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The Impact of Competition on Elephant Musth Strategies: A Game-theoretic Model

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THE IMPACT OF COMPETITION ON ELEPHANT MUSTH STRATEGIES:
A GAME-THEORETIC MODEL

By
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ABSTRACT

Mature male African 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. When a smaller musth bull encounters a larger non-musth bull, however, 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 observed timing strategies in the Amboseli National Park elephant population. We discuss small male musth behavior, musth-estrus coincidence, the effects of estrous female spatial heterogeneity on musth timing, conservation applications, the assumptions underpinning the model and possible modifications to the model for the purpose of determining musth duration.

CHAPTER 1

INTRODUCTION

Musth is a state of heightened aggression that sexually mature male African elephants (*Loxodonta africana*) temporarily enter and is particularly associated with mating behavior (Poole, 1987, 1989a; Poole et al., 2011). While in musth, 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). 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.

The rest of this dissertation proceeds as follows. Chapter 1 introduces some of the basic concepts and terminology associated with game-theoretic modeling using the Hawk-Dove game as a classic example of a pairwise contest. The chapter is then concluded by extending the pairwise contest example to create a simple model of musth behavior. In chapter 2, a more realistic model of musth behavior is presented along with some numerical results. Chapter 3 discusses the assumptions underlying the model presented in chapter 2, and explores the effects of injury risk on equilibrium musth behavior. Lastly, chapter 4 incorporates non-musth strategies into the male strategy set, and in doing so proposes a possible mechanism for determining equilibrium musth duration. It should be noted that while the material presented in chapters 2 and 3 (and appendices **A**, **B**, **C** and **D**) has been published (Wyse et al., 2017), the material in chapter 4 (and appendices **E** and **F**) is new to this thesis. For ease of reference, a glossary of symbols is included as appendix **G**.

1.1 Game theory

Game theory is a set of modeling techniques used to understand the cooperative and competitive behaviors of rational individuals according to some criterion of self-interest (McNamara et al., 1997). Of particular interest is Evolutionary Game Theory (EGT), a branch of Game Theory used to model phenotypic evolution when the fitness of a behavior is dependent on the frequency of behaviors in the population (Maynard Smith, 1982). The ultimate goal of an EGT model is to find an 'Evolutionarily Stable Strategy' or ESS, defined as a strategy with the property that, if the population adopts the ESS, no individual could improve his or her fitness by unilaterally adopting an alternative strategy. 'Strategy' here means a phenotype, that is, a description of what an individual will do in the context of the game.

The most typical EGT model is that of a symmetric pairwise contest. The assumptions for such a model are as follows: The modeled population contains an infinite number of individuals, the individuals reproduce asexually, the population engages in generational contests that take place between two individuals, there is a finite set of strategies which can be adopted by the contestants and the individuals do not differ in the extent to which they benefit from a contest except insofar

as they adopt different strategies (Maynard Smith, 1982). These assumptions clearly do not hold in the case of musth behavior in African Elephants.

Elephant populations are not infinitely large, and indeed the size of the population will be a relevant parameter in the proposed model. Elephants reproduce sexually, not asexually, and many aspects of musth competition occur between more than two individuals, each of which may differ in size and age (and therefore musth competition is not symmetric). Furthermore, whatever strategy set is defined, it must somehow encompass the large range of possible spatial and timing decisions a male can make regarding musth, suggesting that the strategy set will at least be very large, if not continuous. Nonetheless, the basic EGT model of a pairwise contest is a useful starting point to begin deriving a model of musth decision making.

1.1.1 The hawk–dove game

The hawk–dove game is often used as a general model of pairwise contests in an EGT framework. The model assumes an infinite population of individuals, which can be thought of as reproducing in generational cohorts. At some point over the course of a cohort’s time line, each individual will compete in a pairwise contest with another member of the cohort. At stake is a resource of value V , that is, a resource which would increase an individual’s fitness by V . The pairwise contest can be modeled through the construction of the following payoff matrix M :

Table 1.1: The payoff matrix for the Hawk-Dove game, labeled M .

		Opposing individual	
		Hawk	Dove
Focal individual	Hawk	$\frac{1}{2}(V - C)$	V
	Dove	0	$\frac{1}{2}V$

The entries in the above payoff matrix M represent payoffs to an individual who adopts the strategy on the left (the focal individual) when the opponent adopts the strategy listed above. If the focal individual uses the ‘Hawk’ strategy, then the focal individual will escalate in aggression against the opponent until either the opponent retreats, or until a potentially injurious fight ensues. If, however, the focal individual adopts the ‘Dove’ strategy, then the focal individual attempts to split the resource with the opponent, and will retreat if the opponent acts aggressively. With both strategies available to both contestants, there are four possible results.

i) Hawk vs. Hawk: If both contestants choose the ‘Hawk’ strategy, a confrontation will occur. The payoff to the focal individual in such an outcome is $\frac{1}{2}(V - C)$. The payoff is derived based

on the assumption that each contestant has an equal probability of winning, and therefore the expected payoff should be $\frac{1}{2}V$, minus the expected cost of fighting, represented with the constant $\frac{1}{2}C$.

ii) Hawk vs Dove: If the focal individual uses strategy 'Hawk', while the opposing contestant uses 'Dove', then the expected payoff to the focal contestant is V , as the opposing individual will retreat from the focal individual's aggression and forfeit the resource.

iii) Dove vs Dove: If both contestants use the 'Dove' strategy, then the expected payoff to the focal contestant is $\frac{1}{2}V$. This can be interpreted as the two contestants splitting a divisible resource, or displaying against each other until one individual retreats, with the focal contestant winning with probability $\frac{1}{2}$.

iv) Dove vs Hawk: If the focal contestant plays 'Dove' against an opponent using the 'Hawk' strategy, then the focal individual will retreat when faced with the escalated aggression of the opposing contestant. The focal individual will therefore receive an expected payoff of 0 in this situation.

The goal of this model is to predict, given the payoffs an individual receives in each situation, what the frequency of strategies will be among the population. More specifically, we would like to find an Evolutionarily Stable State, meaning a stable composition of strategies. To accomplish this, the model assumes that individuals can only adopt pure strategies, meaning that each individual must either be a 'Hawk' or a 'Dove' (the alternative would be to allow individuals to adopt probabilistic strategies, where an individual may be a 'Hawk' with probability p and a 'Dove' with probability $1 - p$). Assuming each individual adopts a pure strategy, the model then assumes that success in the pairwise contest brings reproductive success, and that the offspring of a particular strategist will use the parent strategy. This is the assumption of asexual reproduction, but can be more broadly interpreted as 'like begets like'. Mathematically, the replicator equations are often employed to model this process (Cressman and Tao, 2014).

Suppose a population exists with some initial distribution of strategies. In the case of the Hawk–Dove game, this initial distribution can be described with a single real number p , where $0 \leq p \leq 1$, representing the proportion of individuals in the population that employ the 'Hawk' strategy. $1 - p$ is therefore the proportion of 'Doves' in the population. Over time, the proportion of 'Hawk' strategists grows or shrinks depending on the relative success of the 'Hawk' strategy, while the proportion of 'Dove' strategists likewise shrinks or grows such that the sum of the two proportions remains 1. The replicator equations are meant to model this dynamic using a system

of ODEs, derived from the expected payoff the two different types of strategists could expect to receive from a pairwise contest. Consider the following payoffs:

$$E(H) = pM(H, H) + (1 - p)M(H, D)$$

$$E(D) = pM(D, H) + (1 - p)M(D, D).$$

Above, $E(H)$ is the expected value a 'Hawk' strategist can expect to receive from a pairwise contest, while $E(D)$ is the expected payoff a 'Dove' strategist receives from a contest. $M(H, H)$ is the value in the 'Hawk vs Hawk' entry of the payoff matrix M , while $M(D, H)$, $M(H, D)$ and $M(D, D)$ are the values in the 'Dove vs Hawk', 'Hawk vs Dove' and 'Dove vs Dove' entries of the payoff matrix, respectively.

Let A be the weighted average of $E(H)$ and $E(D)$, so that:

$$A = pE(H) + (1 - p)E(D).$$

The replicator equations are then defined so that strategies which earn an above average fitness payoff increase as a proportion of the total population, while strategies with a below average payoff decrease as a proportion of the population. In the case of the hawk-dove game, there is only one equation:

$$\dot{p} = (E(H) - A)p.$$

This means that the evolutionary trajectory of a set of strategies can be calculated numerically, and an Evolutionarily Stable State can be found by letting the evolutionary trajectory approach a stable node. However, in some cases, an Evolutionarily Stable State can be found through analysis alone, without resorting to numerical methods. Consider what must be true for p to be an equilibrium point of the replicator equations. We must have:

$$\dot{p} = 0 \Rightarrow p = 0 \text{ or } E(H) = A.$$

$$\text{If } p \neq 0 \text{ then } E(H) = A = pE(H) + (1 - p)E(D) \Rightarrow$$

$$p = 1 \text{ or } E(H) = E(D).$$

This implies that there are three equilibria, $p = 0$, $p = 1$, and $p = p^*$ such that $E(H) = E(D)$ (in the case of the Hawk–Dove game, this is $p^* = \frac{V}{C}$). Because there is only one ODE, at least one of the nodes must be stable, and will therefore be an Evolutionarily Stable State.

Alternatively, one can consider the definition of an ESS (an Evolutionarily Stable Strategy, rather than an Evolutionarily Stable State), that is, a strategy such that, if adopted by the entire population, no individual could improve his or her fitness by unilaterally adopting an alternative strategy.

