Evolutionarily Stable Dispersal Timing: Effects of Dispersal Costs and Kin Competition

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1 Abstract

Dispersal is the permanent relocation of individuals or propagules away from the natal habitat. Previous studies have investigated which biological factors most affect dispersal. However, few studies have addressed the timing of dispersal. We present a game-theoretical model of the time at which individuals should disperse from the natal area. This model includes the effects of kin competition (i.e., sibling rivalry) and dispersal costs such as time and risk of death.

In our model, siblings in a brood decide sequentially whether to disperse from or remain in their natal area. This decision occurs each day of a finite breeding season, where the most 'dominant' sibling makes their decision first and every sibling has complete knowledge of all previous decisions. We find strict Nash Equilibria such that each sibling optimizes their own expected future reproductive success, demonstrating the evolutionarily stable dispersal timing for each sibling. Finally, we use sensitivity analysis to draw conclusions about how evolutionarily stable dispersal timing is affected by: semelparity/iteroparity, kin competition, parental care, dominance level, and inbreeding avoidance.

2 Introduction

Movement is critical to survival and reproduction in most, if not all, species. These movements are classified based on their purpose: foraging is movement to find food; migration is seasonal movement to a more suitable habitat; and dispersal is the permanent movement of individuals (or propagules) away from the natal habitat. Amongst all the types of movement, dispersal may be the most significant from an evolutionary perspective. Dispersal can be either active or passive, depending on the means of locomotion, and adult or natal, depending on the timing of dispersal. Passive dispersal occurs when the disperser cannot control their own movement; this is common in plants since plants are stationary and must rely on propagules (e.g., seeds, spores) to spread out over space. Active dispersal occurs when the disperser can move about without assistance and is more common in mammals and birds, since those individuals

can control their movement. Adult dispersal is the movement of a reproductive individual or group from one area to another between reproducive cycles. This allows offspring to be born in different areas and thus allows for the genepool of the parent(s) to be spread over space, potentially boosting generational fitness. Finally, in natal dispersal, offspring themselves move away from the natal patch, usually before first reproduction. Natal dispersal is usually separated into phases. The departure phase includes the preparation for and eventual movement out of the natal habitat, the transfer phase includes the movement itself, and the settlement phase includes the cessation of movement in the new habitat [3].

Understanding dispersal is essential since dispersal plays a major role in both ecology and evolution. From an ecological perspective, dispersal costs influence the survival and reproduction of individuals. From an evolutionary perspective, survival of the fittest favors genes corresponding to stronger dispersal strategies. Mathematical models of dispersal help us understand and predict which dispersal strategies are evolutionarily stable. This is especially important as climate change causes rapid changes in environments, potentially changing which dispersal strategies are successful.

Prior research has attempted to describe natal dispersal [7]. Some of the factors used to explain dispersal include the propensity to avoid inbreeding, the role of kin competition in driving variable sibling behavior, and the costs of dispersal. Bonte et al. (2012) recognizes dispersal costs levied at the departure, transfer, and settlment phase of dispersal [3]. These costs include the time spent in dispersal (time cost), the risk of death due to predation or exhaustion (risk cost), the energy expended (energy cost), and the cost of giving up advantages associated with remaining in the natal habitat such as local adaptation or social status (opportunity costs)[3].

Other research stresses the importance of kin competition in driving natal dispersal [9]. Siblings compete for the care provided by the parent and sometimes for their parents' territory. This competition for the parental habitat is commonly associated in biological theory with dominance-delayed dispersal, in which more dominant offspring are more likely to succeed their parents [10]. Studies have shown that the incentive to avoid kin competition can drive dispersal, even when limited knowledge of areas outside the natal habitat implies potentially greater dispersal costs [9]. Another important driver of dispersal is the incentive to avoid inbreeding. When genetically similar individuals mate, there is higher potential for malatorious recessive alleles to be passed to offspring. Like kin competition, research suggests that inbreeding avoidance alone can sometimes cause dispersal [2][21].

Researchers have created many models attempting to describe natal dispersal. The current literature contains models describing the effects of iteroparity and semelparity [19], kin competition [11][14], inbreeding avoidance [14], and dispersal costs [11][14] on the evolutionarily stable dispersal rate. Other studies have investigated how the evolutionarily stable dispersal rate changes in fragmented environments [4]. When combined, mathematical models and field studies help prove information and predictions about dispersal rate, distance,

motivation, and method, or more generally describe the who, where, why, and how of natal dispersal.

We aim to help answer the question of "when." Specifically, when (i.e., on what day) should individuals disperse from the natal area during their first breeding cycle? Field research suggests that the timing of natal dispersal varies between individuals, sometimes even within a group of siblings [20][22][16]. These findings suggest that dispersal timing is important and that we should not treat dispersal as a yes or no decision. As individuals grow in the natal habitat, they trade time for energy. This energy can be invested in better locomotive machinery, potentially helping find prey or avoid predation [24]. This time investment, however, comes before departure and is thus subject to the effects of kin competition. Moreover, children retain the option of remaining philopatric (i.e., never dispersing), which can be evolutionarily stable, especially if the children believe they can inherit the habitat of their parent [18], but comes at the cost of potential inbreeding.

An evolutionarily stable dispersal strategy (**ESDS**) must maximize the fitness in the context of these factors. A game-theoretical approach is ideal for this, since an ESDS can be found by finding pure Nash equilibria. The players are siblings of a nest/brood, and the best action of one child depends on the actions of her siblings. These sibling interactions determine the effects of kin competition, and the environment dictates costs like risk of death, time cost, and the fitness penalty of inbreeding. Since the specific way in which these factors affect individual fitness and behavior will undoubtedly vary across species and environments, we incorporate these factors as parameters of the model, meaning that they can be changed to suit the species in question.

The purpose of our model is to find evolutionarily stable (**ES**) departure dates for all siblings in a litter and then illuminate the reasoning at play for when individuals decided to disperse. Similarly to the approach taken in McNamara et. al. (2000), we draw conclusions about the decision-making at play after the ESDS has been found [17]. This helps avoid biases about individual decision-making when constructing the model; we let the biological principles and simplifying assumptions of the model describe each individual's choices. Specifically, we want our model to answer how the following affect evolutionarily stable dispersal timing: semelparity/iteroparity, kin competition, parental care, dominance level, inbreeding avoidance, and length of the breeding season.

We hope that the relations we find between these variables and the ES dispersal timing will highlight the importance of dispersal timing in mathematical models and the need for further research in the area.

3   The Model

3.1   Assumptions of the Model

This model aims to analyze the effects of semelparity/iteroparity, kin competition, parental care, dominance level, inbreeding avoidance, and length of the

breeding season on the timing of dispersal. For this model, time is given in days, and all decisions are made at the beginning of each day. We examine behavior over a breeding cycle (B.C.) of fixed length in which children mature and disperse in a single B.C. Once a child reaches maturity, she will attempt to reproduce in the current B.C., though maturing later will result in a lower reproductive success rate. We do not distinguish behavior by sex or include difficulties with mate finding; we assume that all adults that can reproduce will reproduce. Young are cared for equally by the parent so that each child receives an equal amount of resources (food, protection, instruction, etc.). The resources provided by the parent are finite and are split evenly among the children. Once the children reach juvenile stage, they can disperse time before the end of the B.C. Dispersal forces the disperser to provide her own resources, and since the dispersed child no longer shares parental care, the remaining philopatric siblings get a larger individual share of parental care resources. This decision to disperse is assumed to be permanent; that is, a child must either remain philopatric or disperse sometime before the B.C. Dispersal is assumed to be a risky but rewarding process, meaning that some percent of dispersers will die in the process and that successful dispersal conveys a fitness reward (which we assume to be constant).

