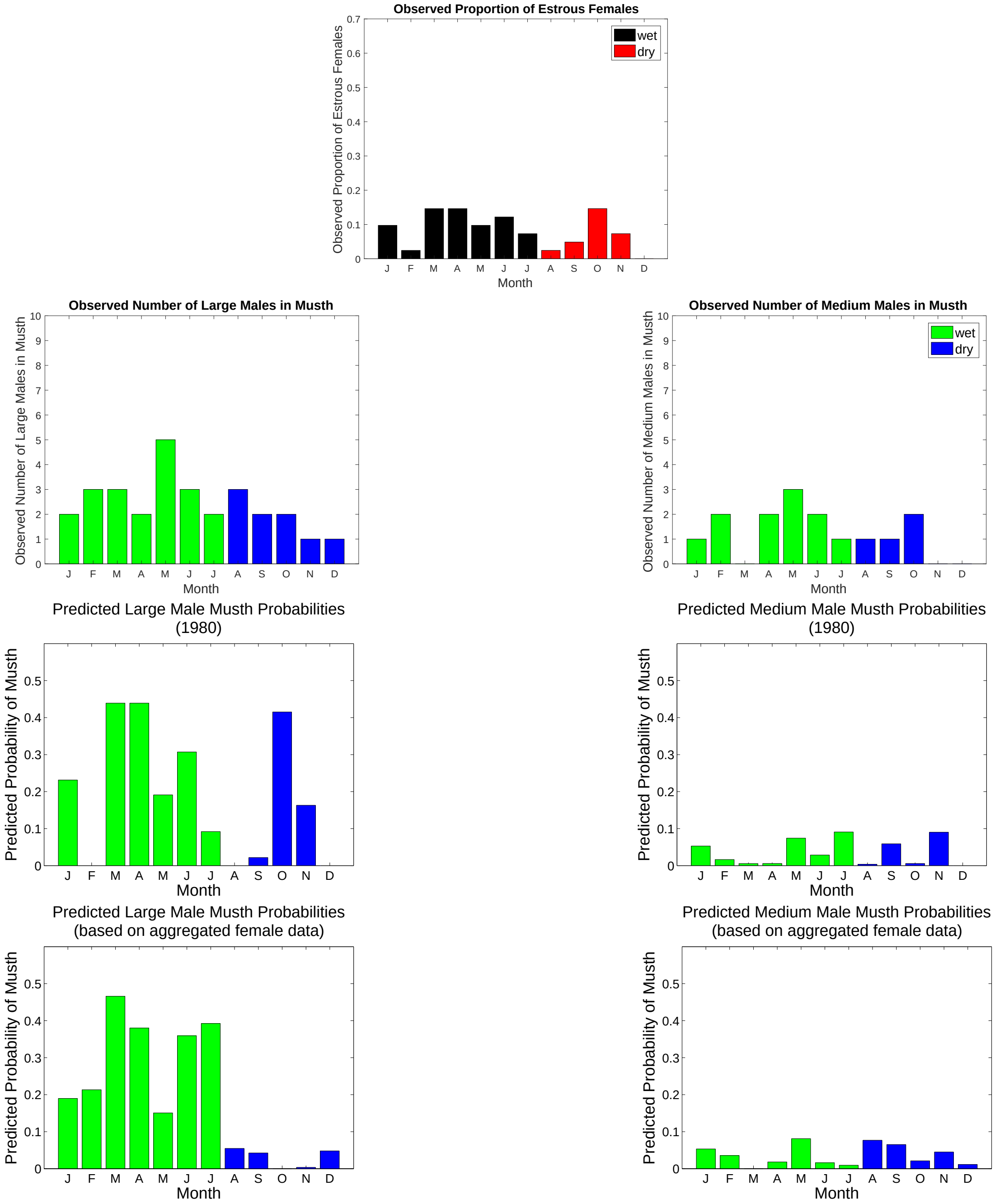


Figure 9: The observed number of estrous females each month in 1980 (top), the observed and predicted number of large musth males each month in 1980 (bottom three rows, left). The observed and predicted number of medium musth males each month in 1980 (bottom three rows, right). Calculated with $T_L =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

