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Natal dispersal and new group formation in capybaras (*Hydrochoerus hydrochaeris*) in a seasonally flooded savanna of Venezuela

by

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A Dissertation Submitted to the Graduate School of the
University of Missouri- St. Louis in partial fulfillment of the requirements for the degree
Doctor of Philosophy in Biology with an emphasis in Animal Behavior

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ABSTRACT

This study examines natal dispersal and new group formation in capybaras (*Hydrochoerus hydrochaeris*) in a seasonally flooded savanna in Venezuela. The first section describes a novel approach to the study of dispersal that could be applied to many taxa. Dispersal is considered in three stages (emigration, transience, and immigration) and its proximate and ultimate mechanisms are clearly differentiated. The second chapter describes dispersal behavior in capybaras, including which individuals disperse, when, and to where.

In the third chapter, I evaluate dispersal in capybaras with respect to social subordination and social cohesion hypotheses. In this population, some support was found for the social subordination hypothesis, although results were not always straightforward. Little evidence was found for the social cohesion hypothesis. All dispersers were male and very few males were philopatric. Taken together, these data suggest that young dispersing males are more aggressive (both initiating and receiving more aggression) and less tolerated by adult males than are females of similar age. This population appears to have two behavioral classes of individuals that follow gender roles: aggressive-dispersive males; and tolerant-philopatric females. The aggression initiated by young males is suggestive of a social variation of the ontogenetic switch hypothesis wherein maturing males switch from being submissive juveniles to aggressive subadults. While most social hypotheses for dispersal focus on the reactions of juveniles to adults, this study suggests a primary role of the behavioral maturation of the disperser.

In the final chapter, the ultimate drivers of dispersal are considered in light of the behavioral data collected. The tendency for aggressive interactions to be intra-sexual

suggests mate competition is an important driver of dispersal in this species. Although genetic data are not yet available, the high costs of dispersal and differences between natal and breeding groups further support the mate competition hypothesis for the evolution of dispersal in capybaras.

Understanding dispersal in this highly social species provides valuable insight concerning the relationship between habitat and social structure. In the context of extensive, and often rapid, anthropogenic environmental changes, the ability to predict a species response to change becomes increasingly important.

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I also thank Dr. Patricia Parker for setting a standard of excellence as a scientist and mentor that I will always admire and strive to achieve in my own way. When I struggled with decisions, Patty offered an open door, an open mind, and a valuable perspective.

The support and encouragement of my other committee members, Bette Loiselle, Stan Braude, and George Taylor, kept me on track and enabled me to finish this project and stand by my decisions with confidence. I turned to each of these people at crucial moments with numerous questions and I always found a helping hand and left their offices knowing that the current challenge could be managed successfully.

This work was made possible with financial support from several institutions. I received the Henry Cowley Scholarship from the International Center for Tropical

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CHAPTER 1

A conceptual framework for the study of dispersal: Capybaras as a case study

INTRODUCTION

Despite an abundance of empirical studies on dispersal, few consistent patterns have emerged (for a recent review see Bowler and Benton 2005). This lack of pattern has led to the development of models based on simplified assumptions, which over-simplify the process and represent dispersal as little more than a probability of moving and an average distance moved. In many species, however, dispersal is mediated by combinations of factors and can be condition-dependent (Ims and Hjermann 2001). An individual with conditional dispersal may have an advantage in its ability to withstand environmental stochasticity (Ronce et al 2001). Furthermore, in the context of extensive, and sometimes rapid, anthropogenic changes in the environment, the ability to predict a species response to change becomes increasingly valuable. The links between dispersal and population dynamics make understanding the causes and consequences of dispersal vital for such endeavors (Bowler and Benton 2005).

The factors that influence dispersal are likely to either vary among species, if not among individuals, or vary in their importance in different species (Dobson 1982). Thus, 'universal' hypotheses about dispersal based on single underlying mechanisms have limited applicability (Bekoff 1977). The complexity of dispersal leads to the juxtaposition of several hypotheses and multiple selection pressures potentially acting simultaneously. Furthermore, since the hypotheses are not mutually exclusive, a combination of mechanisms may operate in a given species or in the same population over time (Gaines

and McClenaghan 1980). Potential causes are too often considered as alternatives rather than as interacting forces. For instance, risk of inbreeding depression may select for dispersal, which also reduces kin competition (Perrin and Goudet 2001).

Studies that parcel out one aspect of dispersal to examine it closely face the subsequent challenge of placing it in its proper context and establishing necessary experimental controls. Results are rarely straightforward, precisely because of the interacting influences within that context. For example, capybaras display group territoriality in a naturally harsh environment with potentially high natural inbreeding, dominance hierarchies with high reproductive skew, risks of infanticide, and at least some level of female choice. Putting all these social and ecological parameters together and identifying the key components in the evolution of dispersal can lead be very difficult.

The purpose of this paper is to suggest a framework from which to approach the study of dispersal. This is not intended to be a review paper of mechanisms or proposed causes of dispersal, but rather a way of integrating stages and processes for one species or for interspecific comparisons. Reviews of dispersal (Chepko-Sade and Halpin 1987, Johnson and Gaines 1990, Clobert et al. 2001, Bowler and Benton 2005) frequently read like laundry lists of examples rather than cohesive syntheses of a single theme (but see Bowler and Benton 2005). A recent volume of collected papers reviews the current understanding of dispersal, but the individual approaches of each chapter's author leaves the reader with the challenge of unifying all of the ideas into one conceptual framework (Clobert et al 2001). This challenge motivated the present work. A common framework

will allow researchers to communicate effectively and place our work and that of others in relative juxtaposition.

First, we need to realize that the dispersal process has three distinct phases: emigration, transience or travel, and immigration or settlement. The proximate cues and ultimate causation of each stage should be examined as integrated but potentially distinct. I will provide examples from a study of the natal dispersal of capybaras (*Hydrochoerus hydrochaeris*) for illustration. Many of the other examples are specific to social vertebrates, but the general approach applies to other taxa. I will provide examples to illustrate the scope of this approach.

Three Distinct Stages

Dispersal is often collapsed into a single parameter, despite the fact that it is a process composed of three interdependent stages: the 'decision' to leave the current patch (emigration), movement between patches (transience), and the 'decision' to enter and remain in a new patch (immigration), each of which may display different condition dependencies (Benton and Bowler 2005). Bowler and Benton (2005) argue for this separation of stages, but the argument gets lost in their extensive review of dispersal. Other authors have proposed this distinction of the stages of dispersal, at least in some restricted contexts (plants, Van der Pijl 1982; predation risk, Weisser 2001; condition-dependent dispersal, Ims and Hjermann 2001). In a review of dispersal strategies in plants, Van der Pijl (1982) looked at the strategies of the parent plant to disperse the seeds and the establishment of those seeds as two distinct processes. Weisser (2001) considered animal dispersal in stages but in the somewhat limited context of the predation risk at each stage. Ims and Hjermann (2001) discuss the importance of dispersal

stages with respect to social cues in the sense that cues may act on different stages differently. As an example, shifting focus from emigration to immigration changes the predictions for the effects of density. From an emigration perspective, higher density should increase competition and favor emigration and thus favor dispersal (e.g., in lizards, Lena et al. 1998; in Iberian lynx, Ferreras et al. 2004). From an immigration perspective, higher density may mean fewer empty habitat patches and less chance for settlement and thus favors philopatry (blind mole rats, Zuri and Terkel 1998; alpine butterflies, Roland et al. 2000).

Holekamp's (1986) test of several different hypotheses for proximal causes for dispersal in Belding's ground squirrels illustrates the need to consider dispersal stages separately. Belding's ground squirrels show support for the ontogenetic switch hypothesis, wherein juveniles disperse when some threshold body condition is reached. If this is true, then cues for settlement must necessarily be entirely different from cues for emigration (Holekamp 1986). In sciurids in general, conspecific aggression apparently plays only a minor role in facilitating dispersal, but it may strongly influence settlement by dispersers in immigration areas (reviewed in Holekamp 1986).

Existing models of dispersal tend to follow one of two forms, either condensing the entire process, without breaking it into these sub-parts, or focusing on only one phase, either emigration or immigration (Rousset 2001). While this may be necessary because of the inherent constraints of modeling, this approach may dilute, or even ignore, the importance of individual stages. Dispersal is sometimes quantified as merely a probability of moving and a distance moved. Depending on the question of interest, this may be sufficient. If the goal is to predict the effects of some change in population

dynamics, viewing the stages of dispersal separately is likely to shed light on critical details. For example, 25% of young capybaras might successfully disperse an average of 3 kilometers from their natal territory. In one case, these numbers could reflect 30% of the young males emigrating from the natal territory, 5% experiencing mortality during transience, resulting in 25% immigrating to a breeding territory. One could easily imagine the same 25% successful dispersal resulting from 50% emigration and 50% of those not surviving to immigration.

Four Classes of Study

Any phenomenon in plant and animal behavioral studies can be broken down into natural history (description); consequences (costs and benefits); proximate cues; and ultimate causation. Examining dispersal with Tinbergen's four questions (Alcock 2001) in mind leads to the conceptual framework presented here (Table 1). The four aspects of animal behavior that most ethologists strive to understand are the development of the behavior, its immediate mechanisms, its function or current selective advantage, and its evolutionary history or original selective advantage. The framework proposed here addresses these four questions, but in a somewhat new structure, by approaching them from the progression of the scientific process: natural history description, consequences, proximate mechanisms, and origin.

Any scientific study of behavior naturally begins with the observation and description of the phenomenon of interest (Row A, Table 1.) In the case of dispersal, this would include the identification of which individuals disperse, how far they travel, and/or where they settle. The consequences of dispersal (Row B, Table 1) include the costs and benefits of dispersal both to the individual and to the group. Study of these consequences

would answer the functional question of ethology's four central questions. The proximate mechanisms of dispersal (Row C, Table 1) may include genetic control, learning, and/or sensory-motor cues and studies of this nature answer two more questions – those of immediate cause and development. Finally, the goal of study may be to elucidate the evolutionary history or origin of a particular behavioral trait (Row D, Table 1), and thus answer the fourth question: evolution of behavior.

A major point of the framework presented here is the clear distinction between the proximate (or immediate) costs and benefits of, or cues for, dispersal behavior. Review papers have clearly outlined the potential costs and benefits of dispersal that may then lead to hypotheses for the selective pressures shaping the behavior (Shields 1987). Extensive work has also looked for the cues that lead to emigration, revealing variability between the sexes (e.g., lizards, Lena et al. 1998), among populations (e.g., capybaras, Salas 1999), and among species (e.g., social canids, Bekoff 1977). But does knowledge of the current benefit of dispersal or a proximate cue necessarily lead us directly to the ultimate cause? In most species dispersal leads to a reduction in inbreeding depression, but some would argue that inbreeding avoidance was not the selective pressure that led to dispersal (Moore and Ali 1984).

Likewise, once dispersal has evolved, via whatever ultimate mechanism, the proximate cues may be shaped by a different mechanism. For example, in Bekoff's (1977) review of dispersal in mammals he describes three marmot species that all show dispersal by young animals, but at different times, with the most social of the three delaying dispersal the longest. This suggests that perhaps the ultimate pressure to

disperse is the same across the three species, but the proximate cue for when to disperse varies according to their level of sociality.

When considering competition as a cause for dispersal, this distinction between immediate benefit and original selective pressure can become particularly blurred. Increasing densities that lead to critically limited resources or increased aggression during direct competition for those resources could be the proximate cue that triggers dispersal (Christian 1970). The alleviation of competition, especially kin competition, could also be the selective pressure that led to the evolution of dispersal in the first place (Moore and Ali 1984). Unfortunately, many papers treat these as one in the same and don't clarify which they are testing in their studies (Ferrerias et al. 2004; Lena et al 1998).

EMIGRATION

The first step to any dispersal study is to determine which individuals are dispersing and when (Box 1A, Table 1). Data that might be gathered in this type of study are the descriptions of any sex-bias in dispersal, the age of the average disperser, and/or the season in which dispersers tend to emigrate. In addition, emigration may occur in some particular social context, such as when mammalian females are preparing to give birth to the next litter of offspring. The description would also include any variation in the probably of individuals emigrating.

In capybaras, emigration is strongly male-biased, with only a few philopatric males identified in one cohort and no definitive female emigration. All emigrants were either juvenile or subadult males, varying in age from 9 to 19 months (Table 2; also see Chapter 2).

The consequences of emigration (see Box 1B, Table 1) are typically considered from the perspective of the natal group. For instance, once a young, potential mate emigrates, the natal group should experience reduced risk of inbreeding depression and reduced kin competition. Several researchers advocate studying philopatry, rather than dispersal, because from the perspective of the natal group, the individuals that remain are having a greater effect than those that leave, whether they dispersed or died. For example, in capybaras, strongly male-biased dispersal, accompanied by female philopatry, intuitively should lead to social groups being classified as female kin-clusters with unrelated males, although the genetic work has not been done to confirm this (Salas 1999).

The proximate mechanism for the initiation of emigration or decision to leave the natal group (see Box 1C in Table 1) addresses Tinbergen's two proximate questions: immediate cause and development of a behavior (Alcock 2001). Studies of the proximate cues for dispersal are abundant, and yet general patterns are difficult to identify. The Genetic-Behavioral Polymorphism Hypothesis (reviewed in Gaines and McClenaghan 1980) proposes a largely genetic basis for emigration and is supported, at least in part, in planthoppers (Denno et al. 1996). The use of public information for emigration decisions has been shown such that emigration rate increased when local offspring quantity or quality decreased (Doligez et al 2002). The ontogenetic switch hypothesis predicts the emigration of young individuals when they reach some threshold body condition (Holekamp 1986). Other proximate hypotheses base their predictions on familiarity or kin recognition (Bollinger et al 1993), density (Christian 1970), competition (Dobson 1982), or predation pressure (Sloggertt and Weisser 2002).

Among the most-tested social hypotheses for emigration are the social subordination (Christian 1970) and the social cohesion (Bekoff 1977) hypotheses. The social subordination hypothesis predicts emigration to increase as density increases; direct competition for limited resources then leads the lesser competitors, typically the young or subordinate individuals, to react to increased aggression by emigrating. This has been tested and supported in several species (microtine rodents, Christian 1970; fox, White and Harris 1994; house mice, Zuri and Terkel 1998; Iberian lynx, Ferreras et al. 2004; Florida panther, Maehr et al. 2002).

The social cohesion hypothesis grew out of a number of studies that did not support the subordination hypothesis in social mammals, in particular canids and sciurids (Bekoff 1977). This hypothesis predicts that individuals that do not effectively establish strong social ties in the natal group would be the more likely to emigrate without increased aggression being directed toward them. Support for this hypothesis has been found in coyotes (Bekoff 1977) and foxes (Harris and White 1992).

In capybaras, emigration of young males correlates with the onset of agonism such that subadult males are more likely to both initiate and receive aggression when compared to younger males or females (Figure 1, also see Chapter 3). These data suggest that while increased aggression may be involved, the young emigrant is driven to leave the natal group by some developmental change in agonism, perhaps consistent with a social version of the ontogenetic switch hypothesis mentioned earlier (see Chapter 3).

Finally, in this conceptual model, the ultimate causes or selective pressures that lead to emigration are considered (Box 1D in Table 1.) The most frequently cited ultimate causes of dispersal are inbreeding avoidance, competition for resources or mates,

kin competition, and habitat variability patterns. From the perspective of emigration, each of these may apply and can be tested in terms of the average fitness of dispersers relative to philopatric individuals.

The inbreeding avoidance hypothesis, in particular, deals with emigration more so than immigration, since once the natal group is avoided, one could argue that one breeding group is as good as another in terms of avoidance of inbreeding. The avoidance of inbreeding has been supported with genetic data as the driving force for the evolution of dispersal in meadow voles (Bollinger et al. 1993) and Townsend's voles (Lambin 1994).

In capybaras, there is some evidence to suggest that competition for mates has played a role in the evolutionary history of emigration. Data show that males emigrate as they reach the subadult stage and move to social groups with fewer adult males than their natal territory (Figure 2; also see Chapter 2). The avoidance of inbreeding is not likely the ultimate cause as suggested by two lines of evidence. First, dispersal distances are often less than 1 kilometer, which is not likely sufficient to avoid mating with second order relatives (Chapter 4). Second, at least some males remain philopatric and attempt mating within their natal social group (Chapter 2). However, additional data and genetic studies are needed to confirm these conclusions.

TRANSIENCE

Intuitively, it may seem odd to consider transience as its own stage, since an individual emigrating from one area and immigrating to another would obviously have to be 'transient' in between. However, movement and survival while traveling through the matrix of habitat in between territories or social groups is likely to require a set of tactics

and decisions unique to that stage. Some individuals might make temporary forays from the natal territory into the surrounding habitat before effectively emigrating (foxes, Woollard and Harris 1990; capybaras, pers. obs.). The behavior of dispersing foxes on exploratory nights is markedly different to that on a normal night's activity, moving faster and farther than non-dispersers, with reduced resting or foraging (Woollard and Harris 1990). In addition, movement is not always under the control of the disperser, but is sometimes the result of wind or some unwitting assistant, as is the case of pseudo-scorpions attaching under the wings of beetles to achieve long distance movements (Haack and Wilkinson 1987). The timing of this transient period can also vary widely, from a few hours to several years.

Capybara males in transition between groups behave somewhat differently from established group members (see Chapter 2). At least two young males were seen making temporary forays away from their natal group before dispersing. Once emigrated from their natal site, subadult males tend to stay at the edge of other social groups, perhaps scent marking in order to familiarize the group with their scent. Staying relatively close to established territories and groups might also afford the transient the benefit of the vigilance of the social group (Yaber and Herrera 1994).

With regard to consequences, the mortality risk associated with dispersal is often highest during transience, when individuals do not have the protection of their natal group or an established territory. In capybaras this risk is evidenced by the greater number of injuries seen on dispersing individuals than on similarly aged, philopatric individuals (Figure 3; also see Chapter 4). Anecdotal evidence also suggests greater

mortality in dispersers: several young males (the dispersing sex) were found dead outside their natal territory, but no young females (the philopatric sex) were found deceased.

The proximate cues used to determine direction of movement, distance traveled, or time spent traveling during this transient phase are most likely due to a combination of habitat and social cues. An individual disperser may follow habitat corridors, engage in random walk patterns, or travel from territory to territory in search of a suitable breeding area. Or there may be some inspection of several available sites and apparent comparison among them (J. Stamps, pers. comm.). Unfortunately, data of these movements are difficult to obtain, but advances in radio-telemetry and satellite tracking are adding to our understanding of these movements every year.

Speaking of the 'ultimate cause' of transience is a bit nonsensical, since anything that selects for emigration requires the movements that follow. However, the particular strategies that an individual disperser employs to search for a settlement site during this stage may be under unique selective pressure. For example, the increased predation risk of lone foxes may be the force that leads to their increased pace and reduced foraging during this time. In capybaras, it could be predation pressure that leads them to remain close to the edges of established territories as they travel.

IMMIGRATION

Immigration or settlement into a breeding group or area can take many forms. The disperser may simply choose the first available habitat away from the natal site and never leave. As mentioned above, there may be some inspection of several available sites and apparent comparison among them before a decision is made to remain in one. The characteristics of the chosen site that play a role in the decision could range from

availability of any number of resources to the social structure of the current residents.