3.2   Birth, growth, and departure timing

An adult produces n offspring every B.C. Each B.C. has a length of T_{max} days. Thus, 0 represents the birth date of young, and T_{max} represents the birth date of the next season's young. An adult can expect to reproduce an average of N times over her life. A parent cares for offspring until the end of the season, at which care ceases as the parent shifts care to the children of the next B.C. The time at which children becomes juveniles (that is, dispersal becomes possible) is defined to be t_0, where $0 < t_0 \leq T_{max}$

Parental care is quantified in terms of "resources," which can be thought of as all the food, protection, and instruction needed for a child to reach adulthood. $R(d_i)$ gives the accumulated resources of child i who received parental care for d days while in the natal habitat. $R_{min} = R(t_0)$ is defined to be the minimum resources required for dispersal, and R_{max} is defined to be the value of $R(d_i)$ at which reproduction becomes possible.

To incorporate kin competition, we assume that resources provided by the parent each day are split evenly among the remaining non-dispersed children, which is given by $n(t)$. This is distinct from the constant n, which is the initial number of siblings. In general, $n(0) = n$, and $n(t) \leq n$ for all $t \in [0, T_{max}]$ Thus, $R(d_i)$ can be defined as

$$R(d_i) = R_{min} + \sum_{t=0}^{d_i} \frac{r}{n(t)} \tag{1}$$

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3.3 Sequence of decisions

Children make the choice of whether to disperse or remain philopatric each day after reaching time t_0. If a child chooses to remain philopatric on a given day d, she can either choose to disperse or remain philopatric on the next day. If the child chooses to remain philopatric until T_{max}, then she has opted not to disperse. However, if the child chooses to disperse on d, then she will remain dispersed and her departure date is known by all other children. Children make a choice each day in a set order until they decide to disperse, and these choices are common knowledge to all children remaining in the natal area. The siblings are numbered according to the order in which decisions are made, and the order of siblings denotes dominance level. Thus, sibling 1, who is the most dominant, makes her decision, and, after observing her choice, sibling 2, who is more submissive, makes her decision. This continues for all undispersed children and repeats each day until all remaining children have reached maturity. As such, d_1 represents the departure date of sibling 1, and in general d_i represents the departure date of the child choosing in the ith position.

3.4 Nondispersing behavior

Since we are interested in comparing the risk cost of dispersal with philopatry, we assume that a philopatric individual always survives. A nondispering player i matures after z_i days, and thus $R(z_i) = R_{max}$. Due to the resource splitting described in equation (1), z_i will be smaller if more children disperse earlier, since child i will receive a larger share of resources. Since we assume that all children will eventually reach maturity $z_i \leq T_{max}$. Having reached maturity, player i now reproduces.

3.5 Dispersing behavior

For simplicity, we assume the risk costs of transfer and settlement are levied together in the settlement phase. This allows us to use a single survival function. A disperser departing on d_i no longer receives parental resources and instead provides for herself, gaining c resources each day until she reaches R_{max}. The amount of time spent collecting c resources in her new environment is given by the variable $q_i = \lceil \frac{R_{max} - R(d_i)}{c} \rceil$. Each of the q_i settlement days has a survival cost, so the expected probability of survival, p_i, is given by

$$p_i = \left(\frac{R(d_i)}{R(d_i) + K} \right)^{q_i} \tag{2}$$

where $K > 0$ represents the risk of death. After q_i days, player i reproduces in her new habitat, provided she survives.

3.6 Reproduction and fitness

To describe reproductive fitness, we introduce a function with constants f and b. f represents the expected number of surviving children that an individual can

Symbol	Value	Biological Interpretation
N	1	# of breeding cycles (**B.C.**s) over lifetime
n	4	Initial # of children per brood/litter
T_{max}	120	Breeding cycle length in days
R_{min}	40	Minimum resources for dispersal
R_{max}	136	Resources required for reproduction
r	2.4	Parent-provided resources/day in natal area
c	2	Child-provided resources/day in settlement
K	0.5	Risk of death during dispersal
b	0.8	Dispersal fecundity bonus
f	4	# of surviving children per B.C.

Table 1: Model parameters and values used in analysis

expect to have in each B.C., and b represents the boost to fitness one obtains by avoiding inbreeding (which can only occur if an individual disperses).

Individuals can only reproduce when they are mature, and an individual that disperses at time d_i reaches maturity at time $d_i + q_i$, at which point her expected future reproductive success (**EFRS**) is

$$\mu(d_i) = p_i \left(f + b\right) \left[\frac{T_{max} - d_i - q_i}{T_{max}} + (N - 1)\right] \tag{3}$$

The first factor in equation (3) denotes the chance of surviving dispersal, and the second factor gives the fecundity per B.C. The third factor represents the number of times an individual can expect to breed, which includes the first breeding cycle where $\frac{T_{max} - d_i - q_i}{T_{max}}$ denotes the time cost of reaching maturity and the subsequent $(N - 1)$ breeding cycles.

If an individual remains philopatric, we say $d_i = \varnothing$ since there is no departure date. In this case, the nondisperser reaches maturity at some time z_i, at which point her EFRS is

$$\mu(\varnothing) = f \left[\frac{T_{max} - z_i}{T_{max}} + (N - 1)\right] \tag{4}$$

Equation (4) behaves similarly to equation (3). The first factor of (4) represents the fecundity per B.C., and the second factor is the number of breeding cycles with the time cost of maturing.

The parameters of the model, as well as the values we use for sensitivity analysis, are summarized in the Table 1.

4 Finding an ESS

4.1 Analyzing the Model

Lemma 1. *Reproductive success is increasing with resources on any given dispersal date.*

Proof. Suppose an player i on day d_i chooses to remain philopatric, and that on this day a total of a individuals remain philopatric ($1 \leq a \leq n$). On day d_i, she therefore obtains $\frac{r}{a}$ resources, bringing her total to $R(d_i) + \frac{r}{a}$. If we assume the individual disperses on $d_i + 1$, then we can describe her payoff with the function $\mu(R(d_i) + \frac{r}{a})$. Since $R(d_i) + \frac{r}{a+1}$ represents the maximum accumulated resources strictly smaller than $R(d_i) + \frac{r}{a}$, then if the expression

$$\mu\left(R(d_i) + \frac{r}{a}\right) - \mu\left(R(d_i) + \frac{r}{a+1}\right) \tag{5}$$

is strictly positive, then EFRS will be increasing with resources, since all differences in resources must be greater than (5). Using the formula for $\mu(R(d_i))$, we can expand equation (3) to get

$$p_{i_a}\left[\frac{T_{max} - (d_i + 1) - q_a)}{T_{max}}(f + b) + (N - 1)(f + b)\right] - \tag{6}$$
$$p_{i_{a+1}}\left[\frac{T_{max} - (d + 1) - q_{a+1})}{T_{max}}(f + b) + (N - 1)(f + b)\right]$$

where p_{i_a} and $p_{i_{a+1}}$ represent the probability of survival given resources were split a and $a + 1$ ways on day d, respectively, and q_{i_a} and $q_{i_{a+1}}$ represent the number of days spent in given a and $a + 1$ resource splitting.