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

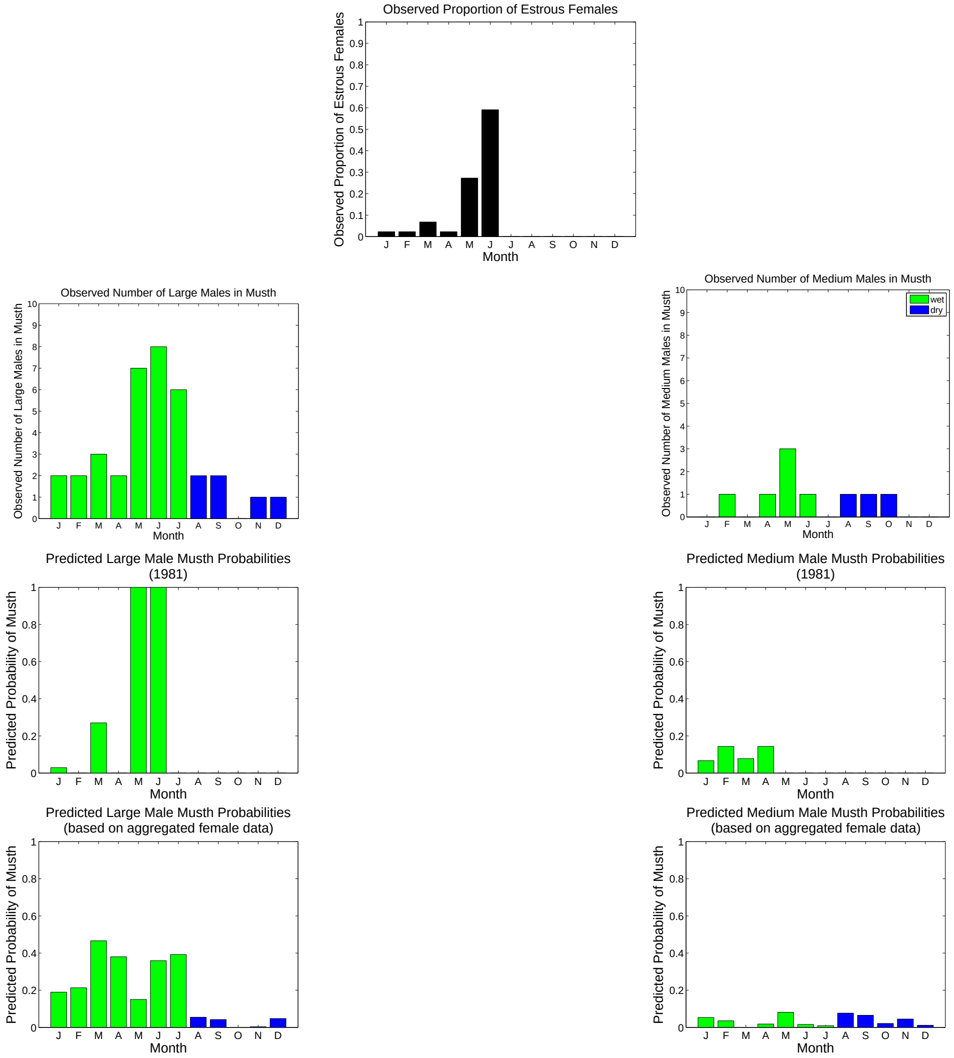


Figure 10: The observed number of estrous females each month in 1981 (top), the observed and predicted number of large males in musth each month in 1981 (bottom three rows, left). The observed and predicted number of medium males in musth each month in 1981 (bottom three rows, right). Calculated with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