Mathematically, this is expressed as follows:

- i) Let strategy u be adopted by the population (in this case, u could be either 'Hawk' or 'Dove').
- ii). Suppose a single individual adopts strategy v . Because the rest of the population is using strategy u , we know that the payoff to the invading strategist in the pairwise contest will be $M(v, u)$, while if the invading strategist had continued using the population strategy, the payoff would be $M(u, u)$. Therefore, in order for u to be an ESS, we must have:

$$M(u, u) > M(v, u) \quad \forall v \neq u$$

or, if $M(v, u) = M(u, u)$, then

$$M(u, v) > M(v, v).$$

In the case of the 'Hawk–Dove' game, there are only two available strategies, 'Hawk' and 'Dove'. We can easily verify that 'Dove' cannot be an ESS, because $M(D, D) = \frac{V}{2} < V = M(H, D)$. 'Hawk' can be an ESS, but only if the cost parameter C is less than the value of the resource V . In particular, if $C < V$, then $M(H, H) = \frac{1}{2}(V - C) > 0 = M(D, H)$, and therefore H is an ESS. If $C > V$, however, then $M(H, H) = \frac{1}{2}(V - C) < 0 = M(D, H)$, in which case H is not an ESS.

If $V < C$, then there is no ESS, or more specifically, there is no ESS under the assumption that each individual must always play a pure strategy. However, the game can be modified to allow individuals in the population to play probabilistic strategies, that is, an individual can adopt any strategy $p \in [0, 1]$ such that they play 'Hawk' with probability p and play 'Dove' with probability

$1 - p$. With this change an ESS can be found by using the criteria listed above. Assume that the population adopts strategy $p \in [0, 1]$.

Then, once again, the expected payoffs associated with an individual playing strategy 'Hawk' or 'Dove' are:

$$E(H) = pM(H, H) + (1 - p)M(H, D)$$

$$E(D) = pM(D, H) + (1 - p)M(D, D).$$

Therefore, the expected payoff associated with an individual playing strategy v in a population of p strategists is:

$$E(v, p) = vE(H) + (1 - v)E(D).$$

For p to be an ESS, we must apply the above ESS definition to our payoff formula, we have:

$$E(p, p) > E(v, p) \quad \forall v \neq p$$

or, if $E(v, p) = E(p, p)$, then

$$E(p, v) > E(v, v).$$

In order for a strategy v to maximize $E(v, p)$, we look at the derivative of E with respect to the individual's strategy choice v . We have: $\frac{\partial}{\partial v} E(v, p) = E(H) - E(D)$.

If the population strategy p is such that $E(H) > E(D)$, then the derivative is always positive and the individual maximizes fitness by choosing strategy $v = 1$. If the population strategy is such that $E(D) > E(H)$, then the individual strategy that maximizes fitness is $v = 0$. Thus, if p is an ESS, p must satisfy at least one of the following: $p = 0$, $p = 1$ or p is chosen so that $E(H) = E(D)$. Note that these are the same three possibilities we had when using the replicator equations to find a stable proportion p of the population utilizing the strategy 'Hawk'.

Thus, for the pairwise contest model represented above, regardless of whether or not one allows probabilistic behavior and attempts to find an ESS, or instead tries to find stable proportions of a population utilizing pure deterministic strategies, the equilibrium behavior of the population is found in the same way.

1.1.2 A simple model of musth

The pairwise 'Hawk–Dove' model is a standard example of EGT modeling techniques applied to a type of behavior that can exist in animal species. With some modification, this basic model can be used as the foundation of a (very simple) model of musth behavior.

Consider an infinite population of male elephants, made up of individuals which age in generational cohorts. When a male enters the population he is "small", but after one round becomes "medium". After a second round the male grows to become "large", and after the third round the male is removed from the population. Suppose that in each round every individual "enters musth", and in doing so is placed into a group composed of six (rather than two) males in total, where they will compete for reproductive access to females. Once a group has been formed, the participating males must choose between 2 patches of differing quality with regards to mating opportunities. If two males enter the same area, they compete, and the winning male receives the entire payoff (that is, he is the only male allowed to mate in the area). Assume also that each group is made up of 2 small males, 2 medium sized males and 2 large males.

At the end of each round, a new cohort of small males must be added to the population. Each individual of the new cohort has a lifetime strategy which will determine his behavior as a small male, medium male and large male. The proportion of males using a given lifetime strategy in the new cohort is directly proportional to the relative success of that lifetime strategy in the previous round. Furthermore, assume that small males always lose to medium or large sized males, and that medium males always lose to large males. This means that a large male need only consider the actions of the other large male when considering his own movement strategy.

Let there be two areas, A_1 and A_2 , with maximum payoffs V_1 and V_2 such that $V_1 \geq V_2$. Every round, the two large males must choose which area to compete in. The payoff matrix is as follows:

Table 1.2: The large male payoff matrix

		Opposing Male	
		A_1	A_2
Focal Male	A_1	$\frac{1}{2}V_1$	V_1
	A_2	V_2	$\frac{1}{2}V_2$

Notice that if $V_2 < \frac{1}{2}V_1$, then the ESS will have both large males spending all their time in A_1 . Consider the case where $V_2 > \frac{1}{2}V_1$.

Let p be the probability that the opposing male competes in A_1 , $1-p$ is therefore the probability that the opposing male competes in A_2 . Alternatively, p could be interpreted as the proportion of large males using the strategy "compete in A_1 ", and $1-p$ would therefore be the proportion of large males using the strategy "compete in A_2 ". In either case, the expected payoff to the focal male for competing in A_1 is given by:

$$E(A_1) = \frac{1}{2}V_1p + V_1(1-p)$$

While the expected payoff to the focal male for competing in A_2 is given by:

$$E(A_2) = V_2p + \frac{1}{2}V_2(1-p)$$

At an ESS, we must have:

$$\begin{aligned} E(A_1) &= E(A_2) \Rightarrow \\ \frac{1}{2}V_1p + V_1(1-p) &= V_2p + \frac{1}{2}V_2(1-p) \Rightarrow \\ p(\frac{1}{2}V_1 - V_2) &= (1-p)(\frac{1}{2}V_2 - V_1) \end{aligned}$$

Let $C_1 = \frac{1}{2}V_1 - V_2$ (always negative) and let $C_2 = \frac{1}{2}V_2 - V_1$ (always negative). This means we now have:

$$\begin{aligned} pC_1 &= (1-p)C_2 = C_2 - pC_2 \Rightarrow \\ p(C_1 + C_2) &= C_2 \Rightarrow \\ p &= \frac{C_2}{C_1 + C_2}. \end{aligned}$$

Note that because C_1 and C_2 are both always negative, p is always positive and less than one. Also note that we have:

$$\begin{aligned} p &= \frac{\frac{1}{2}V_2 - V_1}{\frac{1}{2}V_2 - V_1 + \frac{1}{2}V_1 - V_2} = \frac{\frac{1}{2}(V_2 - 2V_1)}{-\frac{1}{2}V_2 - \frac{1}{2}V_1} = \frac{-\frac{1}{2}(2V_1 - V_2)}{-\frac{1}{2}(V_1 + V_2)} = \\ \frac{2V_1 - V_2}{V_1 + V_2} &> \frac{V_1}{V_1 + V_2} > \frac{V_1}{2V_1} = \frac{1}{2}. \end{aligned}$$

And therefore $1 > p > \frac{1}{2}$. This means that the probability that a given large male will choose to compete in the more intrinsically valuable patch will be above .5 when the large male population is at an ESS.

Now consider the same game between the two medium sized males. The payoff matrix in this game is exactly the same as the previous payoff matrix, except the payoffs are contingent on avoiding the large males as well. If it is assumed that the large male behavior has reached an equilibrium, then both large males will be going to area A_1 with probability p . Thus we have:

Table 1.3: The medium male payoff matrix

		Opposing	Male
		A_1	A_2
Focal	A_1	$(1-p)^2 \frac{1}{2} V_1$	$(1-p)^2 V_1$
Male	A_2	$p^2 V_2$	$p^2 \frac{1}{2} V_2$

Note that this game is coupled to the game between the large males. For example, the payoff going to the focal male in row 1 column 1 is multiplied by a factor of $(1-p)^2$, because the focal male only receives a payoff if both of the large males are in A_2 .

Also notice that because $p > \frac{1}{2} > 1-p$ and $V_2 > \frac{1}{2} V_1$, a pure A_1 ESS still does not exist. A pure A_2 ESS, however, could exist if $p^2 \frac{1}{2} V_2 > (1-p)^2 V_1 \Rightarrow V_2 > \frac{2(1-p)^2}{p^2} V_1$.

If we assume no pure ESS exists, however, then we can again find a mixed ESS. Let q denote the probability that the opposing male competes in A_1 . Once again we find the expected payoff for the focal male for each strategy choice:

$$E(A_1) = (1-p)^2 \frac{1}{2} V_1 q + (1-p)^2 V_1 (1-q)$$

$$E(A_2) = p^2 V_2 q + \frac{1}{2} V_2 p^2 (1-q)$$

$$E(A_1) = E(A_2) \Rightarrow$$

$$(1-p)^2 \frac{1}{2} V_1 q + (1-p)^2 V_1 (1-q) = p^2 V_2 q + \frac{1}{2} V_2 p^2 (1-q) \Rightarrow$$

$$(1-p)^2 \frac{1}{2} V_1 q - p^2 V_2 q = \frac{1}{2} V_2 p^2 (1-q) - (1-p)^2 V_1 (1-q) \Rightarrow$$

$$q[\frac{1}{2}(1-p)^2 V_1 - p^2 V_2] = (1-q)[\frac{1}{2} V_2 p^2 - (1-p)^2 V_1].$$

If we let $K_1 = \frac{1}{2}(1-p)^2 V_1 - p^2 V_2$ and $K_2 = \frac{1}{2} V_2 p^2 - (1-p)^2 V_1$, then, as before we end up with:

$$q = \frac{K_2}{K_1 + K_2}.$$

Note that we are assuming $p^2 \frac{1}{2} V_2 < (1-p)^2 V_1$ (that is, we are assuming that if the opposing medium sized male chooses to go to A2, it would be better for the focal male to choose area A1 over A2. If this were not the case, there would be a pure A_2 ESS), and therefore both K_1 and K_2 are negative and $0 < q < 1$.