Equation (7) will be non-negative if $p_{i_a} \geq p_{i_{a+1}}$ and $q_{i_a} \leq q_{i_{a+1}}$ and will be positive if either of these inequalities are strict. Using the formulas for p_i and q_i, we get that

$$q_{i_a} = \frac{R_{max} - R(d) - \frac{r}{a}}{c}$$
$$q_{i_{a+1}} = \frac{R_{max} - R(d) - \frac{r}{a+1}}{c}$$
$$p_{i_a} = \left(\frac{R(d) + \frac{r}{a}}{R(d) + \frac{r}{a} + K}\right)^{q_a}$$
$$p_{i_{a+1}} = \left(\frac{R(d) + \frac{r}{a+1}}{R(d) + \frac{r}{a+1} + K}\right)^{q_{a+1}}$$

And so the difference in settlement times, $q_{i_{a+1}} - q_{i_a}$ is given by

$$q_{i_{a+1}} - q_{i_a} = \frac{r}{c}\left(\frac{1}{a^2 + a}\right) \tag{7}$$

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which is strictly positive. Similarly, the difference $p_{i_a} - p_{i_{a+1}}$ is strictly positive. To understand why, consider that $p_{i_{a+1}}$ is simply p_{i_a}, except that the numerator and denominator are decreased by $\left(\frac{r}{a} - \frac{r}{a+1}\right)$. This smaller base is being raised to a larger exponent since $q_{i_a} < q_{i_{a+1}}$, meaning that the fraction $p_{i_{a+1}}$ is less than p_{i_a}. Both conditions are thus met, proving the lemma. ∎

Theorem 1. *Players disperse in the reverse order they make decisions in.*

Proof. Suppose that at a certain time t there are m remaining players. At t, player i must decide whether to remain philopatric or disperse. If i disperses, she gets some payoff $\mu(R(d_i))$ which does not depend on the decisions of the other players. If she does disperse, her EFRS is at least $\mu(R(d_i) + \frac{r}{a})$, where a ($1 \le a \le m$) represents the number of philopatric children after $m - a$ players have chosen to disperse. Assume that player i has a greater payoff by not dispersing. Since player i will choose not to disperse, by Lemma 1 her payoff is increasing with $\frac{r}{a}$. Thus,

$$\mu\left(R(d_i) + \frac{r}{1}\right) > \mu\left(R(d_i) + \frac{r}{2}\right) \; . \; . \; . > \mu\left(R(d_i) + \frac{r}{m}\right) \qquad (8)$$

Because not dispersing yield a greater payoff for plaery i, we have that for some value of a the incremental resource gain offsets the loss of waiting another day, or that

$$\mu\left(R(d_i) + \frac{r}{a}\right) > \mu(R(d_i)) \ge \mu\left(R(d_i) + \frac{r}{a+1}\right) \qquad (9)$$

Supposing that a players have made the decision to remain philopatric, any player deciding afterwards will choose to disperse, since dispersing now yields a higher payoff.

Because the decisions are made sequentially by player order, the first a players will choose to remain, which forces the next $m - a$ players to disperse since it now yields a higher EFRS. Since player 1 always chooses first, she is guaranteed to become one of the a philopatric children. The same logic applies to player 2, who will remain if and only if $a \ge 2$. In general, player i will remain if and only if $a \ge i$. As a decreases over time, only the first a players will remain philopatric, which is what we intended to show. ∎

4.2   Fast Nash Algorithm

The prior proof provides the framework for an algorithm to find the ESDS. In general, the number of unique outcomes for a game lasting T_{max} days and having n players is equal to $T_{max}{}^n$. However, by instead solving for the value of a satisfying equation (9) at each stage, we can compute the ESDS in $O(T_{max} \times n)$ time.

We do this by analyzing the decisions of players in reverse order. Since player n must always disperse before (or possibly at the same time as) other players, the daily resources obtained by player n will always be $\frac{r}{n}$ resources. We can

calculate the EFRS of player n for any given dispersal date d_n as simply $\mu(\frac{rd}{n})$. By iterating over all $d_n \in [0, T_{max} - 1]$, we find a d_n that maximizes EFRS.

Next, we look at player $n - 1$, who by Theorem 1 will disperse on some $d_{n-1} \in [d_n, T_{max} - 1]$. d_{n-1} can be found by calculating $\mu(\frac{rd_n}{n} + \frac{rd_{n-1}}{n-1})$ for all $d_{n-1} \in [d_n, T_{max} - 1]$ and finding the d_{n-1} that maximizes $\mu(\frac{rd_n}{n} + \frac{rd_{n-1}}{n-1})$. This yields a vector of departure times $D = \langle d_1, d_2, \ . \ . \ . \ d_{n-1}, d_n \rangle$ where, by Theorem 1, for all players $i, j \in [1, n], i < j \rightarrow d_i \leq d_j$. This is repeated for all players, and since each player's EFRS is maximized, this method will produce a Nash equilibrium. A more complete description of how this algorithm works can be found in the README file found in the GitHub repository linked in the Appendix.

This process is implemented in the Python code linked in the Appendix (see README for more details). Once we know d_i and $R(d_i)$ for each player i, we can easily calculate the EFRS of each. Since the arithmetic involved in computation takes a constant amount of time, the complexity of this process depends only on the dimension of the matrix. As such, the time complexity of the Fast Nash Algorithm is $O(T_{max} \times n)$ in both space and time complexity.

4.3   Uniqueness of the Nash Equilibrium

For a dispersal strategy to be an ESDS, it must correspond to a pure NE. We now investigate conditions under which the NE produced by this algorithm is a pure NE.

Theorem 2. *The Nash equilibrium found through the Fast Nash algorithm will be unique if, for player i's payoff-maximizing departure date d_i, the equations*

$$\left(R(d_i) + \frac{d_j - d_i}{n\,(d_n)} + K \right)^{q_j} R(d_i)^{q_i} \left(NT_{max} - q_i - d_i \right) =$$

$$\left(R(d_i) + K \right)^{q_i} \left(R(d_i) + \frac{d_j - d_i}{n\,(d_n)} \right)^{q_j} \left(NT_{max} - q_j - d_j \right) \tag{10}$$

and

$$\left(NT_{max} - z_i \right) \left(R(d_i) + K \right)^{q_i} = \left(1 + \frac{b}{f} \right) \left(NT_{max} - d_i - q_i \right) \left(R(d_i) \right)^{q_i} \tag{11}$$

have no solutions for all $d_i \neq d_j$, where q_i and q_j represent the corresponding settlement times and z_i represents the time required to reach maturity without dispersing.

Proof. The proof of this theorem follows simply from the payoff equations described in (3) and (4). Comparing the payoff generated by an optimal departure date d_i found via the Fast Nash algorithm with the payoff obtained by never dispersing, then the individual will be indifferent between dispersing and not

dispersing if and only if

$$\left(\frac{R\left(d_i\right)}{R\left(d_i\right)+K}\right)^{q_i}\left[\left(\frac{T_{max}-d_i-q_i}{T_{max}}\right)(f+b)+(N-1)(f+b)\right]= \qquad (12)$$
$$\left[f\left(\frac{T_{max}-z_i}{T_{max}}\right)+f(N-1)\right]$$

This equation can be simplified and rearrange to the form described in 11. Similarly, if we compare all other dispersal dates $d_j \neq d_i$, then the individual will be indifferent to two dispersal dates if and only if

$$\left(\frac{R\left(d_i\right)}{R\left(d_i\right)+K}\right)^{q_i}\left[\left(\frac{T_{max}-d_i-q_i}{T_{max}}\right)(f+b)+(N-1)(f+b)\right]= \qquad (13)$$
$$\left(\frac{R\left(d_j\right)}{R\left(d_j\right)+K}\right)^{q_j}\left[\left(\frac{T_{max}-d_j-q_j}{T_{max}}\right)(f+b)+(N-1)(f+b)\right]$$

If we, without loss of generality, assume d_i to be the earliest such instance of a payoff-maxizing dispersal time, then we have that $d_i < d_j$. By equation1 we have that player i obtains $\frac{r}{i}$ daily resources between the previous player's dispersal and i's dispersal, then equation (14) becomes, for player p dispersing on day d_i,

$$\left(\frac{R\left(d_i\right)}{R\left(d_i\right)+K}\right)^{q_i}\left[\left(\frac{T_{max}-d_i-q_i}{T_{max}}\right)(f+b)+(N-1)(f+b)\right]=$$
$$\qquad (14)$$
$$\left(\frac{R\left(d_i\right)+\frac{r(d_j-d_i)}{i}}{R\left(d_i\right)+\frac{r(d_j-d_i)}{i}+K}\right)^{q_j}\left[\left(\frac{T_{max}-d_j-q_j}{T_{max}}\right)(f+b)+(N-1)(f+b)\right]$$

which simplifies to equation 10.

