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Male Dispersal Decisions: An Agent-based General Model
and Suggested Refinements for White-faced Capuchin Monkeys

(Cebus capucinus)

A thesis submitted in partial satisfaction
of the requirements for the degree Master of Arts
in Anthropology

by

Kotrina Kajokaite

2014

ABSTRACT OF THE THESIS

Male Dispersal Decisions: An Agent-based General Model
and Suggested Refinements for White-faced Capuchin Monkeys
(*Cebus capucinus*)

by

Kotrina Kajokaite

Master of Arts in Anthropology

University of California, Los Angeles, 2014

Professor Susan Perry, Chair

Kokko and Ekman (2002) presented the first mathematical model that attempts to quantify the direct fitness benefits of dispersal and contrast them to the benefits of philopatry. The model is general and lends itself, with some specific adjustments, to application for various species. Here I present a transformation of this general mathematical model into a dynamic agent-based model (ABM). I explain how the mathematical model is used to inform the construction of the ABM and present the results of running the ABM across a wide variety of parameter values (a total of 21 different simulation scenarios). I discuss the ways in which the ABM replicates Kokko and Ekman's (2002) model's predictions, and the ways in which it does not. I suggest

how to resolve these differences in future simulations. Finally, I explore what factors of white-faced capuchin (*Cebus capucinus*) life histories should be incorporated into the ABM in order to study the relative benefits of dispersal and philopatry in this species.

The thesis of Kotrina Kajokaite is approved.

Joseph H. Manson

Karthik Panchanathan

Brooke Scelza

Susan Perry, Committee Chair

University of California, Los Angeles

2014

To my parents, Donaldas Kajokas and Danute Kajokiene,
who supported my decision to disperse
so early and so far.

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PART I

INTRODUCTION

Lifetime reproductive success often depends on the decision to stay in or leave one's current social environment. Dispersal is a fine-tuned life-history trait, which involves individuals evaluating their current situation and deciding to leave in search of better conditions. Ultimately, what they seek is a chance to reproduce. This is true for many mammalian species. Among mammals, differential allocation of resources contributes to a general pattern of sex-biased dispersal, with one sex leaving their natal site or group in search of new breeding opportunities (Greenwood 1980). Since leaving a familiar environment and one's relatives is often a dangerous endeavor, staying home, or at least staying home longer, can be a safer choice. Therefore, individuals face a complicated question – should they stay or should they go? – and the answer is a function of their own physical and behavioral traits, their social environment, and the trade-offs they have to make in either case.

Dispersal has wide-ranging consequences at both the individual and population levels. It restructures relationships among individuals and groups (Cheney and Seyfarth 1983) by cutting ties between migrating individuals and those who stay; it also facilitates new relationships when migrants join other groups. This inevitably influences individual reproductive histories and broader mating patterns. The most dramatic effects are observed in species where infanticide is a male mating strategy; in these species, the immigration of new males into a group usually means the loss of nursing infants for the group's females (sea lions: Campagna et al. 1988; langurs: Hrdy 1974; capuchin

monkeys: Manson et al. 2004; lions: Packer and Pusey 1983; gorillas: Robbins et al. 2013; wolverines: Persson et al. 2003).

The movement of individuals ensures gene flow within and between populations. The spatial distribution of the groups and their sizes in the population is restructured by animals migrating from their natal groups, roaming the territory alone or together, and, finally, either entering or forming new groups (Taylor and Taylor 1977). Importantly, the immigrants bring new genetic material into the groups they enter, altering a population's genetic structure (Greenwood 1980; Melnik 1987).

Costs and benefits of dispersal

Dispersal results in a change in the animal's physical and social environment. This can have various consequences for the emigrants: they must adapt to new physical and social environments, and face many risks before finding a new home. We can analyze the factors contributing to the decision to disperse in terms of fitness costs and benefits.

One of the costs of dispersal is an increase in mortality risk (Lawson Handley and Perrin 2007). In normally gregarious species, migrants that spend considerable time alone during dispersal increase their vulnerability to predation, since they can no longer rely on the detection and dilution benefits that group life affords. The longer the period that the migrant spends alone between social groups, the more likely he is to die of predation.

Travelling through unfavorable and unfamiliar habitats can also pose costs. Foraging can become more difficult in unfamiliar territory (Lawson Handley and Perrin 2007) and animals might not be able to obtain an adequate amount of calories. Other

resident conspecifics in such territories put migrating animals at a disadvantage, especially if resource acquisition requires complex interactions with the environment. Newly dispersed lone individuals cannot rely on kin cooperation while competing with other conspecifics (Lawson Handley and Perrin 2007).

The ubiquity of dispersal across the animal kingdom implies that, under certain conditions, the benefits of dispersal outweigh the costs. The principal benefit of dispersal is thought to be inbreeding avoidance (Bischof 1975; Greenwood 1980; Pusey 1980; Packer 1979; 1987; Melnik 1987; Wolff 1994; Lawson Handley and Perrin 2007). Usually, most potential mates in an animal's natal group are also its close genetic kin. S. Wright (1921) demonstrated that regular mating between full cousins or more closely related individuals often results in increased homozygosity. In such cases, deleterious recessive traits are more likely to be expressed in the offspring, resulting in increased morbidity and reduced fecundity. This reduction in the viability and fertility of offspring due to mating between close relatives is known as inbreeding depression (Crnokrak and Roff 1999). Dispersal, which typically occurs before breeding, reduces an individual's chances of mating with close relatives.

Another potential benefit of dispersal is increased access to mates. In most mammals, males are more likely to disperse before breeding whereas females are usually philopatric (Greenwood 1980; Dobson 1982; Smale et al. 1997; Lawson Handley and Perrin 2007). This is due to differential allocation of resources between males and females. Female reproductive success is mostly influenced by access to resources (Trivers 1972), because they pay larger costs of gestation, lactation, and care for their offspring than males. Males, on the other hand, compete with each other for access to

females, and this usually leads to short male tenures (Wolff 1994). As a result, females are selected to be philopatric, because they run little risk of being co-resident with their fathers, and thus risking close inbreeding (Clutton-Brock 1989; Wolff 1994). Males benefit from dispersal more than females, because they compete more intensely among themselves for access to reproductive females (Packer 1979; Greenwood 1980; Wolff 1994). The cost of philopatry for males (lost mating opportunities) would be comparable to that of increased mortality risk when dispersing. Reproductive enhancement associated with dispersal can potentially outweigh the costs associated with increased mortality during the migration period (Greenwood 1980; Wolff 1994).

Factors affecting the timing of dispersal

Dispersal facilitates an increase in an individual's reproductive success through inbreeding avoidance and/or enhanced access to more mates. The decision of whether to leave should be determined by the costs and benefits of dispersal in a particular system, but the decision of *when* to leave is affected by additional factors.

In some species the dispersing sex leaves right at sexual maturity, but in many species dispersal time is highly variable: some individuals depart while very young whereas others delay dispersal until they are much older (Lawson Handley and Perrin 2007). Since staying in one's natal group potentially means postponing one's reproduction, there has to be some benefit from delayed dispersal that outweighs the cost on direct fitness (Kokko and Ekman 2002). In addition to understanding the direct fitness benefits gained through dispersal, it is also important to understand how fitness benefits

vary depending on the timing of dispersal, and whether there are direct fitness benefits associated with delayed dispersal.

What benefits can delayed dispersal offer?

1. Ecological constraints hypothesis

If dispersal does not confer reproductive opportunities immediately, staying in one's natal group might be better. In such conditions, individuals who stay do not pay the reproductive costs associated with delayed dispersal, because reproductive opportunities are rare. The majority of the dispersers do not become breeders immediately. This is known as the *ecological constraints* hypothesis (Emlen 1982), which predicts that the frequency of nonbreeders in a population will depend on constraints placed on becoming a breeder in a stable, saturated habitat, and the constraints of the environment present in an erratic, unpredictable habitat. Hatchwell (2000) identifies some of the possible ecological constraints: high dispersal costs, a shortage of territory vacancies, a shortage of breeding partners, and the low probability of successful breeding once a territory has been obtained.

Emlen (1982) suggests that at least four variables have to be taken into account when considering dispersal vs. philopatry:

- 1) the risks of dispersal itself;
- 2) the probability of acquiring a suitable territory (area, group) after dispersal;
- 3) the probability of successfully finding a mate;
- 4) the likelihood of successful reproduction.

When variable 1) is high, or one of the other variables is low, the benefits of philopatry are predicted to increase due to inclusive fitness benefits that a philopatric individual acquires through helping his kin (Emlen 1982). Whereas variable 1) mostly concerns environmental pressure (e.g., high extrinsic mortality rates associated with dispersal), the rest are associated with the population structure itself.

Brown (1969) similarly distinguishes between three levels of population densities; at the highest level of density, some dispersers form a floating population of nonbreeding individuals, because the competition for breeding position is very high.

In such situations, staying in one's natal group is potentially a better choice, because although breeding is also delayed in one's natal group, the advantages of growing a bigger body size and gaining experience in a safe environment might later put these individuals at an advantage in competitions for breeding position (Emlen 1982).

2. Benefits of philopatry hypothesis

The ecological constraints hypothesis does not explain why some individuals delay dispersal in populations where the habitat is not saturated with ready-to-breed individuals (Stacey and Ligon 1987; 1991). The *benefit of philopatry* hypothesis posits that individuals will delay dispersal when there is a benefit associated with staying in a natal group or territory. There has to be some benefit to staying longer that outweighs the cost of not reproducing as early as possible and is not dependent on habitat saturation alone.

Stacey and Ligon (1987) propose that philopatry does not depend on habitat saturation, but on access to critical resources (e.g., a high-quality territory). They suggest

that if there is a possibility of inheriting a high-quality territory in the future, this will increase the net benefits of philopatry relative to the net benefits of dispersal (Stacey and Ligon 1991). Although younger dispersers might start reproducing earlier, those who wait a few years and inherit the high-quality territory of their parents might do better in terms of lifetime reproductive success (Heg et al. 2011).