The timing of settlement could also vary. Individual dispersers may stay transient for some period of time before settling – perhaps until some body condition or age is reached or until the breeding season.

For social species, describing the immigration of individuals into their breeding site presents several challenges to researchers, and is less common in the literature. It requires that all individuals in a social group be identified so that newcomers are recognizable. Otherwise, a disperser must be followed from its natal site, through transience, and into its breeding territory. In my capybara study, I was able to follow several individuals from their natal group to their secondary social group and observe their behavior as recent immigrants. These young males spent more time at the edge of the new group compared to their last few weeks in their natal territory (Figure 4, see also Chapter 2). However, one individual was observed spending almost a full year in transience before immigrating into an existing group.

As is the case with emigration, the consequences of immigration can be viewed from the perspective of the immigrant or the group or neighborhood it joins. The settler gains the benefits of that territory – be they resources such as food or mates or refuges for predator avoidance. The neighborhood or social group joined may gain genetic variability or perhaps suffer social disturbance or outbreeding depression. In social species, resident males might suffer increased competition with each immigrant. In capybaras, an additional male in a social group increases the overall vigilance of the group, which benefits all group-members (Yaber and Herrera 1994).

The proximate cues for the decision to settle in an area or join a social group can include both habitat and social features of the area. There may be conspecific attraction wherein an individual uses the presence of conspecifics as an indicator of suitable habitat (e.g., corvids, Williams and Rabenold 2005). Furthermore, the presence of young conspecifics may be an indicator of not only suitable habitat, but habitat sufficient for fecundity (Doligez et al. 2002). Even heterospecific performance is sometimes used as a habitat indicator, if the heterospecific shares ecological needs (Parejo et al. 2005).

In capybaras, there appear to be two social forces working toward the selection of a disperser's breeding group. The territory holders put up a 'social fence' by aggressively expelling unfamiliar intruders. But the young immigrant can apparently get around this 'fence' and often enters a group with fewer adult males than his natal group (Figure 2; see also Chapter 4). It could be that fewer males mean fewer territory holders to expel the intruder, but females and subadults also defend the territory and there is no difference in numbers of individuals in these latter two categories between natal and breeding groups. Alternatively, the immigrant might select a group that has fewer adult males ahead of him in the queue to dominance.

Isolating the historical ultimate cause of immigration to a particular site or social group can be difficult. The theoretical literature on ideal free distribution and ideal despotic distribution lend valuable insights (Holt and Barfield 2001). For social animals, the benefits of group living and cooperation must be balanced by the cost of competing with group-members. In capybaras, one study found that the fecundity of females increases as group size increases, indicating that cooperation is beneficial to individuals (Herrera and Macdonald 1987). Furthermore, the increased likelihood of injury or death

of transient individuals suggests the benefit of protection by the group (Chapter 2).

However, whether the ultimate pressure for inclusion in a group is reduced risk of predation for all group-members or the drive for males to become the dominant breeding individual (or some combination of the two) is not known.

CONCLUSION

The study of dispersal has been in need of a unifying conceptual framework that views dispersal as a process and differentiates clearly among the three stages of this process. By identifying specifically to which part of this overall framework a particular study or bit of data belongs, we, as researchers, can more effectively communicate with one another. In particular, we can be clear about the goals and limitations of a study. We can also be clear about how gathering additional empirical data can further the understanding of other parts of the framework. This could encourage modelers and empirical researchers to collaborate and improve the ability of models to predict effects of change or disturbance on a population.

In capybaras, ontogenetic onset of aggression correlates well with emigration, but in no way explains immigration. By viewing the process of dispersal according to the framework presented here, one can easily separate the two stages and appreciate the different selective pressures acting at each stage. Furthermore, one can appreciate that while the proximate cues for emigration may be linked to agonistic onset, it is the process of immigration that suggests that there are strong selective pressure for group-living and cooperation.

Table 1. A conceptual framework for the study of dispersal. Dispersal can be viewed as occurring in three distinct phases, listed along the top of the table. For each stage, study typically progresses from observations of dispersal patterns, to descriptions of the costs and benefits of dispersal to the individual disperser and both the natal group and breeding group, as listed along the left side of the table. The separation of the proximate mechanisms of dispersal and ultimate origin of dispersal illustrates the need to be clear which is being described and tested in any particular study. Within each box are examples of questions that would be answered by study of the particular aspect of each stage in the process of dispersal.

	1. EMIGRATION	2. TRANSIENCE	3. IMMIGRATION
A. OBSERVATION / DESCRIPTION	Who? When?	How long? Where? How to survive?	Where? When? How?
B. CONSEQUENCES (COSTS/BENEFITS)	For the individual? For those left behind?	For the individual?	For the individual? For the group entered?
C. PROXIMATE MECHANISMS	Making the decision to leave	What direction to go?	Choosing to settle
D. ULTIMATE ORIGIN	Selective force to leave	Selective pressure for the mechanism	Selective force to settle

Table 2. Emigration by capybaras in a seasonally flooded savanna of Venezuela. The numbers of individuals dispersed include only those that successfully immigrated into a secondary group. For greater detail of these results, refer to Chapter 2.

Gender	# Groups Represented	Philopatric	Dispersed	Mean Emigration Age (Months)
Male	10	3	19	14.1
Female	13	25	0	N/A

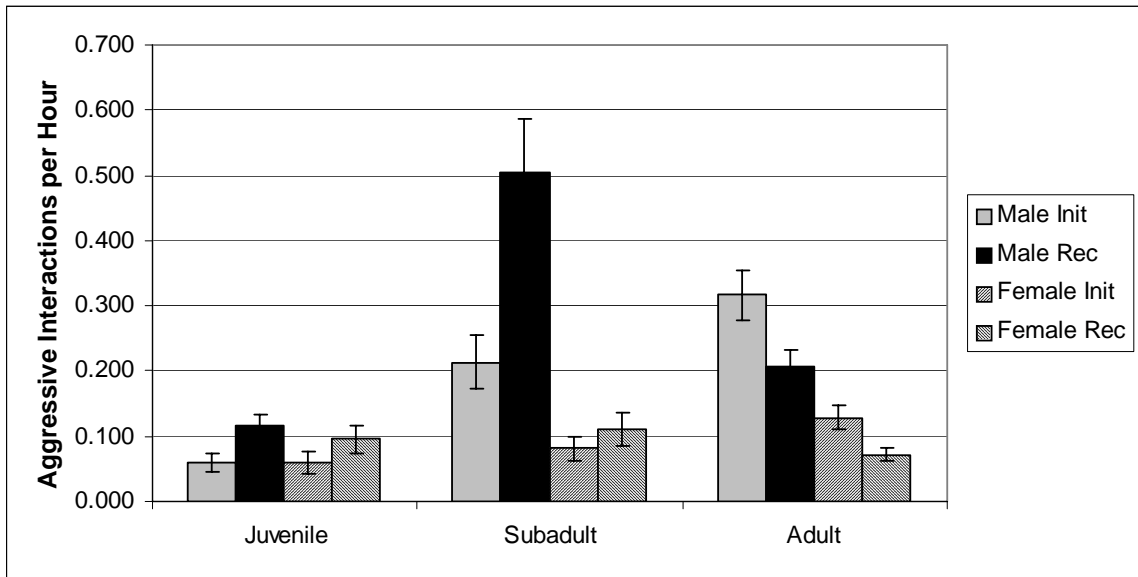


Figure 1. Aggressive interactions per hour of observation for each age / sex class of capybaras. For each class, the interactions are further divided into those initiated by that class and those received. Subadult males receive more aggression than any other class (Planned contrasts ANOVA, $p < .001$). Mean and standard error are shown.

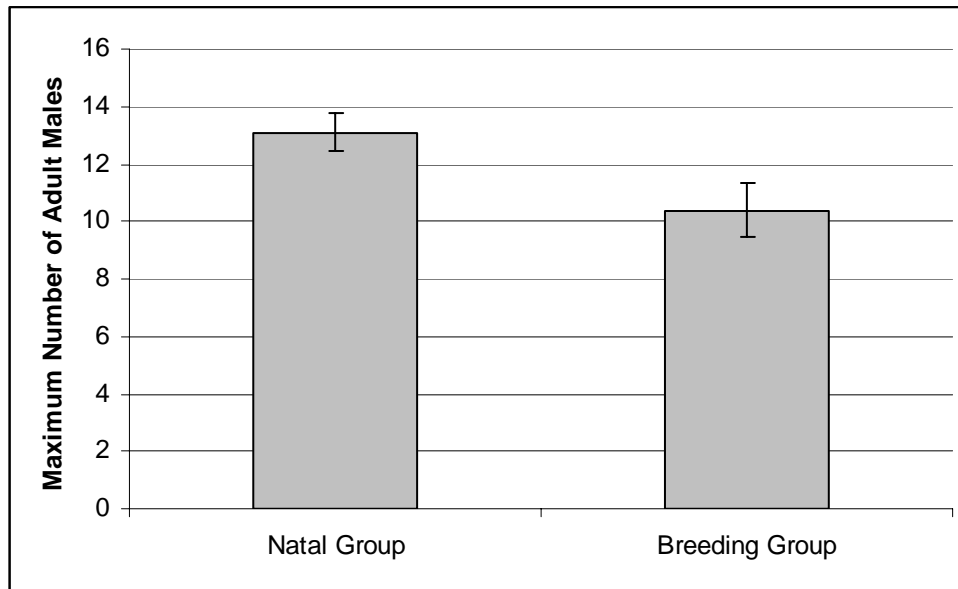


Figure 2. The maximum number of adult male capybaras present at any one time in the natal and breeding groups of dispersed males. Mean and standard error are shown.

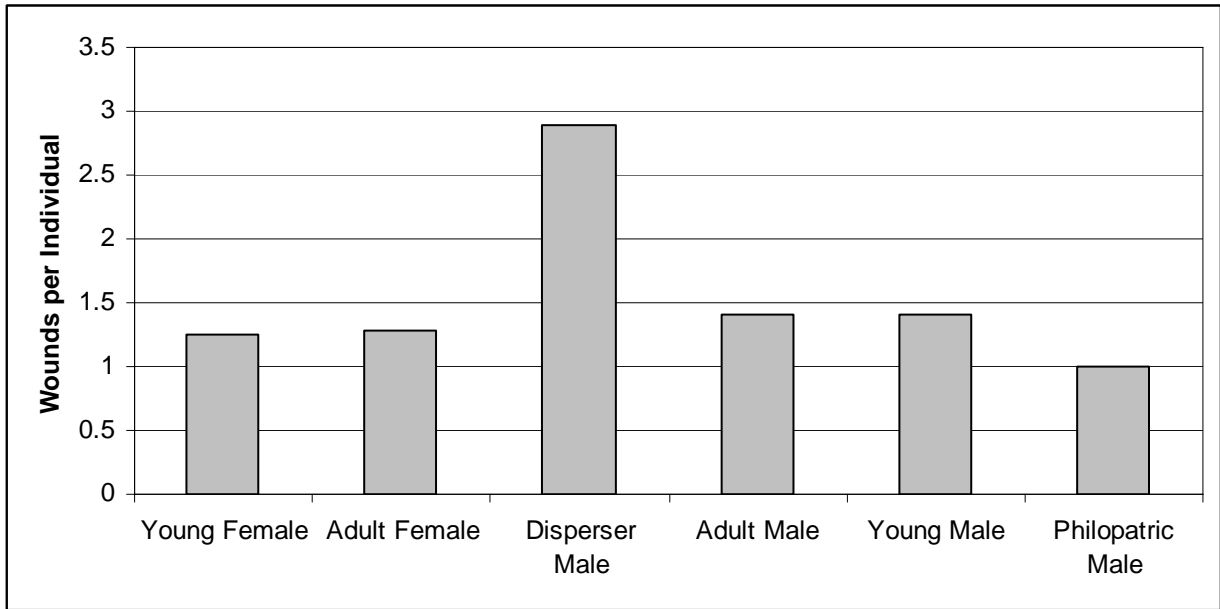


Figure 3. Average wounds per individual capybara of each sex and age class. An individual was classified as ‘young’ if it was marked as a juvenile and then observed until approximately two years of age. ‘Adults’ were marked as adults and their exact age is not known. Those labeled ‘disperser’ or ‘philopatric’ were marked as juveniles and followed until adulthood.

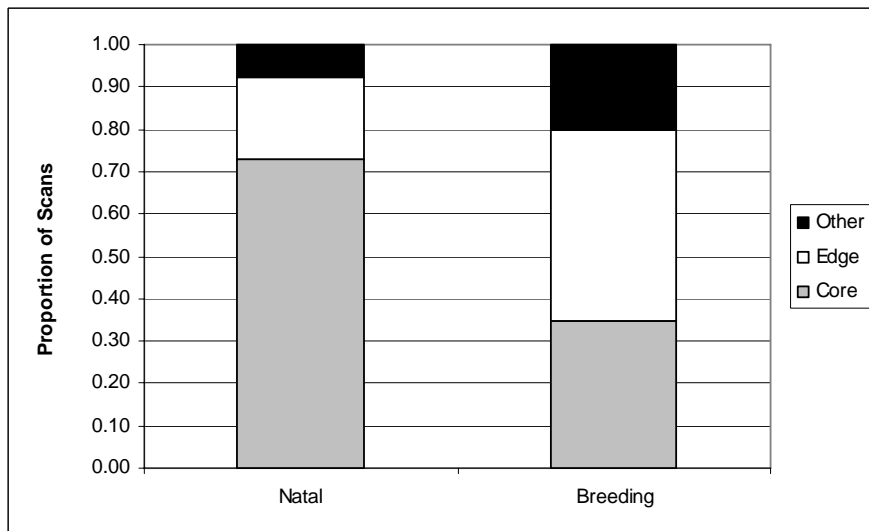


Figure 4. Times spent at the core, edge, or ‘other’ in the natal group and breeding group for 10 dispersing male capybaras. ‘Other’ represents either the periphery of the group, away from the group but still in the territory, or out of sight but present. Data were collected at least 60 days prior to emigration from the natal group and at least 30 days following immigration into the secondary group.

CHAPTER 2

A description of natal dispersal and group fissions in capybaras (*Hydrochoerus hydrochaeris*) in a seasonally flooded savannah of Venezuela

INTRODUCTION

Dispersal is the movement of an individual between breeding areas or social groups. Dispersal may occur without effective gene flow, but effective gene flow rarely occurs without dispersal. Whatever aspect of a population's behavior, genetics, or ecology one might study, dispersal likely plays a role in its maintenance or origin. Furthermore, dispersal is impacted by a variety of natural history parameters, including mating system, habitat requirements, diet, and social structure. Therefore, understanding the dispersal mechanisms plus the proximate cues and ultimate causes of dispersal in any particular species can inform numerous other aspects of their behavioral ecology and population genetics.

Gadgil (1971) called dispersal "one of the most important and amongst the least understood factors of population biology", and many researchers have been drawn to explore it. Yet our knowledge of the genetic and social implications of dispersal is still incomplete (for reviews see Greenwood 1980, Shields 1987, Van Vuren 1998). Social roles (e.g., dominance) and intra-specific competition can be important determinants of dispersal patterns (Shields 1987). Dispersal, in turn, will dictate the mating opportunities of individuals and thus the genetic structure of a population. Examining the dispersal patterns of a species may be a critical component to understanding natural group dynamics and long-term stability of genetic structure within a population or species (i.e.

avoidance of inbreeding depression) (Durant 2000). Furthermore, in the context of extensive and sometimes rapid anthropogenic changes in the environment, the ability to predict a species response to change becomes increasingly valuable, if not critical. The links between dispersal and population dynamics make understanding the causes and consequences of dispersal vital for predicting population-level response to change (Bowler and Benton 2005).

This study specifically focuses on natal dispersal: the movement between the natal area or social group and the area or social group where breeding first takes place. Predicting which individuals will disperse from a social group, and at what age, typically involves identifying the needs that are not being met in that group. For instance, the individuals least likely to have access to adequate food, space, and preferred mates will be the individuals most likely to leave, or to attempt to leave (Christian 1970). Then the likelihood of actually emigrating becomes dependent upon the likelihood that those needs will be met by another social group and that membership in the other social group is attainable. With respect to alleviating intraspecific competition, juveniles are likely to be less competitive than adults and thus more likely to disperse, as is the case in most birds and mammals (Gaines and McCleneghan 1980). The timing of dispersal can be reliant on the motivation behind it, for example, for inbreeding avoidance individuals must disperse before or concurrent with reaching sexual maturity. But timing is also constrained by the available food resources either during dispersal or prior to dispersal so that fat stores are sufficient to sustain the individual in sub-optimal habitat while traveling. In habitat with long vegetative growing seasons, animals have ample time in the first year to build fat stores and may disperse at fairly young ages (Barash 1977). Likewise, in areas with

shorter growing seasons, dispersal may be delayed to the second or third growing season to allow body condition to build.

With respect to 'who' disperses, several generalizations have been made based on other life-history characteristics. Many studies in both birds and mammals have suggested that the mating system plays a large role in determining dispersal strategies, or perhaps vice versa. Some researchers propose that polygynous or polyandrous species are expected to show sex-biased dispersal, while socially monogamous species are expected to have uniform dispersal (Shields 1987). Others contend that for the purposes of inbreeding avoidance, most species should show sex-biased dispersal, and the mating system will then determine which sex disperses (Greenwood 1980). Birds, which are often socially monogamous, tend to have social systems in which the male is defending a territory to which he is attempting to attract the female (a resource defense system). Because the male therefore benefits from familiarity with and extended occupancy of the territory, males are more likely to be the philopatric sex. Mammals, which tend toward polygyny, are more likely to have males defending access to females rather than to a resource, and as such are not tied to an area (a mate defense system). Females, on the other hand, may not be capable of enduring the costs of dispersal given the demands of parental care, and thus females are philopatric and males disperse in many mammals. Naturally, exceptions can be found on either side, with some birds showing male-biased dispersal (lesser snow geese, Cooke *et al* 1975) and some mammals showing female-biased dispersal (white-lined bats, Tannenbaum 1975; greater white-toothed shrew, Favre *et al.* 1997; pikas, Peacock and Ray 2001; chimpanzee, Pusey and Packer 1987). In

several species juveniles of both sexes disperse (plains zebras, Klingel 1969; rodents, various species, Greenwood 1980).

Dispersal distances are often very variable, with most individuals moving only short distances and a few individuals moving very long distances (i.e., long distance dispersal). Sex-biased dispersal is illustrated by the fact that distances of one sex are significantly and often greater than that of the other. The 'philopatric' sex might remain in their natal range or territory or within just a few range-lengths. In some species, individuals may engage in exploratory movement away from the natal territory but return to it prior to a complete dispersal event (e.g. foxes, Woollard and Harris 1990).

Dispersers are faced with the risks of crossing unknown habitat to interact with unknown conspecifics. The benefits of membership in the new group likely outweigh the costs of getting there and gaining acceptance.