Lastly, by applying the same reasoning to the small male population, we derive the payoff matrix:

Table 1.4: The small male payoff matrix

		Opposing	Male
		A_1	A_2
Focal	A_1	$(1-q)^2(1-p)^2 \frac{1}{2} V_1$	$(1-q)^2(1-p)^2 V_1$
Male	A_2	$q^2 p^2 V_2$	$q^2 p^2 \frac{1}{2} V_2$

If we let w be the probability that the opposing small male chooses A_1 , we get:

$$E(A_1) = (1-q)^2(1-p)^2 \frac{1}{2} V_1 w + (1-q)^2(1-p)^2 V_1 (1-w), \text{ and}$$

$$E(A_2) = q^2 p^2 V_2 w + \frac{1}{2} V_2 q^2 p^2 (1-w) \Rightarrow$$

$$w = \frac{B_2}{B_1 + B_2}, \text{ where}$$

$$B_1 = \frac{1}{2}(1-q)^2(1-p)^2 V_1 - q^2 p^2 V_2, \text{ and}$$

$$B_2 = \frac{1}{2} V_2 p^2 q^2 - (1-p)^2(1-q)^2 V_1.$$

Thus, by reducing the above six player game into a sequence of three coupled pairwise contests, we can find the life-history ESS for the population. If we call the life-history ESS $\vec{u}$, then $\vec{u} = \langle p, q, w \rangle$. Additionally, one question of interest to evolutionary biologists is to what extent do larger males dominate reproduction. In this (very simple) model we can offer a partial answer to that question by calculating the expected payoff for each size class (recall that at equilibrium $E(A_1) = E(A_2)$ for all size classes):

$$E_L(A_1) = \frac{1}{2} V_1 p + V_1 (1-p)$$

$$E_M(A_1) = (1-p)^2 \frac{1}{2} V_1 q + (1-p)^2 V_1 (1-q)$$

$$E_S(A_1) = (1-q)^2(1-p)^2 \frac{1}{2} V_1 w + (1-q)^2(1-p)^2 V_1 (1-w).$$

Lastly, in this simple model we assumed an infinitely large population from which six individuals are chosen. The purpose of this assumption is that, in the case of a population of pure strategists, a given type of strategist can make up any proportion of the population, and therefore the proportion can be treated as a continuous variable. For example, if p is the proportion of large males who always go to area A1, then if the population is infinitely large we have $p \in [0, 1]$. However, if there are only n large males, where n is some finite positive integer, then $p \in \{0, \frac{1}{n}, \frac{2}{n}, \dots, 1\}$, and cannot be treated as continuous.

This restriction, however, is only relevant if we limit the players to pure strategies. If we allow probabilistic strategies, then the probabilities are the relevant variable and are continuous. In the next chapter, where a model with a finite population of male elephants is considered, we could limit the population to pure strategies by thinking of the finite population as being selected from an infinite population. For simplicity, however, we will instead allow the individuals to adopt probabilistic strategies.

CHAPTER 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 $i = 1, \dots, M$ and $j = 1, \dots, N$, 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 η_j , ξ_j or μ_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 $\vec{\eta} = \langle \eta_1, \eta_2, \dots, \eta_N \rangle$, $\vec{\xi} = \langle \xi_1, \xi_2, \dots, \xi_N \rangle$ and $\vec{\mu} = \langle \mu_1, \mu_2, \dots, \mu_N \rangle$, respectively.
3. The expected number of time periods that a large, medium or small male will spend in musth is denoted by $T_L = \sum_{j=1}^{j=N} \eta_j$, $T_M = \sum_{j=1}^{j=N} \xi_j$ or $T_S = \sum_{j=1}^{j=N} \mu_j$, 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 $\vec{p}_j = \langle p_{1j}, p_{2j}, \dots, p_{Mj} \rangle$, $\vec{q}_j = \langle q_{1j}, q_{2j}, \dots, q_{Mj} \rangle$ and $\vec{w}_j = \langle w_{1j}, w_{2j}, \dots, w_{Mj} \rangle$, respectively.
5. Males mate only while in musth. This is a simplification of natural mating behavior (Hollister-Smith et al., 2007) (see Discussion).

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 will be modified later in the manuscript (see Discussion).
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 Discussion).

With these 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, Γ_L, Γ_M and Γ_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):

$$E_L(i, j) = \frac{V_{i,j}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - \eta_j p_{ij})^{\Gamma_L}) \quad (2.1)$$

$$E_M(i, j) = \frac{V_{i,j}}{\Gamma_M q_{ij} \xi_j} (1 - (1 - \xi_j q_{ij})^{\Gamma_M}) (1 - \eta_j p_{ij})^{\Gamma_L} \quad (2.2)$$

$$E_S(i, j) = \frac{V_{i,j}}{\Gamma_S w_{ij} \mu_j} (1 - (1 - \mu_j w_{ij})^{\Gamma_S}) (1 - \eta_j p_{ij})^{\Gamma_L} (1 - \xi_j q_{ij})^{\Gamma_M} \quad (2.3)$$

2.2 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 $(\vec{\eta}, \vec{\xi}$ and $\vec{\mu})$. 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.

2.2.1 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 Γ_S equal to the number of males in category 2; we set Γ_M equal to the number of males in category 3; and we set Γ_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 2.1):

Table 2.1: The observed number of estrous females by month as reported by Poole (1989b)

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

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.

2.3 Results

The spatial ESS was to compete in each area with equal probability. The timing ESS is depicted in Figure 2.1.

As can be seen in Figure 2.1, 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).

2.3.1 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

Figure 2.1: 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 $\Gamma_S = 42$.

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 2.2.

The results displayed in Figure 2.2 are similar to those of Figure 2.1, though with some noteworthy differences. The large males are nearly unaffected by the increased population size, though the large musth male population does occupy the two viable dry season months a little more frequently. The change in the medium male strategy is more noticeable, as the medium males appear less frequently during the earlier dry season months and more frequently in the later dry season, and also are less prevalent during the wet season. The small males also have some noteworthy qualitative changes, as they almost stop being in musth in October, which was a common month to be in musth in Figure 2.1.

Figure 2.2: 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 2.3. The results of Figure 2.3 are further discussed in section 3.1.2.

2.3.2 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

Figure 2.3: 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 2.1.

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 $M = 4$):

Table 2.2: The space–time distribution of estrous females derived from Croze and Moss (2011)

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

Using these 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 2.4.

The two simulations in Figure 2.4 show different basic patterns of behavior, with the second simulation having the large, medium and small males predominantly timing musth in the wet, dry and wet seasons respectively, similar to the distributions seen in Figures 2.1 and 2.2. The results in the first simulation predict that the large, medium and small males predominantly time musth 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 spent in musth by small males. 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 dense (spatial) concentrations of estrous females can make dry season months viable as part of a 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 2.5. The second comparison is

Figure 2.4: 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.

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 2.6.

2.3.3 The Samburu population

The behavioral data on which the above model is based were drawn exclusively 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 Ng'iro river), and reports the number of adult individuals observed in each area

Figure 2.5: 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 $T_S = 0.133$.

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

Figure 2.6: 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 $T_S = 0.133$.

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 2.1 ($T_L = 2.3, T_M = 0.433, T_S = 0.133$). The results are displayed in Figure 2.7.

Figure 2.7: 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 2.1. The model assumes spatial heterogeneity among estrous females.

The results depicted in Figure 2.7 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 ($M = 9$).

2.4 Discussion

2.4.1 Coincidence of musth and estrus timing

Figure 2.1 displays the timing strategies used by the different size classes of males at the resulting space-time ESS with the first parameter set, as well as the proportion of estrous females available each month. Note that the temporal distribution of musth males is such that large males are in musth predominantly during the wet season (January through to July), medium sized males are in musth predominantly during the dry season (August through to December), and small males are in musth predominantly during the wet season, all of which fits with observed musth timing behavior in the Amboseli population (Poole, 1989a).

Poole (1987) found that the observed number of musth males per month was coincident with the observed number of estrous females per month. To test if the model results replicate this pattern, the expected number of musth males for each month was calculated using the formula:

$$\text{Musth males in month } j = \Gamma_L \eta_j + \Gamma_M \xi_j + \Gamma_S \mu_j.$$

The results were computed using $T_L = 2.3$, $T_M = .433$ and $T_S = 0.133$, and are depicted in the second panel of Figure 2.8.

Interestingly, although the model can predict a temporal co-occurrence between the number of males in musth and the number of females in estrus, this is dependent on the musth duration parameters. For example, if the simulation is run with $T_L = 4$, $T_M = 1.2$ and $T_S = 0.5$, a similar pattern of large and small males entering musth in the wet season and medium males entering musth in the dry season emerges. However, the number of males in musth each month is not strongly coincident with the number of estrous females, as can be seen in the third panel of Figure 2.8. For comparison, Figure 2.9 is based on data from Poole (1987), and shows the observed number of musth males and estrous females per month over several years.

Poole (1989a) reported a mean and mode of 3 musth males per month, while the predicted mean was 6 (rounded up from 5.7) with a modal average of 6 (3 months, found by rounding the expected number of males each month to the nearest integer). Possible reasons for the discrepancy between the different averages include a.) musth duration parameters were based on median values as reported in Poole et al. (2011) rather than mean values, b.) the musth duration data set and the population data set are measuring the Amboseli population at different times, and c.) the

Figure 2.8: The observed proportion of estrous females by month as reported by Poole (1989b) (top), the expected number of musth males by month using $T_L = 2.3$, $T_M = 0.433$ and $T_S = 0.133$ (middle), and the expected number of musth males by month using $T_L = 4$, $T_M = 1.2$ and $T_S = 0.5$ (bottom). The expected number of musth males by month is computed using the formula $\Gamma_L \eta_j + \Gamma_M \xi_j + \Gamma_S \mu_j$.

numbers reported in Poole (1989a) were only musth males sighted, which could underestimate the total number of musth males in a given month.