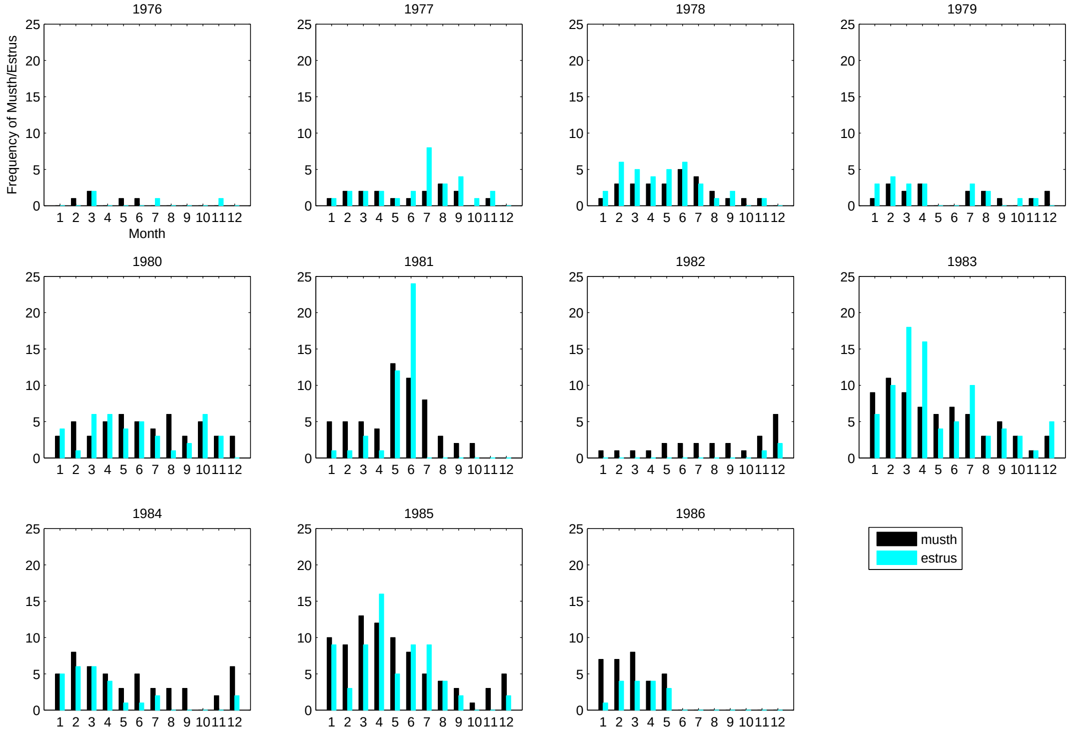


Figure 11: The number of estrous females observed by month versus the number of musth males observed by month. Based on Figure from Poole (1987).

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

The simulations that use aggregated data to estimate the expected distribution of estrous females appear to perform better than the simulations that use year–specific data. The aggregated data simulations for both 1980 and 1981 have only one month that can be rejected for the large males and no months rejected for the medium males. Additionally, the model predictions also appear to fit the 1981 data better than the 1980 data, which can be observed by increasing the false discovery rate to $\alpha = 0.2$. If the larger $\alpha$ value is used on the aggregated data simulations, the number 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 $\alpha = 0.2$

There are, however, some important caveats for the above simulations. Firstly, the spatial distribution of estrous females is based on the observed distribution of all females as reported in Croze and Moss (2011), which both assumes that the number of estrous females in an area is proportional to the number of females in an area, and does not capture any yearly variation in the spatial distribution of estrous females that may have existed in 1980 or 1981. Furthermore, the age categories from Poole (1989a) may not be ideal approximations for size designations. Using the age–size designations derived from Croze and Moss (2011) and Poole (1989a), there are no small males among the 23 individuals from Poole (1982). Yet in the same group of males Poole (1982) noted three distinct subgroups of males.