∎

It is clear that having multiple maximum payoff (and thus a mixed Nash equilibrium) is much more likely to occur if $b = 0$ or $k = 0$. These parameters describe the benefits and costs, respectively, of dispersing, so this is expected behavior. The following corollaries provide more intuition for finding situations where multiple maximum payoffs are likely to occur.

Corollary 1. *For the player i's EFRS maximizing d_i, and potentially EFRS maximizing d_j where $d_j > d_i$, if $\frac{r}{ic} = 1$ then $d_j + q_j = d_i + q_i$.*

Proof. Let $g = d_j - d_i$ be the difference in dispersal times. Suppose at d_i, player i has obtained $R(d_i)$ resources, then between times d_i and d_j player i obtains $\frac{gr}{i}$ for a total of $R(d_i) + \frac{gr}{i}$ resources. Then

$$q_i = \lceil \frac{R_{max} - R(d_i)}{c} \rceil \qquad (15)$$

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and

$$q_j = \lceil \frac{R_{max} - R(d_i) - \frac{gr}{i}}{c} \rceil \qquad (16)$$

Since $g = d_j - d_i \in \mathbf{N}$, if $\frac{r}{ic} = 1$ then $q_i - q_j = g = d_j - d_i$ and thus $d_j + q_j = d_i + q_i$. ∎

We interpret this result as the following: if the daily resources obtained by remaining philopatric (i.e., $\frac{r}{i}$) match the resources obtained in dispersal, namely c, then R_{max} will be reached at the same time regardless of dispersal timing. This corollary provides conditions in which the second term of equation 15 equals 1. If this is the case, the conditions for multiple maximum payoffs reduces to

$$\left(R(d_i) + \frac{d_j - d_i}{n(d_n)} + K \right)^{q_j} R(d_i)^{q_i} = (R(d_i) + K)^{q_i} \left(R(d_i) + \frac{d_j - d_i}{n(d_n)} \right)^{q_j} \qquad (17)$$

which is precisely equation 10 with the final terms on each side removed. This means that if $\frac{r}{ic} = 1$ and the survivability of dispersing on d_i equals the survivability of dispersing on d_j (which will always occur if $K = 0$), then we will have a mixed maximum payoff.

Corollary 2. *For the player picking in the ith position (denoted player i), payoff maximizing d_i, and z_i representing the date at which player i will reach R_{max} without dispersing, if $\frac{r}{ic} = 1$ then $z_i = d_i + q_i$.*

Proof. Suppose that at d_i, player i has obtained $R(d_i)$ resources. Then i needs $R_{max} - R(d_i)$ resources to reach maturity, which will be obtained in q_i days provided an individual disperses and $z_i - d_i = \frac{r(R_{max} - R(d_i))}{i}$ days provided an individual does not disperse. Setting $q_i = z_i$ gives $\frac{r(R_{max} - R(d_i))}{i} = \frac{R_{max} - R(d_i)}{c}$. Thus, if $\frac{r}{ic} = 1$ then $z_i = d_i + q_i$. ∎

We use this proof to use the following result:

Corollary 3. *If $\frac{r}{ic} = 1$ and $\left(1 + \frac{b}{f}\right)\left(\frac{R(d_i)}{R(d_i)+K}\right)^{q_i} \neq 1$, then equation 11 has no solutions, and thus an individual can never equally prefer dispersal to non-dispersal.*

Proof. This follows directly from equation 11. Since the $(NT_{max} - z_i)$ on the left hand side equals (by Corollary 2) the $(NT_{max} - d_i - q_i)$ on the right and both are strictly positive, we cancel from both sides. The equation reduces to $\left(1 + \frac{b}{f}\right)\left(\frac{R(d_i)}{R(d_i)+K}\right)^{q_i} = 1$. If this is false, then equal preference dispersal and nondispersal is impossible. ∎

In our sensitivity analysis, we use a computational version of these equations (see README) to check each Nash equilibrium found for uniqueness, since only unique Nash equilibria are guaranteed to be evolutionarily stable. Situations in which the Nash equilibrium is not unique are described in the Discussion section.

4.4 Computationally Verifying the Fast Nash Algorithm

Even though the result produced by the Fash Nash Algorithm will always be a Nash equilibrium, we still wanted to test this computationally. Using Python's Treelib library, we implemented algorithms to build a game tree, compute individual payoffs, and find the NE through backwards induction. We then ran tests to check if the NE generated by the Fast Nash Algorithm and backwards induction algorithm matched. We assigned each parameter up to 4 different values, and then ran 220,000 unique tests. The values tested were similar to the ones found in Table 1, with the exception of T_{max}. Since the backwards induction algorithm were implemented runs in $O(T_{max}{}^n)$ time, we could only check T_{max} in a range of 1 to 3. In all instances, the NE found by the both algorithms matched, giving us confidence that both algorithms always produce the same NE are and implemented correctly.

5 Relationship between Nash Equilibria and Maximum Group Payoff

The NE found by the Fast Nash Algorithm represents an ESDS within the context of a single brood. This strategy maximizes the individual EFRS, but not necessarily the group EFRS. Since siblings share similar genotypes, the selfish strategies brought about by kin competition may not maximize the success of the genotype. This is in contrast to other dispersal models, which maximize the fitness of a genotype corresponding to a dispersal strategy [11], [12], [14]. Even though our model does not aim to maximize the success of the genotype, we can make conjectures about the optimal gene success by asking whether our ESDSs also correspond to the maximal sum of EFRSs across all players. We ran tests comparing the group EFRS maximizing strategy with the ESDS for varying parameter values. We tested all combinations of parameters b and K for integers $0 < b$ and $K \leq 20$, and all combinations of parameters T_{max} and n for integers $n \leq 2$ and $T_{max} \leq 6$. Since this analysis cannot be done through the Fast Nash Algorithm, we were forced to use backwards induction and greatly restrict the values of n and T_{max} we can use. We also set f to 20 we were vary b in a range of 1 to 20 and wanted to maintain that $b \leq f$.
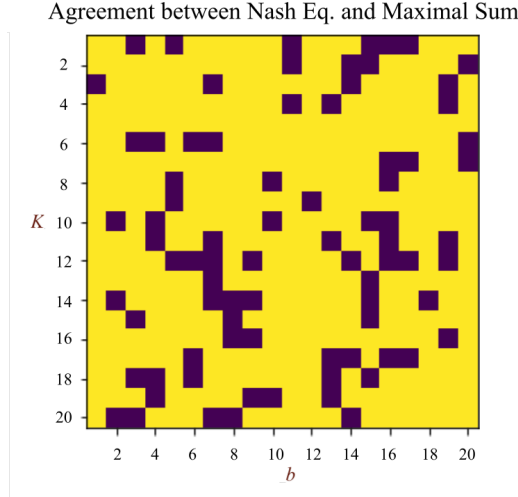
Agreement between Nash Eq. and Maximal Sum

Figure 1: Values of b and K corresponding to where the group EFRS maximizing strategy is the same as the Nash equilibrium are colored yellow. Instances where they are different are colored purple. Values are as in Table 1, except $n = 3$, $T_{max} = 2$, and $f = 20$.