Capybaras (*Hydrochoerus hydrochaeris*) are excellent subjects for studying dispersal because of their large body size (large enough to observe from a distance) and social organization. They are terrestrial, diurnal, territorial, and highly social and polygynous, allowing for capture in groups of large numbers, and they apparently disperse several kilometers from their natal ranges (Herrera 1992, Salas 1999). Although they have been locally extirpated from some areas, capybara densities are high in some private ranches of the *llanos*, the seasonally flooded savannas of northern South America. Furthermore, previous studies (described below) suggest that capybaras may represent an example of behavioral variation that warrants conservation as its own form of biodiversity (Buchholz and Clemmons 1997).

Capybaras are polygynous mammals with male dominance hierarchies and at least some communal breeding by females. Overall, males are more aggressive than females (Salas 1999), even as subadults (Chapter 3). Thus, based on adult behavior, the males appear to follow the 'threat of eviction' model while the females are following the 'beneficial sharing' (Cant and Johnstone 1999) Male subordinate reproduction is restrained by the threat of being evicted from the group by the dominant male. The females mutually cooperate and apparently experience greater fecundity in larger groups (Herrera and Macdonald 1987). Based on adult behavior, one would expect male-biased dispersal, if not in probability, at least in distance (Greenwood 1990).

Previous work on capybaras suggests two different possible scenarios. One study demonstrated equal proportions of male and females dispersing, perhaps in kin groups, with dispersal distances averaging 5.6 km (Herrera and Macdonald 1987, Herrera 1992). Another study revealed male-biased dispersal with 75% female philopatry (Salas 1999). The latter study described capybara social structure as female kin-clusters with associations of un-related males. One possibility is a scenario involving a sort of melding of the two patterns wherein juvenile and sub-adult males leave their natal groups and live as floaters until reaching sexual maturity, at which point they corral young and/or adult females from an existing group to create a new social unit, similar to the system seen in plains zebras (Klingel 1969).

This corralling of young may represent a sort of social facilitation of dispersal (Holekamp 1986). This hypothesis suggests that, at the time of dispersal, transients would appear in natal areas to facilitate emigration in young animals. Juveniles believed to be following such transients out of their natal areas should remain in closer physical

proximity to them, and/or follow them around more, than do other animals in the population. Thus, this hypothesis predicts that males should follow conspecifics more frequently and/or follow them longer distances than do females.

The current study set out to describe the natal dispersal pattern of capybaras in order to test hypotheses for the proximate cues and past selection pressures in this species (Chapters 3 and 4). Due to the mixed results of previous studies, no a priori assumptions were made with regard to which individuals would disperse, or how far. Data were collected for both males and females beginning at ages young enough to be reasonably certain that individuals were still in their natal groups. In addition to providing basic information on who disperses, when, and to where, I also gathered more detailed accounts of individual's behavior during dispersal.

METHODS

Study Species

Capybaras (*Hydrochoerus hydrochaeris*; formerly known as *Hydrochaeris hydrochaeris*, ICZN 1998) are large (~50kg) caviomorph rodents that live in groups averaging around 10 individuals with large variation in group size (approximately 4 to 40 individuals; Herrera and Macdonald 1987, Salas 1999). These groups are stable; that is membership remains more or less unchanged for over a year, with each group consisting of a dominant male, several females, their young and one or more subordinate males (Herrera and Macdonald 1987). At El Frio ranch in Venezuela, these subordinate males were proper group members, as opposed to 'floaters', for at least two years (Herrera 1986). A rigid dominance hierarchy is evident among the males, with the dominant individual being larger and obtaining significantly more matings than subordinates

(Herrera and Macdonald 1989). The subordinate males apparently queue for dominance, with age being the significant correlate with dominance (Salas 1999), although size may be an important factor as well (Herrera and Macdonald 1993). The mating system is polygynous and there may be a certain degree of cooperative breeding, in the sense that young are maintained in 'creches' and lactating females indiscriminately nurse their own and alien young (Macdonald 1981; Salas 1999).

Capybaras are capable of breeding throughout the year. At other sites, peaks in breeding occur at seasonal transitions, with a significant increase in mating in April-May leading to births in September-October. At the site of the current study, these peaks were much less pronounced (Congdon, unpublished data).

Capybaras live in non-overlapping territories defended by all adult group members, including subordinate males (Herrera 1986, Herrera and Macdonald 1989, 1993). A territory typically includes a grazing patch, bush or shade, and a section of a pond or river (Herrera and Macdonald 1989). In the dry season, the scarcity of water can lead groups to congregate at water holes in groups of up to 100 individuals with little aggression being exhibited (Herrera and Macdonald 1987). The availability of a water source appears to be very important in that it is used for predator avoidance, wallowing for temperature regulation, and mating (Herrera 1986). Since the availability of these water sources varies across sites, it may be expected that territorial spatial relationships and population densities also vary between sites and could have consequences for dispersal patterns. Some researchers describe capybaras as the hippopotamus of the New World (Salas 1999), filling the niche of the large, semi-aquatic herbivore.

Study Site

Hato El Cedral is located approximately 200 km west of San Fernando, Apure State in Venezuela, and covers close to 50,000 hectares. A population of approximately 10,000 capybaras comprising several hundred social groups is distributed throughout the ranch, although groups tend to concentrate around large, permanent water bodies, particularly in the dry season. The large size of the ranch and lack of fencing low enough to restrict capybara movement allow for studies under semi-natural conditions but with poaching controlled (Ojasti 1991; E. Herrera, pers. comm.). The core study area was in the approximate center of the ranch, such that dispersing individuals were more likely to settle within ranch boundaries post-dispersal.

The ranch is located in the seasonally flooded savannas (*llanos*) of Venezuela. Despite the apparent flatness of the land, there are three distinct kinds of terrain, differing in their height, soil and vegetation cover. Highest are '*bancos*', banks of former rivers or parts thereof, usually covered in tall grasses or bushes. The '*bajios*' comprise some 75% of the landscape and are covered in short, highly palatable grasses. The lowest lands, '*esteros*', are swamps, ponds and lakes, many of which dry up completely in the dry season. Isolated patches of woodland are also scattered around the ranch and gallery forests line the major rivers. Banks and woodlands are usually not flooded, while *bajios* tend to be covered by a few centimeters of water except in the height of the dry season. Many private ranches, including El Cedral, manipulate the water levels with dikes, keeping some areas with water year-round and draining others for cattle.

Capture and Identification

All capturing and marking of individuals was done during the dry season, when we could effectively reach most areas via horseback. A pilot study was conducted in

2004 and 103 individuals were marked. In 2005 another 187 were marked for the major part of the study. Young animals weighing less than 10 kg were avoided for fear of injuring them or disrupting their maternal bond while they were still nursing. Thus, individuals that were targeted for the dispersal study were between 10 and 20 kg, which ensures they were still young enough to be in their natal group. Based on previous work (Ojasti 1973), animals of that size would be approximately 5 – 8 months old and were born at the end of the wet season.

Individuals were captured using traditional methods: chasing from horseback and lassoing. Due to the scattering effect of this method, it was not possible to mark entire social groups. A total of 290 individuals were captured and tagged and another 8 were identified by natural scars or some other obvious feature. Once captured, individuals could be restrained by hand for processing, which took no more than a few minutes and was done at the site of capture. Animals were weighed and marked with numbered tags of varying colors. Several measurements and ear notch tissue samples were also taken during processing. Each individual's sex was determined with palpation of the gonads. Approximate age was determined by weight for those individuals less than 35 kg (see Table 1 for details; Ojasti 1973). All others were classified as adults, but age estimates for live adult individuals are not currently available.

Social groups with at least three juveniles marked, and for which there was reasonable accessibility, were chosen as focal groups. Initially 13 social groups were spaced along an east to west dirt road. Each group had from 3 to 17 individuals marked. Immediately following the marking procedure, only group location and composition were

noted for several days, to ensure that membership had stabilized following the disturbance of capture.

Behavioral Observations

Behavior observations were conducted from April through June 2004 and from April 2005 through June 2006, for a total of 1180 hours. On average, each focal group was observed for 74 hours. The openness of the terrain made it possible to observe the entire social group at once, with the exception of individuals that might be hiding under bushes, where the social behaviors of interest were unlikely to take place due to lack of space. Each observation session began with noting group location, using a Garmin 12XL Global Positioning System, compass, and digital range-finder to calculate the coordinates of the approximate center of the group.

Two methods were used for documenting social behavior: focal individual observations and focal group observations. Focal *individual* observations were conducted for each marked animal for 10 minutes, noting nearest neighbors, all occurrences of social behaviors, and event behaviors such as scent marking. Every attempt was made to watch each individual at least once per week, with most being observed two to three times per week.

Focal groups were observed as often as possible, which resulted in some being observed three to four times per week and others only once per week. If a group could not be found for more than 4 weeks, it was no longer considered 'focal' and the data was used only anecdotally. During focal group observations, all occurrences of social interactions involving a marked individual were documented for all individuals in the group noting general age class and sex (if possible) for any un-marked participants.

Interactions between two unmarked individuals were noted on an opportunistic basis. For every behavior several parameters were noted: date, time, initiator, recipient, behavior, outcome (e.g., of a fight), and any additional notes. In the ethogram a 'courtship' was reclassified as a 'mating' if the male mounted the female more than 4 times, based on previous data that at least 7 mounts are required for ejaculation (Ojasti 1973, Salas 1999). This is also the definition used by Salas (1999) and allows comparisons. The detailed ethogram used was modified from several previous ethograms and is available upon request to the author. Table 1 lists the social behaviors and definitions relevant to this study.

Only two aspects of the social data are presented here. First, courting behavior was used as a definitive indication of a disperser's immigration into a secondary group. Second, as a measure of potential social facilitation, following behavior was recorded during all behavioral observations. Although this would not tell us positively whether social facilitation of dispersal is occurring, the lack of following behaviors without agonism could rule out this possibility.

Detecting Dispersal

For the purposes of this study, natal dispersal is defined as the movement of individuals away from their natal area or social group to the area or social group where breeding first takes place (Clobert *et al.* 2001). This species' high levels of sociality and territoriality led me to define dispersal by establishment in a new social group, rather than by spatial location or absolute distance moved. Because successful breeding (i.e., paternity) has not yet been determined in this study, the group where a male first attempted to court a female was considered his breeding group. Searches of the study

area to detect dispersers were conducted at least once per week, and more frequently when an individual had recently disappeared from a group. The road and trail system of the ranch allowed for fairly extensive searching, aided by sightings by ranch workers who could cover more ground on horseback than I could with a truck.

Individuals that were marked as juveniles and eventually dispersed will be referred to as 'dispersers', including when examining their behavior prior to dispersal. Individuals that were marked as juveniles and were later defined as philopatric will be referred to as 'philopatric individuals'. When comparing behaviors relative to the time of dispersal, philopatric individuals are considered relative to the average age of dispersal, or 15 months. Because all dispersers were males and only two philopatric males provide enough behavioral data for consideration, the confounding variable of gender is ever-present in these analyses and their interpretation. Only disperser males and philopatric females yield enough data to analyze statistically, while philopatric males are considered separately and subjectively.

Many juveniles that were marked either disappeared or lost their ear tags, so that they could not be classified as either 'dispersed' or 'philopatric'. These individuals were excluded from analysis. Additionally, individuals that were initially captured and marked as subadults or adults could not be classified because their natal group was not known. However, these known individuals added value to the study by giving identity to the partner of social interactions with the focal individuals.

Territories

Distance between territories was measured as straight-line distances between approximate centers of the territory and taken to the nearest 50m. More accurate

measurements would be misleading, as the groups varied in their dispersion throughout the day and seasons. Also noted were the number of other territories between the natal and secondary group of a disperser. In some cases this was difficult to estimate due to the irregular shape of territories and non-linear movements. Nonetheless, as an initial and relative measure of dispersal distance, it may prove informative.

Data Analysis

Data analysis was performed with SPSS v15. Due to small sample sizes and non-normality of data, nonparametric tests were used most often unless otherwise noted. In some cases, samples were too restricted to warrant statistical analysis, but are compared qualitatively.

RESULTS

By observing marked juveniles until they reached adulthood, we were able to identify a total of 23 males from 10 groups as either philopatric or dispersed. As shown in Table 2, 20 males dispersed and only three remained philopatric. Of the three that remained in their natal groups, one attempted mating and was thus undeniably 'philopatric'. The other two were 22 and 28 months old, while the oldest confirmed disperser was 19 months, with the mean dispersal age being 14.1 months (Table 3). Although it is possible that these two individuals would eventually emigrate from their natal group, they have clearly remained past the average dispersal age of 14 months. Of 26 females from 13 groups observed for the same period of time, none dispersed. A number of males and females did disappear from their natal territories, but they were never seen again despite extensive searching of the area. Since we can not confirm mortality or long-distance dispersal, these animals were excluded from further analysis.

One female did appear to move between groups as an adult, but because she was not marked as a juvenile, it could not be determined if this was natal dispersal or breeding dispersal and so this data point was excluded from further analysis.

The age, date and approximate season of each disperser and dispersal event are provided in Table 3. The age of emigration ranged from 9 to 19 months, based on age estimated by weight at the time of capture (Ojasti 1973). In 8 of 12 cases emigration took place during a transition between seasons, with the remainder emigrating during the wet season (Table 3). The table also includes the number of days a disperser is transient correlates with the season of emigration (Spearman's Correlation ρ , $p = .031$) such that individuals that emigrate in the wet season, when the area is flooded and dry land is limited, tend to spend more days in transition before effectively immigrating into a new group. Individuals that emigrate during the transition from dry to wet, or during the transition from wet to dry, tend to immigrate more immediately into a group. A comparison of those individuals that emigrated during the wet season with those that emigrated during either seasonal transition reveals a significantly longer transience period for the wet season emigrants (Mann-Whitney U, $p = .038$, Table 3 last column).

Dispersal distance was calculated both geometrically (the straight-line distance) and functionally (the number of existing territories between the natal and breeding territory; Table 4). Dispersal distances ranged from 200 to 3000 meters, as measured from the center of the natal group to the center of the breeding group. It should be noted that three males moved from their natal group to a neighboring group.

Dispersal strategies

The frequency of 'following' behavior (see Table 1 for a definition) by young individuals was used as a preliminary measure of potential social facilitation of dispersal. Figure 1 shows the number of follows per hour by males and females prior to dispersal age. The difference is not statistically significant, but there is a trend for females to engage in more following behavior than males may (Mann-Whitney U, $p = .095$).

Most dispersers traveled alone, although there were some situations that may represent exceptions. Three individuals from the same natal group (group C) did appear together in another group (Group LB) the following year. One of these individuals, a male, moved further on to another group and was defined a disperser (individual number 17). The other two disappeared, one adult female and one young male. This situation may have been a case of group fission initially, and then dispersal by #17. However, it could also have been a case of joint dispersal by all three, followed by secondary dispersal by #17 and disappearance of the other two. Unfortunately, due to the lack of other marked individuals in Group LB, it could not be determined if the initial change was group fission or group transfer. In another case, two individuals moved from the same natal group to the same post-natal, but they did were never seen traveling together nor did they appear to have any particular bond in the latter group.

Most dispersers made excursions away from their natal group before leaving permanently and some floated between two or more groups before settling, but none for more than a few weeks. Several dispersers were satellite members of their secondary group before becoming core members. Satellite members are individuals that are routinely seen within the territory, thereby benefiting from the resources within that territory, but are always peripheral to the rest of the group (See table 1 for detailed

definitions). One adult male in this study did appear to be a floater as defined in Table 1. This male spent time in more than one territory, interacting with territory holders in each.

Following dispersal, males that immigrated into a new group were seen more often at the edge or periphery of that group in comparison to the core (Figure 3). This is in direct opposition to their tendency to be seen most often in the core of their natal group (Chapter 4).

Group fission was witnessed in at least one case and possibly a second. These group splits were not considered dispersal and included both males and females of varying ages. In one case, the original group was seen as a whole for a couple weeks, then split into stable subunits, and was seen only once or twice more as a whole. During this time, some individuals were repeatedly with only one subunit, recognizable by their separation along a road. Other individuals moved back and forth between the two. When individuals no longer switched between the two subunits, they were considered separate territories.

In a less comprehensively documented case of fission, a set of individuals was marked and repeatedly seen together in the dry season of 2004, along with several unmarked individuals. No observations were made (break in data collection) for several months and then in the dry season of 2005 at least one adult female and two young (approximately 14 to 18 months of age) males were seen with several unmarked individuals a couple hundred meters east of the original 2004 group. At least two females from the original group were still at the original location. Throughout 2005 these two groups never mixed and a third group established a territory between them.

In another ambiguous situation, a large group marked in the dry season of 2005 moved at least 1 kilometer south during the next wet season, when their original territory flooded. Unfortunately, the flooding made it impossible to conduct observations or even census effectively to the south. When the water receded, many of the group members returned to the original territory, but some stayed to the south, including one marked female. Due to the unclear circumstances, this was not considered dispersal by the female, but a possible group fission, whether seasonal or permanent is not clear.

Young dispersing males were more frequently seen with obvious wounds than were any other group of individuals, including young females, adults, or philopatric males (Figure 2). Over the course of this study, two young males were found dead outside their natal territory. Two dead females were found, both as adults and within their natal territory. Exact cause of death could not be determined in any case, but appeared natural, i.e., not from a car accident or poaching attempt.

DISCUSSION

As expected for a polygynous mammal (Greenwood 1980), capybaras demonstrate male-biased dispersal with potential fission at large group-sizes. Other studies have reported that dispersal takes place at the end of the wet season (Herrera 1992), but this study revealed movements at both seasonal transitions, from wet to dry and dry to wet. This variation could be due to the water management within the ranch. At the study site, a series of dykes and levies keep some areas wet, or at least green, year round. This mitigation of seasonal patterns may explain the lack of synchronized breeding and subsequent lack of synchronized dispersal.

Although this study did involve the disappearance (or loss of identifying ear tags) of many female juveniles, none were observed successfully immigrating in to a secondary group. The near equal proportions of marked males and females that disappeared allowed me to exclude these individuals in my evaluation of sex-biased dispersal. However, the possibility remains that some of these females in fact dispersed, but were never found. The apparent high costs of dispersal, as evidenced by the injury rates and mortality in young males, does suggest that if females were dispersing, we would likely have seen more injuries and/or dead females away from their natal group.

The short distances dispersed by many capybara males raises the question of the effectiveness of dispersal in terms of avoiding inbreeding depression. Other species have been shown to display this mammalian pattern of male-biased dispersal but with short distances (plateau pikas, American pikas, and banner-tailed kangaroo rats (Dobson et al. 1998), and perhaps capybaras. It has been suggested that habitat uniformity might limit the benefits of dispersal or increase the costs of long-distance dispersal (plateau pikas, Dobson et al. 1998). In birds, short dispersal distances and viscous populations may be selected for when predator-risk is high or assessing territory quality is difficult (Yaber and Rabenold 2002). Vigilance behavior in capybaras does suggest that predation risk may have been a selective pressure, at least in the past (Yaber and Herrera 1994). Currently, only a few natural predators large enough to take a subadult capybara remain in any significant numbers in the ranch, most notably anacondas and pumas. In the past, jaguars were likely predators of adult capybaras, but have been extirpated from the ranch by humans.