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

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

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

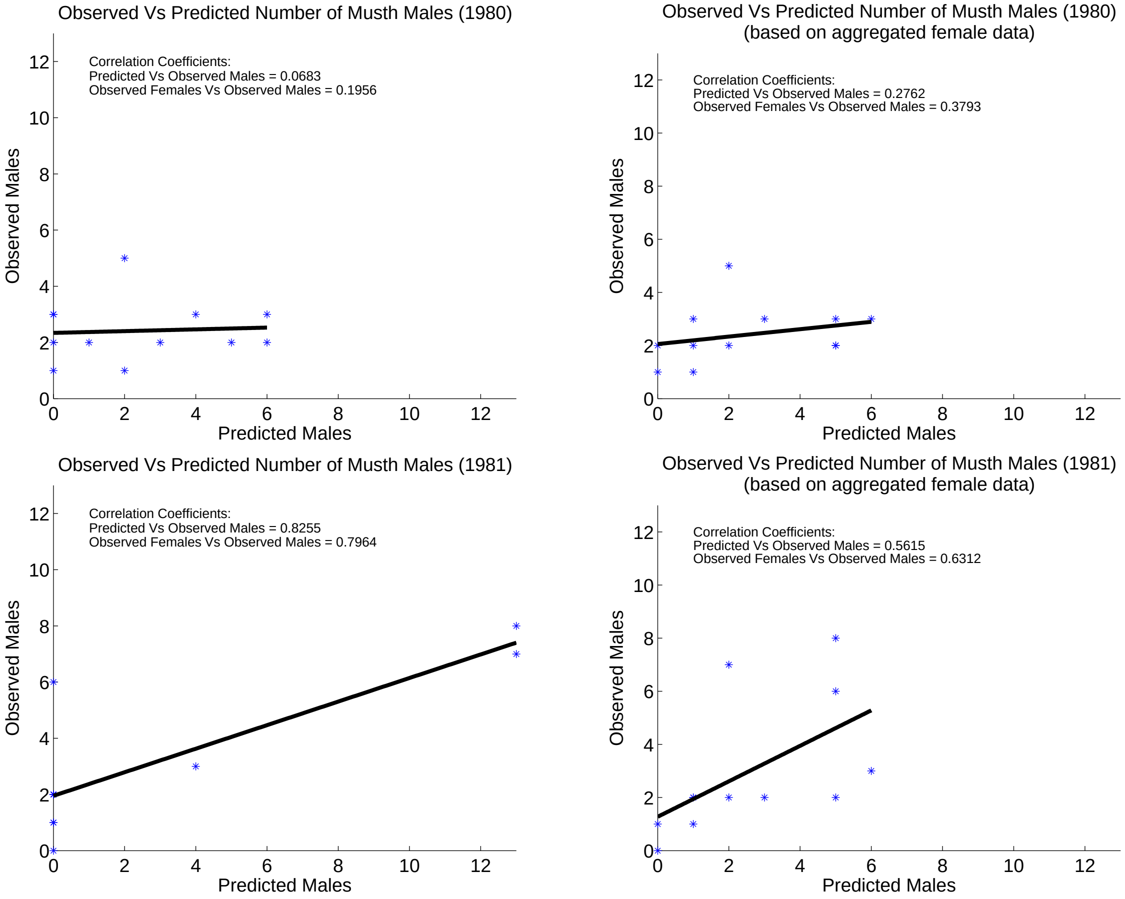


Figure 12: The observed number of large males in musth each month versus the predicted number of large males in musth each month for 1980 (year–specific data, top left) 1980 (Aggregated data, top right), 1981 (year–specific data, bottom left) and 1981 (Aggregated data, bottom right). Additionally, The 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.

### *4.5. Injury Risk*

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

**B**). The injury risk model assumes that the probability of injury is dependent on the size difference of the competing males. $\lambda$ is the probability that a musth male will be injured while competing against a musth male of equal size, $\beta$ is the probability a musth male will be injured competing against a musth male that is one size class larger, while $\omega$ is the probability that a musth male will be injured competing against a male that is two size classes larger. Furthermore, while large male musth duration is taken as a parameter, the medium and small males may adjust their expected musth duration as a strategic variable while seeking to maximize their expected lifetime payoffs. Three examples of an ESS from the injury risk model are shown in Figure 13. The results are discussed further in Section 5.2.