Age-related asymmetries in resource holding potential (RHP) might select for delayed dispersal (Zack and Stutchbury 1992). If early dispersers are poor competitors due to age-related traits like body size, it might be beneficial for them to wait in their natal territory until they are better competitors and can gain more from independent breeding (Heg et al. 2011).

3. Life-history trait hypothesis

In the context of dispersal, the *life-history hypothesis* (Brown 1969) explains how life-history traits affect dispersal patterns. This is, in essence, a unifying name for a number of specific hypotheses that share a basis in life-history theory. For example, Arnold and Owens (1998) demonstrate that low mortality rates play a key role in favoring cooperative breeding in bird taxa. Where mortality risks are low, it becomes worthwhile to spend time accruing inclusive fitness benefits by caring for younger siblings, because there is a high probability of surviving to reproduce later.

Often, life-history hypotheses are considered alongside the ecological constraints hypothesis (Hatchwell and Komdeur 2000), where life-history traits predispose cooperative breeding behavior and delayed dispersal, and ecological factors facilitate it—i.e., the rate of change in breeder identity will depend on breeder mortality (a life-history

trait) and habitat saturation (an ecological constraint).

The dispersal pattern within any particular species is a function of these various costs and benefits. When studying a dispersal pattern in any particular species, the costs and benefits of dispersal and philopatry discussed above provide us with a useful toolkit, which, if properly used, can help us to understand why individuals are leaving and how they are timing their departure.

Safe Havens model and agent-based model

Kokko and Ekman (2002) present a mathematical model evaluating three different routes to breeding: (1) departing to search for new territories as a floater, (2) staying and queuing to inherit the natal territory, and (3) staying and eventually shifting to a breeding vacancy in a neighboring territory. The model quantifies the benefits of philopatry for subordinates of various ranks and contrasts these benefits to those of dispersal. The Kokko and Ekman model is the first attempt to quantify the direct fitness benefits of dispersal and philopatry, allowing one to study under which conditions, and at which dominance rank, an individual will favor philopatry over dispersal. Kokko and Ekman conclude that a natal territory could function as a safe haven, in which individuals can wait for breeding opportunities (their model will henceforth be referred to as the Safe Havens model).

I have constructed an agent-based model (henceforth, ABM) that is based on the Safe Havens model. Kokko and Ekman's (2002) mathematical model quantifies lifetime fitness benefits and determines at which rank the benefits of dispersal exceed the benefits

of philopatry. In other words, it describes how big the groups should be in a given species under given social and ecological conditions. The ABM attempts to transform the mathematical model into a dynamic one, in which a population of dispersing individuals is tracked over a long period of time, calculating the reproductive success of those who disperse and those who stay. The ABM qualitatively captures the Safe Havens model's predictions and explores the different parameter values evaluating the conditions under which either dispersal or philopatry is favored.

METHODS

Description of the model

Agent-based models are computer simulations in which the interactions of individual agents result in the emergence of group behaviors and social structures (Epstein 1996). In agent-based models, agents and groups interact according to defined rules, while their states and population structure are tracked over time. Such models are useful in studying complex biological systems, because they enable us to explore aspects of the world that are hard to examine observationally or experimentally, due to temporal, ethical, and logistical constraints (Peck 2004).

The ABM based on the Safe Havens model has a fixed number of 50 groups, and each group has a fixed number of 20 males. The model only includes males, which are divided into different categories according to their life history: alpha males, group-living subordinate males, and floater males. Males transition between these categories. Alpha males hold rank 1 and are the only breeders in the population, as in the Safe Havens

model. The next male in the hierarchy is the first-ranking subordinate, and the rest of the males form a linear dominance hierarchy. Once a male leaves his natal group he becomes a floater. The number of floater males is not fixed and emerges through the mortality and emigration rates of the subordinate males. The model simulates life-history events from the Safe Havens model, in which males make decisions whether to disperse or not based on the rank position in which they find themselves.

Since alpha males are the only breeders in the population, becoming alpha is used as an approximation of lifetime reproductive success. The alpha position and breeding position are used interchangeably in the model description. The model tracks the routes through which males become alpha males in order to evaluate under which conditions philopatry is favored over dispersal.

The rest of the model description follows the standardized ODD (Overview, Design Concepts, and Details) protocol for describing individual and agent-based models (Grimm et al. 2006; 2010).

Overview, Design Concepts, and Details for Safe Haven Agent-Based Model

1. Purpose

The model is designed to explore the conditions under which males in a female philopatric system either stay in their natal group or disperse to search for other breeding opportunities. The model is based on the Kokko and Ekman (2002) mathematical model, which quantifies the benefits of philopatry and the benefits of dispersal, and it simulates three different routes to breeding:

- 1) staying in one's natal group and inheriting the breeding position (*inheritance route*);
- 2) staying in one's natal group and eventually acquiring a breeding position by directly shifting to a nearby group (*shifter route*);
- 3) leaving one's group in search of breeding opportunities elsewhere (*floater route*).

2. Entities, state variables and scales

The model has one entity: males who are striving for alpha status. Although space is not explicitly modeled, the males live in 50 social groups, each containing 20 males. Besides group-residing males, there are floater males who do not belong to any group but compete for breeding positions.

Time is represented discretely in this model. During each time period, agents execute the commands described in the schedule. One discrete time step includes all life-history events (described in *Process overview and scheduling*). The length of one time step is not specified, but it should represent a year in an agent's life. However, senescence is not modeled, and agents' attributes do not change as a function of how long they have been in the simulation. The simulation lasts 10,000 time steps.

The model entities are characterized by the state variables described in Table 1.

Table 1. State variables for ABM entities.

Entity	State variable	Description
Agents	Male	Each male is classified according to his demographic status: alpha, subordinate, or floater.
	Emigration thresholds	Each male has a number from 1 to 20, representing a decision rule he uses when he considers migration. If a male's current rank is lower than

	his emigration threshold, he becomes a floater.
Groups observed	Each male becomes aware of and competes for a breeding position only in the groups he is monitoring. The number of groups each male monitors is determined by his demographic status (alpha, subordinate, or floater) and rank.
Age	This is the number of time steps that the agent has been alive in the simulation.
Status	All males are divided into two types: floaters and group-living males.
Rank	All group-living males have a rank: rank 1 represents the alpha male, rank 2 represents the first-ranking subordinate, and so on. The lowest-ranking male holds rank 20.

3. Process overview and scheduling

This model proceeds in discrete time steps, and entities execute procedures according to the following order. For each time step:

1) Age of agents is incremented by 1.

2) Mortality (for all agents simultaneously):

- Mortality probability for breeders is applied to first ranking individuals (alpha males) in each group.

- Mortality probability for subordinates is applied to the rest of the group-living males.

- Mortality probability for floaters is applied to the males who live outside the groups.

- After mortality probabilities are applied, all group-living males move up in the hierarchy if there is an open space above them. No one moves up to rank 1 position, which is filled using a *contest for breeding position function*.

3) Contest for open breeding positions:

- If any of the groups has a vacant rank 1 position (alpha position), a new alpha is picked from a competitors pool comprising floaters, subordinate males from the group in which there is a vacancy, and subordinate males from other groups who have this group in their “groups observed” list.

- After a new alpha is selected, any subordinate males that have an open rank position above them in the hierarchy move up to that position.

4) Emigration (for subordinate group-living males only):

- All subordinate group-living males compare their current rank with the emigration threshold they are assigned at birth.

- If their rank is lower than their emigration threshold, the males disperse to become floater males.

- Group-living males check if there are any open rank positions above them and move up if there are.

5) Birth:

- Births occur in the groups that have subordinate male spots available after all subordinates move up in the hierarchy due to death or the selection of a new alpha—i.e., every group has 20 spots, and some of those spots will be free after *mortality*, *contest for breeding position*, and *emigration* probabilities are applied.

- New individuals are born who inherit the same emigration probability threshold as the current alpha male, with a mutation rate of 5%.

Description of the parameters

Mortality

Mortality is a number between 0 and 1 that represents a probability of dying applied to each agent, depending on his demographic status (alpha, subordinate, or floater) and rank, at every time step. There are three parameters of mortality in the model: μ_B is the mortality of the breeder, while μ_S and μ_F represent the mortality of group-living subordinates and the mortality of floaters, respectively.

Mortality of the breeder (μ_B). As in the Safe Havens model, the ABM assumes that the parameter μ_B incorporates not only the extrinsic mortality of the individual who holds alpha position in the group, but also includes the rates of take-overs that lead to a change in the dominant individual's identity (Kokko and Ekman 2002). The breeder mortality represents how often we can expect to see a top dominant position vacancy in any given group. If μ_B is set to 0.2, we can expect to observe a vacancy in a particular group once every five time steps on average. Therefore, high μ_B values will result in frequent turnover, and low values will result in less frequent changes in the dominant's identity.

The breeder mortality parameter also means that alpha males can neither return to the floater pool nor become subordinate males; they can only die and be removed from the population.

Mortality of subordinates and floaters (μ_S and μ_F). Differences between the mortality of subordinate group-living males and floater males represent one of the potential benefits of staying in a natal group. If floater males experience higher mortality, the benefits of philopatry increase. If the mortality rates are the same for both of these groups, then the benefits of dispersal might increase if the floater males are also able to monitor more groups and be aware of more potential breeding positions in comparison to group-living subordinate males.

Sigma parameter (σ_n). Group-living subordinate mortality can be further adjusted using the σ_n parameter. This parameter scales mortality down the hierarchy, so that the mortality of the lower-ranking subordinate is higher by factor σ_n (Kokko and Ekman 2002). If σ_n is equal to 1, then all of the males in the group experience the same mortality, but if $\sigma_n > 1$, then each male's mortality is higher than the mortality of the male right above him in the hierarchy by the factor σ_n .