Two previous studies have examined the dispersal of capybaras and revealed possible variation or condition-dependent patterns. Based on research conducted at Hato El Frio, approximately 60 km from the site of the current study, Herrera and Macdonald (1987) proposed that dispersal might occur in groups consisting of both males and females. Herrera and Macdonald's (1987) work suggests a form of social facilitation of dispersal in capybaras. Natal dispersal may occur when young animals follow conspecifics leaving the natal area, so that dispersal is triggered by 'transient' conspecifics. This hypothesis predicts that young males should follow conspecifics more frequently and/or follow them longer distances than do females (Holekamp 1986). Furthermore, these young dispersers should not show agonistic behavior toward their facilitators. However, in the current Cedral study population, young males approaching dispersal age actually show more aggression toward conspecifics than do females (Chapter 3).

Research conducted by Salas (1999), at the site of the current study, showed that all males dispersed as juveniles while only 25% of females dispersed, with most females remaining philopatric (Salas 1999). These results from El Cedral are more typical of the male biased dispersal found in most mammals (for reviews see Michener 1983, Shields 1987, Chepko-Sade and Halpin 1987). Furthermore, most sub-adult males in this system were solitary, comprising a floater population that was not observed in the El Frio study nor in the current study. The current study found significant male-biased dispersal, with 20 of 23 juvenile males dispersing and none of 26 juvenile females of the same cohort dispersing (Table 2).

The presence of extra-group males, or 'floaters', in capybara populations may vary with the level of habitat saturation. During the Salas (1999) study, censuses were taken along a 3 km transect and yielded an average of over 1000 individuals. During the current study, that transect was recreated as closely as possible and never showed more than 600 individuals, indicating a lower density and possibly lesser degree of habitat saturation. In addition, however, many of the floater individuals identified by Salas 1999 would be classified as satellite group members in this study, due to their regular occurrence in only one territory. Others would be potential dispersers, as they were young males that were seen moving from one territory to the next, without on-going observations to determine their fate. During the current study, 'floating' was apparently a temporary state before immigrating into a social group, rather than a long-term strategy. As apparent in Table 3, three individuals spent several months in transition before entering into a secondary group after dispersing from their natal group. While other studies might term these 'floaters,' I consider these individuals dispersers in transition.

While this study has led to a greater understanding of the mechanisms of emigration in capybaras, the processes of searching for a breeding territory, evaluating potential territories, and immigrating into an existing social group remain a mystery. Understanding the whole process will likely require radio-telemetry or similar technology to follow individuals over the long-term, coupled with behavioral observations of social interactions. Capybaras provide us with several opportunities. First, they are large-bodied herbivores that are not yet threatened with extinction, thereby providing the chance to study population dynamics relative to social evolution. Second, they are of economic value as a source of food and leather, providing an example of potentially sustainable

harvest in a species with high sociality. Finally, they provide an example of behavioral plasticity and variation that is its own form of biodiversity and worthy of conserving.

Table 1. Ethogram and definitions of relevant behaviors and terms for capybaras. A complete ethogram is available upon request to the author.

Two event behaviors are considered different bouts if they are separated by another defined behavior, a change in participant, or at least 5 minutes, unless otherwise noted.

Social Behavior

Follow	One individual walks behind another individual in the same direction. The lead individual does not increase pace to a run.
Court	Male closely follows the female with his head held high and his chin close to her rump and mounts less than four times, or not at all. Distinguish from 'mate'. (~Salas 1999)
Mate	Male closely follows the female with his head held high and his chin close to her rump. The female lowers her rump and the male mounts her. Male mounts at least four times. Distinguish from 'court'. (~Salas 1999)

Location

Out of Sight	Animal is known present, but not visible (e.g. behind a tree or under water). More than 30% OOS in one focal session will nullify that session.
Core	Imagining a line from the spatial group center to the focal animal, at least one other individual is farther away from the center OR there are animals in two opposite compass directions.
Edge	No other individuals are farther away from the center of the group than the focal individual but the focal is not peripheral
Periphery	The focal animal is farther away from other group members than the average distance between any two group members, but closer than any neighboring group. Less than 100m from the nearest group member.
Away	The focal individual's location is known but is beyond the periphery of the group's current location. More than 100m from group and/or out of the known territory.

Age Classes

Baby / Infant	Socially dependent on mother or females, typically < 4 kg. Field identification: stay close to female or other babies, ~3 kg or less.
Juvenile	Independence to 11.9 months; up to 24.9 kg Field identification: noticeably / undoubtedly smaller than an adult.
Subadult	12 to 17.9 months; 25.0 to 35.9 kg Field identification: males have visible testes but no morrillo; females same size as known subadult
Adult	18.0 months and older; 36.0 kg and heavier Field identification – males have visible testes and prominent morrillo; females are same body size as adult males but with no visible testes.

Group Membership / Changes

- Disperser Individual no longer associates with its natal group and is repeatedly seen outside its natal territory. If that individual engages in courtship or mating in the secondary group, it is considered an immigrant to that group.
- Philopatric An individual remains in its natal group until adulthood AND / OR is observed courting or mating in the natal group AND / OR gives birth in the natal territory.
- Member An individual is repeatedly seen in only one group, interacts with other group members, and may engage in courtship or mating.
- Satellite
Group
Member An individual repeatedly seen in the territory but rarely observed interacting with other group members. These individuals are often peripheral or at the edge of the group. They are not seen in any other group's territory (see Floater).
- Floater An individual is observed in more than one territory and may interact with members of either territories' social group. If this individual immigrates into a social group, attempts to mate, and stays, then it will be reclassified as a 'disperser'.

Table 2. Number of dispersed and philopatric capybaras for each sex.

Gender	# Groups Represented	# Juveniles Marked	Philopatric	Dispersed	Disappeared
Male	10	74	3	20	45
Female	13	66	26	0	40

Table 3. Approximate age, date and season of emigration of male capybaras from their natal territories.

Individual Identification	Emigration Age (months)	Emigration Date	Emigration Season	Days in Transition
17	unknown	unknown	unknown	180+
108	14	9/24/05	Wet	67
109	19	3/7/06	Dry to Wet Transition	27
125	11	7/22/05	Wet	141
168	15	11/6/05	Wet to Dry Transition	18
172	14	11/14/05	Wet to Dry Transition	22
201	16	12/18/05	Wet to Dry Transition	Unknown
202	unknown	unknown	unknown	180+
203	17	4/9/06	Dry to Wet Transition	15
210	13	11/25/05	Wet to Dry Transition	20
211	11	8/16/05	Wet	32
214	12	8/10/05	Wet	20
220	18	4/25/06	Dry to Wet Transition	Unknown
908	9	4/8/06	Dry to Wet Transition	3
Mean	14.1			

Table 4. Dispersal distances of identified individual capybaras in terms of straight-line distance and the number of territories in between the natal and breeding territories. Distances were calculated from the spatial center of the territory.

Individual Identification	Straight-Line Distance (m)	Number of Territories
17	500	1
108	1400	3
109	1550	3
125	2500	7
128	3000	10
168	200	0
172	200	0
203	400	0
210	500	1
211	800	1
212	1500	8
214	1250	2
218	700	1
237	2000	8
265	1500	8
908	1700	4
Mean	1230	3.4

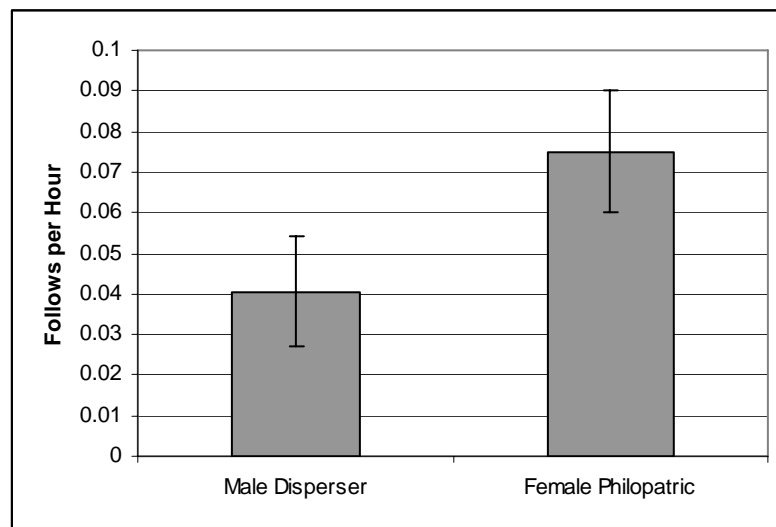


Figure 1. Following behavior by future male dispersers and females prior to dispersal age. Mean and standard error are shown.

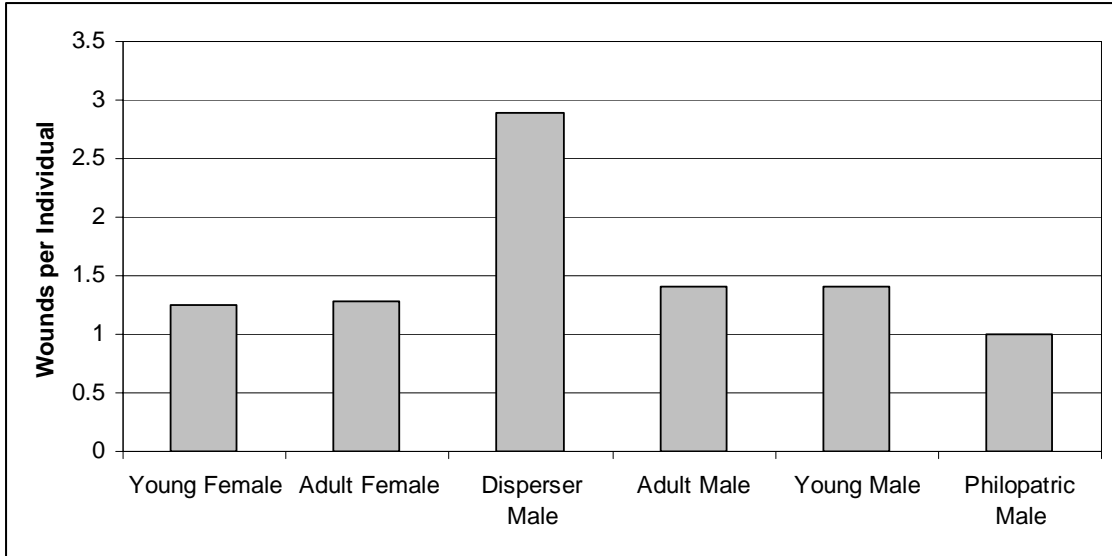


Figure 2. Average wounds per individual of each gender, classified as either ‘young’ which were marked as juveniles and observed until approximately two years of age, ‘adult’ which were marked as adults and their exact age is not known, and labeled ‘disperser’ or ‘philopatric’ if that fate is known.

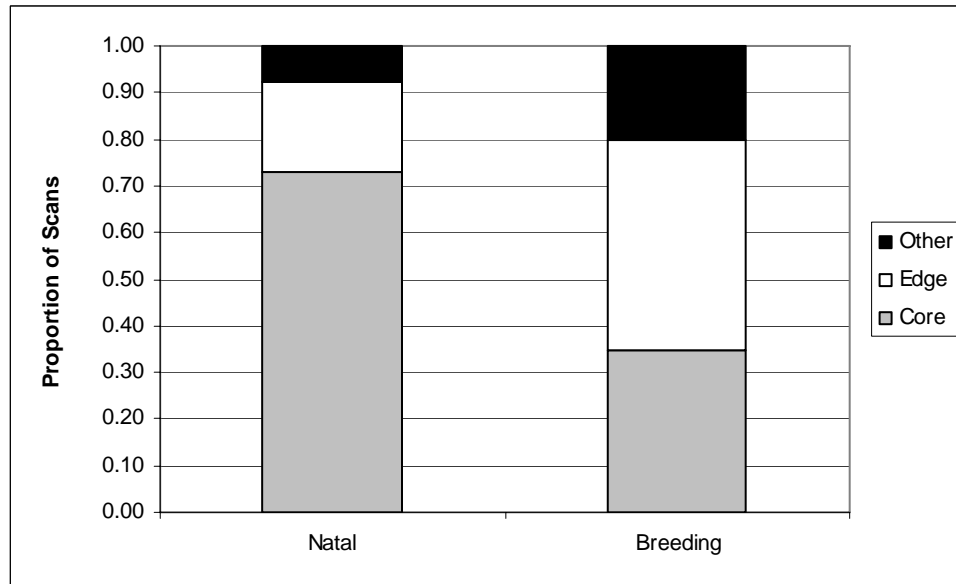


Figure 3. Proportion of scans in each relative location within the group of dispersing males only, prior to emigration (Natal groups) and following immigration (Breeding groups). Thus, these are disperser males only.

CHAPTER 3

Natal dispersal in capybaras (*Hydrochoerus hydrochaeris*): social interactions as proximate cues for emigration

INTRODUCTION

Dispersal is a behavior that has the rare ability to affect and/or be affected by almost every aspect of an individual's natural history and evolutionary future. Dispersal may occur without effective gene flow, but effective gene flow cannot occur without dispersal. Gadgil (1971) called dispersal "one of the most important and amongst the least understood factors of population biology", and many researchers have been drawn to explore it. Yet our knowledge of the genetic and social implications of dispersal is still incomplete (for reviews see Shields 1987, Clobert et al. 2001, Bowler and Benton 2005). Social roles (e.g., dominance) and intra-specific competition can be important determinants of dispersal patterns (Shields 1987). Dispersal, in turn, will dictate the mating opportunities of individuals and thus the genetic structure of a population. Examining the dispersal patterns of a species may be a critical component to understanding natural group dynamics and long-term stability of genetic structure within a population or species (i.e. avoidance of inbreeding depression) (Durant 2000). In mathematical models, by introducing dispersal between populations, population stability, as measured by persistence in time, can be increased by several orders of magnitude (Roff 1975).

Unfortunately, despite an abundance of empirical work on dispersal, few consistent patterns have emerged other than the very general statements of Greenwood (1980) that males should disperse in mammals and females in birds. This lack of pattern

may have led to the simplest assumptions being incorporated into models (Bowler and Benton 2005), and thus the models over-simplifying the process and representing dispersal by nothing more than a probability and a distance. In many species, however, dispersal is mediated by combinations of factors and can be condition-dependent (reviewed in Bowler and Benton 2005). Individuals with conditional dispersal may have an advantage in their ability to withstand environmental stochasticity (Ronce et al 2001). Furthermore, in the context of extensive and sometimes rapid anthropogenic changes in the environment, the ability to predict a species response to change becomes increasingly valuable. The links between dispersal and population dynamics make understanding the causes and consequences of dispersal vital for predicting population-level response to change (Bowler and Benton 2005).

How does an animal make the decision to disperse away from the safety and familiarity of its natal territory? What internal or external cue does an individual use to initiate this movement? These questions have been discussed often but are difficult to thoroughly assess in the field with natural populations. And while the evolution of dispersal behavior is a vibrant field of inquiry, understanding the proximate mechanisms is often overlooked as somehow less important. Indeed, the evolutionary significance of a behavior does have longer reaching impact, but the immediate cues involved in its activation are the characteristics that are subject to changing environments and the basis for current selection, whether natural or anthropogenic. A greater understanding of the behavioral basis underlying dispersal decisions is necessary to predict the movement of individuals within a spatial system (Bowler and Benton 2005).

“The study of the proximate causes of dispersal, in particular, the social environment in which animals are observed prior to dispersal, would be indicative of the ultimate cause of dispersal” (Bowler and Benton 2005). For example, a dispersal strategy that is sensitive to the presence of opposite sex kin would be suggestive of inbreeding avoidance (Lambin 1994). When driven by kin competition, both sexes may disperse, and the dispersal rate may be sensitive to the numbers of all kin, or promoted by the numbers of the more competitive sex (e.g. Lena et al. 1998). Thus, examining proximate cues leads us to hypotheses for selective pressures and ultimate causation.

In social species the potential exists for conspecific interactions to drive the initiation of dispersal. Two primary behavioral hypotheses have been put forth to explain the initiation of dispersal in such species: the social subordination hypothesis (Christian 1970) and the social cohesion hypothesis (Bekoff 1977). These hypotheses do not specify the role of physiological processes in this behavior, but rather focus on the differential social experiences that lead young animals to make the decision to emigrate away from the safety and familiarity of their natal group or site. Using social cues to dictate emigration allows for immediate adjustment to changes in density, group size, or any demographic stochasticity, as opposed to the comparatively slow and potentially fatal body-condition cues.

The clearest example of a socially motivated dispersal pattern is via Christian’s (1970) social subordination hypothesis wherein subordinate individuals are driven to disperse from territories held by more dominant individuals. Under this hypothesis, behavior is controlled by experience and hormonal effects that lead testosterone-rich, territorial males to behave as dominant individuals, resulting in the dispersal of stressed,

subordinate males. The hypothesis makes no assumption of genetic differences between dispersers and non-dispersers.

The social subordination hypothesis was originally proposed to explain dispersal in microtine rodents with cyclic variations in population density (Christian 1970; Gaines 1980). It predicted that the levels of aggression and population density will be positively correlated. Dispersal rates will be higher during phases of peak density than during phases of increasing density and aggression and dispersal will be due to physiological responses to density. Dispersers will be predominantly subadult males that have just attained sexual maturity and are social subordinates. Tests of this hypothesis often measure density and dispersal rather than direct behavioral interactions due to the difficulty of observing behavior in natural populations (Gaines 1980; Holekamp 1986).

It is worth noting that Christian's (1970) original paper does not directly predict that direct aggression by the dominant individual will drive out dispersers, perhaps due to the particular system under consideration – microtine rodents. Later work with social species that allowed direct behavioral observations explored the role of social interactions. In these cases, it is predicted that dispersers will receive more aggression than philopatric individuals, particularly immediately prior to dispersal. The timing of dispersal may still correlate with group size, in so far as group size correlates with aggression. Dispersers may be more likely to avoid close contact with conspecifics in order to avoid aggression (see Results).

Many studies have been limited by the inability to directly observe aggressive interactions and have used observations of wounding, spatial and temporal overlap of disperser and potential aggressors, or general levels of aggressive interaction in the entire

population as correlates of dispersal in support of this hypothesis (Holekamp 1986). These measures are all indirect and potentially misleading. Wounding could be from interspecific interactions. Potential aggression does not necessarily mean actual aggression. And general population levels of aggression may be restricted to the adults, or not specific to the dispersing sex. Ferreras et al. (2004) state that social subordination hypothesis is supported as the proximate cue for dispersal but direct aggression from adults to subordinate lynx (*Lynx pardinus*) was never detected. A few studies have observed aggression involving dispersers and concluded that natal dispersal by males resulted from direct conflict with other males (Gunnison's prairie dogs, Rayer 1985; blind mole rat, Zuri and Terkel 1998; Iberian lynx, Ferreras 2005; fox, Woollard and Harris 1990).