We hypothesized that the strategies would match when K is large and b is low, since this implies that dispersal carries a high risk and low reward. When the probability of survival becomes sufficiently small, players choose not to disperse (see Figure 3b), and since there is no variability in players' dispersal timings the group and individual EFRSs should be maximized. Suprisingly, there was no clear pattern in whether the ESS matches the total fitness maximizing strategy. As shown in Figure 1, when b and K were varied, the strategies matched in 69% of test cases. When T_{max} and n were varied with b, f and K held at values of 4, 20, and 0.5 respectively, the strategies matched in 80% of the 30 test cases, though no obvious trend emerged.
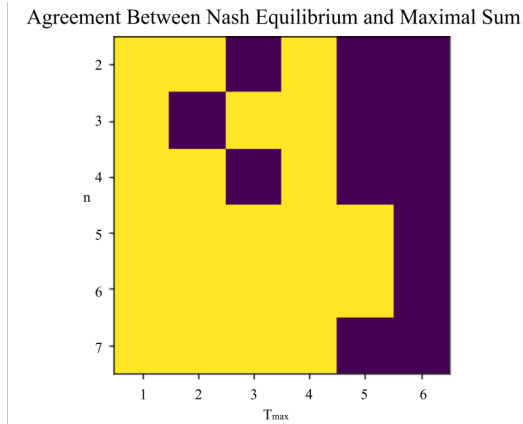
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Figure 2: Values of n and T_{max} corresponding to where the group EFRS maximizing strategy is the same as the Nash equilibrium are colored yellow. Instances where they are different are colored purple. Values are as in Table 1.

Testing the agreement between the Nash equilibria and maximal sum under varying n and T_{max} is difficult because the algorithm to do this runs in $O(T_{max}{}^n)$. For the values we were able to compute, agreement became less common for higher values of T_{max}. It is possible that instances of agreement in the testable cases were due to the relatively small number of options in the strategy vector for low values of T_{max}. More work is needed to confirm whether instances of agreements disappear for large values of T_{max}.

6   Sensitivity Analysis

6.1   Justification for Parameter Values

We performed the sensitivity analysis using the following baseline values given in Table 1. The values were chosen by combining data found in observational studies with values that yielded mathematically interesting results. Since field observation of peregrine falcons is readily available, we decided to use their biological statistics as base parameters for the model. For example, peregrine falcon parents usually watch over a nest of 3-4 eggs such that we chose $n = 4$. Approximately 45 days after hatching, the chicks fledge, and most leave the nest around 60 days later [6]. Thus, our parameter $R_{min} = 40$ represents this pre-fledge period, and with $r = \frac{12}{5}$ and $n = 4$, it will take 67 days to reach R_{min} or 50 days if $n = 3$. Taking the average of these and adding the 60 days most peregrine chicks spend post-fledging with their parents yields our estimate of 120 for T_{max}. Not only does this estimate of 120 days fit well for the peregrine falcon, but most breeding seasons occur during warmer months, which can last from 90 to 200 days in areas that experience seasonal changes [8]. This demonstrates that our set value for T_{max} is well-fit to many non-tropical

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species and can yield biologically relevant results beyond the peregrine falcon. The remaining parameters set only by biological interpretation include c, f, and b. Since offspring are still maturing throughout their first breeding cycle, we set c such that the daily resources that offspring can collect by themselves after dispersal is less than the r resources that an adult is capable of collecting. Finally, since the expected future reproductive success is an indicator of the number of offspring each sibling in the game is capable of producing, it was important to set f and b such that the EFRS can be interpreted as the expected number of surviving children an individual can expect to have over their lifetime. We then set f as the average number of offspring for the peregrine falcon ($f = n$) and set b to be one-fifth of f. We decided upon this ratio because observational studies often contradict each other regarding whether dispersers have a higher fecundity. The low ratio demonstrates that b can have a more flexible biological meaning, such as the increased fitness of each player's offspring that have avoided inbreeding or that are born into a superior natal habitat.

We set the remaining parameters of K and N to values that created mathematically interesting results. The biological basis for the number of breeding cycles in one lifetime began with field observations of the peregrine falcon. Since adult peregrine falcons breed only in the summer and generally have year-to-year survival of 75% with a maximum lifespan of 20 years, leading to an average of 4 breeding cycles per adult, we initially set $N = 4$. Our results with $N = 4$ matched very well with the observed data, which usually observe peregrine dispersal at around days post hatching [6]. In our results, four siblings dispersed after at least 100 days, and three dispersed after 115. Upon further investigation, we noted that larger values of N resulted in progressively later dispersal times. This is to be expected from our model since larger N allows an individual to invest more into survival by accumulating resources, and since the time spent obtaining resources only incurs a cost only in the first B.C., having more breeding cycles reduces the relative cost of this investment.

The reverse is also true, and a value of $N = 1$ leads to greater variability in dispersal timings between siblings. This variety led to more descriptive results when varying each parameter to demonstrate the effect on EFRS strategy, and as such we chose $N = 1$ as a baseline. In fact, using the parameters in Table 1, the standard deviation in dispersal times was 19.6 days, which is nearly 17% of the entire breeding cycle. The earliest dispersal date was at day 10, and the latest was at day 65.
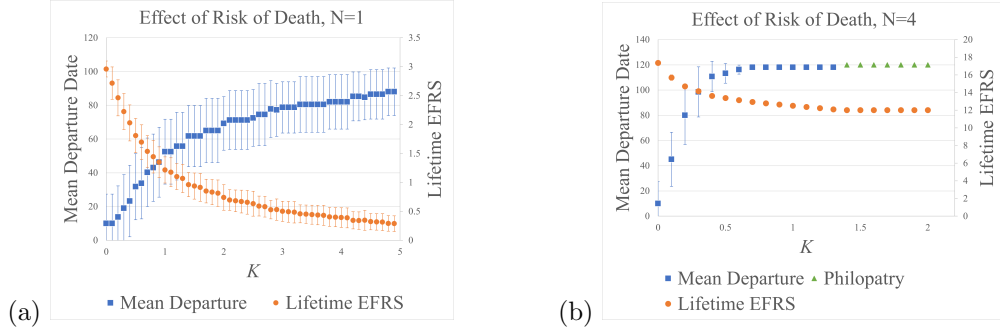
Figure 3: ESSs as the risk of death constant (K) increases for B.C.s of $N = 1$ (left) and $N = 4$ (right) for parameter values as shown in Table 1.

Before we analyze the effect of varying each parameter on departure date and EFRS and interpret the biological significance, it is essential to graphically demonstrate how we set the K and N values to be the most mathematically interesting and how this is connected to the EFRS payout function. We first set $N = 4$, since this matches the typical number of breeding cycles of the peregrine falcon. We then examined the effect that an increasing K would have upon the departure dates and EFRS. We had expected that a large K would greatly impact the timing of and propensity for dispersal due to the rapid decrease in survivability, since $p_i = \left(\frac{R(d_i)}{R(d_i)+K}\right)^{q_i}$. In particular, we expected that the model would lead to later departure dates as K increased because large K incentivizes individuals to minimize q_i, which is done by dispersing later in the B.C. However, we did not know the strength of this effect as K increased; Figure 3a demonstrates that with $N = 4$ and the rest of parameters set as described in the table, philopatry will occur when $K > 1.4$, and $K < 0.75$ will demonstrate greater variation in departure date based on error bar height. Due to the high sensitivity that K has on departure date, we set $K = 0.5$.