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

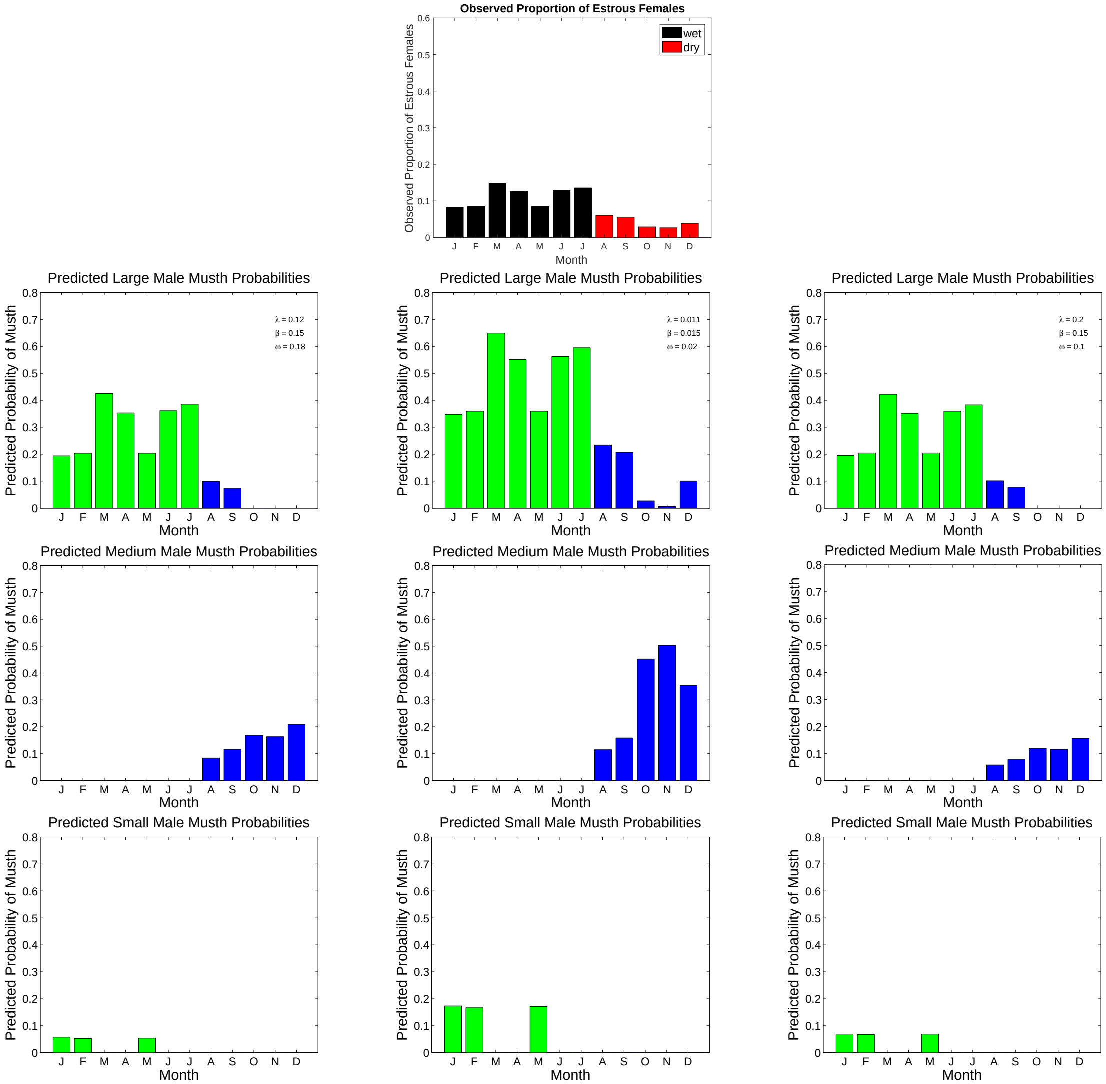


Figure 13: The observed proportion of estrous females by month as reported by Poole (1989b) (top). The predicted equilibrium probabilities of being in musth by month for large, medium and small males assuming $T_L = 2.3$, $\lambda = 0.12$, $\beta = 0.15$, $\omega = 0.18$ (probability of injury increases 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

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

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

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

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

### *5.2. Costless musth*

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

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

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

Consider four possible answers to the question of what determines musth duration:

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

2.) Male elephants enter musth in such a way as to maximize a trade–off between current benefits (greater access to estrous females gained by entering musth now) versus expected future benefits (access to estrous females in the future), which are decreased due to a resulting shorter lifespan (or slowed growth in physical size) caused by the physiological costs of musth.