Groups observed

One way the advantages of dispersal increase in the model is when floater males observe more groups than group-living males. Living in the group offers safety from predators and benefits associated with nepotism, but the group-living males might be

restricted to their group's range, which means they will have access to information about fewer other social groups than floater males. While floater males often experience increased mortality risk, they might be able to range farther than a large social group and have the opportunity to sample more territory, acquiring information about a larger number of social groups. If floaters have opportunities to acquire knowledge about more groups than group-living males, they might be aware of more potential open breeding positions.

In order to describe the relationship between the number of groups observed by the floaters versus the number of groups observed by group-living subordinate males, I use two parameters: T_f and T_s , where T_f is the number of territories that floater males are able to observe, and T_s is the number of territories that males living in social groups are able to observe in addition to the territory in which they are currently residing (Kokko and Ekman 2002).

Propensities to acquire breeding position

Individuals might differ in their abilities to acquire a breeding (alpha) position. The model parameterizes state-dependent propensities that describe the relative abilities of different types of males to acquire a breeding position (Kokko and Ekman 2002). Males will differ in these propensities depending on their rank and on their demographic situation: a floater, a subordinate from the group where an alpha position is vacant, and a subordinate from a neighboring group.

There are three parameters that describe the propensities of males. Since it is a relative scale, we need to choose a reference point. Kokko and Ekman (2002) use the

first-ranking subordinate from a neighboring group in relation to the breeding position in question, and assign a propensity of 1 to this individual. There are two other types of males that might compete for this position: floater males and the first-ranking subordinate male from a group where the breeding position is vacant. There are also lower-ranking subordinate males who might contest the breeding position (both from the group where the alpha position is vacant and also from other groups that observe the focal group).

Therefore, there are three parameters that address these relationships among all male types: α , β and γ .

Parameter α describes the propensity of natal subordinate males to acquire a breeding position in their natal group. If philopatric subordinate males and subordinate males from other groups are equally likely to attain a breeding position, then α is set to 1—i.e., if the highest-ranking natal subordinate is a candidate for a breeding position in his own natal group, he has the same propensity to become the breeder as the first-ranking subordinate from a neighboring group. However, if there is inbreeding avoidance, then we can expect that philopatric males will acquire breeding positions in their natal groups less often than males from other groups. A value of α from 0 to 1 captures the strength of inbreeding avoidance that puts these males at a disadvantage in comparison to males from other groups. The ABM is agnostic about the mechanism that facilitates the reduced propensity of natal subordinates to become breeders in their natal group. As in the Safe Havens model, the assumption in the ABM is that only males who hold the alpha position reproduce, and α below value 1 describes systems where natal males are less viable candidates to occupy the alpha/breeder position than males from other groups.

An opposite situation can be found in species where there is no inbreeding avoidance and residence in one's natal group actually confers an advantage of acquiring a breeding position there. In this case, values of α above 1 should capture the strength of advantage that the philopatric males experience in comparison to subordinate males from other groups.

Parameter β represents the competitive ability of the floater males in comparison to a first-ranking subordinate that is not natal to the group where a vacancy in alpha position occurs. If β is equal to 1, then floaters are equally competitive to that subordinate male. However, we can expect that the floater males might be disadvantaged because they are less familiar with the territory of the breeding position. The specific mechanism will depend on the species and its ecology, but one example of a disadvantage could be reduced fighting ability due to malnutrition while living in a new territory. The values between 0 and 1 will capture the strength of the decrease in competitive ability when a floater is contesting a breeding position in comparison to a subordinate non-natal male. The values of β above 1 describe species where floaters have an advantage in comparison to the group-living males. In such cases, subordinates might be disadvantaged due to inbreeding avoidance not only in their own group (captured by α), but also in the neighboring groups. Floaters might also be able to explore the territory better because, unlike group-living males, they are not constrained by group activities (Kokko and Ekman 2002).

Parameter γ captures how individuals compare to each other in the same social group, within a dominance hierarchy. If γ is equal to 1, all of the subordinates have the same propensity to become alpha, and rank does not affect the chances of acquiring alpha position. If γ is equal to 0, then the breeding position acquisition is strictly based on hierarchy and the subordinates below the first-ranking subordinate cannot become breeders. The values between 0 and 1 capture the strength of the queue rigidity, with the queue becoming more rigid when γ approaches 0 and more relaxed when γ approaches 1.

Base simulation. For the base simulation, parameters were set to make the conditions for each of the three routes to breeding equal. The mortality of both subordinate males and floater males were set to a probability of 0.1. Both types of males (subordinates and floaters) observed the same number of groups: floaters observed 3 groups, while subordinates observed their current group of residence and 2 other groups. When competing for a breeding position, natal subordinate males, subordinate males from other groups, and floater males were equally likely to attain a breeding position (α and β were set to 1). The γ parameter was set to 0.5, which means that each subordinate male under the first-ranking subordinate has half of the propensity of the male ranking immediately above him. Mortality of the alpha male was set to the same value as group-living subordinate males (0.1).

In the subsequent simulations one or two parameter values were altered in order to see how a change in conditions affects the dispersal and alpha position acquisition patterns.

Table 2. Description of the simulations and parameters.

Simulation	Parameter(s) adjusted	Description
1.		Base simulation.
2.	$\mu_F = 0.2$	Floater mortality is increased to 0.2.
3.	$\mu_F = 0.3$	Floater mortality is increased to 0.3.
4.	$T_S = 0$	Subordinate males do not observe any territories other than the one in which they reside.
5.	$T_f = 6$	Floaters see twice as many territories (6) as subordinate males (3).
6.	$T_f = 9$	Floaters see three times as many territories (9) as subordinate males (3).
7.	$\alpha = 0$	Subordinate males are not able to become alpha in their natal group.
8.	$\alpha = 0.5$	Subordinate males are less competitive for the alpha position in their natal group in comparison to subordinate males from other groups and floater males.
9.	$\alpha = 2$	Subordinate males are more competitive for the alpha position in their natal group in comparison to subordinate males from other groups and floater males.
10.	$\beta = 0.5$	Floater males are less competitive for breeding positions than subordinate males,
11.	$\beta = 2$	Floater males are more competitive for breeding positions than subordinate males
12.	$\gamma = 0$	The hierarchy in groups is strict, and only first-ranking subordinates are able to compete for breeding position.
13.	$\gamma = 1$	A male's rank does not predict his propensity to acquire a breeding position. All males within a group have the same propensity.
14.	$\mu_F = 0.2$ and $T_f = 6$	Floaters are twice as likely to die, but they observe twice as many territories as subordinate males.
15.	$\mu_F = 0.2$ and $T_f = 9$	Floaters are twice as likely to die, but they observe three times as many territories as subordinate males.
16.	$\mu_F = 0.3$ and $T_f = 6$	Floaters are three times as likely to die, but they observe twice as many territories, compared to subordinate males.
17.	$\mu_F = 0.3$ and $T_f = 9$	Floaters are three times as likely to die, but they observe three times as many territories as subordinate males.
18.	$\mu_F = 0.2$ and $\beta = 0.5$	Floaters are twice as likely to die as subordinate males, and have half the propensity when competing for breeding positions.

19.	$\mu_F = 0.2$ and $\beta = 2$	Floaters are twice as likely to die as subordinate males, but have twice the propensity when competing for breeding positions.
20.	$\mu_F = 0.3$ and $\beta = 0.5$	Floaters are three times as likely to die as subordinate males, and have half the propensity when competing for breeding positions.
21.	$\mu_F = 0.3$ and $\beta = 2$	Floaters are three times as likely to die as subordinate males, but have twice the propensity when competing for breeding positions.

4. Design concepts

Basic principles. The basic principle addressed by the model is the comparison of three different routes to breeding, examining which leads to higher fitness payoffs (fitness here is approximated by attaining a breeding position which is the only way to sire offspring). The three routes represent two main strategies: philopatry and dispersal.

The philopatry strategy has two potential routes to breeding: either a group-living male stays in his group and becomes alpha when the current one dies, or he shifts to a neighboring group once a breeding position opens. Dispersing males join the floater pool and compete for breeding positions in the groups they are monitoring.

Emergence. This concept is addressed through seeing which emigration thresholds emerge as dominant at the end of the simulation. Depending on the initial parameters, the selection in the model is on the emigration strategy thresholds. The most common emigration threshold shows how long of a queue should form for any given set of parameters. The higher the lowest acceptable rank (i.e., the rank below which a male will emigrate), the shorter the within-group queue, and the larger the proportion of floaters in the male population.

Adaptation. The adaptive behavior is modeled via competition for alpha positions. This behavior is based on the understanding (not included in the model) that acquiring a breeding position leads to mating and offspring (increased fitness) that inherit the same emigration threshold.

The trait under selection is emigration threshold. By achieving alpha position, males pass this trait to their offspring. The fitness of the male is measured by the spread of his emigration threshold in the population.

Objectives. The objective is to increase fitness.

Predictions/Learning. Agents in this model lack the ability to predict the outcomes of future social interactions. They do not integrate information across time periods.

Sensing. Agents can compete for breeding positions in the groups they are monitoring at the time.

Interaction. There are no direct interactions between agents. Agents interact indirectly when competing for the breeding position; they do not communicate with one another during competition.

Stochasticity. Mortality, picking a new breeder from the list of competitors, and mutations all have stochastic elements.

Collectives. Social groups are collectives in the model. They are defined by the modeler as a set of individuals with certain properties. Along with rank, membership in the group defines the propensities of individuals to compete for breeding position.