We also explored the effect of K for $N = 1$ to determine if our model favors different dispersal strategies when comparing semelparous and iteroparous species. Figure 3a shows dispersal was selected for even large values of K with greater disparity regarding departure and EFRS payout between siblings. Thus, $N = 1$ was chosen as the official value to report more mathematically diverse results when conducting our sensitivity analysis, but additional comparison of large N values will be presented in order to demonstrate the biological implications of our model regarding semelparity and iteroparity, respectively.
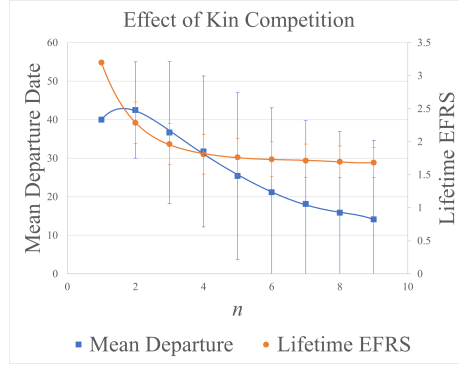
6.2 Effect of Kin Competition

Figure 4: ESS departure dates for increasing number of siblings per brood for parameter values as shown in Table 1.

With our official parameters values set as seen in Table 1, we began the sensitivity analysis for each parameter regarding the EFRS and departure timing. Since our model quantifies the effect of kin competition as a slower accumulation of parental resources in the natal area for larger values of n, we expected departure dates to occur earlier as litter size increased. Figure 4 demonstrates this effect, and excluding $n = 1$, who experienced no kin competition, $n = 2$ and $n = 6$ indicate the least and greatest variance in departure regarding dispersal date with a standard deviation of 12.5 days and 21.9 days, respectively. This can imply that two siblings experience little competition within their natal area such that there is less pressure to disperse when compared to $n = 6$. For $n > 6$, the variation in dispersal dates decreases as the more submissive siblings depart as soon as they reach R_{min}. due to the immense cost of kin competition. Finally, although the overall EFRS payout decreased as n increased, the small error in payout demonstrates that n has a stronger effect on departure date compared to EFRS.
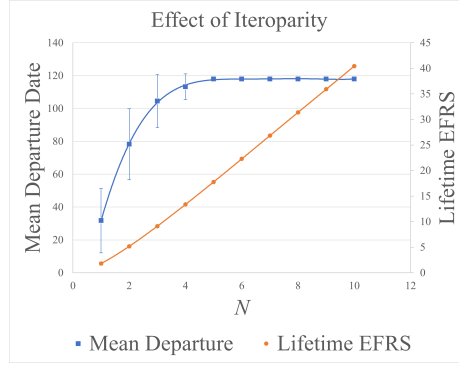
6.3 Effect of Iteroparity

Figure 5: ESSs for an increasing number of B.C.s (right) for parameter values as shown in Table 1.

Figure 5 then explores the strength of N regarding departure date and expected EFRS payout. Based upon our EFRS function, we expected that larger N values would result in philopatry or a departure date close to T_{max} since preceding breeding cycles will hold more value regarding EFRS potential when compared to a semelparous species. From a biological perspective, this plot demonstrates that iteroparous species should focus on resource accumulation and higher survivability, trading lower fecundity in their first breeding cycle for future payout, whereas semelparous species benefit from exiting the natal area to avoid inbreeding. We conclude that N has a strong effect regarding the distribution of departure dates for $N < 5$. Although there is low variance in EFRS, the relationship is almost perfectly linear, with an R^2 value of 0.9987.
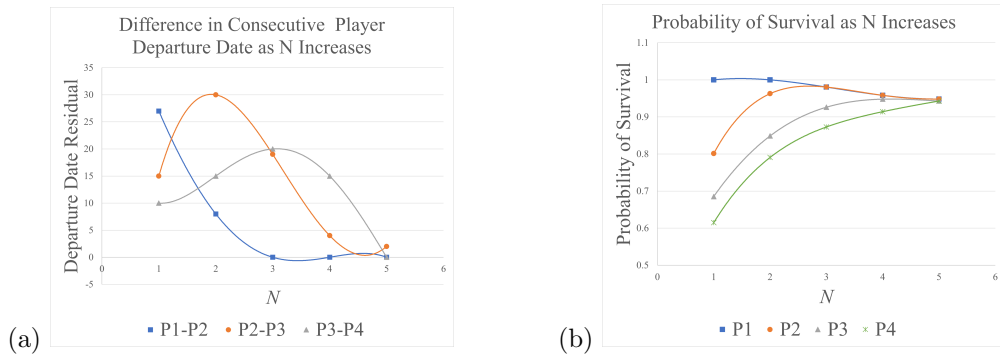

(a)   (b)

Figure 6: The difference in ES departure dates (left) and survival probability (right) between consecutive individuals as the number of B.C.s increases for parameter values as shown in Table 1.

Figure 6a illustrates the difference in departure date between consecutive players as N changes. As expected, larger values of N resulted in less variation in departure dates. This is because when N is large, the relative benefit of reproducing in the same breeding cycle as disperal becomes small. Therefore all players disperse at the latest possible date, maximizing their probability of survival and allowing them the benefit of dispersal for all subsequent breeding cycles. However, we did not expect to see different maxima regarding departure residuals. Based on the plot, we can see that the maxima correspond to the more dominant player. In particular, the pressure from player 1 on player 2 to disperse early is maximized when $N = 1$, the pressure from player 2 on player 3 to disperse early is maximized when $N = 2$, etc., until $N > n$ such that the difference in departure dates tends towards zero.

When exploring the reason behind this trend, we analyzed each player's survival probability as N increased, and found that each player would have a survival rate within 0.5% of 0.948 for $N > n$. Thus, we can conclude that dominance has a decreasing effect on survival probability as the number of breeding cycles increases because there is low variance in departure dates when $N > n$.

6.4   Effect of Parental Care

(a) Individual Departure Date as Parental Care Increases

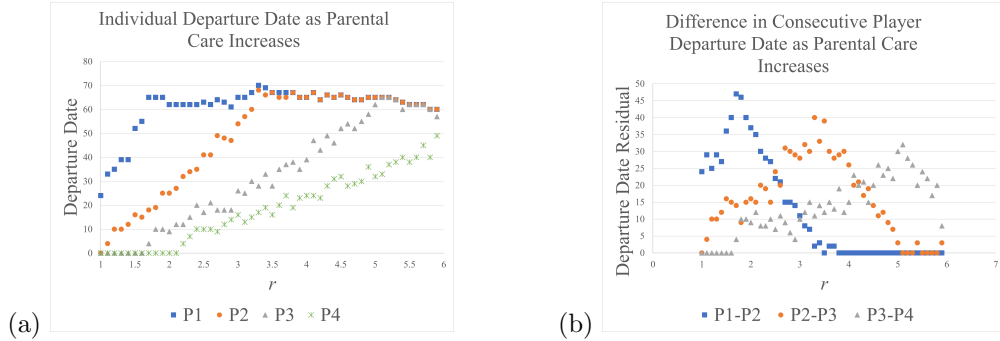(b) Difference in Consecutive Player Departure Date as Parental Care Increases

Figure 7: The difference in departure date between consecutive individuals as parental care increases for parameter values as shown in Table 1.

Our model uses the resource accumulation stage to include the effect of parental care. Offspring that remain in the natal area receive r resources shared evenly each day. We expected that an increase in parental care would result in later departure dates since the effect of kin competition would be mitigated as r increased. Figure 7a demonstrates this expected effect where an increase in parental care decreases the incentive for early dispersal.