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

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

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

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

The second and third possible explanations are similar in that they both require evaluation from a life–history perspective. Poole (1989a) reports that those medium males which time musth to coincide with the dry season stay in musth for longer than those medium males that are in musth during the wet season. This behavior may be unexpected from a physiological cost perspective, as costs are likely to be easier to offset during the wet season due to the greater abundance of food; but is not surprising if competing against a larger male is more dangerous than competing against a similarly sized male, as larger males are more likely to be in musth during the wet season. Alternatively, male elephants that are unwell or in poor physiological condition will skip or shorten their musth periods (Poole, 1989a), suggesting that physiological costs can be a binding constraint.

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

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

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

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

A reasonable conclusion, therefore, is that for a given musth duration, the predictions of a model that incorporates physiological cost concerns is unlikely to contradict the basic characteristics of the wet-dry-wet temporal musth distribution that is predicted without considering physiological costs. The possibility that physiological costs are the primary concern limiting the musth duration of sexually active males is therefore potentially consistent with the above observed and predicted musth distributions, though further examination is necessary to determine if such concerns can adequately account for differences in musth duration.

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

### *5.3. Other assumptions*

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

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

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

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

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

### *5.4. Conservation applications*

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

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

Other scenarios could also be explored with regard to changes in land availability or quality, for example due to expansion of agriculture or human habitation. Lastly, the model, when paired with additional knowledge of the region or population, could be used to better understand how elephant populations may react to extended periods of drought or to attempts at mitigating drought, such as the use of artificial water sources.

## 6. Acknowledgments

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

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

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

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

$$\tbinom{\gamma_L-1}{\gamma-1}(p_{ij})^{\gamma-1}(1-p_{ij})^{\gamma_L-\gamma}.$$

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

$$\Sigma_{\gamma=1}^{\gamma=\gamma_L}\frac{V_{ij}}{\gamma}\tbinom{\gamma_L-1}{\gamma-1}(p_{ij})^{\gamma-1}(1-p_{ij})^{\gamma_L-\gamma} =$$

$$\Sigma_{\gamma=1}^{\gamma=\gamma_L}\frac{V_{ij}}{\gamma_L}\tbinom{\gamma_L}{\gamma}(p_{ij})^{\gamma-1}(1-p_{ij})^{\gamma_L-\gamma} =$$

$$\Sigma_{\gamma=1}^{\gamma=\gamma_L}\frac{V_{ij}}{\gamma_L p_{ij}}\tbinom{\gamma_L}{\gamma}(p_{ij})^{\gamma}(1-p_{ij})^{\gamma_L-\gamma} =$$

$$\frac{V_{ij}}{\gamma_L p_{ij}}\Sigma_{\gamma=1}^{\gamma=\gamma_L}\tbinom{\gamma_L}{\gamma}(p_{ij})^{\gamma}(1-p_{ij})^{\gamma_L-\gamma}.$$

The above summation is identical to the probability mass function for $\gamma_L$ Bernoulli trials, except that the summation starts at $j = 1$ rather than $j = 0$. Therefore the sum must be equal to 1 minus the $j = 0$ term, and the expected value becomes:

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

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

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

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

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

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

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

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

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

Now, consider the two terms in the summation above, the first is:

$$\Sigma_{\gamma_L=1}^{\gamma_L=\Gamma_L}\binom{\Gamma_L}{\gamma_L}(\eta_j)^{\gamma_L}(1 - \eta_j)^{\Gamma_L - \gamma_L}$$

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

$$\Sigma_{\gamma_L=1}^{\gamma_L=\Gamma_L}\binom{\Gamma_L}{\gamma_L}(\eta_j)^{\gamma_L}(1 - \eta_j)^{\Gamma_L - \gamma_L} = 1 - (1 - \eta_j)^{\Gamma_L}$$

Now consider the second term in the summation:

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

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

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

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

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

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

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

Combining these expressions gives:

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

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

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

## B. Finding probability of survival (injury risk model)

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

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

It should be noted, however, that inducing cautious behavior over a short time horizon requires larger risk parameters than for a longer time horizon, and therefore $\lambda$, $\beta$ and $\omega$ (see assumption 10) should be considered over-estimates of injury risk facing an adult male elephant. Nonetheless, the shorter time frame should be sufficient for observing the qualitative effects that injury risk can have on musth seasonality and spatial distribution.