The model predicts that the number of large males in musth per month will be related to the number of estrous females. This does not, however, necessarily extend to the rest of the population, as medium males will attempt to avoid large males, and therefore will be in musth during periods of time when few estrous females are available (the dry season). Similarly, although small males will

Figure 2.9: The number of estrous females observed by month versus the number of musth males observed by month. Based on Figure from Poole (1987).

try to avoid medium sized males and therefore will usually enter musth during the wet season, the months chosen by small males will generally be the wet season months with the smallest number of large males (and therefore the smallest number of available estrous females). Thus, as long as the population of large males is sufficient to influence the musth behavior of the medium and small males, both the medium and small male timing strategies will coincide poorly with female estrus timing. The overall population co-occurrence is caused primarily by the fact that larger males spend much more time in musth than medium or small males.

2.4.2 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). The above model offers two possible 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, in contrast to the case 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 optimal strategy for small males than for other size classes.

The latter phenomenon can be seen by inspecting Figures 2.1 and 2.2, and also by considering the effect of changing musth duration on the small males shown in Figure 2.4. Figures 2.1 and 2.2 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 strategies adopted by the small and medium sized male populations. Similarly, the effect of changing the musth-duration parameters shown in Figure 2.4 is largest for the small males. In Figure 2.4, the simulation with shorter musth-duration parameters has the 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.

Similar results can be observed with other changes to the male population and musth-duration parameters. The reason that small male strategies are usually the most influenced by parameter changes is because they are affected by every size class. With the modeling assumptions used, large males cannot lose a musth competition against medium or small sized males, and therefore changes to the medium or small male populations have no effect on the large male ESS. Medium males, however, are influenced by changes to both the large and medium sized male populations, but not by changes to the small male population. Lastly, small males always lose musth competitions against large and medium sized males, and therefore anything that influences the strategies or populations of those two groups will have an impact on the small male strategy as well. Because natural conditions such as male and female population size may vary over time, the optimal behavior for smaller males may not be as consistent as that of large and medium sized males, and therefore small male musth behavior may have evolved to be less predictable.

2.4.3 The effect of a non-uniform estrous female distribution

Figure 2.4 displays the results of simulations made with a non-uniform distribution of estrous females. The most noticeable impact of the non-uniform spatial distribution was to obscure, or even eliminate, the wet-dry-wet temporal distribution observed in the spatially uniform case. The reason that spatial variation of estrous females can obscure the previous timing behavior is that it introduces an alternative dimension in which musth males can avoid larger competitors; that is, a medium (or small) sized male can avoid large males by visiting areas that have a relatively small number of estrous females (and are therefore unlikely to contain large male competitors), even if

the time period contains a large number of estrous females overall. Similarly, if several female elephants congregate in a single area, then it could be worthwhile for a large male to enter musth even if, overall, the time period has relatively few estrous females.

The effect of the non-uniform V_{ij} values is most obvious in the simulation with shorter musth-duration parameters, in which both medium and small sized males are likely to go into musth during the dry season. This timing distribution is contrary to both observed behavior and the results of other simulations. However, when the musth-duration parameters are increased, the wet-dry-wet distribution returns. The shorter musth duration parameters are based on the median observed musth durations reported in Poole et al. (2011), while the longer musth duration parameters were selected to exhibit the effect of parameter variation and are the same musth duration parameters used in the third panel of Figure 2.8.

The predicted musth behavior from the short musth-duration simulation shown in Figure 2.4 has the small males entering musth more frequently in the dry season rather than the wet season. One possible reason for this discrepancy with reported behavior is the assumption that the number of estrous females in an area is proportional to the number of families in the area. Poole et al. (2011) note that females are more likely to enter estrus following periods of high rainfall, probably because the heavier rainfall stimulates vegetation growth. It may be the case, therefore, that family groups are less likely to contain estrous females when foraging in lower quality areas (which have less vegetation), and therefore the spatial distribution of estrous females may differ from the overall distribution of the female population.

2.4.4 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 over two years (1980–1981). Each male was classified as either "large" or "medium" (there were no small males) 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 2.10.

The observed musth behavior differs from the predicted musth behavior shown in Figure 2.1. However, the results in Figure 2.1 were computed using male population values from Poole (1989a), which used data collected in 1986. Furthermore, Figure 2.1 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 2.4. Most

Figure 2.10: The observed number of estrous females per month, and the observed number of large and medium males in musth per month in 1980.

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 2.11.

Additionally, similar simulations were carried out using data from 1981, as shown in Figure 2.12. 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.

To further compare the predicted musth timing probabilities shown in Figures 2.11 and 2.12 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

Figure 2.11: 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 2.9.

using a false discovery rate of $\alpha = 0.05$ and a significance threshold of $q^* = 0.05$. The number of months for which the predicted musth probability can be rejected are displayed in Table 2.3.

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 α value is used on the aggregated data simulations,

Figure 2.12: 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 2.9.

the number of rejections increases for 1980 though not for 1981, as can be seen in Table 2.4.

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

Table 2.3: The number of monthly probabilities rejected and accepted for each simulation

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

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

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 couple of days, could be forced out of musth by other males and entered and exited musth multiple times while associating with females. These groups could be considered similar to the large, medium and small designations used in the model, suggesting that some of the medium sized males in the graphs above should be classified as small, and perhaps also that some of the large males should be considered 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 in this manuscript 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 2.13.

Figure 2.13: 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.

CHAPTER 3

ASSUMPTIONS AND APPLICATIONS

3.1 Costless musth

In creating the above model, several simplifying assumptions were made regarding musth behavior that do not always hold in the wild, but were useful for modeling purposes. 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 made in the model 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 and therefore be sub-optimal from a life-history perspective. Additionally, though musth competitions 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 attempt a non-musth strategy, where the male stays out of musth so as to avoid attention from musth males, but still tries 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 than 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 doing so.
- 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 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 strategy 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 chance 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 will sometimes enter musth at an earlier age than observed in the wild (Poole and Granli, 1989) and large males are known to suppress musth in smaller males (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, 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 is unusual from a physiological cost perspective, as physiological costs are likely easier to offset during the wet season, but is not unusual if competing against a larger male is more dangerous than competing against a similarly sized male. Alternatively, male elephants that are unwell or in poor physiological condition will skip or shorten their musth periods (Poole, 1989a), suggesting that in some cases physiological cost 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 a positive injury risk associated with musth, but it remains unclear how significant it may be and how it may affect the ESS. 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. λ is the probability that a musth male will be injured while competing against a musth male of equal size, β is the probability a musth male will be injured competing against a musth male that is one size class larger, while ω 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 expected lifetime payoff. Three examples of an ESS from the injury risk model are shown in Figure 3.1.

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 λ 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 3.1 depicts two simulations where the probability of injury increases when the focal male is significantly

Figure 3.1: 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).

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 a model is not presented in this manuscript. 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 conclude that a male can likewise more easily offset the physiological cost of musth during months with (or following) heavy rainfall, meaning that a male would benefit from entering musth in rainy months both due to more prevalent vegetation and because of the greater access to estrous females. Because large males are unaffected by the actions of smaller males, inserting physiological costs into the above model should not significantly alter the incentives facing 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 likely (barring unusually low numbers of large males or implausibly high physiological costs) avoid the larger males by entering musth more frequently during the drier time periods, and small males would thus likely enter musth during the wet season to avoid the 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 a non-musth strategy, also requires a significant modeling effort to understand, which is undertaken in chapter 4 (though without any numerical results). In addition to the model in chapter 4, there

is empirical evidence that such a trade-off is an important constraint on musth duration, which is also discussed in the next chapter.

3.1.1 Other assumptions

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

Females do 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 must 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.

3.1.2 Conservation applications

The model presented in this manuscript 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 from 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.

Similar phenomena could be predicted 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.

CHAPTER 4

INCORPORATING NON-MUSTH STRATEGIES

In section 3.1, the possibility that sexually active males choose between a musth strategy and a non-musth strategy is briefly discussed. Here we develop such a model, and discuss empirical evidence that such a trade-off is an important constraint on musth-duration, though numerical results are still in progress and therefore remain a matter for future work.

4.1 Evidence of non-musth mating strategies

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 popular among cow/calf groups. This implies a physiological cost associated with a male spending time outside of a "bull area," as the available forage provides a sub-optimal diet for an adult male. 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 their time around females in musth, 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 low-ranking males are in fact more likely to obtain a copulation as non-musth non-guarders in situations where the available estrous females are already monopolized by a high ranking male. This is because, as non-musth males, they are allowed to get closer to the estrous female. Additionally, Poole (1989a) observes a size-dependent non-musth dominance hierarchy among sexually active males, similar to the musth hierarchy described previously, and also records the deterioration of physical condition associated with long musth periods. Lastly, Poole (1989b) observes that estrous females will actively avoid sexually active non-musth males, suggesting a penalty to non-musth sexually active males even when they can avoid male musth and non-musth competitors.

Collectively, this evidence points to an additional strategic element not incorporated in the previous models. A given male can choose to be in musth, and in doing so pay greater physi-

ological costs but gain a competitive advantage over non-musth males in agonistic interactions. Alternatively, the male can be a sexually active non-musth male, and in doing so have less costly physiological expenses and may possibly avoid the attention of musth males (though probably losing any agonistic interactions that he gets into against musth males), at the cost of estrous females resisting his mating attempts.