In species that do not show the density fluctuations seen in microtine rodents, conspecific aggression appears to promote dispersal in at least four additional natural situations: where parental aggression towards weaned offspring increases because adults become occupied with subsequent pregnancy or offspring; where young males may be expelled by a new male, usually just after his immigration into the group; where emigration is actually breeding or saturation dispersal rather than natal dispersal; or where one or more critical resources are in short supply (reviewed in Holekamp 1986). While the first two situations are specific to particular individuals (offspring of gestating females) or social groups (those experiencing a change in dominance or saturation); the latter two can be population wide and very similar to the social subordination hypothesis. Saturation dispersal is the emigration of surplus individuals from a population at or near its carrying capacity (Gaines 1980). At or near carrying capacity, resources tend to be

limited, leading to the next situation. If critical resources are in short supply, competition is likely to increase and the younger and more subordinate individuals are least likely to be able to achieve access to those resources. In other words, the behavioral expectation of increased aggression and young subordinate dispersal is equivalent to the predictions of Christian's (1970) original social subordination hypothesis.

Studies of social mammals and their lack of aggressive interactions led Bekoff (1977) to propose what was later termed the social cohesion hypothesis, which is more an explanation for philopatry than for dispersal. It was proposed first in canids and then extended to marmots (Bekoff 1977). Essentially, animals that do not form social bonds with conspecifics in early life stages, for whatever reason, are more likely to disperse or less likely to be philopatric. Bekoff refers to these individuals as 'asocial types', which sounds more negative than perhaps it should. These types presumably represent a natural behavioral variant in the population, rather than some aberrant personality.

The social cohesion hypothesis predicts that asocial individuals have the highest dispersal rates with no association between population density and dispersal (because the agonism of competition is not the driver). If there is a variation in group size, and dominant-subordinate relationships, then larger demes have greater variation in behavioral types and higher dispersal rates. This hypothesis has been supported in some groups of canids (coyote, Bekoff 1977) and Richardson's ground squirrels (Michener and Sheppard 1972). It is unclear if the adults are avoiding the juveniles or vice versa. If the young subordinates are attempting to initiate interactions with the adults but being refuted, one would expect to see at least mild aggression directed toward the young, which would then be difficult to distinguish from the social subordination hypothesis.

However, if the avoidance is mutual, so that no aggressive rebuffering occurs, we could conclude that these individuals are less social than their philopatric counterparts.

I tested both of these hypotheses in capybaras, a social rodent species native to South America. Capybaras are excellent subjects for studying dispersal for both logistic and theoretical reasons. They are terrestrial, diurnal, and territorial, allowing for capture in groups of large numbers. They also are highly social, with a polygynous mating system and groups averaging 10 individuals, but ranging from 4 to 40 (Herrera and Macdonald 1987). Adult behavior has been thoroughly described elsewhere (Ojasti 1973, Herrera 1986, Salas 1999), with limited information available with regard to juvenile behavior and natal dispersal (Ojasti 1973, Herrera 1992). Although previous studies have revealed some variation (Herrera 1992; Salas 1999), the capybara population studied here shows markedly male-biased dispersal, with no confirmed female dispersers and rare male philopatry (Chapter 2).

The capybaras of this study are normally harvested annually, likely keeping their density below saturation (Salas 1999). It is therefore unlikely that saturation dispersal is taking place. However, the population does appear to be at a level sufficient to induce competition for resources. Although this population may have plentiful food supply for most of the year, being that they are grazers in a grassland, the limited resources of water, shade, and adequate forage are aggressively defended by all adult members of social groups (Herrera and Macdonald 1987). Each territory contains all three of these habitat features, and it may be acceptance into that territory, with its resident females, that is the 'resource' which the males are most likely to fight over (Herrera and Macdonald 1989).

Adult male capybaras establish a dominance hierarchy within social groups that is aggressively maintained (Herrera 1986; Herrera and Macdonald 1993). This aggressiveness between adult males sharing a territory suggests that their social interactions are structured according to competition for some resource. Being that capybaras have a polygynous mating system with high reproductive skew in favor of the dominant (Herrera 1992; Salas 1999), the resource in question is likely females. Intuitively, as young male capybaras reach sexual maturity and begin to compete for the females of their group, they are likely to be the recipients of increasing aggression from older males. Thus, the social subordination hypothesis is likely to apply to capybara males.

However, the dominance hierarchy in capybara males correlates closely with age (Salas 1999), not with body size (but see Herrera and Macdonald 1993). And while males are more aggressive than females (see Results; Salas 1999), the escalation of mild aggression to fights that result in injury was rarely observed. Furthermore, selection would seem to favor subordinate males that submit to the dominant rather than escalate to battle that they would undoubtedly lose.

Adult female capybaras, on the other hand, are at least partially cooperative. In the wild, females maintain the young in 'creches' and will nurse both their own and alien young (Macdonald 1981). However, in captivity, if females with newborns are introduced to a second, unfamiliar female, infanticide by the latter is likely (Nogueira et al 1999). If the two females had been housed together since weaning, infanticide did not occur; and female infanticide had not previously been documented in the wild, but did occur (pers. obs.). Thus, the female relationship appears to be maintained through familiarity and

cooperation, rather than competitive aggression. If a female does disperse, the predicted social cue would be a lack of cohesiveness with the group, or behaviors associated with the social cohesion hypothesis (Bekoff 1977). Males also cooperate in vigilance behavior and alarm calling as adults. In additions, the juveniles engage in social play. In social canids, species that play more as juveniles show stronger social bonds and greater sociality as adults (Bekoff 1977).

The social correlates of dispersal in capybaras were examined in several ways. Behavioral data were collected both before and after dispersal by recording aggression, affiliation, avoidance behaviors, and play. Location data were recorded in absolute terms and relative to other group members. Nearest neighbor data were also used as an indicator of an individual's tolerance of others and cohesiveness within the group.

Applying the social subordination hypothesis to capybaras, I predicted several differences between young dispersive males and young philopatric females. If this hypothesis is supported, larger or more dense groups should experience increased competition (given equal distribution of resources), leading to increased aggression and dispersers emigrating at younger ages. In comparison to philopatric individuals, young dispersive males should receive more aggression from adults, particularly from adult males. Just prior to dispersal, these individuals may avoid conspecifics by staying at the edge of the group and maintaining greater distances to their nearest neighbor.

The social cohesion hypothesis predicts that dispersing individuals will be those that engage in fewer interactions – both agonistic and affiliative. In capybaras, non-sexual affiliative interactions may include allomarking, allogrooming, social play, head nuzzling, and/or inspections. If this hypothesis is true, larger group sizes would not

necessarily lead to greater aggression toward younger, subordinate individuals. In comparison to philopatric individuals, young dispersive males should engage in fewer social behaviors overall, particularly fewer affiliative behaviors. They should also engage in less play and inspection behavior. These individuals may also spend more time at the edge of the group with fewer conspecifics in close proximity.

METHODS

Study Species

Capybaras are large (~50kg) caviomorph rodents that live in groups averaging around 10 individuals with large variation in group size (approximately 4 to 40 individuals; Herrera and Macdonald 1987). These groups are stable, i.e. membership remains more or less unchanged for over a year, with each group consisting of a dominant male, several females, their young and one or more subordinate males (Herrera and Macdonald 1987). At El Frio ranch in Venezuela, these subordinate males were proper group members, as opposed to 'floaters', for at least two years (Herrera 1986). A rigid dominance hierarchy is evident among the males, with the dominant individual being older, larger and obtaining significantly more matings than subordinates (Herrera and Macdonald 1989; Salas 1999). The subordinate males apparently queue for dominance (Herrera and Macdonald 1993), with age being the only significant correlate with dominance once it is corrected for size (Salas 1999). The mating system is polygynous and there may be a certain degree of cooperative breeding, in the sense that young are maintained in 'creches' and lactating females indiscriminately nurse their own and alien young (Macdonald 1981; Salas 1999).

Capybaras live in non-overlapping territories defended by all adult group members, including subordinate males (Herrera 1986, Herrera and Macdonald 1989, 1993). A territory typically includes a grazing patch, bush or shade, and a section of a pond or river (Herrera and Macdonald 1989). In the dry season, the scarcity of water can lead groups to congregate at water holes in groups of up to 100 individuals with little aggression being exhibited (Herrera 1986; Herrera and Macdonald 1987). The availability of a water source appears to be very important in that it is used for predator avoidance, wallowing for temperature regulation, and mating (Macdonald 1981; Herrera 1986). Some researchers describe capybaras as the hippopotamus of the New World (Salas 1999), filling the niche of the large, semi-aquatic herbivore. Since the availability of these water sources varies across sites, it may be expected that territorial spatial relationships and population densities also vary between sites and could have consequences for dispersal patterns.

Two previous studies have examined the dispersal of capybaras and revealed possible variation or condition-dependent patterns. Based on research conducted at Hato El Frio, approximately 60 km from the site of the current study, Herrera and Macdonald (1987) proposed that dispersal might occur in groups consisting of both males and females. Anecdotal evidence suggested a scenario wherein a subordinate adult male is joined by several yearlings to form a new group with the adult male as the dominant individual (Herrera and Macdonald 1987). In a mark-recapture study, Herrera (1992) found no sex-bias in dispersal. On the other hand, research conducted by Salas (1999), at the site of the current study, showed that all males dispersed as juveniles while only 25% of females dispersed, with most females remaining philopatric (Salas 1999). These results

from El Cedral are more typical of the male biased dispersal found in most mammals (for reviews see Greenwood 1980, Shields 1987, Chepko-Sade and Halpin 1987).

Furthermore, most sub-adult males in the Salas (1999) study were solitary, comprising a floater population that was not observed in the El Frio study nor in the current study. The presence of floaters may be an indication of saturation, but this can not be confirmed. The current study found significant male-biased dispersal, with 20 of 23 juvenile males dispersing and none of 26 juvenile females of the same cohort dispersing (Chapter 2).

Study Site

Hato El Cedral (7°25'N, 69°20'N) is located approximately 200 km west of San Fernando, Apure State, and covers close to 50,000 hectares. A population of approximately 10,000 capybaras comprising several hundred social groups is distributed throughout the ranch, although groups tend to concentrate around large, permanent water bodies, particularly in the dry season (Ojasti 1973; Macdonald 1981; Herrera and Macdonald 1987). The large size of the ranch and lack of fencing low enough to restrict capybara movement (they can go under the fencing) allow for studies under natural conditions but with poaching controlled (Ojasti 1991; E. Herrera, pers. comm.). The core study area was in the approximate center of the ranch, such that dispersing individuals were more likely to settle within ranch boundaries post-dispersal.

The ranch is located in the seasonally flooded savannas (*llanos*) of Venezuela. Despite the apparent flatness of the land, there are three distinct kinds of terrain, differing in their height, soil and vegetation cover. Highest are '*bancos*', banks of former rivers or parts thereof, usually covered in tall grasses or bushes. The '*bajios*' comprise some 75% of the landscape and are covered in short, highly palatable grasses. And the lowest lands,

'*esteros*', are swamps, ponds and lakes, many of which dry up completely in the dry season. Isolated patches of woodland are also scattered around the ranch and gallery forests line the major rivers. Banks and woodlands are usually not flooded, while *bajios* tend to be covered by a few centimeters of water except in the height of the dry season. Many private ranches, including El Cedral, manipulate the water levels with dykes, keeping some areas with water year-round and draining others for cattle.

Capture and Identification

Individuals were captured using traditional methods: chasing from horseback and lassoing. All capturing procedures were conducted during the transition of the wet to dry season. At this time of year, the ground has dried enough for the horses to effectively round-up groups, but the drought is not yet severe enough to put the capybaras in danger of over-heating during the stress of capture. Due to the scattering effect of this method, it was not possible to mark entire social groups.

A total of 290 individuals were captured and tagged and another 8 individuals were identified by some natural scar or obvious feature (Chapter 2). Once captured, individuals could be restrained by hand for processing, which took no more than a few minutes and was done at the site of capture. Each animal was weighed and marked with one tag in each ear of varying color and unique numbers. Several measurements and ear notch tissue samples were also taken for another study. Each individual's sex was determined with palpation of the abdomen to expose the penis or lack thereof. Approximate age was determined by weight for those individuals less than 35 kg (see Table 1 for details; Ojasti 1973). All others were classified as adults but more accurate age estimates for adult live individuals are not currently available.

Social groups with at least three juveniles marked and reasonable accessibility were chosen as focal groups. Initially 13 focal groups were spaced along an east to west dirt road with from 3 to 17 individuals marked. An additional four to seven group in the area were monitored for composition but could not be accessed for capturing.

Immediately following the marking procedure, only group location and composition were noted for several days, to ensure that membership had stabilized following the disturbance of capture.

Behavioral Observations

Behavioral observations were conducted from April through June 2004 and from April 2005 through June 2006, for a total of 1180 hours over 15 consecutive months. On average, each focal group was observed for 74 hours. The openness of the terrain made it possible to observe the entire social group at once, with the exception of individuals that might be hiding under bushes, where the social behaviors of interest were unlikely to take place due to lack of space. Each observation session began with noting group location, using a Garmin 12XL Global Positioning System, compass, and digital range-finder to calculate the coordinates of the approximate center of the group. Group composition and relative location (core, edge, or periphery, see Table 1) of each marked individual were noted every hour.

Two methods were used for documenting social behavior: focal individual observations and focal group observations. Focal *individual* observations were conducted for each marked animal for 10 minutes, noting nearest neighbors, all occurrences of social behaviors, and event behaviors such as scent marking. During focal *group* observations, all occurrences of social interactions involving a marked individual were

documented for all individuals in the group noting general age class and sex (if possible) for any un-marked participants. Focal group observations continued for a maximum of four hours or until the group moved out of sight. Interactions between two unmarked individuals were noted on an opportunistic basis. For every behavior several parameters were noted: date, time, initiator, recipient, behavior, outcome (e.g., of a fight), and any additional notes. Note in the ethogram that a 'courtship' was re-classified as a 'mating' if the male mounted the female more than 4 times, based on previous data that at least 7 mounts are required for ejaculation (Ojasti xxxx, Salas 1999). This is also the definition used by Salas (1999) and allows comparisons. The detailed ethogram used was modified from several previous ethograms and is available upon request to the author. Table 1 lists the social behaviors and definitions relevant to this study.

Detecting Dispersal

For the purposes of this study, natal dispersal is defined as the movement of individuals away from their natal area or social group to the area or social group where breeding first takes place (Clobert *et al.* 2001). This species' high levels of sociality and territoriality led me to define dispersal by establishment in a new social group, rather than by spatial location or absolute distance moved. Because successful breeding (i.e., paternity) could not be determined in this study, the group where a male first attempted to court a female was considered its breeding group. Searches of the study area to detect dispersers were conducted at least once per week year-round, more frequently when an individual had recently disappeared from a group. The road and trail system of the ranch allowed for fairly extensive searching, aided by sightings by ranch workers that could cover more ground on horseback than I could with a truck.

For the remainder of this paper, individuals that were marked as juveniles and eventually dispersed will be referred to as ‘dispersers’, including when examining their behavior prior to dispersal. Individuals that were marked as juveniles and were later defined as philopatric will be referred to as ‘philopatric individuals’. When comparing behaviors relative to the time of dispersal, philopatric individuals are considered relative to the average age of dispersal, or 15 months. Because all dispersers were males and only two philopatric males yielded enough behavioral data for consideration, the confounding variable of gender is ever-present in these analyses and their interpretation. Only disperser males and philopatric females yield enough data to analyze statistically, while philopatric males are considered separately and anecdotally.

Many juveniles that were marked either disappeared or lost their ear tags, so that they could not be classified as either ‘dispersed’ or ‘philopatric’. These individuals were excluded from analysis. Additionally, individuals that were initially captured and marked as subadults or adults could not be classified because their natal group was not known. However, these known individuals added value to the study by giving identity to the partner of social interactions with the focal individuals.

Data Analysis

To look for group effects, social groups were compared in terms of their overall size and the number of males, both measured as maximum present and average number present (see Table 1 for definitions of group membership). Age ratio was compared by calculating the maximum number of adults present relative to the maximum number of juveniles. Sex ratio of adults was similarly taken as the maximum number of males

relative to the maximum number of females. Finally, aggressive interactions per hour of observation were calculated for each group and compared.

The social correlates of dispersal were measured in several ways, including all social interactions together, aggressive interactions initiated or received, avoidance or evasive behaviors, affiliative behaviors initiated or received, location within the group, and the number of near neighbors. Aggressive behaviors include fights, chases of varying speed and duration, and threat posture. Affiliative behaviors include courtship, mating, nursing, allogrooming, allomarking, head-nuzzling, and social play. Any behaviors associated with courtship or nursing were excluded from the analysis since the nutritional and reproductive function superced the social function. They are also gender-biased: only males can court and only females can nurse.

Statistical comparisons were performed in two ways. First, age classes of juveniles, subadults, and adults for both sexes were compared with regard to each class of behaviors in order to maximize sample sizes and use all marked individuals, whether their fate as dispersers or philopatric individuals was known or not. Males that successfully dispersed were then compared to philopatric females with regard to each class of behaviors, for a closer look at their differences. Philopatric males were not included in these analyses because there were only two for which complete data were available. Hence, these individuals are described anecdotally only.

One way to look at aggression in individuals is its change over time relative to dispersal. Based on preliminary results, two months was used as a reasonable time-frame so that behaviors were compared in five time blocks: from marking to two months before dispersal or average dispersal age; two months before dispersal or average dispersal age;

transience between groups during dispersal; two months following immigration into a new group; and the remainder of the study. This study was terminated when all of the focal males had at least attempted to court a female in either their natal or secondary group. Due to the relatively short duration of the study following immigration (from three weeks for one individual to six months for another), immigrants would likely remain young subordinates in the post-natal group. Thus, individuals marked as adults were used as a representative of a sixth time frame, or that of full and established group membership. Because preliminary results showed that adult males are initiating the majority of the aggression toward dispersing males, only interactions with adult males were considered in this analysis.

In addition to outright aggression, capybaras display avoidance behaviors wherein the initiator appears to do nothing other than approach the focal individual and the focal walks or runs away immediately. These behaviors were considered separately from aggression because the intent of the initiator is not known, so they are considered from the perspective of the recipient, or the 'avoider'. If the young pre-dispersal individuals are avoiding adults, then this behavior may be a sort of 'ghost of aggression past' and support the social subordination hypothesis. On the other hand, if the adults are avoiding young individuals that may be seeking social interaction, then the social cohesion hypothesis would be supported.

Data analysis was performed with SPSS v15. Due to small sample sizes and non-normality of data, nonparametric tests were used most often unless otherwise noted.

RESULTS

Social Group Comparisons

The natal social groups of all marked juveniles did not differ in sex ratio, age ratio, maximum number of males, maximum group size, or average group size over the observation period (in all cases Chi squared, $p > .05$). Groups do differ significantly in the number of aggressive interactions per hour ($p < .001$). Further exploring this difference in aggression levels, a correlation analysis was done for aggression with dispersal age or dispersal date, revealing no such correlation (Pearson, $p = .657$ and $p = .773$ respectively.) Comparing groups with philopatric males to those without showed no differences in average group size (Mann-Whitney U, $p = .548$), maximum group size ($p = .381$), maximum number of males ($p = .381$), sex ratio ($p = .905$), age ratio ($p = .714$) or aggressive interactions per hour ($p = 1.00$). Finally, because several groups had multiple dispersers it could be shown that group identity does not affect dispersal age or date (One Way ANOVA, $p = .404$ and $p = .158$ respectively). Based on this lack of differences between groups, individual animals are considered independent samples for the rest of the analyses, regardless of their natal group.