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

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

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

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

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

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

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

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

10.) The risk of a given male being injured in a musth competition is dependent entirely on the size disparity between the given male and the opposing male. If both males are the same size, then the probability of injury is $\lambda$. If the opposing male is one size class larger, the probability of injury is $\beta$ while a disadvantage of two size classes gives a probability of injury of $\omega$. If the focal male is larger than the opposing male, the probability of injury to the focal male is 0.

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

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

13.) At the end of every year $\Gamma_S$ small males are added to the adult male population.

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

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

$$(1 - \lambda)^{\gamma}$$

(recall that $\lambda$ is the probability that a male is injured while competing against a male of the same size).

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

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

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

The above equivalence can be found by applying the binomial theorem, as in Appendix **A**. This probability of survival, however, is conditional on there being $\gamma_M$ males in musth during time period $j$ (counting the focal male). This probability must therefore be multiplied by the probability that there are in fact $\gamma_M$ males in musth during time period $j$. Summing over all possible values of $\gamma_M$ then determines the probability of survival for the focal male. This gives:

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

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

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

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

Where $\beta$ is the probability that a focal male will be killed given that he is competing against a musth male that is one size class above the focal male. For small males the survival probability is given by:

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

Where $\omega$ is the probability a focal male will be killed given that he is competing against a musth male that is two size classes larger.

To incorporate these probabilities into the payoff functions, expected future benefits must be added to the payoff expressions. For medium sized males, the expected value of going to an area $i$ during time period $j$ is now given by:

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

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

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

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

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

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

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

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

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

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

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

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

### C. The numerical process

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

1.) Begin by considering only the large males.

2.) Select an initial population timing strategy $\vec{\eta}$, then select an initial population spatial strategy $\vec{p_j}$ for each of the phases.

3.) Select the area $A_{h1}$ with the highest expected payoff out of all the areas during phase 1.

4.) Set $p_{h1} = p_{h1} + \epsilon$.

5.) Select the area $A_{l1}$ with the lowest expected payoff out of all the areas during phase 1 (not including areas $A_{i1}$ for which $p_{i1} = 0$).

6.) Set $p_{l1} = p_{l1} - \epsilon$.

7.) Repeat steps 3-6 until $E_L(h,1) = E_L(l,1)$, (or until $p_{h1} = 1$).

8.) Repeat steps 3-7 for each of the remaining phases.

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

$$\text{yearly payoff} = \eta_1 E_1 + \eta_2 E_2 + ... + \eta_N E_N$$

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

$0 \leq \eta_j \leq 1$, and
$\Sigma_{j=1}^{j=N} \eta_j \tau = T_L \Rightarrow \Sigma_{j=1}^{j=N} \eta_j = \frac{T_L}{\tau}$

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

$\Sigma_{j=1}^{j=N} \eta_j = T_L$.

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

9.) Select the time phase $h$ which has the highest payoff $E_h$(excluding phases $j$ such that $\eta_j = 1$).
10.) Set $\eta_h = \eta_h + \epsilon$.
11.) Select the time phase $l$ which has the lowest payoff $E_l$ (excluding phases $j$ for which $\eta_j = 0$).
12.) Set $\eta_l = \eta_l - \epsilon$.
13.) Repeat steps 3-7 for time phase $h$ and time phase $l$.
14.) Repeat steps 9-13 until $E_h = E_l$.
15.) Once step 14 is complete, the population of large males will be at a space-time ESS. Repeat steps 1-14 for medium sized males (replacing $\eta$ with $\xi$, $p$ with $q$, $T_L$ with $T_M$ and $E_L(i,j)$ with $E_M(i,j)$).
16.) Once step 15 is complete, the population of large and medium sized males will be at a space-time ESS. Repeat steps 1-14 for small males (replacing $\eta$ with $\mu$, $p$ 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

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

Let $E_{L^*}(i,j) = \dfrac{V_{ij}}{(\Gamma_L - 1)v_{ij}}\left(1-(1-v_{ij})^{\Gamma_L-1}\right)(1-u_{ij}) +$ $u_{ij}\Sigma_{\gamma=1}^{\gamma=\Gamma_L-1}\dfrac{V_{ij}}{\gamma+1}\binom{\Gamma_L-2}{\gamma-1}(v_{ij})^{\gamma-1}(1-v_{ij})^{\Gamma_L-1-\gamma}$.