Observation. The data collected for each simulation run:

- 1) mean and standard deviation of alpha male tenure length (number of time steps)
- 2) mean and standard deviation age of alpha at the start of the tenure
- 3) mean and standard deviation age of alpha at the start of the tenure when the male attains alpha rank via the floater route
- 4) mean and standard deviation age of alpha at the start of the tenure when the male attains alpha rank via the inheritance route
- 5) mean and standard deviation age of alpha at the start of the tenure when the male attains alpha rank via the shifter route
- 6) mean and standard deviation age at leaving the natal group
- 7) mean and standard deviation age at death
- 8) number of alpha males
- 9) number of alpha males via the floater route
- 10) number of alpha males via the inheritance route
- 11) number of alpha males via the shifter route
- 12) number of floaters every 1000 time steps (10 values)
- 13) number of group males every 1000 time steps (10 values)
- 14) mean and standard deviation of emigration threshold every 1000 time steps (10 values)

RESULTS

There were 21 different simulations and each of them was replicated at least 35 times (range 35-42) in order to get more accurate values and account for variance. The final dataset contained data from a total of 763 simulation runs, and the results reported below include data from all simulations.

Number of males in the simulations. The number of group-living males was fixed at 1000 at any given point in time, which means there were no fluctuations in the group-living male population size when measured at the beginning of each time step. There was an alpha male for each of the 50 groups, and the remaining 950 group-living males were subordinates forming a linear dominance hierarchy in each group. The fixed number of group-living males is ensured by *birth function*: at every time step, the number of newborn males is equal to the sum of dead and emigrated males in the group-living male population.

The floater male number emerged through group-living male emigration and did not have any floor or ceiling values. The mean number of floater males in all simulations, as measured once every 1000 time steps, is 58458 (range 26059 – 81382). Even the lowest observed average number of floaters, 26058, in simulation 20, is 2.5 larger than the fixed number of group-living males. Half of the simulations had a floater population more than eight times higher than the group-living male population.

Proportion of alpha males by competitor category. Since the alpha male's mortality (μ_B) was set to the same value in all of the simulations, there was very little variation in how many alphas were simulated in each run. A mean number of alphas simulated for 10000 time steps for all simulations was 50045, with standard deviation of

44. For each open alpha position the *contest for breeding position function* considered all subordinate males from the group where the alpha position was vacant, subordinate male candidates from neighboring groups that had the focal group in the list of groups they observe (the length of the list is set by the T_s parameter), and floater candidates who had this group in the list of groups they observe (the length of the list is set by the T_f parameter). Figure 1 demonstrates that the floater males become alpha disproportionately across all simulations.

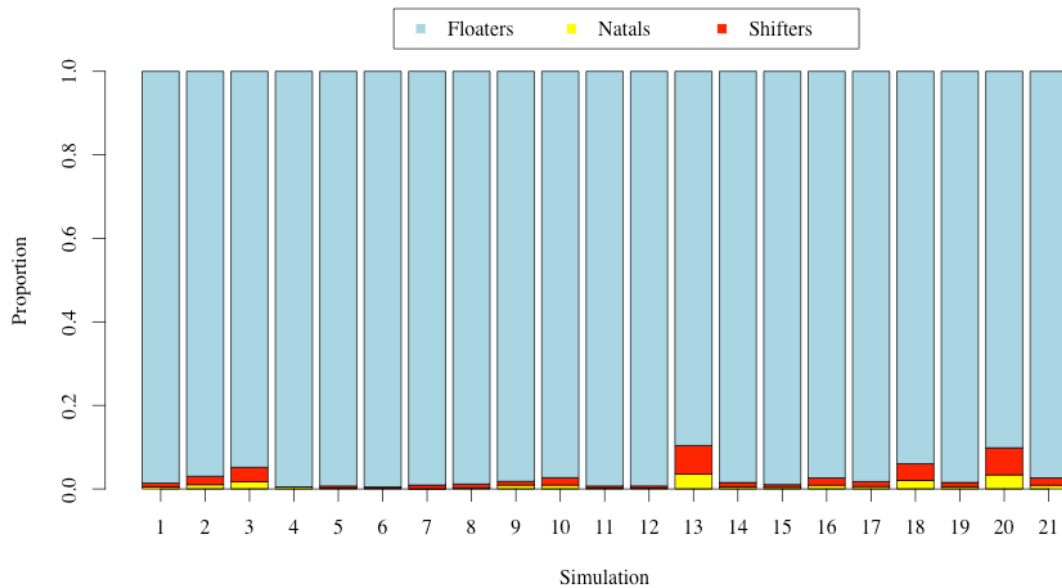


Figure 1: Proportion of alpha males by male category. The average number of alpha males simulated in each simulation was 50045, with a minimum of 49968 (simulation 21) and a maximum of 50130 (simulation 17). Each of the bins represents all alpha males simulated in one of the simulations (averaged across all replicates) and the colors represent a proportion of those alpha males that came via floater, inheritance, or shifter routes. Across all 21 simulations, the majority of alpha males came from the floater pool.

Emigration thresholds. Each male is assigned a random number between 1 and 20 at the start of the simulation as his emigration threshold. This number indicates the lowest

rank position at which this male has to find himself in order to stay in the group. This means that every time the *emigration function* is implemented, males compare their current rank to their emigration threshold, and if their current rank is lower than the threshold, they become floaters. In the initial population, thresholds are distributed uniformly among the males. After 10000 time steps I took an average of all thresholds present in the population to assess if selection had changed their distribution, since only alpha males are able to pass their thresholds to their offspring.

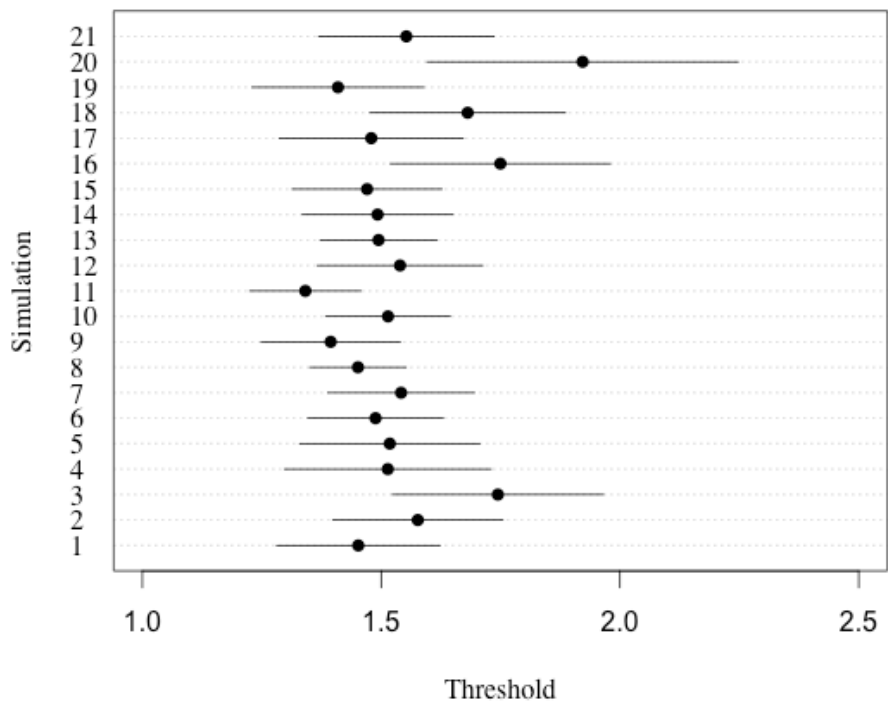


Figure 2: The ABM's averaged thresholds and their standard deviations for each simulation. The average was taken after 10000 time steps. Standard deviations were calculated for each simulation across all replicates of that simulation.

The average threshold for all 21 simulations across all replicates measured at 10000 time steps was between 1 and 2. The average threshold in the population falls to a number between 1 and 2 by the 1000th time step. Figure 2 demonstrates the variation among the ABM thresholds averaged after 10000 time steps and their standard deviations across their replicates.

Emigration thresholds and the Safe Havens model predictions. The Kokko and Ekman (2002) Safe Havens model provides predictions for the rank in the dominance hierarchy at which the benefits of dispersal exceed the benefits of philopatry, and an individual who finds himself at that rank would do better to disperse rather than stay.

Emigration thresholds in the ABM are not equivalent to the predictions of the Safe Havens model, but qualitatively they produce the same results. Emigration thresholds fluctuate in the same pattern as the Safe Havens model's predictions, and the correlation between the two variables is 0.82 (Figure 3).

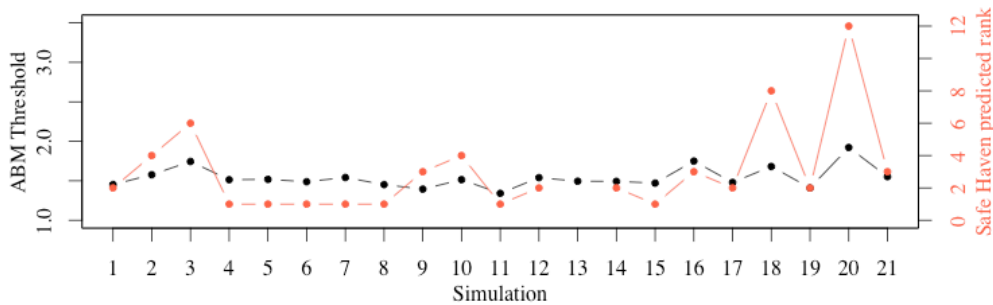


Figure 3: The ABM thresholds for 21 simulations and the Safe Havens model's predicted ranks at which the benefits of dispersal exceed the benefits of philopatry, calculated using parameters for each of the 21 simulations. The correlation between these two variables is 0.82. Simulation 13 does not have a prediction from the Safe Havens model, because under the parameters of this simulation (equal mortality and equal number of groups observed for floaters and group-living males, equal propensities to acquire alpha position for every male in the simulation) the Safe Havens model predicts that the benefits of philopatry and the benefits of dispersal are equal for all males, and the dispersal decision does not affect a male's reproductive success, because reproductive success is influenced neither by the male's demographic status nor by his rank.