Social Interactions

Initially, all social interactions regardless of type or intensity were considered. Over the entire observation period, corresponding to approximately four to 21 months of age, dispersing males are more interactive than philopatric females (Mann-Whitney U, $p = .010$, Figure 1). However, looking prior to dispersal or prior to average dispersal age in philopatric individuals, no difference was detected (Mann-Whitney U, $p = .959$). The two philopatric males that were observed for at least 5 hours appeared to fall somewhere in

between the other two classes, but were not analyzed statistically due to the small sample size. The third philopatric male was not visible enough to make any statements.

Due to the ambiguous nature of social inspection behaviors, they were analyzed separately from either aggression or affiliation. A repeated measures ANOVA of age and sex classes showed a significant interaction between inspection direction and gender ($p = .003$). Males initiate more inspections than they receive (Wilcoxon Signed Rank Test, $p = .019$) but females do not differ in the number that they initiate or receive ($p = .126$). Over the entire study period, disperser males initiate more inspections than philopatric females (Mann-Whitney U, $p = .047$), but this difference was not significant prior to dispersal date or similar age of philopatric individuals ($p = .904$).

Agonism

Aggressive interactions were considered separately. Comparing gender and age classes over the entire observation period revealed several differences (Figure 2). First, a significant three-way interaction of aggression initiated or received, age, and gender was detected (Repeated Measures ANOVA, $p = .004$). Transforming the repeated variable of aggression initiated and received into an average, there were significant effects of age ($p < .001$), gender ($p < .001$), and an interaction ($p = .002$). Specifically, subadults and adults both engage in more aggression than juveniles, males more than females, and collectively individuals receive more aggression than they initiate. However, adults initiate more than they receive ($p = .003$) while juveniles and subadult males receive more than they initiate (Repeated measures ANOVA $p = .002$ and $p = .002$) but subadult females show no difference in aggressions received or initiated (Wilcoxon Signed Rank Test, $p = .497$). In juveniles, no difference in aggression is seen between males and females (ANOVA $p =$

.595) but, in subadults and adults, males interact aggressively more than females ($p = .001$ and $p < .001$ respectively). A planned contrasts ANOVA of subadult males shows that they receive more aggression than any other group ($p < .001$).

A fresh variable was created by taking the logarithm of interactions received (R) over interactions initiated (I), thus giving a measure of the discrepancy between the two (Figure 3). Taking the log of the variable resulted in normality so that parametric statistics could be used. This R/I Index was significantly greater in juveniles and subadults than in adults and there was no difference detected between the genders (ANOVA with age $p < .001$ and gender $p = .606$). This greater discrepancy between aggression received and initiated in younger animals could either be due to relatively few interactions being initiated or relatively many being received. A planned contrasts ANOVA revealed a greater R/I Index for subadult males over any other group ($p = .004$).

Next, the initiators of the aggression toward focal individuals was considered (Figure 4). Subadult males receive a greater proportion of their aggression from adult males (as opposed to adult females) than do subadult females (Z score, $0 < .01$). Furthermore, for both sexes, same-sex aggression is more common than male-female aggression (Chi Square Test, $p < .01$). Juveniles appear to interact equally with other juveniles of either sex, but these data are less conclusive due to the difficulty in identifying the sex of unmarked juveniles and thus the lower sample-size than any other category.

In individuals that were marked as juveniles and later defined as either dispersers or philopatric, over the entire observation period, disperser males both initiate and receive more aggression and have a higher R/I Index than do philopatric females (Figure 5,

Mann-Whitney U, initiate $p = .026$, receive $p < .001$, R/I index $p = .055$). Disperser males receive more aggression than they initiate (Wilcoxon Signed Ranks Test, $p = .017$), but philopatric females do not ($p = .679$).

Considering only the time before dispersal or similar age, dispersal males show a marginal trend to initiate more aggression than philopatric females (Mann-Whitney U, $p = .066$). This difference becomes significant if only the last two months prior to dispersal and corresponding age in philopatric individuals is considered (Figure 6, Mann-Whitney U $p = .047$). Disperser males do not receive more aggression than philopatric females, whether considering the entire time-frame before dispersal (Mann-Whitney U, $p = .217$) or only the last two months ($p = .270$).

Aggression initiated by adult males toward disperser males and philopatric females does not differ, whether calculated as proportion of aggression received (Mann-Whitney U, $p = .370$) or rates of aggression per hour ($p = .139$). However, disperser males do receive more aggression from adult males than from adult females (Wilcoxon Signed Ranks Test, $p = .050$) while in philopatric females the difference in sex of initiator is not significant ($p = .327$; Figure 7).

Looking at the change in aggression by adult males over time, philopatric females show no significant differences in aggression initiated (Friedman Test, $p = .655$) or received ($p = .698$) across the five time frames (see Methods for details). Adult females do initiate more aggression than young females (Friedman Test, $p < .001$), but do not receive more ($p = .563$). Dispersing males show an increase in aggression both initiated and received during the juvenile stage, pre-dispersal, and transience (Friedman Test, $p = .016$ for both), but then stabilize at levels similar to adult males for the post-dispersal and

young member stages, once they have immigrated into a new group (Friedman Test, initiated $p = .584$, received $p = .116$, Figure 8). There is a particular peak in received aggression while they are transient.

Looking at sex and age classes of avoidance behavior, subadult males again show a peak, as with outright aggression (Figure 9). An ANOVA revealed a significant effect of age such that subadults avoid conspecifics more than either juveniles or adults ($p < .001$). Overall, males display more avoidance behaviors than females ($p = .001$), but this difference is driven by the subadults, with no difference in juveniles and the reverse trend in adults (i.e., adult females avoid more than adult males). A planned contrasts ANOVA showed that subadult males engage in more avoidance behaviors than any other group ($p < .001$). Looking at the initiators of the avoidance, or the individuals that are being avoided, subadult males avoid other males more than they avoid females (Chi Squared, $p < .01$) while subadult females show no differentiation between avoiding males and females ($p < .01$).

Disperser males and philopatric females do not differ in their avoidance behavior prior to dispersal or average dispersal age, whether considering the entire study period (Mann-Whitney U, $p = .436$) or in the last two months prior to dispersal ($p = .519$). The initiators of this avoidance could not be evaluated statistically due to the prevalence of zeroes in the data set. Avoidance behaviors over the same five time intervals used for aggression show that disperser males increase their avoidance drastically when they are transient and then decline, but not to their natal levels, as subordinate members of a group (Figure 10, ANOVA, $p = .048$). Philopatric females decrease their avoidance behavior as they get older (ANOVA $p = .002$).

Affiliative interactions were investigated in similar ways as aggression, first with classes of age and gender, then with individual dispersers and philopatric individuals. Affiliative behaviors included play, nuzzles, allogrooming and allomarking. A repeated measures ANOVA with affiliation initiated or received, age class, and gender showed no interaction between variables ($p = .680$). Overall, individuals initiate more than they receive ($p = .003$). Juveniles engage in more affiliative behaviors than subadults or adults, primarily because of their tendency to play ($p < .001$). No difference in overall affiliation was detected between males and females ($p = .391$).

Looking specifically at disperser males and philopatric females, no significant differences in affiliation were detected for the entire study period (Mann-Whitney U, initiated $p = .452$, received $p = .363$, R/I index $p = .816$) or before dispersal date or age (initiated $p = .274$, received $p = .641$, R/I index $p = .691$) or for the two month time period immediately prior to dispersal (initiate $p = .606$, received $p = .438$, R/I Index $p = .438$).

Comparing the tendency for same-sex pairs of individuals to engage in aggressive versus affiliative interactions showed that both males and females are more likely to interact aggressively rather than affiliatively (Chi Squared Test, $p < .01$). However, females are more likely to behave in an affiliative or neutral manner than are males ($p < .01$). Over 80% of male-male interactions are aggressive while only 60% of female-female interactions are aggressive.

In addition to being included in the affiliative behaviors, play was analyzed in isolation because of its potential importance in determining later social relationships. No difference was detected between dispersal males and philopatric females in the frequency

of play (Mann-Whitney U, $p = .528$). In many cases, the initiator and recipient of play could not be determined because it appeared mutual, and so individuals were not distinguished in this way. Play bouts were almost exclusively between juveniles or subadults, so adults were excluded from this analysis.

Another measure of the avoidance of potential aggression is the relative location of an individual within the group, either in the core, at the edge, peripheral, or away. All young individuals spend more time in the core than at the edge (Wilcoxon Signed Ranks Test, $p < .001$). Disperser males spend a greater proportion of their time in the core of their natal group than do philopatric females and philopatric males spend even less time in the core (Kruskal-Wallis Test, $p = .019$, Figure 11). In this case there was sufficient data for all three philopatric males so they were included in the analysis.

Near neighbors were defined as individuals within two body lengths of the focal individual and were used as a measure of tolerance of individuals to one another (See Table 1). Looking at all marked individuals, juveniles had more near neighbors than did subadults, which had more than adults, and this was true for both males and females (ANOVA, age $p < .001$; gender $p = .257$). Looking at adult neighbors only, since adults are more likely to be aggressive and less tolerant, females had more adult neighbors than did males, with no effect of age (ANOVA, age $p = .663$, gender $p = .028$, interaction $p = .111$). Specifically comparing subadult males to subadult females as the potential dispersal age, males again had fewer adult neighbors than did females (Mann-Whitney U, $p = .007$). The proportion of scans with at least one neighbor is also greater for juveniles and subadults than for adults (ANOVA, age $p = .018$, gender $p = .028$, interaction $p = .169$; Figure 12). Comparing disperser males to philopatric females two months prior to

dispersal or to average dispersal age (Figure 13), dispersers have marginally fewer adult near neighbors than do philopatric females ($p = .068$) and marginally fewer scans with at least one neighbor ($p = .068$). Philopatric males were never seen with a near neighbor, but there were only two philopatric males.

Table 2 shows a comparison of the behavior of philopatric females, disperser males, and philopatric males in the first two years of life, the time frame of this study. In only one case was there sufficient data to compare philopatric males statistically with the other two groups, thus this latter comparison is largely anecdotal and strong conclusions cannot be drawn from it.

DISCUSSION

These data show that young males and females are experiencing differing social environments during maturation that correlates with their likelihood and timing of dispersal. Males are overall more interactive and more aggressive than females, a trend that continues into adulthood. The increase in a male's aggression does coincide roughly with dispersal, while age and season of dispersal vary. Age of dispersal ranges from 9 to 19 months and the only season that appears unsuitable is the height of the dry season (Chapter 2). While the social cohesion hypothesis is clearly not appropriate for this system, the data do not agree completely with the social subordination either.

The social cohesion hypothesis was refuted by some of our data and supported with other. Differences in affiliative behavior between dispersers and philopatric individuals can be completely explained by gender differences and do not relate to dispersal date or age. Looking at all social interactions together, dispersing males are more interactive than philopatric females, which is contrary to the predictions of the

hypothesis. Furthermore, disperser males are more often in the core of the group than philopatric females. However, disperser males do have fewer near neighbors than philopatric females, which does fit with this hypothesis. Given that only one comparison supports this hypothesis, these data do not support a lack of cohesiveness as a major force in determining dispersal in capybaras.

At first glance these results seem to support the social subordination hypothesis as it was first proposed by Christian (1970). This hypothesis proposes that aggression is the manifestation of competition between males. In capybaras, a polygynous mammal, this competition is most likely for access to females (Greenwood 1980). While Christian's original hypothesis looked for this aggression to occur during peak density, in capybaras there is no clear relationship between group size and aggression. On the contrary, during the crowded conditions around water holes in the dry season, aggression is actually lower and there is a greater tolerance of extra-group individuals (Herrera 1986). The relationship of this crowding and lack of aggressiveness remains to be investigated further.

The role of population density was not directly tested with this study, but capybaras do undergo significant density fluctuations through the year which can be compared to the timing of dispersal. Density is greatest during the peak of the dry season, when several groups may be crowded together around shrinking bodies of water (Herrera 1986). In other sites, where dry land during the wet season is a limited resource, density increases at these sites during the peak of the wet season (Aldana-Dominguez et al. 2002). In this study, dispersal took place most often during the transition between seasons, when there was more of a balance of dry land with good forage and available

water (Chapter 2). This suggests that the availability of resources (both forage and water) dictated the timing of dispersal more than the local density. These results taken together suggest that the motivating force for dispersal is related to aggression, but that aggression is not exacerbated by increased population density.

In microtine rodents, for which the social subordination hypothesis was first proposed, dispersers had more wounds but were generally less aggressive than resident animals (Christian 1970). That is, they received more aggression but did not initiate it. In capybaras, however, subadult males *initiate* more aggression than juveniles or females of any age. They are not passive recipients, but are provoking at least some of the aggression received from adults. Future dispersers in particular initiate more aggression during their last two months in their natal groups. This increased aggressiveness is maintained into adulthood, even as young subordinates in their secondary group.

Interestingly, these future dispersers spend more time in the core of the group, and yet have fewer near neighbors than do philopatric females. This result must be viewed in light of the definitions of 'core' and 'near neighbor' used here (see Methods). In other words, while dispersers are in the spatial middle of the group, with at least one individual farther away from the spatial center than themselves, they are spaced from other individuals by at least two body lengths. Other studies have shown that juveniles tend to be at the core of social groups, while most individuals at the periphery are males (Macdonald 1981). This may represent a transition for these young males as they are accustomed to being in the core as young but are less and less tolerated in close proximity to older individuals. These results further suggest that the young males are more

interactive and more aggressive, but less tolerated by other group members as they approach dispersal age.

Several factors suggest that the aggression in males is not due to the other dispersal-related scenarios described by Holekamp (1986). The capybaras of this study are harvested each year, keeping their density well below saturation (Salas 1999), so that the dispersal witnessed was natal, not saturation dispersal. Furthermore, while females may be more likely to act aggressively toward their maturing young when they are preparing to give birth, aggression by males far exceeded female aggression, making maternal aggression unlikely to be the determining force of emigration. Finally, take over of a group by a new male was not seen in this study, despite the numerous occurrences of dispersal. However, this may be another contributing factor leading to increased dispersal. A preliminary study of the results of removal by harvest of a dominant male did show that aggression in the group increased as a new dominance order was established (Salas 1999). This increase may also be true if the dominant male is expelled by a new male.

Taken collectively, these results suggest that capybaras have at least two behavioral variants that coincide with gender: aggressive-dispersive males and tolerant (maybe even cooperative)-philopatric females. A similar suite of traits was identified in wild house mice by Rusu and Krackow (2005) wherein agonistic onset in males coincided with dispersal. Young male house mice behave amicably, with what these authors term a submissive-philopatric strategy. As they mature, this strategy switches to an agonistic-dispersive strategy which seems to be driven by a shift in their emotional reaction norm – measured as ‘anxiety’ in that study. In other words, the levels of

aggression from adults don't change, but the young males' response to that aggression changes and their 'coping' strategy is dispersal. They further suggest that at least in that species, the young male is likely to challenge the dominant, territory-holding male before dispersing.

This scenario fits well with my behavioral data on wild capybaras, although I did not test emotional anxiety. Juvenile male capybaras engage in similar levels of play and affiliation as same-age females, both with very low levels of agonism. As they mature, females do not significantly shift their behavior, except to reduce play, and while aggression from adults does increase, it does so equally for males and females. Subadult males, however, increase their agonistic behavior, initiating more aggressive interactions, particularly with other males. It is at this age as well that they disperse. Thus, capybaras are exhibiting a switch from juvenile affiliative behavior to agonistic behavior that coincides with dispersal. It thus appears that the physiological cue that increases agonism may be related to the cue that encourages dispersal. Or perhaps an agonistic 'personality' in itself is a driver of dispersal, particularly in species with social dominance maintained via aggression.

This relationship between dispersal and aggression may be due to an ontogenetic reduction of juveniles' response thresholds to relatively constant levels of conspecific aggression. This hypothesis predicts that juvenile males should terminate agonistic interactions initiated by conspecifics more quickly or frequently than do juvenile females (Holekamp 1986). The tendency for capybara subadult males to engage in more avoidance behaviors than subadult females could be an indication of this change in response threshold. Furthermore, the decrease in female avoidance behavior over time

could be an indication of their threshold changing in the opposite direction as they mature. Perhaps the natural increase in testosterone as a male matures leads to an aggressive and dispersive behavioral morph that is independent of group size or available resources. However, the tendency for most individuals to disperse at a seasonal transition (Chapter 2), with a wide range in ages and well after the testes descend (Congdon, in prep), suggests that there is an environmental cue being used as well. There could be a role for the ontogenetic switch hypothesis (Holekamp 1986) wherein individuals disperse in response to some physical change in body size or weight, which would be dependent on available resources.

The ontogenetic switch hypothesis (Holekamp 1986) proposes that natal dispersal is triggered by ontogenetic change in the animal's internal milieu, rather than by a particular stimulus configuration (e.g., resource shortage or conspecific aggression) in its external environment. Specifically, this hypothesis proposes the existence of a sex-linked mechanism causing dispersal and associated behaviors to occur in males when they attain some minimal body mass or store some minimal amount of energy as fat. In Belding's ground squirrels, this hypothesis states that dispersers should be heavier, or exhibit different patterns of mass gain, than animals of equivalent ages still residing in their natal areas. The hypothesis also predicts the existence of an unambiguous sex difference in frequencies of all behaviors tightly associated with the dispersal event. In Belding's ground squirrels, male emigrants were heavier than males of equivalent ages still in their natal groups. If body mass in young capybaras could be monitored in the wild, we might expect a correlation between body condition and dispersal date. This would be in direct contrast to the dispersers from cycling microtine rodent populations which generally

weighed less than resident animals (Gaines and McCleneghan 1980), intuitively due to the higher density and/or resource shortages that promote dispersal in the social subordination hypothesis.

Philopatric males might provide an opportunity to explore this ontogenetic switch in behavioral morph hypothesis more fully, but their rareness makes this difficult. The only parameter for which enough data were available to compare them statistically to dispersing males was their tendency to stay out of the core of the social group. However, taken collectively, the set of anecdotal data does suggest that these males behave differently from dispersing males and warrant further investigation. It may be that these philopatric males do not experience the increased agonism, perhaps have less testosterone.

Further data on reproductive success is needed to determine the fitness consequences of each behavioral type in males. However, our behavioral data do show that at least one philopatric male was able to achieve a first mating attempt (having mounted a female over 11 times in succession) earlier than dispersing males (Chapter 4). A relatively complex set of trade-offs may balance the fitness of philopatric and dispersive males. Philopatric males risk mating with a relative and may only be accepted by younger females (Bedoya 2007), who are inexperienced and possibly poor mothers. Older females may be better able to protect newborns from predators and infanticidal males (pers. obs.).