In Figure 7b, we demonstrate the time difference in departure dates between consecutive players. Biologically, this plot illustrates the effect of receding dominance, whereby the most dominant siblings remain in the natal area and benefit

longer from parental care compared to more submissive siblings. In fact, the more submissive siblings must commit to early departure until r is sufficiently large such that kin competition is reduced and all offspring depart on the same day. This is seen where $r > 3.8$ for players 1 and 2 and where $r > 5$ for player 3. Under such conditions, these players all depart together on day 60. In addition, the local maxima demonstrate the largest difference in departure date between consecutive players. This implies that the more dominant sibling influences the departure date of the more submissive sibling to the greatest extent at each maxima. The decrease of the local maxima represents that a more submissive consecutive player is only partially influenced by the preceding player; in actuality, her departure date is influenced by all players that are more dominant.

6.5 Effect of Resource Availability During Settlement

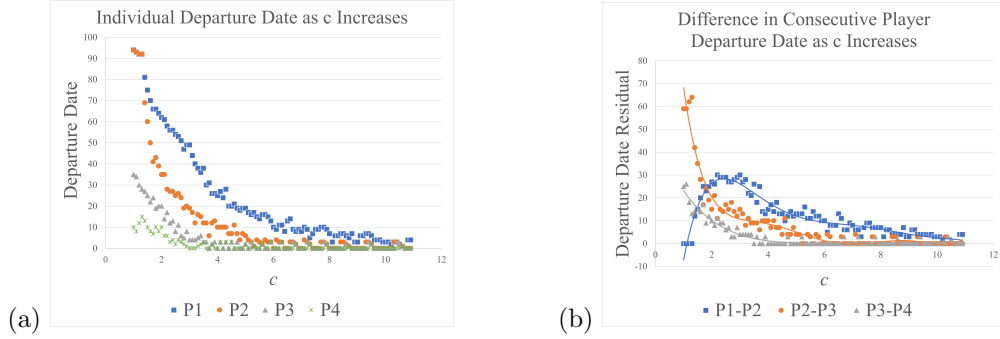(a)   (b)

Figure 8: ES departure dates by individual (left) and the difference in departure between consecutive individuals (right) as offspring become more capable of accumulating resources for parameter values as shown in Table 1.

Since survivability is a function of q_i and q_i is a function of c, it is important to determine the effect that c has upon departure date and EFRS. We expected that larger values of c would increase the incentive to disperse earlier. Figure 4a demonstrates this effect on the individual level, and the Fast Nash Algorithm calculates mean survivability and EFRS that are stricly increasing with c.

Figure 8b then illustrates the difference in departure date between consecutive players as children increase their ability to acquire resources. The decreasing functions for more submissive siblings demonstrate that an increasing c will result in departure times that are earlier and closer together. The difference in departure day between player 1 and player 2 shows a more complex relationship where the two most dominant siblings experience increasing kin competition such that player 1 forces player 2 to depart earlier for c values close to $r = 12/5$, particularly for $11/5 < c < 3$. This is an interesting result because it demonstrates that c may have a larger effect within the model regarding the variance in departure date between the most dominant siblings rather than mean EFRS.

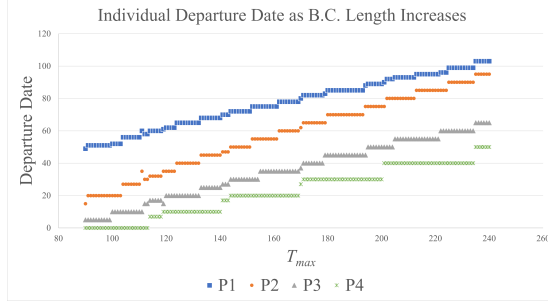## 6.6 Effect of Length of Breeding Season

Figure 9: ES departure dates by individual as B.C. length increases for parameter values as shown in Table 1.

Since breeding season length can differ due to seasonal variation, we also decided to analyze T_{max}'s effect on EFRS. Because our model includes a time cost in the first B.C., we expected that larger T_{max} values would result in larger EFRS values. Our Fast Nash calculations confirmed a strictly increasing EFRS with increasing T_{max}. We also posited that longer breeding cycles would result in later departure dates since a child would have more time to accumulate resources and could spend more time in transfer or settlement. Figure 9 demonstrates that individual departure date did increase with T_{max}, but it also shows an unexpected result regarding modes of departure distributions. As such, the parameter is highly affected by increases in player dominance. Dominant siblings are more sensitive to changes in T_{max} when compared to submissive siblings. This is determined by the modality of departure datets, where fewer modes demonstrates less variation in evolutionarily stable departure strategy. However, we can explain this phenomenon in terms of our model: the most dominant sibling has the greatest decision-making power at any given moment because she makes the first decision, and each consecutive sibling must make her own decision based upon the decision of more dominant siblings. The idea that dominant offspring experience a more diverse series of strategies is comparable to dominance-delayed dispersal in biological theory, where a child can remain in the natal area in order to benefit from nepotism but risks fecundity in that season [10].
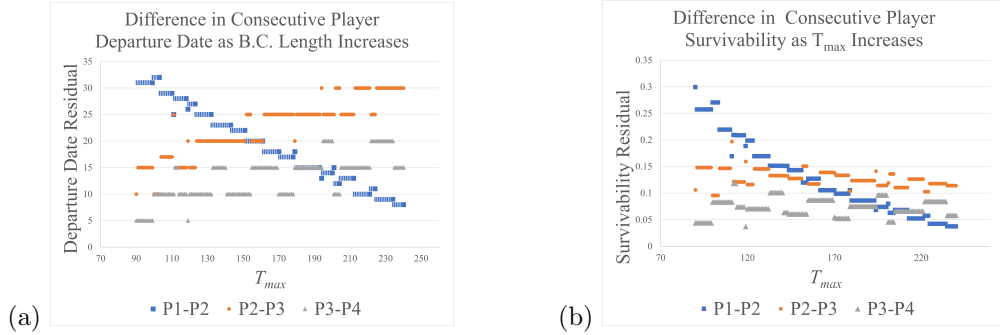
Figure 10: Difference in ES departure dates by consecutive players as B.C. length increases (left) and the difference in survival between consecutive individuals (right) for parameter values as shown in Table 1.

Figure 9 demonstrated that mean departure dates increased with B.C. length, and the increasing modal variation with dominance level prompted an interest in analyzing the departure dates of two consecutive players. Thus, we created Figure 10a to analyze the differences in departure date between consecutive players. This plot demonstrated that shorter breeding seasons result in the greatest departure variation between the most dominant siblings while the opposite holds true for more submissive siblings. We were unsure why there would be such a stark difference between these strategies, so we examined the other factors of the EFRS function that might influence the players. When examining the difference in survival between consecutive players, as shown in Figure 10b, we discovered that player 2 opted to disperse at a time closer to player 1 as T_{max} increased in order to increase their survival probability. In fact, player 2's survival probability went from 0.701 when $T_{max} = 90$ days to 0.963 when $T_{max} = 240$ days. On the other hand, when comparing the difference in survival probability between more submissive players, it remained within the same 5% range for all T_{max}. Since there was no direct survival benefit for a more submissive sibling to disperse at a time closer to the previous sibling, the departure dates followed the mean pattern for later departure as B.C. length increased.