Agent-based model results. Simulation 1 is a base simulation in which the philopatric males and floater males experience the same mortality, observe the same number of groups, and have the same propensity when competing for alpha position. Simulations 2 and 3 increase only floater male mortality, which increases the average threshold in the population after 10000 time steps. Increasing the number of groups observed by floater males (simulations 4, 5, and 6) decreases the averaged thresholds. Decreasing floater male propensity to acquire an alpha position (β parameter) in comparison to subordinate males increases the average threshold in the population (simulation 10). We see the opposite effect—a decrease in the threshold—when floater males have twice the propensity of the subordinates (simulation 11). The biggest increase in the population's average threshold is observed when the mortality of the floaters increases and the propensity of the floaters (β parameter) decreases (simulations 18 and 20), and the opposite effect is observed when the mortality of the floaters increases but the propensity to acquire alpha position is doubled in comparison to subordinate males (simulations 19 and 21).

The floater population was highest when floaters observed more territories (simulations 4, 5, and 6). Changing only the relative propensity of floaters and group-living males (simulations 7-13) does not affect emigration rates and keeps them very high. Increased floater mortality (simulations 2, 3, 16, 17, 20, and 12) is the single most important factor in determining the size of the floater population. If floater mortality is high, adding a benefit of more territories (simulations 16 and 17) or changing floater propensities (simulations 20 and 21) does not increase the floater population.

DISCUSSION

Number of floater males in the simulation. Across all simulation scenarios, regardless of whether dispersing males experienced higher mortality, observed fewer groups, or had a lower propensity to acquire a breeding position in comparison to group-living males, the numbers of floaters were at least 2.5 times higher than those of group-living males. In each simulation, the number of floater males increased through the first 1000 time steps, and varied only slightly for the remaining 9000 time steps.

This is mostly due to a fixed group-living male population number and the operation of the *birth function*. Each time step starts with mortality, which removes about 10% of the group-living males on average, since the mortality of group-living males is fixed and only the mortality of floaters, in comparison to group-living males, varies. The reason for fixing group-living male mortality is that, for the model, absolute mortality rate does not matter as much as the relationship between group-living male mortality and floater mortality (e.g., equal rates; floater mortality double that of group-living male mortality; etc.)

After mortality is completed, 10% of the 1000 group-living male spots are “empty” and available. Some of them will be alpha positions, which are filled through the *contest for breeding position function* with either floaters or group-living subordinate males. After all alpha positions are full again, the subordinate males check if their emigration thresholds are equal to or higher than their rank. Those males whose thresholds are lower than their rank disperse and join the floater pool.

The *birth function* is executed at the end of every time step and the number of new males born is equal to the number of “empty” spaces in the group-living male population, which is significantly reduced from 1000 by mortality and emigration. This means that at the next time step all these newborn males will be available to disperse again, and as a result of the emigration thresholds that they disproportionately inherit (see discussion on emigration thresholds below), the floater population grows very rapidly. The number of males born at every time step through the *birth function* seems to be one of the main reasons why the floater population grows so quickly.

Proportion of floater males among alpha males. The strong preponderance of former floaters among alpha males can be explained by inspecting how the *contest for breeding position function* assigns a new alpha from a competitors’ list. A new competitors’ list is assembled for every vacant alpha position; the list consists of all the males within the social group where alpha position is vacant, all of the males from other social groups that observe this particular group, and all of the floater males that observe this particular group.

Each male in the competitors’ list is assigned a propensity according to his demographic status (either floater or group-living subordinate) and his rank (if γ is less than 1, lower ranking subordinates have smaller propensities than the males above them). Then the propensities are converted into a probability, by dividing each propensity by the sum of all propensities. This ensures that, during this contest, every male has a probability to become alpha that is proportional to his propensity. For example, if group-living subordinate male A has a propensity of 1, and the floater male B has a propensity

of 0.8, then once these are converted into probabilities, the male A will have a higher probability than male B.

However, such assignment of probabilities does not take into account the number of competitors drawn from each category. The number of group-living males does not fluctuate dramatically across each competitors' list, because there is a fixed number of groups and a fixed number of subordinates in each group. However, the floater number varies greatly across different simulations, and, more importantly, there are always more floaters than group-living males (as little as 2.5 times more and as much as 8 times more).

This means that, in the competitors' lists, there will be more floaters than shifters or inheritor males. Thus, even if an individual shifter or inheritor has a higher probability than an individual floater of becoming alpha male, each *vacant alpha position* has a higher probability of being filled by a floater than by a shifter or an inheritor. This explains the pattern we observe in Figure 1, with floater males taking the biggest proportion of alpha positions across all simulations.

Why do the simulations produce average emigration thresholds between 1 and 2?

Individual males compete among themselves for the alpha position. For any particular male, if he survives long enough and a vacancy in alpha position occurs among the groups that he observes, his propensity, defined by demographic status and rank, has the biggest influence on his chances of acquiring a breeding position. However, because of the properties of the model, emigration thresholds compete on a different level from individual males. For the reasons described below, the pool of floaters comes to consist

disproportionately of males with low emigration thresholds (i.e., males whose minimal acceptable dominance rank is high).

The simulation starts with a population of 1000 males, all living in 50 social groups, and each group starts with thresholds, ranging from 1-20, assigned randomly to individuals of different ranks. It is true, then, that for any threshold from 1 to 20, the smaller it is, the less likely it is to be assigned to a rank that is equal or higher. For example, in the first time step, all males who have threshold 1 will disperse, because only subordinate males disperse and the only conditions under which a male with threshold 1 will stay in the group is if he is alpha (but alpha males never disperse). In the same way, the other low thresholds will also be more likely to disperse in comparison to high thresholds, although their probability of finding themselves at a rank equal to their threshold or higher is greater than that of threshold 1.

The result of this process is that the most common threshold in the floater pool will be 1. When the competitors' list for the *contest for breeding position function* is assembled, we can expect that the largest proportion of the floaters will have a threshold of 1 as well, which means that the breeding position is most likely to go to a male with a threshold 1, even though emigration thresholds have no direct effect on the outcome of the *contest for breeding position function*.

Once a male with a threshold 1 becomes alpha and the *birth function* is executed, the majority of his offspring will have a threshold 1 as well (with a mutation rate of 5%). The offspring are given the lowest available ranks within the group, which means that at the next emigration round, all of these males will join the floater pool, further increasing the frequency of threshold 1 in the floater population. The smaller the other thresholds

are, the closer will their trajectory of selection be to threshold 1, with probability decreasing down the threshold list.

After 10000 time steps the population threshold pool is dominated by the smallest emigration thresholds. Since the majority of the alpha males are former floaters, their success rapidly increases the frequency of small thresholds, particularly threshold 1. Thus, the average thresholds present in the population after 10000 steps will be pulled towards 1 due to the disproportionate representation of threshold 1 in the population.

Replicating the Safe Havens model. The ABM's emigration thresholds are not equivalent to the Safe Havens model's predictions. Kokko and Ekman's (2002) model predicts at which subordinate rank the benefits of dispersal exceed the benefits of philopatry. The ABM's thresholds primarily capture which emigration thresholds are the most successful in the population at becoming alpha through the floater route. However, the ABM thresholds qualitatively conform to the Safe Havens model's predictions concerning how the changes in the parameters affect the success of males at different subordinate ranks.

It is difficult to interpret the ABM results in light of the Safe Havens model, because the former is not a replicate of the latter. We do observe a decrease in dispersal when mortality risk for floaters doubles or triples in comparison to group-living males. The benefits of being able to observe more groups when floating increases dispersal. Variation in propensity to acquire alpha position favors dispersal when floaters have higher propensities in comparison to group-living males, and favors philopatry when this is reversed. The highest spike in the average emigration threshold indicating benefits of

philopatry is when floaters not only suffer from higher mortality, but also have a lower propensity to acquire alpha position.

How should ABM be adjusted to replicate the Safe Havens predictions? The first step in adjusting the agent-based model is to modify the *contest for breeding position function*. The number of competitors within each category should be taken into account. The propensities for group-living natal males, other group-living males, and floaters should define how the probability of success is partitioned among these three categories. For example, if subordinate males from other groups who are shifting have a propensity of 1, the natal subordinates have a propensity of 0.5, and the floaters have a propensity of 0.8, then the probability of success for those three categories should be divided respectively: $1/(1+0.8+0.5)$, $0.8/(1+0.8+0.5)$, $0.5/(1+0.8+0.5)$. This results in success probabilities of 0.43 for shifter males, 0.35 for floater males, and 0.22 for natal males. Only then should the probability within each category be divided by the number of males that are on the competitors' list in that category. In this way, the propensity to acquire a breeding position describes the propensity of a *category* of males to become alpha, and should not result in floater males dominating the alpha male pool.

Another aspect of the model should also be reconsidered. Fixing the group-living male population size and birthing the males at every time step to fill the missing spots seems to be one of the main aspects contributing to the rapid growth of the floater male population. If there was only one male birth per new alpha, then the propagation of low thresholds would be curbed.

Finally, it would be useful to model group size as an emerging phenomenon. This might be a way to replicate the Safe Havens model's predicted ranks at which males should disperse. Males who make the wrong decision regarding dispersal should do worse than the males who make the right decision. If there is selection for males who make the right decision, over a long period of time we should observe an emerging group size that caps at the predicted rank where the benefits of dispersal exceed those of philopatry.

PART II

FURTHER DIRECTIONS IN APPLYING SAFE HAVENS MODEL TO CAPUCHIN MONKEYS

INTRODUCTION

Models are useful in evaluating the logic of arguments about general phenomena in question, but an important next step is to apply models to empirical data. The Lomas Barbudal dataset is an excellent resource for testing life-history models. It contains behavioral, demographic, and genetic data on more than 444 individual white-faced capuchin monkeys (*Cebus capucinus*), collected over last 24 years. There is detailed information about male migration patterns and other life-history traits related to dispersal. Kokko and Ekman's Safe Havens model (2002) is a general one, which does not apply to any particular species. Building an agent-based model, inspired by the Safe Havens model but tailored specifically to white-faced capuchins, requires considering and including various life-history aspects and tactics characteristic of this species.