Other studies of capybaras have yielded some varying results and provide interesting insights into potential variability in behavior, especially with regard to dispersal and group membership. Herrera (1986; Herrera and Macdonal 1987)) studied

the capybaras of Hato El Frio, approximately 60 kilometers from Hato El Cedral where the current study was conducted. At the time of that study, the capybara population was stable, but the extent of habitat saturation is not known. Herrera (1992) reported dispersal of both males and females, in what appeared to be groups of siblings, or at least young from the same natal territory, dispersing together and for several kilometers. Another study conducted at Hato El Cedral, several years before the current study, reported a high population density and as much as 40% of the males were defined as 'floaters' without stable group membership (Salas 1999). The current study at Cedral found the population reduced to about half the 1998 population and only a small handful of males that appeared to "float" between groups. Furthermore, neither Cedral study showed any dispersing females. Perhaps the differences between these ranches in terms of suitable habitat between territories and habitat saturation are determining the differences in male behavior. If the objective is to conserve the evolutionary potential of populations, capybara dispersal could represent a textbook example of environmentally-determined behavior that deserves protection (Buchholz and Clemmons 1997).

Table 1. Ethogram and definitions of relevant behaviors and terms for a study of capybara dispersal. A complete ethogram is available upon request to the author.

Two event behaviors are considered different bouts if they are separated by another defined behavior, a change in participant, or at least 5 minutes, unless otherwise noted.

Social Behavior

Approach Initiator walks toward an individual, coming within 2 body lengths, and the recipient does not immediately (within 5 seconds) move away. Initiator either stops or engages in some social interaction (i.e. not just passing by).

Inspect Initiator sniffs at another individual, typically but not exclusively at the snout or rump. (~Herrera 1986)

Agonism

Displace An initiator walks toward an individual, who moves away without direct contact. Initiator typically points its snout at the recipient. (~Salas 1999) This definition includes the immediate approach. The initiator may or may not take the place of the recipient.

Rebuff An individual moves its head swiftly toward another individual, as if to bite, moving only its head and/or upper body. Recipient backs away, not necessarily far. Distinguish from 'Lunge'.

Lunge Initiator runs toward an individual, who moves away. Initiator may bite or tooth chatter. Initiator travels less than 10 meters. (~Salas 1999)

Slow chase Initiator walks toward an individual and the recipient moves away. Initiator and recipient travel more than 10 meters (~Salas 1999) Distinguish from 'Follow', where the leader does not change its pace. Lunge may be embedded, but chase overrides it.

Chase Initiator runs toward an individual and the recipient moves away. Both travel more than 10 meters. Initiator may bite or tooth chatter. (~Salas 1999) Slow chase or lunge may be embedded, but fast chase overrides them

Disrupt (Courtship disruption) An individual prevents another male from mating or interrupts him after one or more mounts. (~Salas 1999) Initiator approaches a courting pair, coming within 10m of either male or female, and the male stops courting. The recipient is the courting male.

Attack Initiator bites or tries to bite a recipient and the recipient does not reciprocate. Distinguish from 'fight'.

Fight Animals bite at each other and one eventually flees (or dies). Note flee separately. Typically, both animals jump at each other and embrace for a short time while attempting to bite the opponents face or shoulders. This is normally preceded by a threat. (Salas 1999) Distinguish from 'play'.

Flee An individual walks or runs away from an agonistic encounter, moving at

least two body lengths. While this is embedded within the definitions of other interactions, it may stand alone if the focal animal is not the recipient of the agonism or after a fight.

Threat Initiator assumes a head high, shoulders back posture when approached by another individual (the recipient). May or may not teeth chatter. (~Herrera 1986)

Affiliation

Nuzzle An individual will rub another individual's face or anterior with its own face, but not with the morrillo (snout scent gland).

Allogroom Biting a companion gently, typically around the neck and facial area but could be any body part or ear tag. (~Salas 1999) The recipient does not 'flee'.

Allomark Initiator rubs its morrillo (snout scent gland) against the face or rump of another individual. (~Salas 1999)

Court Male closely follows the female with his head held high and his chin close to her rump and mounts less than four times, maybe not at all. Distinguish from 'mate'. (~Salas 1999)

Mate Male closely follows the female with his head held high and his chin close to her rump. The female lowers her rump and the male mounts her. Male mounts at least four times. Distinguish from 'court'. (~Salas 1999)

Nurse When an individual suckles or attempts to suckle on a female.

Play Any close contact, non-aggressive (no injury or threat posture) interaction between two individuals in which neither individual flees; without injury, submission, or escalation to fighting. It typically involves wrestling-like movement wherein two individuals lunge at one another on their hind feet, embrace and fall over together. May include one or more individuals seeming to spontaneously leap into the air.

Location

Out of Sight Animal is known present, but not visible (e.g. behind a tree or under water). More than 30% OOS in one focal session will nullify that session.

Core Imagining a line from the spatial group center to the focal animal, at least one other individual is farther away from the center OR there are animals in two opposite compass directions.

Edge No other individuals are farther away from the center of the group than the focal individual but the focal is not peripheral

Periphery The focal animal is farther away from other group members than the average distance between any two group members, but closer than any neighboring group. Less than 100m from the nearest group member.

Away The focal individual's location is known but is beyond the periphery of the group's current location. More than 100m from group and/or out of the known territory.

Near Neighbor The closest individual in every direction within two body lengths. If there is a row of individuals so that three or four are all within two body lengths in the same direction, only the closest will be noted. If the focal animal is in the center of a circle of five animals, the focal individual has five near neighbors.

Age Classes

Baby / Infant Socially dependent on mother or females, typically < 4 kg. Field identification: stick closely to female or other babies, ~3 kg or less.

Juvenile Independence to 11.9 months; up to 24.9 kg
Field identification: noticeably / undoubtedly smaller than an adult.

Subadult 12 to 17.9 months; 25.0 to 35.9 kg
Field identification: males have visible testes but no morrillo; females same size as known subadult

Adult 18.0 months and older; 36.0 kg and heavier
Field identification – males have visible testes and prominent morrillo; females are same body size as adult males but with no visible testes and only small morrillo, if any.

Group Membership / Changes

Disperser Individual no longer associates with its natal group and is repeatedly seen outside its natal territory. If that individual engages in courtship or mating in the secondary group, it is considered an immigrant to that group.

Philopatric An individual remains in its natal group until adulthood AND / OR is observed courting or mating in the natal group AND / OR gives birth in the natal territory.

Member An individual is repeatedly seen in only one group, interacts with other group members, and may engage in courtship or mating.

Satellite Group Member An individual repeatedly seen in the territory but rarely observed interacting with other group members. These individuals are often peripheral or at the edge of the group. They are not seen in any other group's territory (see Floater).

Floater An individual is observed in more than one territory and may interact with members of either territories' social group.

Table 2. A comparison of behaviors in three classes of individual capybaras: philopatric females, disperser males, and philopatric males. For philopatric females and disperser males, only statistically significant differences are listed. The comparison of two philopatric males was not statistically analyzed and is anecdotal only, except where noted. Information in parentheses was true for subadults as a whole, but not for the focal individual subgroup.

Behavior	Philopatric Females (Subadult Females)	Dispersed Males (Subadult Males)	Philopatric Males (n = 2)
Over the entire study period – approximately 4 to 21 months of age			
All Social Interactions	Lower	Higher	Low
Aggression	Less aggression	More aggression	In between
Aggression – comparing initiated to received	Initiate and receive ~equally (Less difference between)	Receive much more than initiate (Greater difference between)	Receive more than initiate
Avoidance behaviors	Less (Less)	More (More)	In between
Pre-Dispersal or equivalent age only			
Aggression	Initiate little	Initiate more	Initiate very little, receive in between (n = 1)
Aggression received from adults	Receive equally from males and females	Receive more from males than females	Receive equally from males and females
Avoidance	(Avoid males and females equally)	(Avoid males more than females)	
Time spent in core	Less	More	Less than females (n = 3, significant difference)
Near Neighbors (adults)	Marginally more	Marginally fewer	None
Over Time Stages from Juvenile to Young Adult Group Member			
Aggressive interactions with adult males	No change over time	Increase over time, peak aggression during transience	No change over time
Avoidance	Decrease over time	Increase until in new group, then decrease	No change over time

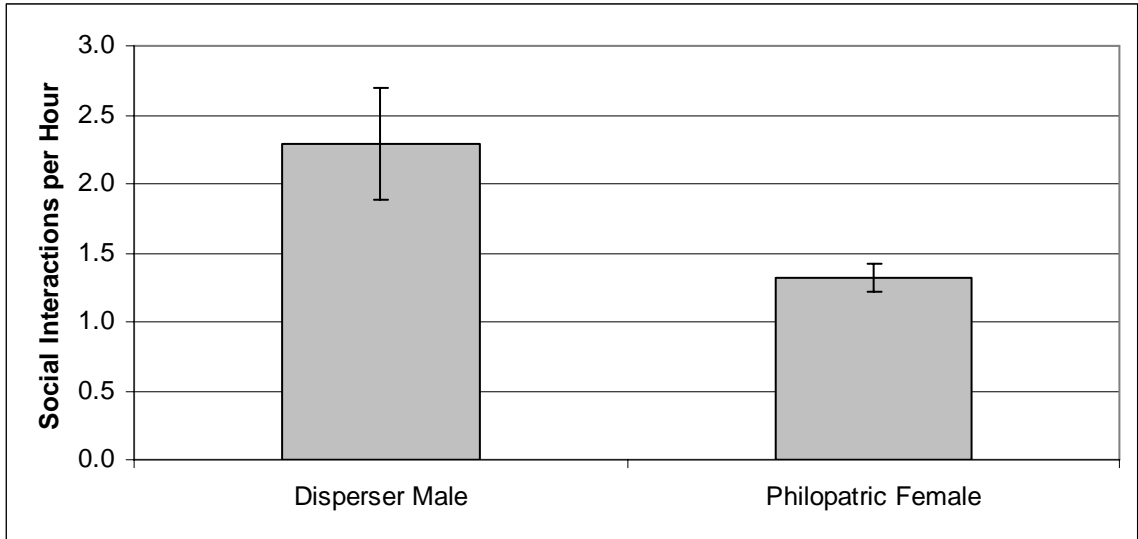


Figure 1. Social interactions per observation hour for Disperser Males and Philopatric Female capybaras for the entire observation period, corresponding to approximately 4 to 21 months of age. Mean and standard error are shown.

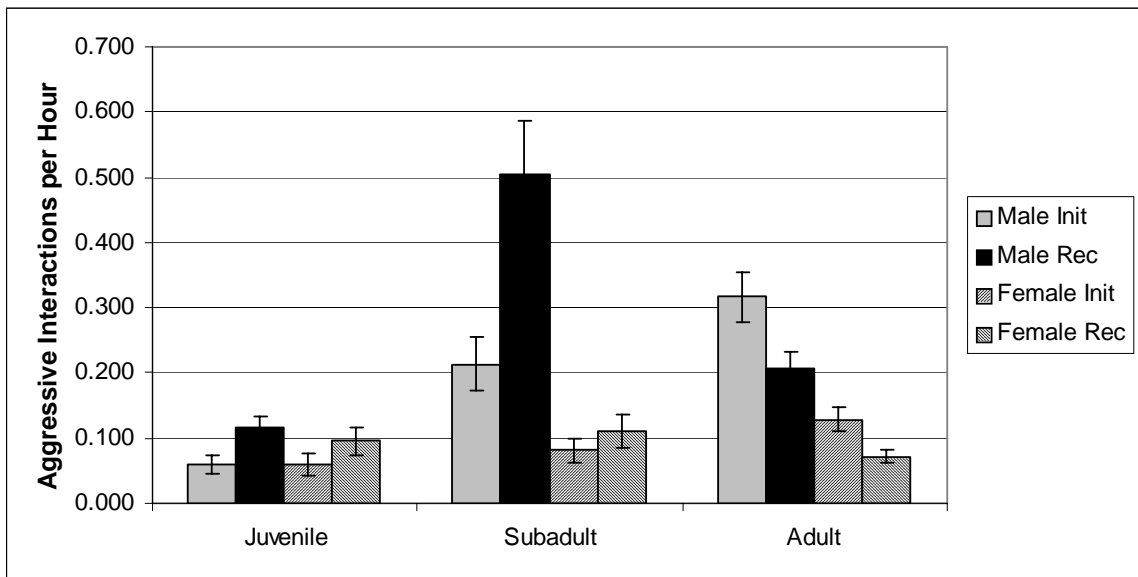


Figure 2. Aggressive interactions across sex and three capybara age classes: juvenile, subadult, and adult. Each age class is divided into males and females and each sex is further divided into interactions initiated and received. Mean and standard error are shown.

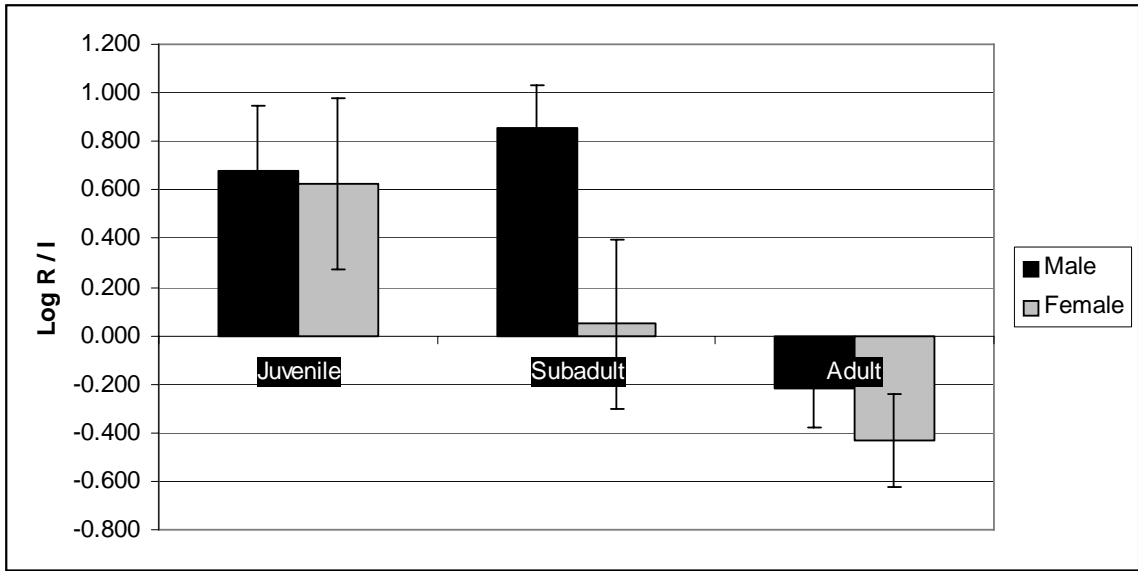


Figure 3. The log of the ratio of aggressive interactions received to those initiated for both sexes of capybaras in each age class. Mean and standard error are shown.

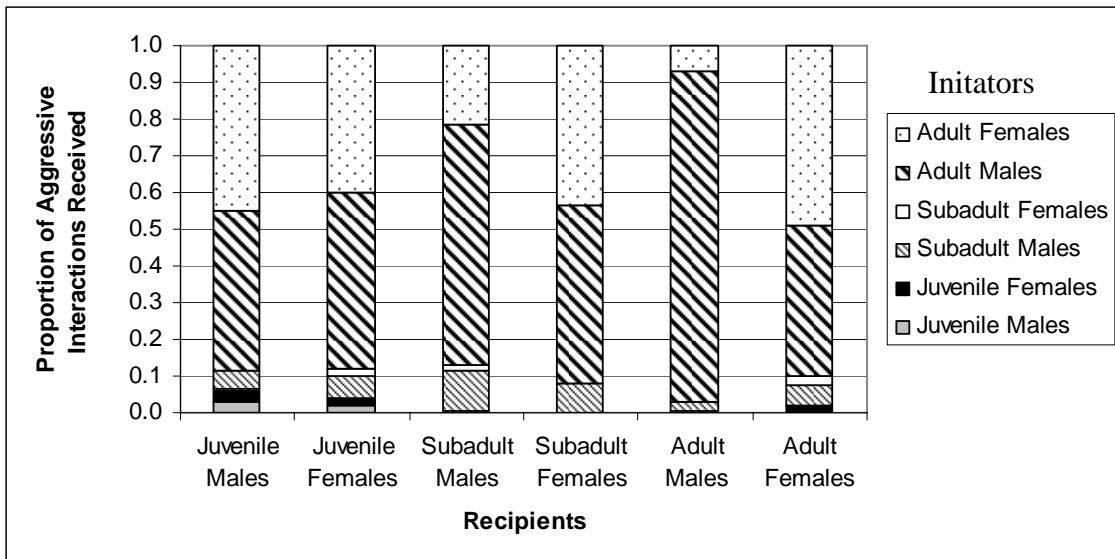


Figure 4. Proportion of aggressive interactions in capybaras received from each initiator class.

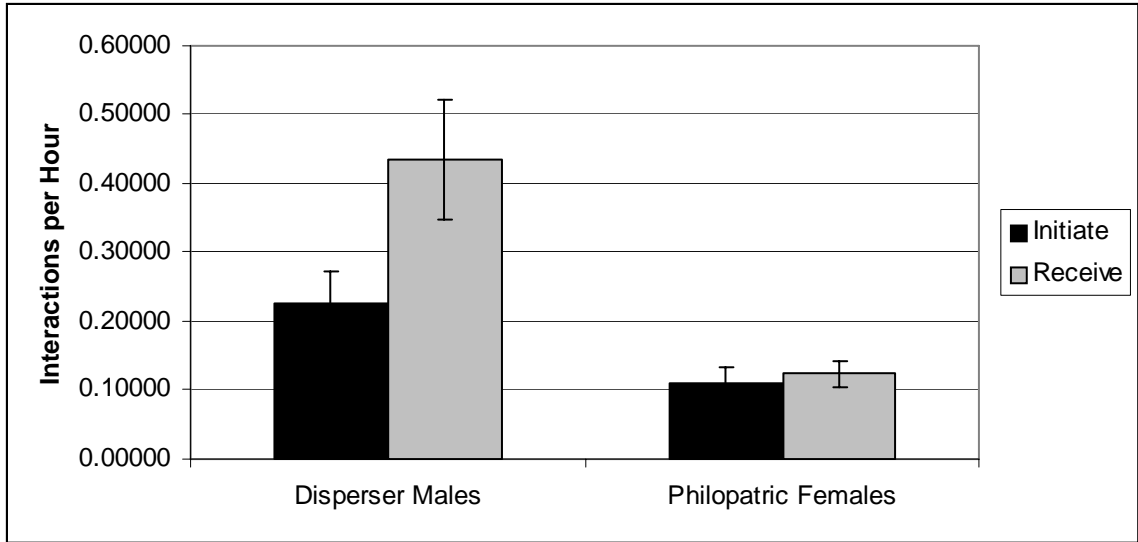


Figure 5. Aggression over the entire study period in disperser males and philopatric female capybaras. Mean and standard error are shown.