4.1.1 Assumptions for the non-musth model

Consider the following set of assumptions:

1. There are M different spatial areas at any time during a year, which is subdivided into N time periods.
2. For $i = 1, \dots, M$ and $j = 1, \dots, N$, let V_{ij} represent the intrinsic value of an area i during time period j in terms of mating opportunities.
3. There are three size classes of males: small, medium and large.
4. Males only mate when sexually active. While sexually active, males may either enter musth or be a non-musth male.
5. Timing strategies for sexually active males of all size classes are vectors of probabilities. Let ω_j , θ_j or ϕ_j be the probability that a large, medium or small male, respectively, will be sexually active during time period j . Then the population strategies for large, medium and small males are $\vec{\omega} = \langle \omega_1, \omega_2, \dots, \omega_N \rangle$, $\vec{\theta} = \langle \theta_1, \theta_2, \dots, \theta_N \rangle$ and $\vec{\phi} = \langle \phi_1, \phi_2, \dots, \phi_N \rangle$, respectively.
6. Timing strategies for musth males of all size classes are vectors of probabilities. Let η_j , ξ_j or μ_j be the probability that a large, medium or small male, respectively, will enter musth during time period j , given that he is sexually active during time period j . Then the population musth timing strategies for large, medium and small males are $\vec{\eta} = \langle \eta_1, \eta_2, \dots, \eta_N \rangle$, $\vec{\xi} = \langle \xi_1, \xi_2, \dots, \xi_N \rangle$ and $\vec{\mu} = \langle \mu_1, \mu_2, \dots, \mu_N \rangle$, respectively.
7. The expected number of time periods that a large, medium or small male will spend in musth is denoted by $T_L = \sum_{j=1}^{j=N} \omega_j \eta_j$, $T_M = \sum_{j=1}^{j=N} \theta_j \xi_j$ or $T_S = \sum_{j=1}^{j=N} \phi_j \mu_j$, respectively.
8. The expected number of time periods that a large, medium or small male will spend as a non-musth male is denoted by $S_L = \sum_{j=1}^{j=N} \omega_j (1 - \eta_j)$, $S_M = \sum_{j=1}^{j=N} \theta_j (1 - \xi_j)$ or $S_S = \sum_{j=1}^{j=N} \phi_j (1 - \mu_j)$, respectively.

9. 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 musth male, respectively, competes in area i in time period j . Then the spatial strategies for large, medium and small musth males are $\vec{p}_j = \langle p_{1j}, p_{2j}, \dots, p_{Mj} \rangle$, $\vec{q}_j = \langle q_{1j}, q_{2j}, \dots, q_{Mj} \rangle$ and $\vec{w}_j = \langle w_{1j}, w_{2j}, \dots, w_{Mj} \rangle$, respectively.
10. When not in musth, each male has a spatial strategy, which can depend on the time period. Let x_{ij}, y_{ij} or z_{ij} be the probability that a large, medium or small non-musth male, respectively, competes in area i in time period j . Then the spatial strategies for large, medium and small non-musth males are $\vec{x}_j = \langle x_{1j}, x_{2j}, \dots, x_{Mj} \rangle$, $\vec{y}_j = \langle y_{1j}, y_{2j}, \dots, y_{Mj} \rangle$ and $\vec{z}_j = \langle z_{1j}, z_{2j}, \dots, z_{Mj} \rangle$, respectively.
11. 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.
12. If multiple non-musth males are in the same area during the same time period, 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.
13. Musth males ignore non-musth males. The only inherent disadvantage to being a non-musth male is that estrous females will run from non-musth males but not musth males. This means that the victorious male from a non-musth competition will successfully mate with a given estrous female with only some small probability ϵ , while a victorious musth male who wins a musth competition mates with probability $1 - \epsilon$. Alternatively, ϵ can be thought of as representing the probability that the non-musth male successfully avoids the musth male and mates with a given estrous female.
14. Males attempt to maximize the expected number of mating opportunities over the entire year.
15. There is no injury risk associated with agonistic interactions (either musth or non-musth). Males are limited in the amount of time they spend being sexually active by physiological costs. In particular, we assume that P_L , P_M , and P_S represent the maximum number of time periods a large, medium or small male could spend in musth without shortening his lifespan or slowing his long-term growth. Furthermore, recall that T_L, T_M , and T_S represent the amount of time a large, medium, or small male spends in musth (see assumption 7), while

S_L, S_M , and S_S represent the amount of time spent as a sexually active non-musth male for the different size classes (see assumption 8). We assume that α is a parameter such that $0 < \alpha < 1$ and $T_L + \alpha S_L = P_L$, $T_M + \alpha S_M = P_M$, and $T_S + \alpha S_S = P_S$. Alternatively, α can be thought of as the ratio of non-musth-related physiological expenses to musth-related physiological expenses, which is discussed later in the chapter.

16. Estrous females will cooperate with whichever musth male wins a musth competitive interaction, but will avoid mating with the non-musth male who wins the non-musth competitive interaction. Again, this means that the winner of the non-musth competition will only get to mate with a given estrous female with some small probability ϵ , while the musth male mates with probability $1 - \epsilon$.

With these 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 strategies $\vec{\omega}$ and $\vec{\eta}$ 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 strategies $\vec{\theta}$ and $\vec{\xi}$ and spatial strategy $\vec{q}_j$ while all other small males are using $\vec{\phi}$, $\vec{\mu}$ and $\vec{w}_j$. Lastly, Γ_L, Γ_M and Γ_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 E for details):

$$E_L(i, j) = \frac{(1 - \epsilon)V_{i,j}}{\Gamma_L p_{ij} \eta_j \omega_j} [1 - (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L}] \quad (4.1)$$

$$E_M(i, j) = \frac{(1 - \epsilon)V_{i,j}}{\Gamma_M q_{ij} \xi_j \theta_j} [1 - (1 - \xi_j q_{ij} \theta_j)^{\Gamma_M}] (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L} \quad (4.2)$$

$$E_S(i, j) = \frac{(1 - \epsilon)V_{i,j}}{\Gamma_S w_{ij} \mu_j \phi_j} [1 - (1 - \mu_j w_{ij} \phi_j)^{\Gamma_S}] (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L} (1 - \xi_j q_{ij} \theta_j)^{\Gamma_M}. \quad (4.3)$$

Similarly, let $F_L(i, j)$ be the expected payoff that a large male would receive as a non-musth male in area i during time period j , given that all the other large males in the population are using timing strategies $\vec{\omega}$ and $\vec{\eta}$ and spatial strategy $\vec{x}_j$. Similarly, let $F_M(i, j)$ and $F_S(i, j)$ 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 strategies $\vec{\theta}$ and $\vec{\xi}$ and spatial strategy $\vec{y}_j$.

while all other small males are using $\vec{\phi}$, $\vec{\mu}$ and $\vec{z}_j$. With these definitions, it can be shown that F_L , F_M and F_S have the following expressions (see Appendix **E** for details):

$$F_L(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij}(1 - \eta_{ij})\omega_j} [1 - (1 - x_{ij}(1 - \eta_j)\omega_j)^{\Gamma_L}] \quad (4.4)$$

$$F_M(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_M y_{ij}(1 - \xi_{ij})\theta_j} [1 - (1 - y_{ij}(1 - \xi_j)\theta_j)^{\Gamma_M}] (1 - x_{ij}(1 - \eta_j)\omega_j)^{\Gamma_L} \quad (4.5)$$

$$F_S(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_S z_{ij}(1 - \mu_{ij})\phi_j} [1 - (1 - z_{ij}(1 - \mu_j)\phi_j)^{\Gamma_S}] (1 - x_{ij}(1 - \eta_j)\omega_j)^{\Gamma_L} (1 - y_{ij}(1 - \xi_j)\theta_j)^{\Gamma_M} \quad (4.6)$$

The expected value formulas defined above are useful because, at an ESS, any two viable musth 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 . Similarly, any two viable non-musth space-time choices $(i, j), (l, k)$ should have an equal expected payoff as well ($F_*(i, j) = F_*(l, k)$). Lastly, at an ESS it should not be possible for a male to increase his expected yearly payoff by increasing (decreasing) the amount of time he spends in musth by decreasing (increasing) the amount of time he spends as a non-musth sexually active male.

A given male's yearly payoff at an ESS is given by $E_*(i, j)T_* + F_*(l, k)S_*$ for any viable choices of $(i, j), (l, k)$. Furthermore, we also have the physiological restriction $T_* + \alpha S_* = P_*$. If a male chooses to increase the amount of time spent in musth by δ , then we have: $T_* + \delta + \alpha(S_* - \frac{\delta}{\alpha}) = P_*$ (that is, to maintain the physiological constraint we must decrease the amount of time spent as a non-musth male by $\frac{\delta}{\alpha}$). This means that the yearly payoff for a male using the modified strategy would be $E_*(i, j)(T_* + \delta) + F_*(l, k)(S_* - \frac{\delta}{\alpha})$. Because, at an ESS, the modified strategy should not be more successful than the original (regardless if δ is positive or negative), we must have $E_*(i, j)\delta - \frac{F_*(l, k)}{\alpha}\delta = 0 \implies E_*(i, j) = \frac{F_*(l, k)}{\alpha}$ for all viable choices $(i, j), (l, k)$.

Because musth males are unaffected by the musth strategies of smaller males, an ESS can be found by first numerically solving for the $\vec{\omega}, \vec{\eta}, \vec{p}$ and $\vec{x}$ strategies for which $E_L(i, j) = \frac{F_L(l, k)}{\alpha}$, then finding the $\vec{\theta}, \vec{\xi}, \vec{q}$ and $\vec{y}$ strategies for which $E_M(i, j) = \frac{F_M(l, k)}{\alpha}$ taking the $\vec{\omega}, \vec{\eta}, \vec{p}$ and $\vec{x}$ strategies from the large male population as environmental constants. Lastly, the ESS is completed by finding the $\vec{\phi}, \vec{\mu}, \vec{w}$ and $\vec{z}$ for which $E_S(i, j) = \frac{F_S(l, k)}{\alpha}$ while using the $\vec{\omega}, \vec{\eta}, \vec{p}, \vec{x}, \vec{\theta}, \vec{\xi}, \vec{q}$ and $\vec{y}$ strategies from the large and medium male populations (for a further description of the numerical process, see Appendix **F**).

Lastly, it is worth deriving the physiological constraint $T_* + \alpha S_* = P_*$. Suppose a male of a given size class incurs energy costs while sexually active, and that this male will cease being sexually active once the energy costs exceed some threshold M_* . If the male incurs costs at a rate of C_m while in musth and C_n while in a sexually active non-musth state (with $C_m > C_n$), then we have $C_m T_* + C_n S_* = M_*$. Furthermore, because P_* is the maximum number of time periods the male can spend in musth, we must have $M_* = C_m P_*$, and therefore $C_m T_* + C_n S_* = C_m P_*$. dividing through by C_m , we have $T_* + \frac{C_n}{C_m} S_* = P_*$ or $T_* + \alpha S_* = P_*$.