ROUTES TO BREEDING IN CAPUCHIN MONKEYS

In capuchin monkeys, females typically spend all of their lives in their natal groups, while male capuchins disperse (Perry 2012). There is great variation in the age at which males leave their natal group (Figure 4). The range of ages at the first migration is very broad (1.7-13), which means that some males leave when they are young juveniles, while others wait till they reach full body size (age 10) and even beyond (Perry 2012).

Figure 4 demonstrates the variation in age at natal dispersal in capuchin males. This is consistent with the Safe Havens model’s assumption of facultative delayed dispersal.

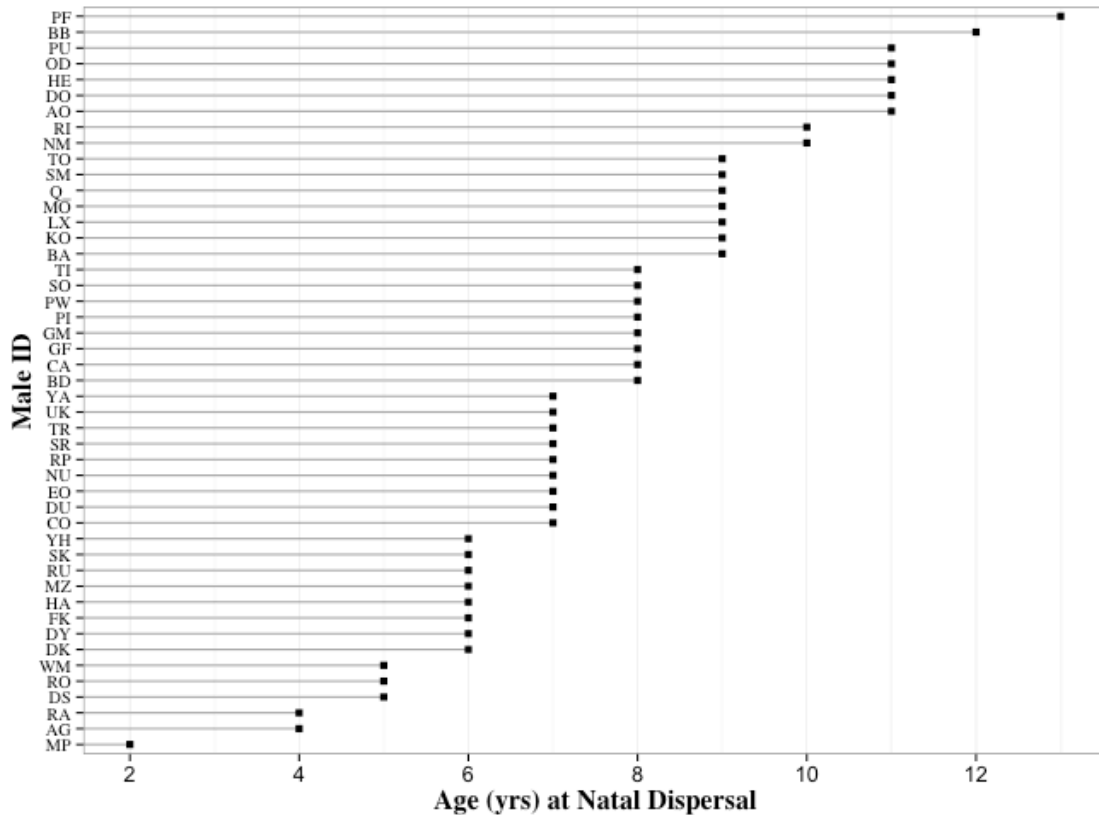


Figure 4: Variance in ages at natal dispersal in the Lomas Barbudal population, years 1996 – 2012. A sample of 47 males from the Lomas Barbudal capuchin monkey dataset (Perry S., unpublished data).

There are five main pathways to becoming an alpha in capuchin monkeys (Table 3):

1. Successfully challenging the alpha in current group of residence.

This is the most commonly observed pathway to becoming alpha for male capuchins (Table 3). Subordinate males who are queuing for an alpha position challenge the current alpha and one of them successfully takes over the position. Only subordinate

males who reside in the group can become alpha through this pathway; both natal and immigrant subordinates are eligible.

2. Invading a neighboring group and defeating its alpha male with the help of allies.

Floater males and subordinate males from any group that is not the focal group can use this pathway to become alpha.

3. Peacefully inheriting when alpha either dies or migrates.

This pathway is available only to subordinate males resident in the group, both natal and immigrant, because it implies no male arriving from outside the group.

4. “Waltzing in.”

If a social group’s adult males all disappear (most likely due to death), then the males who “find” such a group and stay there as alpha are considered to have “waltzed in.” This pathway is available to all types of males.

5. Becoming alpha of a group fission product.

This pathway is available to group resident males, both natal and immigrant. When groups become very large, they sometimes fission along matrilineal lines (Muniz 2010; Perry 2012). A subordinate male has a chance to assume alpha position in one of the fission products.

Table 3. Pathways to alpha position observed in Lomas Barbudal capuchin monkey population from 1992 to 2011, and the percentages of alpha tenures that start through each pathway. The sample includes 87 tenures (Perry, Godoy, and Lammers 2011; Perry, unpublished data)

Pathway to alpha position	% of tenures
1. Successfully challenging the alpha male in the current group of residence	62 %
2. Invading a neighboring group and defeating its alpha males with help of allies	23%
3. Waltz-in	3 %
4. Peacefully inheriting alpha position when the current alpha either dies or migrates	7 %
5. Becoming alpha of a group fission product	5 %

These pathways, considered together, encompass the three routes to alpha position captured by the Safe Havens model; however, there are two additional routes to alpha status for dispersing male capuchins. In the Safe Havens model, a subordinate male who stays in his natal group can become alpha in his own group or can shift to a neighboring group and assume alpha position there. The dispersing males have only one route: to become a floater male who might eventually take over a breeding position in another social group.

Capuchin males who disperse have been observed not only spending time as floater males and eventually taking over alpha position in a social group, but also immigrating to groups without challenging the alpha male (Perry and Manson 2008; Perry 2012). Such immigrant males reside in groups together with natal males and have an opportunity to take over alpha position in their group of residence or shift to a neighboring group.

Therefore, there are five routes to alpha position in capuchins, three identical to the Safe Havens model and two additional ones that have to be incorporated into a capuchin-specific agent-based model:

- 1) Staying in one's natal group and queuing for alpha position there.
- 2) Staying in one's natal group and eventually shifting to alpha position in a neighboring group.
- 3) Leaving one's natal group and becoming a floater who eventually takes over alpha position in a social group.
- 4) Leaving one's natal group and (a) immigrating into another social group without challenging the alpha male upon arrival and (b) queuing along with other immigrants and with natal males in this new group and eventually taking over alpha position.
- 5) Leaving one's natal group and (a) immigrating into another social group without challenging the alpha male upon arrival and (b) eventually taking over the alpha position in a neighboring group (i.e. shifting).

ESTIMATING PARAMETERS FOR CAPUCHIN MONKEYS

Mortality of a breeder (μ_B)

To estimate the μ_B parameter for capuchin monkeys we can use the frequency of turnovers observed at Lomas Barbudal. Turnovers have been observed to happen once a year on average at Lomas Barbudal (Perry 2012) and every 2-4 years in Santa Rosa (Fedigan 1993; Jack and Fedigan 2004), which suggests a μ_B value of 0.5-0.25 (if we

consider only tenures that last at least one year). If we follow the assumption of the Safe Havens model, the estimated value of μ_B would include the situations of alpha male death due to (1) extrinsic reasons, and (2) take-over and eviction. This means that being deposed from alpha rank invariably results in death. Developing the model further, take-overs could be modeled separately from mortality, so that males would get the opportunity to become alpha multiple times in their lives. This would be a more realistic representation of capuchin male life histories.

Mortality of subordinates and floaters (μ_S and μ_F)

When estimating mortality for these two categories of males in capuchin monkeys, we need to assess whether there are any differences in mortality rates if a male lives in a social group or if he is a floater. Males who delay their dispersal might experience nepotistic benefits from residing with their close relatives, such as coalitionary support and enhanced access to food in comparison to non-relatives living in the same group. Males who disperse might experience increased mortality risk, because they start ranging in new territories with which they are not familiar, and finding food patches might be more challenging, though they will experience less feeding competition for the food they may find. They will also lose group-living benefits related to protection from predation and they might spend more time being vigilant for predators. The mortality risk due to predation will still increase even if they are travelling with other males, since all-male groups are generally much smaller than mixed-sex social groups. Also, we know that migrating males experience aggression from group-living males, which can be lethal (Gros-Louis, Perry, and Manson 2003; Perry and Manson 2008).

The Lomas Barbudal dataset has high quality data on mortality rates among group-living males. If there are nepotistic benefits gained from living with matrilineal kin, then there could be possible differences in mortality between philopatric group-males and immigrant group-living males. We need to take age into account, since immigrant males on average will be older than natal males.

The challenging part is to estimate how mortality rates among floater males compare to those among group-living males. The dataset has fewer observations of floater males than group-living males, because it is much more difficult to follow lone individuals or small groups of migrating males. Floater males often disappear from the study area and it is impossible to assess whether they have died or successfully migrated to groups outside the study area.

The primary cause of death among adult males is wounds inflicted by conspecific males (Perry 2012), and males typically have these wounds for a few days before they die from them. Thus, a useful way to assess the differences in risks that group-living males and floater males experience is to compare wounding rates for those two types of males. The Lomas Barbudal dataset contains detailed descriptions of the rates and severity of wounds for both types of males. Since the goal would be to establish whether floater males are exposed to more dangerous conditions than group-living males, the difference in wounding rates between these categories is more relevant than absolute rates.