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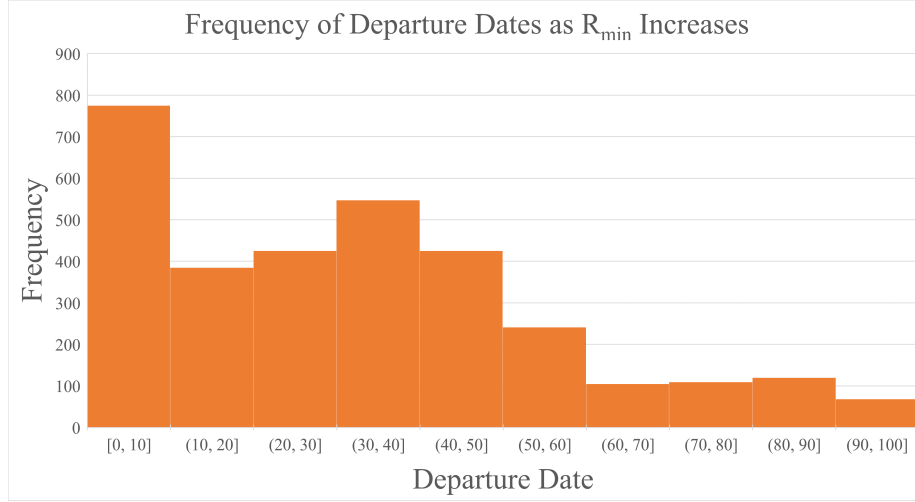## 6.7 Effect of Resources at Earliest Departure

Figure 11: Frequency of ES departure dates as the minimum amount of resources required for dispersal increases for parameter values as shown in Table 1.

When examining the strength of R_{min} regarding departure date and EFRS, we expected that larger values of R_{min} would result in earlier mean departure dates. Since this is easily explained by the fact that survival probability will increase for larger values of $R(d_i)$ and less settlement time will be necessary to gain R_{max} resources, it was important to focus on individual departure dates. Thus, we wanted to determine whether altering R_{min} would result in a specific distribution of departure dates that could demonstrate the frequency of departure regarding resource accumulation. Figure 11 illustrates two large peaks between 0 to 10 days and between 30 to 40 days. This histogram demonstrates that fledglings with greater fitness before the breeding season occurs (i.e., were born earlier and cared for longer) can depart early but fledglings born later that receive little care must depart closer to T_{max} in order to survive. In addition, the relatively small frequency for departure dates greater than 60 days represents that only the player 1 departed late into the B.C. This demonstrates a continuation of the idea that more dominant offspring may delay departure in order to benefit from nepotism or greater fitness [10].

7 Discussion

7.1 Important Results

We created a sequential game-theoretical model that calculates ES dispersal timing for individuals within a brood by maximizing EFRS. By analyzing the

magnitude of each parameter within the model, we discovered the following relationships and demonstrated the biological implications:

1. Strategies that maximize individual fitness also maximize group fitness in certain cases.

   Evolutionarily stable dispersal strategies do not necessarily maximize payoff for all individuals, although sometimes payoff-maximizing strategies are in fact evolutionarily stable. Our analysis of agreement between ESSs and strategies that maximize the total fitness of all offspring showed that these strategies coincided in over 70% of test cases. The number of test cases was limited by computational complexity and time constraints. More work is needed to understand the relationship between ESSs and payoff-maximizing strategies in our model. It would be enlightening to run more tests with variation in other parameters, and especially to test more values of n and T_{max}. The latter would require a faster algorithm for finding payoff-maximizing strategies, which may not be possible.

2. Large values of n, c, and R_{min} result in earlier mean departure times.

   This result implies that there is no single variable that promotes early dispersal timing within our model. We can explain evolutionary significance through a comparison to biological and mathematical literature that includes kin competition and parental pressure.

   For example, our analysis of n implies that larger litter sizes will experience a greater kin competition effect due to the sharing of limited resources within the natal area. As a result, we see in Figure 4 that siblings of large litters ($n > 6$) will disperse as soon as they reach the R_{min} resources on d_i in order to reduce kin competition. Interestingly, the chance of survival for these early dispersers was calculated as 55%, which agrees with one of the results of Hamilton and May (1977) that states even with a chance of death over 50%, dispersal of at least half of offspring will occur in an effort to avoid kin competition.

   Parental pressure has also been demonstrated to affect the timing of dispersal [10]. In this model, Figure 8a illustrates that submissive offspring with high ability to provide for themselves (i.e., when $c > 3$) opted to disperse early to avoid competing with their parents for $r = 12/5$ resources in the natal habitat.

   Finally, larger values of R_{min} resulted in early departure because less settlement time was needed to gain R_{max} resources and survivability increases with larger $R(d_i)$. Interestingly, Figure 11 demonstrated a bimodal distribution of departure timing, which has been observed in empirical studies [20][22]. The greatest departure frequency is between $0 < d < 10$, and this early dispersal may represent that fledglings born early in the breeding cycle are able to disperse earlier [23].

3. Large values of N, r, and T_{max} result in later departure or philopatry.

This demonstrates that no single variable influences the timing of dispersal, which is reflected in the literature [3]. Our results for large N and small N can describe the different ESDSs that iteroparous and semelparous species play. Within our model, iteroparous species have more incentive to delay dispersal until such time as they are likely to survive because they will have several chances to reproduce. Semelparous species should disperse at earlier times in order to spend more of the breeding season finding a suitable habitat and avoiding inbreeding.

Parental care during the fledgling stage also delays dispersal, as shown by large r in Figure 7a. Offspring will delay departure because their chance of survival will increase as they are able to accumulate more resources $(R(d_i))$ before dispersal. This result complements biological theory for cooperative species in which offspring that experience parental care often delay dispersal in order to benefit from greater fitness [10][20].

Finally, longer breeding cycles allow offspring more time in general to develop, disperse, and settle into their new territories. Literature demonstrates that there are costs to each stage of dispersal that may be reflected later as opportunity costs [3]. Since our Fast Nash algorithm calculated an increasing survival rate in settlement for larger T_{max}, our model shows that transfer or opportunity costs levied in settlement are diminished when breeding cycles are longer because offspring have better development.

4. Variation in n, r, T_{max}, and R_{max} can promote dominance-delayed dispersal.

Biological theory on dominance-delayed dispersal states that more dominant individuals may delay dispersal in order to benefit from greater fitness or nepotism [10][20], but other observational studies have demonstrated no correlation between dispersal and temperament [13][5][9]. In our model, dominance decreases with consecutive player. Thus, we were able to determine how varying each parameter affects the departure date of each individual.

An analysis of n demonstrates that for $n > 6$, all individuals will depart on $d_i = 0$. Since our model classifies these early dispersers as more submissive, we can state that more dominant siblings experience delayed departure. In addition, Figure 7a illustrates decreasing local maxima. This represents that the departure date of a more submissive sibling is only partially influenced by the preceding player; in actuality, her departure date is being influenced by every previous decision. When increasing T_{max} in Figure 9, we discover that more dominant individuals experience greater modal variation. This implies that more dominant individuals may have more decision-making power regarding dispersal whereas more submissive or less fit children are pressured to disperse early [1][[15]. Finally, our plot of R_{min} also demonstrates this effect of dominance-delayed dispersal where, for all departure dates past day 57, player 1 was the only sibling to disperse.

7.2 Limitations of the Model

This model calculates expected EFRS for offspring in a single litter, but does not follow the next generations. This means that the model can give an ESDS for a single ecological time-step but does not give one on the evolutionary time scale. There is also no density-dependence in this model, which means that no single game can be generalized to the population. The assumptions of our model also limit its biological applicability. For example, we assume that offspring will receive equal parental care and must disperse in the first breeding cycle, but this is not corroborated by the literature. Furthermore, competition is absent when children accumulate resources outside the natal area, which may be accurate only in some natural environments.

7.3 Future Directions

We plan to revise the model to incorporate specific travel time and corresponding costs such that there is a potential increase in biological applicability. We would like to adjust the current model to include a more sophisticated inbreeding avoidance bonus. We also aim to construct a simultaneous decision-making model in order to compare EFRS strategies when players make decisions simultaneously versus sequentially. Finally, we would like to expand this model to examine group fitness maximum versus individual fitness maximum with spatial arrangement of patches.

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8 Acknowledgements

9 Appendix

The code used in this project and README file can be found in the GitHub repository linked below: https://github.com/WillFowlkes/DynamicsREU2023