CHAPTER 5

CONCLUSION AND FUTURE WORK

In chapter two, a model of musth decision making was introduced that appears to yield insight into the role of competition in shaping the mating behavior of male African elephants. In particular, we investigated the role of avoiding competitors in space and time as a factor in selecting the probabilistic timing strategies adopted by males of differing sizes. The model predictions were then compared to observed data with some success in predicting musth behavior. Further work, however, can be pursued with regards to both improving the predictive capabilities of the model, as well as modifying the model to incorporate other perspectives.

Many of the parameter choices that were made while testing this model, such as the number of areas or time periods, were motivated by the format of existing observational data and could be improved. Most importantly, it is unclear if the age designations used to categorize the males into size classes is optimal, and a more careful selection of size classes may improve results. Such improvements could make the model more useful for understanding phenomena that are important to conservationists and ecologists. Examples of such phenomena include space use by male elephants and the effect that larger males have in regulating the musth behavior of smaller males.

In chapter three, a mortality model was introduced which proposed a possible mechanism through which musth duration could be determined. One advantage of this model is that it could potentially predict gradual changes in musth behavior over an elephant's life-history. For this to be possible, the mortality model would have to be modified to incorporate a larger number of years. If the mortality model was altered to incorporate such a detailed life-history, however, it is likely that the large, medium and small size class designations would have to be replaced with a more sophisticated approach to changes in size.

Additionally, the role of physiological costs in determining musth duration is another avenue for future work. Three possible methods for approaching this issue are: that physiological costs should be conceptualized as lowering fitness by shortening longevity, that physiological costs slow down a male's growth in size, and that physiological costs increase the probability of dying in the year in which the costs are incurred. Even if the effect of physiological costs is not given its own model, it may still play a role in other models (such as the non-musth model described in chapter 4). A

proper conceptualization of physiological costs is therefore likely to be valuable in understanding musth behavior.

Lastly, in chapter four a non-musth model was introduced along with some motivating biological information for why such a model may be plausible. The non-musth model has a number of advantages over the mortality model in that it has the potential to explain several aspects of male behavior simultaneously. Smaller males spend a higher proportion of their time around females in a non-musth state, but as a male grows larger an increasing proportion of this time is spent in musth. It is plausible that the non-musth males are trying to mate with females during this non-musth period, as otherwise it would be difficult to explain why the small males have left the male area. Furthermore, non-musth mating attempts have been observed, and therefore a non-musth model which could explain or incorporate the above facts while also predicting musth duration is worth exploring.

The most important future work outlined by this dissertation is therefore the numerical work implied by the non-musth model discussed in chapter 4. In addition, the question of how to test such a model raises the need for data on non-musth male behavior. Of particular interest is timing data for sexually active non-musth males, that is, dates in which a given male is consorting with females but not in musth, with the size of the male also recorded.

APPENDIX 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 γ 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 γ , however, is dependent on the probabilistic strategies of the large male population. To find the expected value of the payoff function, let there be γ_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:

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

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

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

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

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

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

The above summation is identical to the probability mass function for γ_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 γ_L large males in musth during period j . As, again, γ_L is probabilistic, the expected value of the above formula must be found with respect to γ_L . To find the expected value, note that the focal male will be in musth during time period j , and let there be Γ_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:

$$\begin{aligned} & \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \frac{V_{ij}}{\gamma_L p_{ij}} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L - 1}{\gamma_L - 1} (\eta_j)^{\gamma_L - 1} (1 - \eta_j)^{\Gamma_L - \gamma_L} = \\ & \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \frac{V_{ij}}{\Gamma_L p_{ij}} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L - 1} (1 - \eta_j)^{\Gamma_L - \gamma_L} = \\ & \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} (1 - (1 - p_{ij})^{\gamma_L}) \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} = \\ & \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} - (1 - p_{ij})^{\gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} \\ & = \frac{V_{ij}}{\Gamma_L p_{ij} \eta_j} \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j)^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} - (\eta_j - \eta_j p_{ij})^{\gamma_L} \binom{\Gamma_L}{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} \end{aligned}$$

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

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

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

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

Now consider the second term in the summation:

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

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

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

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 binomial theorem without the $i = \gamma_L = 0$ term is obtained. Therefore:

$$\begin{aligned} & \sum_{\gamma_L=1}^{\gamma_L=\Gamma_L} \binom{\Gamma_L}{\gamma_L} (\eta_j - \eta_j p_{ij})^{\gamma_L} (1 - \eta_j)^{\Gamma_L - \gamma_L} = \\ & [\eta_j - \eta_j p_{ij} + (1 - \eta_j)]^{\Gamma_L} - (1 - \eta_j)^{\Gamma_L} = \\ & (1 - p_{ij} \eta_j)^{\Gamma_L} - (1 - \eta_j)^{\Gamma_L}. \end{aligned}$$

Combining these expressions gives:

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

yielding (2.1). Applying the above reasoning to small and medium males as well yields (2.2)–(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 $T_L = \sum_j \eta_j$ where T_L is a given parameter (for details of the numerical process, see Appendix C).

APPENDIX 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 λ , β and ω (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 $\vec{\eta} = \langle \eta_{2N+1}, \eta_{2N+2}, \dots, \eta_{3N} \rangle$ will enter musth during time period j ($2N+1 \leq j \leq 3N$) with probability η_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 $T = \sum_{j=2N+1}^{j=3N} \eta_j$. 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 $\vec{p}_j = \langle p_{1j}, p_{2j}, \dots, p_{Mj} \rangle$ 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 discussion).

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 $2N + 1 - 3N$), 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 λ . If the opposing male is one size class larger, the probability of injury is β while a disadvantage of two size classes gives a probability of injury of ω . 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 Γ_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 discussion).

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 γ medium sized opponents, then his chances of surviving would be:

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

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

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

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

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

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 γ_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 γ_M males in musth during time period j . Summing over all possible values of γ_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 β 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 ω 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:

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

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

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

To find the expected number of males alive in each time period, assume that each year Γ_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 Γ_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:

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

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

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

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

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

APPENDIX 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 $\vec{\eta}$:

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

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:

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

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

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

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

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 η_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 η with ξ , 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 η with μ , p with w , T_L with T_S and $E_L(i, j)$ with $E_S(i, j)$).

APPENDIX 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:

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

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

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

From appendix **A** we have:

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

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

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

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 Γ_L and let $\sigma = \langle S_1, S_2, \dots, S_{\Gamma_L} \rangle$ 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 probability of being in musth in area i during time period j , and are subject to the constraints $T_L = \sum_{i=1}^{i=M} \sum_{j=1}^{j=N} s_{ij}$ and $\sum_{i=1}^{i=M} s_{ij} \leq 1$ 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 η_j are defined at the beginning of the manuscript.

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.

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

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

$$E(V, \sigma'_n) \geq E(U, \sigma'_n) \quad \forall U \neq V, \text{ and}$$

$$\text{if } E(V, \sigma'_n) = E(U, \sigma'_n) \text{ then } E(V, \sigma'_m) > E(U, \sigma'_m)$$

where $\sigma'_m = \langle V, V, \dots, U, \dots, V \rangle$. 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 than V for both players m and n .

Let $\sigma = \langle V, V, \dots, V \rangle$ and let V be chosen so that $E_L(i, j) = E_L(l, k) \quad \forall (i, j), (l, k)$ 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:

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

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 $\sigma'_m = \langle V, V, \dots, U, \dots, V \rangle$.

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 $E_{L^*}(i, j)$.

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

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 π .

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

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

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 π , so that we have:

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

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 .

APPENDIX E

DERIVATION OF THE NON-MUSTH MODEL

Consider the expected payoff a focal large non-musth male would receive from being sexually active during time period j and in area i . If k large non-musth males will be competing against the focal male in the area during that period, then the payoff function is:

$$F_L(i, j) = \frac{\epsilon V_{ij}}{1+k}$$

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

$$\binom{\lambda-1}{k} (x_{ij})^k (1 - x_{ij})^{\lambda-1-k}.$$

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

$$\begin{aligned} F_L(i, j) &= \sum_{k=0}^{k=\lambda-1} \frac{\epsilon V_{ij}}{1+k} \binom{\lambda-1}{k} (x_{ij})^k (1 - x_{ij})^{\lambda-1-k} \\ &= \frac{\epsilon V_{ij}}{\lambda} \sum_{k=0}^{k=\lambda-1} \binom{\lambda}{k+1} (x_{ij})^k (1 - x_{ij})^{\lambda-1-k} \\ &= \frac{\epsilon V_{ij}}{\lambda x_{ij}} \sum_{k=0}^{k=\lambda-1} \binom{\lambda}{k+1} (x_{ij})^{k+1} (1 - x_{ij})^{\lambda-(k+1)} \\ &= \frac{\epsilon V_{ij}}{\lambda x_{ij}} \sum_{k=1}^{k=\lambda} \binom{\lambda}{k} (x_{ij})^k (1 - x_{ij})^{\lambda-k} \\ &= \frac{\epsilon V_{ij}}{\lambda x_{ij}} (1 - (1 - x_{ij})^\lambda) \end{aligned}$$