Estimating Number of Groups Observed

The challenge of using empirical data to estimate the parameters of how many groups are observed by floaters and group-living males lies in assessing the difference in

the information available to these two types of males. In capuchin monkeys, it is likely that each individual male is aware of a different number of groups. Each individual's personality traits should influence how explorative he is. In this case, even if floater males can range over a larger area and gather information about more groups than group-living males, some floaters might be knowledgeable about fewer groups than some group-living males. However, in the context of the model we are not estimating individual differences; we are interested in differences between two categories of males (floaters and group-living males). If floaters, on average, observe more groups than group-living males, then the benefits of dispersal versus philopatry should increase. *If* and *Ts* are not measuring the actual amount of knowledge about other groups, but rather the opportunities to acquire information about other social groups. These parameters are approximating whether the two types of males have access to the same amount of information or whether males of one of the categories has an advantage.

To estimate how many groups can be observed by group-living capuchin males (*Ts*), we can use information about the distance between a male's natal group and the group in which he acquired alpha position. There are five different pathways for a capuchin male to acquire an alpha position (Table 3). Three of these – successfully challenging the alpha in one's group of residence, inheriting the alpha position and becoming alpha of a group fission product – are variants on becoming alpha in one's own group of residence. Invading neighboring groups and waltzing in requires males to have information about other social groups. Capuchin males have the opportunity to gather information about other groups through intergroup encounters (Perry 1996b; Meunier et al. 2012). Olfactory cues left in the feeding and resting spots might indicate information

about group size and sex ratios in other groups that recently visited those locations, and, most importantly, subordinate males have been observed “visiting” other social groups for some part of the day without making a serious attempt to immigrate into that group (Perry 2012).

The number of territories for capuchin monkeys can be estimated following a similar method to the one used in Kokko & Ekman (2002) for Siberian Jays. First, we calculate the mean number, among social groups, of neighboring groups ($T1$). A neighboring territory for any given focal group is a territory that borders and overlaps with the focal territory. The Lomas Barbudal capuchin dataset has an extensive record of the study groups’ ranging patterns. Starting in 2010, the observers have been carrying GPS devices when following monkeys, collecting data on ranging patterns and developing maps of group ranges.

To calculate $T1$, first we need to count the number of neighboring groups for each study group. The average number is the sum of all numbers of neighboring groups divided by the total number of the groups. Males might become alphas not only in neighboring groups, but in groups that are at least one group away (i.e., the group in which they became alpha and the group from which they transferred both border the neighboring group, but do not border each other). $T2$ is the measure of how many males became alpha at least one territory away, estimated in the same manner as $T1$. At Lomas Barbudal there are no study groups that are two groups away from each other. The group from which we count is the group where the alpha male was resident before taking over alpha position in another group.

Capuchin males sometimes become alpha males in groups that are out of the study territory. Sometimes, males from outside the study territory enter study groups and take over the alpha position. We cannot evaluate how far these males have come, and therefore the estimates of $T1$ and $T2$ will be conservative (Kokko and Ekman 2002).

To combine $T1$ and $T2$ into a measure representing an average number of groups that the group-living males observe (Ts), we need to estimate how often these males move two territories away, relative to how often they move to a neighboring territory. d is a measure that describes the relationship between $T1$ and $T2$. To estimate this measure we need to tally the number of males that became alpha in neighboring groups ($T1$) and the number of males that became alpha in groups lying one group away from that in which they were residing ($T2$). We also need to separate group-living males into two categories: philopatric males and immigrant males. Philopatric males are those that resided in their natal group before becoming alpha male in another group, and immigrant males are those that resided in a non-natal group before transferring into another group to become alpha (i.e., they have immigrated as subordinates). Table 4 summarizes the information we need to tally, where a, b, c, and d represent numbers of males who became alphas within those categories.

Table 4. Distances by territories associated with shifting

	1	2
Philopatric males	a	c
Immigrant males	b	d

The Lomas Barbudal data set contains information on about 103 instances of change in alpha male identity, and a quarter of those changes have a new alpha coming in from outside the group. To obtain d , we assume that $T1$ is equal to $T2$ when we multiply $T2$ by d . That is, when $d = 1$, males have been transferring equally to the neighboring groups and groups two territories away. If $d < 1$, then males transfer to neighboring territories more often. If $d > 1$, males transfer to groups two territories away more often. Then we can obtain d for each type of male:

$$T1 : dT2 = a : b$$

$$d = bT1 / aT2$$

When we have estimated $T1$, $T2$ and d , the calculation of Ts is the sum of $T1$ and d times $T2$. This produces two estimates for Ts : one for philopatric males and one for immigrant males. If the numbers differ, then we take their average to estimate a single value for the Ts parameter.

The number of groups that floater males observe can be estimated using encounters of floater males with social groups. We are interested in whether floater males have opportunities to gather information about a greater number of groups relative to group-living males. For each floater male, we can tally how many groups he had contact with during his floating period (i.e., when a male did not reside in any mixed-sex social group). The average number of groups that floater males have been recorded to come into contact with provides the estimate for the number of groups that floater males observe (Tf).

Estimating propensities to acquire alpha position in capuchin monkeys

To estimate propensities in capuchin monkeys we need to evaluate how different types of males compare to each other in attaining an alpha position. Tallying the number of male-years in each category and types of males that successfully acquired breeding positions will allow us to estimate the three parameters.

For each male we count the years he spent as a philopatric subordinate residing in his natal group, a floater, and/or immigrant subordinate in another group. All of these numbers should be aggregated in Table 5.

Table 5. Male years spent as across different ranks and alpha position acquisition.

	Male years*, first ranked subordinate	Male years,** second ranked subordinate 2	Inherited	Shifted
Philopatric males	a	b	c	d
Immigrant males	e	f	g	h

	Male years, floater	Became Alpha
Floater males	i	j

a – number of male years for first-ranking subordinate. This number will reflect how many years a male spent as first-ranking subordinate.

b – the same for second-ranking subordinate.

c – number of males that became alpha in their natal group.

d – number of males that became alpha in neighboring groups.

f – number of male years for floaters.

g – number of males who became alpha from a floater pool.

* A male will most likely contribute male years to more than one cell.

** There should be as many columns as rank positions for subordinate males in the population.

To estimate α (propensity of natal subordinates to acquire breeding positions), β (propensity of floater males to acquire breeding position) and α' (propensity of immigrant subordinate males to acquire breeding position) we compare the number of top-ranking immigrant males and top-ranking natal males to the frequency with which males acquired breeding position (Table 5).

For example, table 1 specifies that d philopatric and e immigrant males became breeders by territory shifting. When the number of males who were potentially able to shift was a and e , respectively (assuming $\gamma = 0$, i.e., only top-ranking subordinate shifts), the relative propensities to acquire alpha position are calculated in this manner (using constants from Table 5):

1. For floater males:

$$a * T_s : d = e * \beta T_f : h$$

By solving for β , we obtain propensity to acquire alpha position for floater males.

2. For natal subordinates:

$$a * T_s : d = a * \alpha : c$$

By solving for α , we obtain the propensity to acquire an alpha position for natal subordinate males.

3. Immigrant subordinate:

$$a * T_s : d = e * \alpha' : g$$

By solving for α' , we obtain the propensity to acquire alpha position for immigrant subordinate males.

SENESENCE

Neither the Safe Havens model nor the ABM include senescence. Individual life-history parameters do not depend on age. This means that at any time step all of the agents within one category have the same mortality risk and the same propensities to acquire a breeding position, regardless of their age. This is not a realistic assumption for a primate species, and when applying the model to capuchin data, we need to incorporate age effects and senescence.

White-faced capuchin monkeys live up to 55 years in captivity (Hakeem et al. 1996) and in Lomas Barbudal the oldest individual observed was 37 years old (Perry 2012). Capuchins experience a long juvenile period (Fragaszy et al. 2004), which means that senescence is an important part of their life history.

The agents in the model have a variable “age,” but it does not affect any of the their parameters. Different age groups should experience different mortality rates and different propensities when they become competitors for alpha position.

Mortality. For white-faced capuchins, as for most primates, the mortality rate depends on an individual’s age. At Lomas Barbudal the highest mortality rates (up to 49%) are of infants under 1 year of age, mainly due to infanticide risk (Perry et al. 2012). If the infants survive this critical period, the annual mortality rate drops below 5% per year in the second year of life, and by the age of 9 it drops below 1% (Perry 2012; Perry

et al. 2012).

These empirical findings suggest that a simulation of capuchin male life history should include age-specific mortality curves, where an individual's age will influence his mortality risk. The highest risk will be experienced by newborn agents during their first year of life. Mortality drops at two years of age and drops again at 9 years of age.

Propensities to acquire alpha position. In the present version of the ABM, an individual's demographic position and rank influence his propensity to acquire alpha position. In capuchin monkeys, an individual's age influences this parameter.

The youngest recorded sire at Lomas Barbudal was 7.3 years old, but the majority of the males who become sires for the first time are much older, due to high reproductive skew in this population (Muniz et al. 2006; 2010), with the preponderance of the breeding being done by alpha males. Males reach full body size at the age of 10 (Fragaszy et al. 2004; Jack and Fedigan 2004). Although male age at first dispersal varies greatly (Figure 4), the majority of the males (94%) become alpha after age 10 (Figure 5). In fact, the majority of the males who become alpha start their tenure between the ages of 10 and 20 (87%), which suggests that physical condition influences a male's success in rising to the top dominance rank (Figure 5).

However, unlike in baboons (Alberts et al. 2003) and macaques (van Noordwijk and van Schaik 1985; 2001), a capuchin male's dominance rank does not always peak during his physical prime and decline as he senesces. High rates of co-operative take-overs of alpha positions and long alpha tenures held by capuchin males (Perry 2012) suggest that there are more variables associated with a male's acquisition and maintenance of alpha rank than just physical strength. Social relationship managing skills

seem to be crucial for long-term alpha males, with the support of allies helping them stay in the top dominance rank for long periods of time.