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

Proof of lemma:

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

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

From Appendix **A** we have:

$$\frac{V_{ij}}{(\Gamma-1)v_{ij}}\left(1-(1-v_{ij})^{\Gamma-1}\right) = \Sigma_{\gamma=1}^{\gamma=\Gamma-1}\frac{V_{ij}}{\gamma}\binom{\Gamma-2}{\gamma-1}(v_{ij})^{\gamma-1}(1-v_{ij})^{\Gamma-1-\gamma}.$$

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

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

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

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

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

Let the number of individuals in the large male population be $\Gamma_L$ and let $\sigma = \langle S_1, S_2, ..., S_{\Gamma_L}\rangle$ be the population state where $S_n$ is the strategy adopted by individual $n$.

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

$\eta_j$ are defined at the beginning of this paper.

Let $\sigma_n^{'} = \langle S_1, S_2, ..., S_{n-1}, S_{n+1}, ..., S_{\Gamma_L} \rangle$ be the modified population state.

Let $E(S, \sigma_n^{'})$ be the expected yearly payoff that individual $n$ receives when playing strategy $S$ against the modified population state $\sigma_n^{'}$.

We say that a strategy $V$ is a weak ESS if, when we let $\sigma_n^{'} = \langle V, V, ...V \rangle$, we have:

$E(V, \sigma_n^{'}) \geq E(U, \sigma_n^{'})\ \forall U \neq V$, and

if $E(V, \sigma_n^{'}) = E(U, \sigma_n^{'})$ then $E(V, \sigma_m^{'}) > E(U, \sigma_m^{'})$

where $\sigma_m^{'} = \langle V, V, ..., U, ..., V \rangle$. That is, $V$ and $U$ are only equally viable strategies from player $n$'s perspective if individual $n$ is the only player using strategy $U$. If a second individual $m$ adopts strategy $U$, then $U$ will have a lower payoff then $V$ for both players $m$ and $n$.

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

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

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

$$E(V, \sigma_n^{'}) - E(U, \sigma_n^{'}) = \Sigma_{j=1}^{j=M} \Sigma_{i=1}^{i=N} v_{ij} E_L(i,j) - \Sigma_{j=1}^{j=M} \Sigma_{i=1}^{i=N} u_{ij} E_L(i,j) > 0.$$

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

$$E(V, \sigma_n^{'}) = E(U, \sigma_n^{'}).$$

Consider the modified population state $\sigma_m^{'} = \langle V, V, ..., U, ..., V \rangle$.

In order for $V$ to be a weak ESS, we must have $E(V, \sigma_m^{'}) > E(U, \sigma_m^{'})$, or equivalently $E(V, \sigma_m^{'}) - E(U, \sigma_m^{'}) > 0$.

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

We have that $E_{L^*}(i, j) = \dfrac{V_{ij}}{(\Gamma_L - 1)v_{ij}}\left(1 - (1 - v_{ij})^{\Gamma_L - 1}\right)(1 - u_{ij}) +$ $u_{ij}\Sigma_{\gamma=1}^{\gamma=\Gamma_L-1}\dfrac{V_{ij}}{\gamma+1}\binom{\Gamma_L-2}{\gamma-1}(v_{ij})^{\gamma-1}(1 - v_{ij})^{\Gamma_L-1-\gamma}$.

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

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

Consider $E(V, \sigma_m^{'}) - E(U, \sigma_m^{'})$. We have:

$$E(V, \sigma_m^{'}) - E(U, \sigma_m^{'}) = \Sigma_{j=1}^{j=M}\Sigma_{i=1}^{i=N}v_{ij}E_{L^*}(i, j) - \Sigma_{j=1}^{j=M}\Sigma_{i=1}^{i=N}u_{ij}E_{L^*}(i, j)$$

$$= \Sigma_{j=1}^{j=M}\Sigma_{i=1}^{i=N}(v_{ij} - u_{ij})E_{L^*}(i, j).$$

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

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

Thus, we have that $E(V, \sigma_m^{'}) - E(U, \sigma_m^{'}) > 0$ as long as $V \neq U$, and therefore $V$

is a weak ESS.

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

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