We do not, however, know that there are λ large (sexually active) non-musth males during time period j . Let us assume that there are a total of Λ large, sexually active males during time period j . We can therefore find the expected value of being a sexually active non-musth male during time period j by summing the above formula over all possible values of λ . We have:

$$\begin{aligned}
F_L(i, j) &= \sum_{\lambda=1}^{\Lambda} \frac{\epsilon V_{i,j}}{\lambda x_{ij}} (1 - (1 - x_{ij})^\lambda) \binom{\Lambda-1}{\lambda-1} (1 - \eta_{ij})^{\lambda-1} (\eta_{ij})^{\Lambda-\lambda} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \sum_{\lambda=1}^{\Lambda} (1 - (1 - x_{ij})^\lambda) \binom{\Lambda}{\lambda} (1 - \eta_{ij})^\lambda (\eta_{ij})^{\Lambda-\lambda} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \sum_{\lambda=1}^{\Lambda} \binom{\Lambda}{\lambda} (1 - \eta_{ij})^\lambda (\eta_{ij})^{\Lambda-\lambda} - (1 - x_{ij})^\lambda \binom{\Lambda}{\lambda} (1 - \eta_{ij})^\lambda (\eta_{ij})^{\Lambda-\lambda} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \{1 - (\eta_{ij})^\Lambda - \sum_{\lambda=1}^{\Lambda} (1 - x_{ij})^\lambda \binom{\Lambda}{\lambda} (1 - \eta_{ij})^\lambda (\eta_{ij})^{\Lambda-\lambda}\} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \{1 - (\eta_{ij})^\Lambda - \sum_{\lambda=1}^{\Lambda} \binom{\Lambda}{\lambda} (1 - \eta_{ij} - x_{ij} + \eta_{ij} x_{ij})^\lambda (\eta_{ij})^{\Lambda-\lambda}\} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \{1 - (\eta_{ij})^\Lambda - [(1 - x_{ij} + \eta_{ij} x_{ij})^\Lambda - (\eta_{ij})^\Lambda]\} \\
&= \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_{ij})} \{1 - (1 - x_{ij} + \eta_{ij} x_{ij})^\Lambda\}
\end{aligned}$$

Once again, to derive the above expression we assumed that there were Λ sexually active males during time period j . To find the expected value of being a sexually active non-musth male during time period j in a population of Γ_L large males, we must multiply by the probability that there are in fact Λ sexually active males, then sum over all possible values of Λ . We have:

$$\begin{aligned}
F_L(i, j) &= \sum_{\Lambda=1}^{\Gamma_L} \frac{\epsilon V_{i,j}}{\Lambda x_{ij} (1 - \eta_j)} \{1 - (1 - x_{ij} (1 - \eta_j))^\Lambda\} \binom{\Gamma_L-1}{\Lambda-1} (\omega_j)^{\Lambda-1} (1 - \omega_j)^{\Gamma_L-\Lambda} \\
&= \sum_{\Lambda=1}^{\Gamma_L} \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j)} \{1 - (1 - x_{ij} (1 - \eta_j))^\Lambda\} \binom{\Gamma_L}{\Lambda} (\omega_j)^{\Lambda-1} (1 - \omega_j)^{\Gamma_L-\Lambda} \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} \sum_{\Lambda=1}^{\Gamma_L} \{1 - (1 - x_{ij} (1 - \eta_j))^\Lambda\} \binom{\Gamma_L}{\Lambda} (\omega_j)^\Lambda (1 - \omega_j)^{\Gamma_L-\Lambda} \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} \sum_{\Lambda=1}^{\Gamma_L} \binom{\Gamma_L}{\Lambda} (\omega_j)^\Lambda (1 - \omega_j)^{\Gamma_L-\Lambda} - (1 - (1 - \eta_j) x_{ij})^\Lambda \binom{\Gamma_L}{\Lambda} (\omega_j)^\Lambda (1 - \omega_j)^{\Gamma_L-\Lambda} \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} [1 - (1 - \omega_j)^{\Gamma_L} - \sum_{\Lambda=1}^{\Gamma_L} \binom{\Gamma_L}{\Lambda} (1 - (1 - \eta_j) x_{ij})^\Lambda (\omega_j)^\Lambda (1 - \omega_j)^{\Gamma_L-\Lambda}] \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} [1 - (1 - \omega_j)^{\Gamma_L} - \sum_{\Lambda=1}^{\Gamma_L} \binom{\Gamma_L}{\Lambda} (\omega_j - (1 - \eta_j) x_{ij} \omega_j)^\Lambda (1 - \omega_j)^{\Gamma_L-\Lambda}] \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} [1 - (1 - \omega_j)^{\Gamma_L} - ((1 - (1 - \eta_j) x_{ij} \omega_j)^{\Gamma_L} - (1 - \omega_j)^{\Gamma_L})] \\
&= \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} [1 - (1 - (1 - \eta_j) x_{ij} \omega_j)^{\Gamma_L}]
\end{aligned}$$

Using similar methods, expected value formulas for non-musth medium and small males as well as musth males of all size classes can be derived. We therefore have:

$$\begin{aligned}
E_L(i, j) &= \frac{(1 - \epsilon) V_{i,j}}{\Gamma_L p_{ij} \eta_j \omega_j} [1 - (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L}] \\
E_M(i, j) &= \frac{(1 - \epsilon) V_{i,j}}{\Gamma_M q_{ij} \xi_j \theta_j} [1 - (1 - \xi_j q_{ij} \theta_j)^{\Gamma_M}] (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L}
\end{aligned}$$

$$E_S(i, j) = \frac{(1 - \epsilon)V_{i,j}}{\Gamma_S w_{ij} \mu_j \phi_j} [1 - (1 - \mu_j w_{ij} \phi_j)^{\Gamma_S}] (1 - \eta_j p_{ij} \omega_j)^{\Gamma_L} (1 - \xi_j q_{ij} \theta_j)^{\Gamma_M}$$

$$F_L(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_L x_{ij} (1 - \eta_j) \omega_j} [1 - (1 - x_{ij} (1 - \eta_j) \omega_j)^{\Gamma_L}]$$

$$F_M(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_M y_{ij} (1 - \xi_j) \theta_j} [1 - (1 - y_{ij} (1 - \xi_j) \theta_j)^{\Gamma_M}] (1 - x_{ij} (1 - \eta_j) \omega_j)^{\Gamma_L}$$

$$F_S(i, j) = \frac{\epsilon V_{i,j}}{\Gamma_S z_{ij} (1 - \mu_j) \phi_j} [1 - (1 - z_{ij} (1 - \mu_j) \phi_j)^{\Gamma_S}] (1 - x_{ij} (1 - \eta_j) \omega_j)^{\Gamma_L} (1 - y_{ij} (1 - \xi_j) \theta_j)^{\Gamma_M}.$$

Returning to the large males, recall that each large male is maximizing his yearly payoff (denoted E):

$$E = \eta_1 \omega_1 E_1 + (1 - \eta_1) \omega_1 F_1 + \eta_2 \omega_2 E_2 + (1 - \eta_2) \omega_2 F_2 + \dots + \eta_N \omega_N E_N + (1 - \eta_N) \omega_N F_N.$$

Here E_j represents the expected value of being in musth during time period j (recall that at an ESS, all the spatial choices will have an equal payoff) while F_j represents the expected value of being a sexually active non-musth male competing during time period j . Furthermore, we must satisfy the constraints:

$$\sum_{j=1}^{j=N} \eta_j \omega_j = T_L$$

$$\sum_{j=1}^{j=N} (1 - \eta_j) \omega_j = S_L$$

$$T_L + \alpha S_L = P_L, \quad 0 < \alpha < 1.$$

At a musth ESS, $E_i = E_j$ for all viable (i, j) , and at a non-musth ESS we have $F_i = F_j$, for all viable (i, j) . Therefore:

$$E = E_j T_L + F_j S_L.$$

If a male wishes to increase the amount of time spent in musth, he can set $T_L = T_L + \delta$, and $S_L = S_L - \frac{1}{\alpha} \delta$. The resulting yearly payoff would be $E_j(T_L + \delta) + F_j(S_L - \frac{\delta}{\alpha})$, and the net change in payoff would be $E_j \delta - F_j \frac{\delta}{\alpha}$. At an ESS this should be zero, and therefore $E_j = \frac{F_j}{\alpha}$. We can therefore find a complete space/time/musth duration ESS using the algorithm described in Appendix **F**.