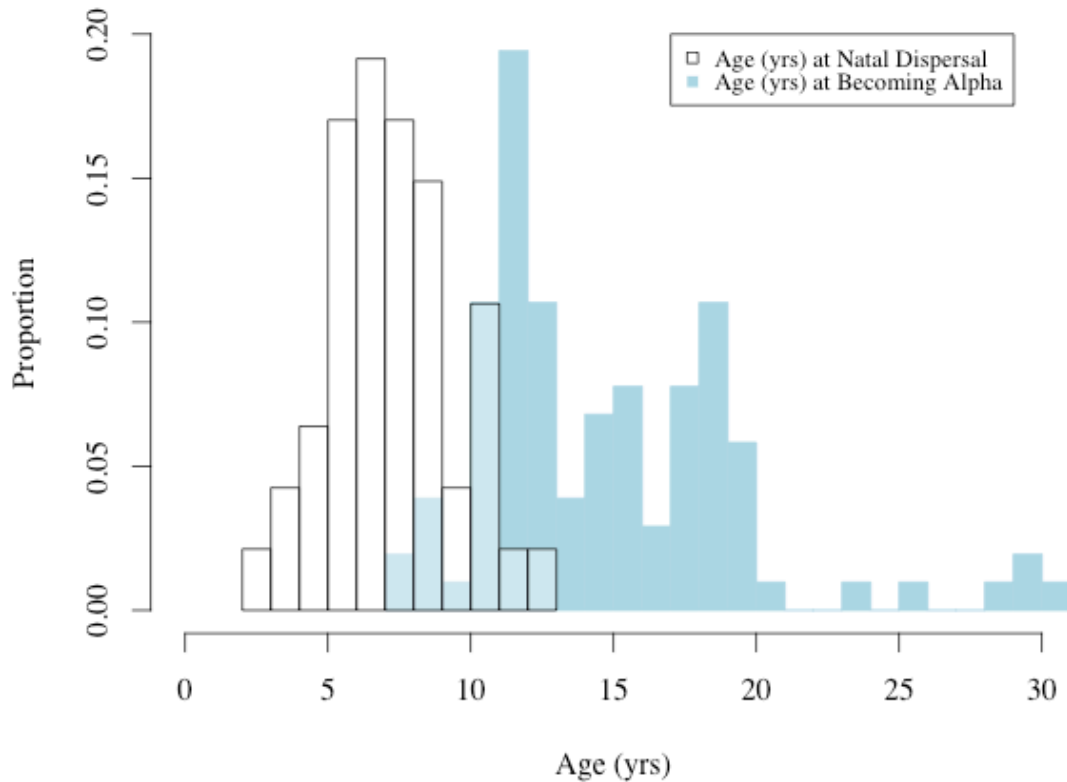


Figure 5: Male capuchins disperse before they are ready to become alpha males. There are two separate samples in this figure. The first sample consists of ages (years) of 47 males at their natal dispersal (white distribution), while the second consists of 46 ages (years) at becoming alpha for the first time (blue distribution). The first distribution (white) illustrates that the majority of males leave their natal group before the age of 10. The second distribution (blue) demonstrates that the prime age range of successfully fighting and acquiring alpha position is 10 and 20. The males in the two distributions are not exactly the same males (Perry S., unpublished data).

In the ABM, an agent's age should influence the time of his first reproduction and his propensity to acquire alpha position.

RELATEDNESS

The agents in the ABM do not have any special relationships to any other agents, and their actions do not influence each other's actions. This assumption is also difficult to justify when applying the model to a primate species, because kin ties are one of the most important factors structuring primate social life and behavior.

Capuchin monkeys usually live in groups of many closely related individuals (Perry and Manson 2008). Residing with one's parents, siblings, half-siblings and other relatives, structures many aspects of capuchin lives. For example, negotiating dominance relationships (Perry 1996a; Perry and Manson 2008), rearing offspring (Manson 1999; Perry and Manson 2008), and deciding with whom and when to migrate (Perry 2012) is usually affected by which kin are present and how many of them there are. In the context of dispersal, the high relatedness of a male to his fellow group members, especially the high relatedness of a male to the females of the group, might favor dispersal over philopatry.

In incorporating relatedness into an agent-based model of capuchin male dispersal, we will need to account for its effects on two aspects of life history: co-migration and reproductive skew.

CO-MIGRATION

Capuchin males leave their current groups of residents either alone or in groups. A migration of a male party consisting of at least two individuals is considered a co-migration. Capuchins migrate multiple times in their lives, usually in the company of other males (Perry 2012). At Lomas Barbudal, the majority of all observed migrations (80%) were co-migrations, and all documented natal migrations were co-migrations

(Perry 2012) .

Adding co-migration to the agent-based model would affect two model parameters directly: mortality and propensity to acquire a breeding position.

Mortality. One of the biggest potential costs of dispersal is increased mortality risk due to the loss of the detection and dilution benefits that group life affords. Dispersing with at least one more individual can potentially reduce this risk, by providing multiple sets of eyes and ears to detect predators. More importantly, migrating males experience intense aggression from other conspecifics that they meet while migrating, and such encounters can be lethal (Gros-Louis et al. 2003; Perry and Manson 2008). Co-migrating groups of individuals can expect to experience fewer injuries and reduce mortality risk due to aggression from conspecifics.

Propensities to acquire alpha position. Co-migrating males not only help each other to reduce mortality risk, but also cooperate in challenging and taking over the top-ranking position in a new group (Perry 2012). About a quarter of the alpha position take-overs are performed by males coming from outside and invading a group (Perry et al. 2011), and all of them are performed by teams of co-migrants (Perry 2012). A lone male who challenges an alpha and his allies in a group where the challenger is not a resident is very unlikely to succeed. However, males with allies have a good chance to take over an alpha position successfully.

The propensities to acquire alpha position in the model should be modified to take into account whether a competitor who is coming from outside to compete for an alpha position is a single individual or an alliance of males. Groups of floater males will be assigned higher propensities in comparison to lone floater males.

The member of co-migrating parties is usually not random, and such parties often consists of kin (Perry 2012). It is possible that males' migration-suitable partners consist disproportionately of kin, but it is also possible that co-migration teams consisting of kin are more stable and more successful in taking over alpha position in a new group. Relatedness might keep the alliance strong and intact even after the take-over is over and only one of its members is a new alpha male and is able to reproduce. Kinship ties among alliance members become important, because (as described below) the other males who helped this alpha to rise to his position now have to wait for at least six years to be able to reproduce due to high reproductive skew in capuchin monkeys (Muniz et al. 2010).

REPRODUCTIVE SKEW

The Safe Havens model incorporates complete reproductive skew – only alpha males breed. Therefore, becoming alpha male is a good approximation of a male's direct fitness measure. Capuchins at Lomas Barbudal are characterized by a very high reproductive skew, with only about 31% of males siring all of the offspring produced, and alpha males responsible for the largest portion (74%) of those offspring (Perry et al. 2011).

Alpha males hold a virtual breeding monopoly for the first six years of their tenure (Muniz et al. 2010). Due to strong aversion to father-daughter inbreeding (Godoy 2010), this monopoly declines when their daughters reach sexual maturity at the age of six years and begin reproducing with the subordinate males. Below alpha rank, there seems to be no correspondence between a subordinate male's rank and his reproductive success (Muniz et al. 2006), although females do prefer immigrant males to their paternal

half-siblings (Perry 2012) (Perry 2012). Subordinate males, who are often the same males who helped the alpha male acquire his rank, start reproducing only once the alpha's daughters become sexually mature.

Adding reproductive skew to the ABM will require classifying alpha males as long-term or short-term in order to distinguish the first years of the alpha's tenure, when he holds a virtual monopoly over breeding, from later years, when his daughters are available for breeding. The maturation of his oldest daughters is the line that divides an alpha male's tenure, and long-term alphas are those who stay in alpha position after their daughters become sexually mature (i.e., longer than 6 years). Alpha males at Lomas Barbudal have been observed to hold tenure up to 17 years (Perry 2012).

In the agent-based model, alpha males up to 6 years should be assigned either complete or almost complete monopoly. After 6 years of tenure, if the alpha has daughters who have reached sexual maturity, they should reproduce with subordinate males. Subordinate males can be further divided into natal subordinates (males who were born in the group and haven't yet migrated) and immigrant subordinates (males who immigrated into the group from outside). The alpha male's sexually mature daughters primarily breed with immigrant subordinate males, but they have also been observed breeding with paternal half-siblings and other more distantly related natal males (Godoy 2010). Relatedness has to be taken into account when we consider breeding between the alpha male's daughters and natal subordinate males.

CONCLUSION

The Lomas Barbudal dataset affords a unique opportunity to apply the agent-based model of benefits of dispersal and philopatry to a long-living primate species. The

ABM has to be modified to take into account some of the aspects of capuchin monkey life history, especially those relevant to dispersal.

First, capuchin monkeys have two additional routes to alpha position. Capuchin floater males can immigrate into social groups at the bottom of the hierarchy and later challenge the alpha male or eventually switch to alpha position in other social groups. Second, aspects of capuchin monkey life history and social behavior, such as senescence, relatedness, co-migration, and reproductive skew, have to be included in order to capture the real-life dynamics of this species. Mortality depends on an individual's age, and the risk of mortality when migrating can be reduced if males migrate with other males. The propensity to acquire alpha position is also influenced by age, relatedness, and co-migration. Finally, the direct fitness of capuchin males is a result of reproductive skew in the population, which is patterned through dominance rank and kinship.

The challenge of creating a useful agent-based model of the benefits of dispersal and philopatry for capuchin males is to take into account the salient aspects of capuchin monkey life history without rendering the model unnecessarily complex, and therefore uninterpretable. One of the main tasks is to incorporate only those aspects of capuchin life history that have the most influence on male dispersal and reproductive success.

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