APPENDIX F

NUMERICAL METHOD FOR SOLVING A SPACE/TIME/MUSTH DURATION ESS

- 1.) choose a set of $\vec{p}, \vec{x}, \vec{\eta}$ and $\vec{\omega}$ values that fulfill $\sum_{j=1}^{j=N} \omega_j = T_L + S_L$ where $T_L + \alpha S_L = P_L$, $\sum_{j=1}^{j=N} \eta_j \omega_j = T_L$, $\sum_{i=1}^{i=M} p_{ij} = \sum_{i=1}^{i=M} x_{ij} = 1$, and $x_{ij}, p_{ij}, \eta_j, \omega_j \in [0, 1]$.
- 2.) Using the above chosen values, find a large musth male spatial ESS using the steps 2 - 8 in the algorithm described in Appendix C.
- 3.) Find a large non-musth male spatial ESS using steps 2 - 8 in the algorithm described in Appendix C, but replacing p with x and E_L with F_L .
- 4.) Consider the following two sets: $\Phi = \{\max(E_1, \frac{F_1}{\alpha}), \max(E_2, \frac{F_2}{\alpha}), \dots, \max(E_N, \frac{F_N}{\alpha})\}$ and $\Theta = \{(E_1 - \frac{F_1}{\alpha}), (E_2 - \frac{F_2}{\alpha}), \dots, (E_N - \frac{F_N}{\alpha})\}$.
- 5.) Pick i, j such that $\max(E_i, \frac{F_i}{\alpha})$ is the highest value in Φ and $\max(E_j, \frac{F_j}{\alpha})$ is the lowest value in Φ . Set $\omega_i = \omega_i + \epsilon_1$, and set $\omega_j = \omega_j - \epsilon_2$. This will decrease $\max(E_i, \frac{F_i}{\alpha})$ and increase $\max(E_j, \frac{F_j}{\alpha})$. If $\omega_i = 1$, $\max(E_i, \frac{F_i}{\alpha})$ should be replaced by the next highest value in Φ . Similarly, if $\omega_j = 0$, $\max(E_j, \frac{F_j}{\alpha})$ should be replaced by the next lowest value in Φ . Note, however, that to maintain our condition that $T_L + \alpha S_L = P_L$, we must choose ϵ_2 carefully given a value of ϵ_1 . Because $\sum_{k=1}^{k=N} \eta_k \omega_k = T_L$, increasing ω_i by ϵ_1 will increase T_L by $\epsilon_1 \eta_i$ and decreasing ω_j by ϵ_2 will decrease T_L by $\epsilon_2 \eta_j$. Additionally, because $S_L = \sum_{k=1}^{k=N} (1 - \eta_k) \omega_k$, S_L will increase by $\epsilon_1 (1 - \eta_i)$ and decrease by $\epsilon_2 (1 - \eta_j)$. We must have $T_L + \epsilon_1 \eta_i - \epsilon_2 \eta_j + \alpha(S_L + \epsilon_1 (1 - \eta_i) - \epsilon_2 (1 - \eta_j)) = P_L \implies \epsilon_1 \eta_i - \epsilon_2 \eta_j + \alpha \epsilon_1 (1 - \eta_i) - \alpha \epsilon_2 (1 - \eta_j) = 0$. Therefore, set $\epsilon_2 = \frac{\epsilon_1 [\eta_i + \alpha(1 - \eta_i)]}{[\eta_j + \alpha(1 - \eta_j)]}$.
- 6.) Repeat steps 2 and 3 for time periods i and j .
- 7.) Pick i, j such that $(E_i - \frac{F_i}{\alpha})$ is the highest value in Θ and $(E_j - \frac{F_j}{\alpha})$ is the lowest value in Θ . Set $\eta_i = \eta_i + \epsilon_1$, and set $\eta_j = \eta_j - \epsilon_2$. This will decrease $(E_i - \frac{F_i}{\alpha})$ and increase $(E_j - \frac{F_j}{\alpha})$. If $\eta_i = 1$, $(E_i - \frac{F_i}{\alpha})$ should be replaced by the next highest value in Θ . Similarly, if $\eta_j = 0$ or $\omega_j = 0$, $(E_j - \frac{F_j}{\alpha})$ should be replaced by the next lowest value in Θ . We must have $T_L + \epsilon_1 \omega_i - \epsilon_2 \omega_j + \alpha(S_L - \epsilon_1 \omega_i + \epsilon_2 \omega_j) = P_L \implies \epsilon_1 \omega_i - \epsilon_2 \omega_j - \alpha \epsilon_1 \omega_i + \alpha \epsilon_2 \omega_j = 0$. Therefore let $\epsilon_2 = \frac{\epsilon_1 \omega_i}{\omega_j}$.
- 8.) Repeat steps 2 and 3 for time periods i and j .
- 9.) Repeat steps 5-8 until $(E_i - \frac{F_i}{\alpha}) = (E_j - \frac{F_j}{\alpha})$ and $\max(E_i, \frac{F_i}{\alpha}) = \max(E_j, \frac{F_j}{\alpha})$ for all viable (i, j) . If $(E_i - \frac{F_i}{\alpha}) > 0$, set $\eta_a = \eta_a + \epsilon_1$ and $\omega_b = \omega_b - \epsilon_2$ for any viable choice of a, b . To maintain

the duration constraint we must have: $T_L + \epsilon_1\omega_a - \epsilon_2\eta_b + \alpha(S_L - \epsilon_1\omega_a - \epsilon_2(1 - \eta_b)) = P_L \implies \epsilon_1\omega_a - \epsilon_2\eta_b - \alpha\epsilon_1\omega_a - \alpha\epsilon_2(1 - \eta_b) = 0$ or $\epsilon_2 = \frac{\epsilon_1\omega_a(1-\alpha)}{\eta_b + \alpha(1-\eta_b)}$. Similarly, if $(E_i - \frac{F_i}{\alpha}) < 0$, set $\eta_a = \eta_a + \epsilon_1$ and $\omega_b = \omega_b - \epsilon_2$ for any viable choice of a, b .

10.) Repeat steps 2 and 3 for time periods a and b .

11.) Repeat steps 5-10 until $(E_i - \frac{F_i}{\alpha}) = 0$.

12.) The resulting $\vec{p}, \vec{x}, \vec{\eta}$, and $\vec{\omega}$ values are a space-time-musth duration ESS for the large males. A medium male ESS can be found by taking the $\vec{p}, \vec{x}, \vec{\eta}$, and $\vec{\omega}$ values and plugging them into the medium male expected value formulas, then repeating steps 1-10 replacing $\vec{p}$ with $\vec{q}$, $\vec{x}$ with $\vec{y}$, $\vec{\eta}$ with $\vec{\xi}$ and $\vec{\omega}$ with $\vec{\theta}$.

13.) A small male ESS can be found by taking the $\vec{p}, \vec{x}, \vec{\eta}, \vec{\omega}, \vec{q}, \vec{y}, \vec{\xi}$ and $\vec{\theta}$ values and plugging them into the small male expected value formulas, then repeating steps 1-10 replacing $\vec{p}$ with $\vec{w}$, $\vec{x}$ with $\vec{z}$, $\vec{\eta}$ with $\vec{\mu}$ and $\vec{\omega}$ with $\vec{\phi}$.

APPENDIX G

GLOSSARY

α : A parameter that determines the relative physiological cost of musth vs. non-musth behavior through the condition $T_* + \alpha S_* = P_*$, where $*$ is an L, M or S (only used in the non-musth model in chapter 4).

β : The probability that a male musth competitor will be seriously injured or killed when competing against a male that is one size class larger (only used in the injury risk model in chapter 3).

ϵ : The probability that the winner of the non-musth male competition in a given area will be able to successfully mate with a given estrous female in the same area (only used in the non-musth model in chapter 4). Note that this is different from the perturbation parameters ϵ_1 and ϵ_2 used in appendix F.

η_j : In the context of the model described in chapter 2, η_j represents the probability that a large male will enter musth during time period j . In the model described in chapter 4, η_j represents the probability that a large male will enter musth during time period j given that he is sexually active during time period j .

θ_j : The probability that a medium sized male will be sexually active during time period j (only used in the non-musth model in chapter 4).

λ : The probability that a male musth competitor will be seriously injured or killed when competing against a male that is of the same size class (only used in the injury risk model in chapter 3).

μ_j : In the context of the model described in chapter 2, μ_j represents the probability that a small male will enter musth during time period j . In the model described in chapter 4, μ_j represents the probability that a small male will enter musth during time period j given that he is sexually active during time period j .

ξ_j : In the context of the model described in chapter 2, ξ_j represents the probability that a medium male will enter musth during time period j . In the model described in chapter 4, ξ_j represents the probability that a medium male will enter musth during time period j given that he is sexually active during time period j .

ϕ_j : The probability that a small sized male will be sexually active during time period j (only used in the non-musth model in chapter 4).

ω : The probability that a male musth competitor will be seriously injured or killed when competing against a male that is two size classes larger (only used in the injury risk model in chapter 3). Note that this is different from ω_j used in chapter 4.

ω_j : The probability that a large male will be sexually active during time period j (only used in the non-musth model in chapter 4).

Γ_L : The number of large males in the population.

Γ_M : The number of medium males in the population.

Γ_S : The number of small males in the population.

$E_L(i, j)$: The expected value a large male could expect to win while in musth in area i during time period j . The formula to calculate $E_L(i, j)$ is given in chapter 2, then is modified in chapter 4.

$E_M(i, j)$: The expected value a medium sized male could expect to win while in musth in area i during time period j . The formula to calculate $E_M(i, j)$ is given in chapter 2, then is modified in chapter 4.

$E_S(i, j)$: The expected value a small male could expect to win while in musth in area i during time period j . The formula to calculate $E_S(i, j)$ is given in chapter 2, then is modified in chapter 4.

$F_L(i, j)$: The expected value a large male could expect to win while sexually active and not in musth in area i during time period j (only used in the non-musth model in chapter 4).

$F_M(i, j)$: The expected value a medium sized male could expect to win while sexually active and not in musth in area i during time period j (only used in the non-musth model in chapter 4).

$F_S(i, j)$: The expected value a small male could expect to win while sexually active and not in musth in area i during time period j (only used in the non-musth model in chapter 4).

M : The number of areas a given male could inhabit during a given time period.

N : The number of time periods in a year.

p_{ij} : The probability that a large male competes in area i during time period j given that he is in musth during time period j .

P_L : The maximum number of time periods a large male can spend in musth (only used in the non-musth model in chapter 4).

P_M : The maximum number of time periods a medium male can spend in musth (only used in the non-musth model in chapter 4).

P_S : The maximum number of time periods a small male can spend in musth (only used in the non-musth model in chapter 4).

q_{ij} : The probability that a medium sized male competes in area i during time period j given that he is in musth during time period j .

S_L : The expected number of time periods a large male spends as a sexually active non-musth competitor.

S_M : The expected number of time periods a medium male spends as a sexually active non-musth competitor.

S_S : The expected number of time periods a small male spends as a sexually active non-musth competitor.

T_L : The expected number of time periods a large male spends in musth.

T_M : The expected number of time periods a medium male spends in musth.

T_S : The expected number of time periods a small male spends in musth.

$V_{i,j}$: The intrinsic value of area i during time period j . Alternatively, the expected number of estrous females in area i during time period j .

w_{ij} : The probability that a small male competes in area i during time period j given that he is in musth during time period j .

x_{ij} : The probability that a large male competes in area i during time period j given that he is sexually active and not in musth during time period j (only used in the non-musth model in chapter 4).

y_{ij} : The probability that a medium sized male competes in area i during time period j given that he is sexually active and not in musth during time period j (only used in the non-musth model in chapter 4).

z_{ij} : The probability that a small male competes in area i during time period j given that he is sexually active and not in musth during time period j (only used in the non-musth model in chapter 4).

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BIOGRAPHICAL SKETCH

John Maxwell Wyse was born in Columbus, Ohio. He studied Mathematics at Goshen College in Indiana. After graduation, his interest in the mathematics of evolution motivated him to join the Biomathematics program at FSU. After receiving his M.S. degree in Biomathematics, he worked under the supervision of Dr. Mike Mesterton-Gibbons for his PhD studies.