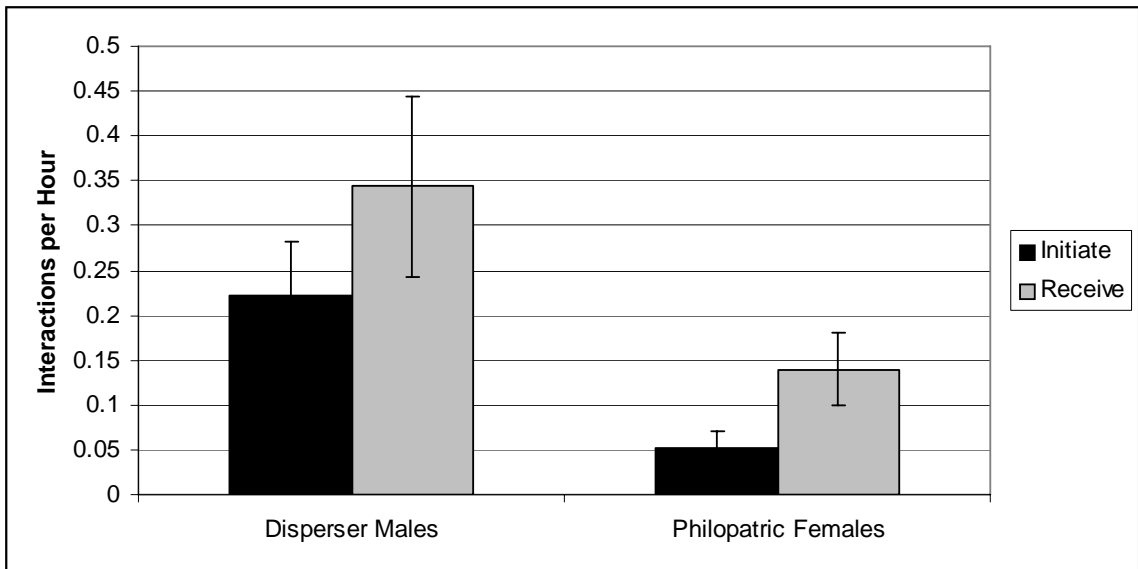


Figure 6. Aggression in the last two months prior to dispersal and the corresponding age in philopatric individual capybaras. Mean and standard error are shown.

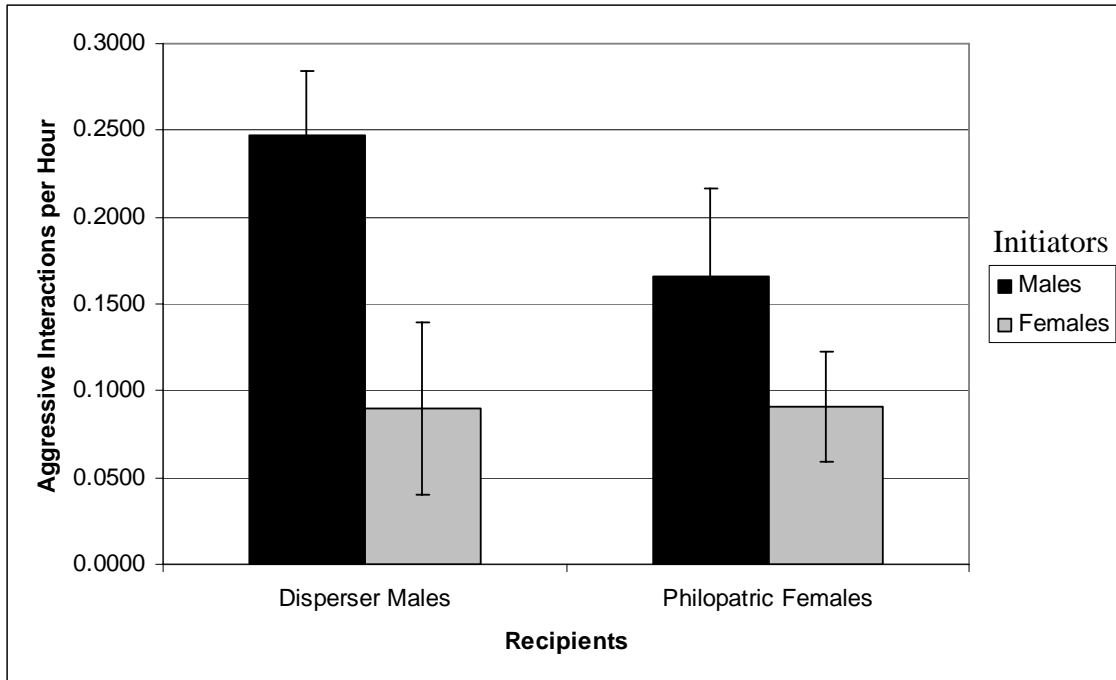
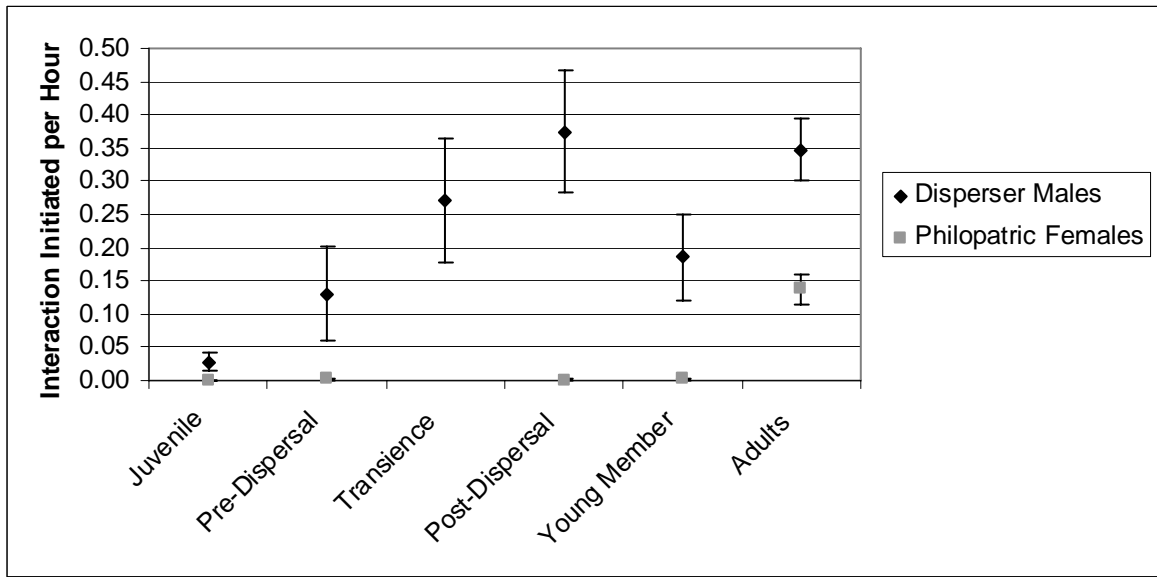


Figure 7. Aggression received from adults by disperser males and philopatric female capybaras. Mean and standard error are shown.

(A)



(B)

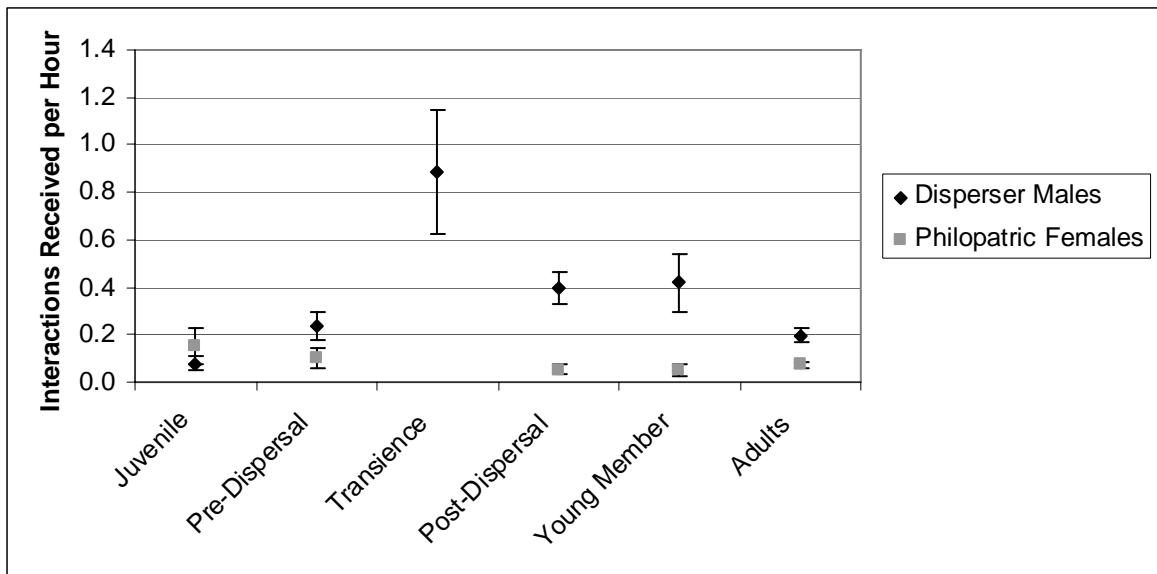


Figure 8(A) and (B). Rates of aggression over time in dispersing males and philopatric female capybaras. (A) shows interactions initiated and (B) shows interactions received. Mean and standard error are shown.

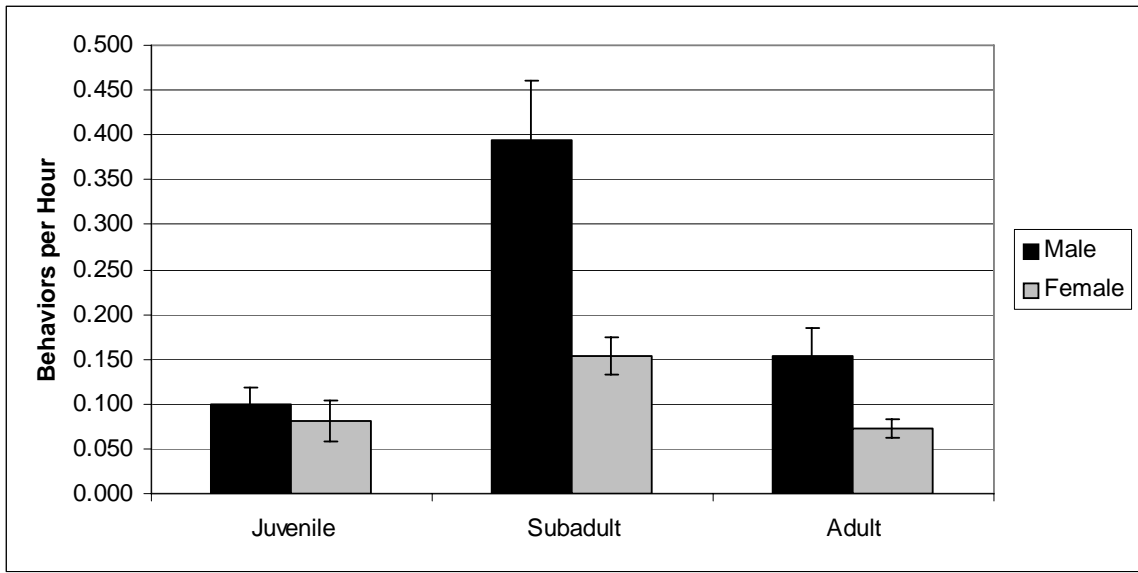


Figure 9. Avoidance behavior in capybaras by age class and sex. Mean and standard error are shown.

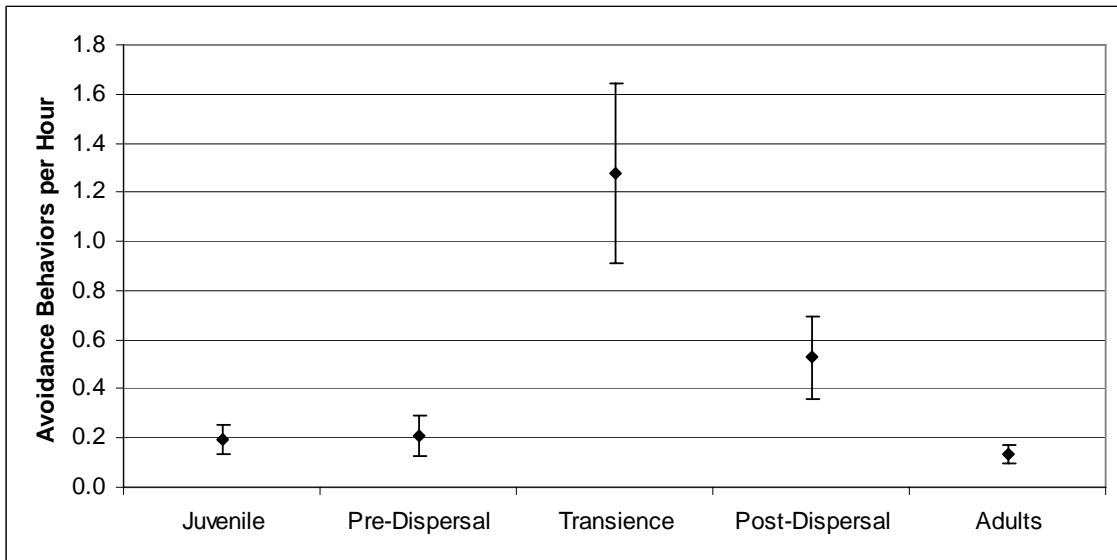


Figure 10. Avoidance behaviors over time in disperser male capybaras. Mean and standard deviation are shown.

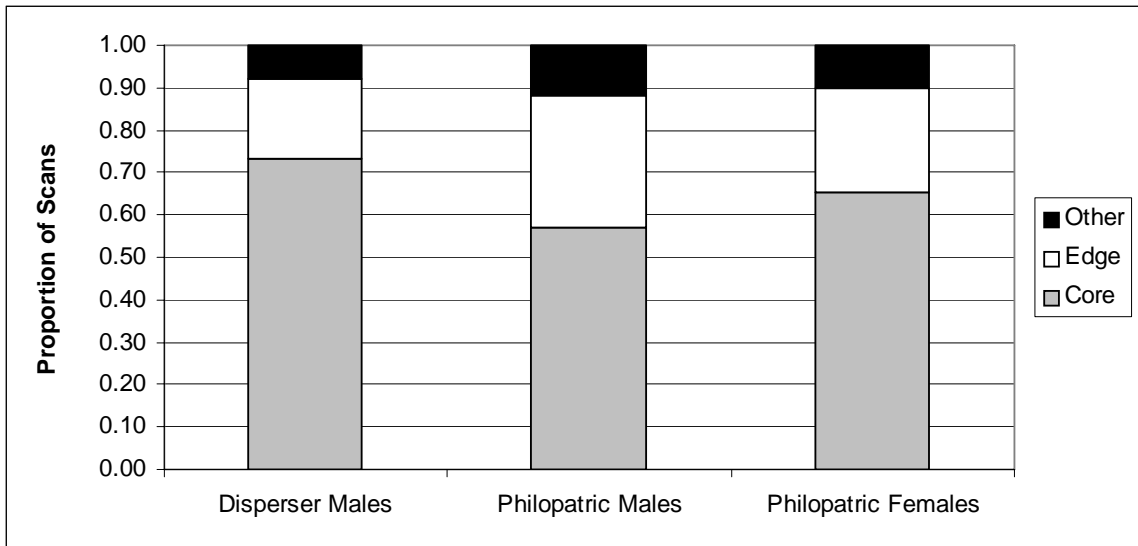


Figure 11. Proportion of time spent by individual capybaras in the core of their social group, at the edge and other. 'Other' includes at the periphery, away from the group, or out of sight at the time of the scan.

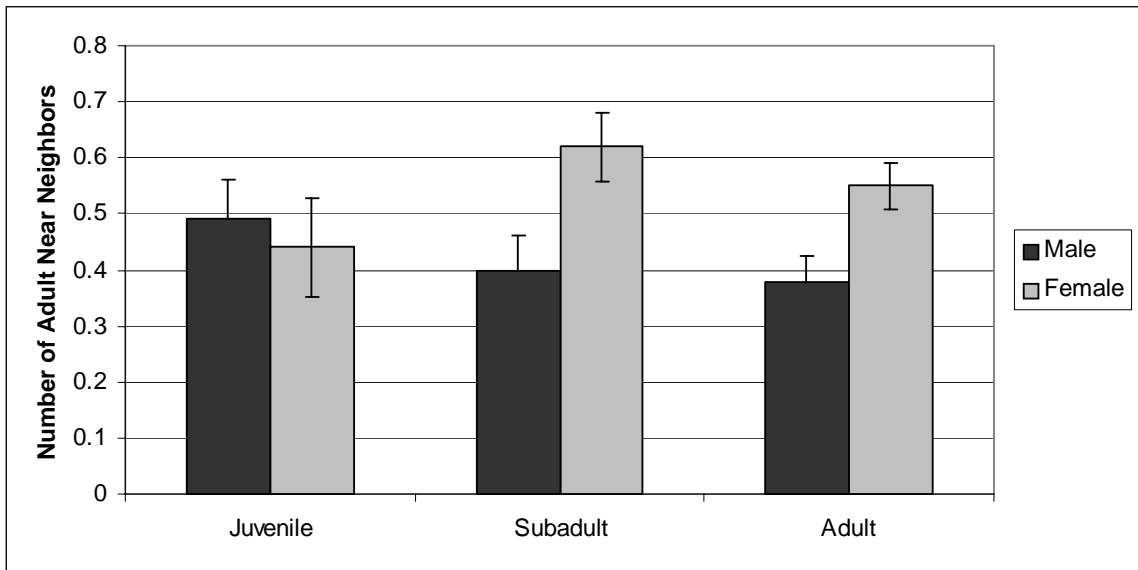


Figure 12. Average number of adult near neighbors (within two body lengths) for each gender and age class of capybara. Mean and standard error are shown.

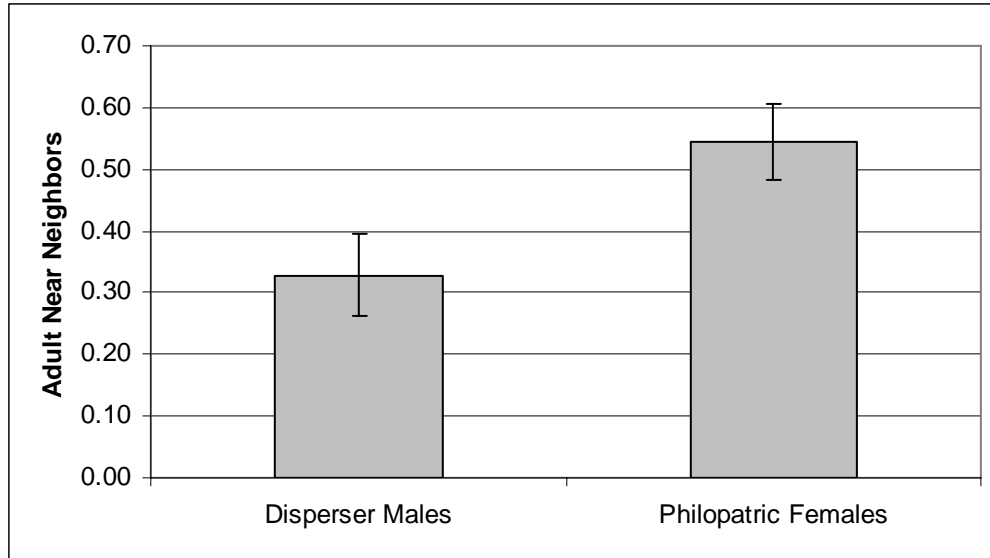


Figure 13. Average number of adult near neighbors (within two body lengths) for disperser males and philopatric females two months prior to average dispersal age. Mean and standard error are shown.

CHAPTER 4

A Search for Ultimate Drivers of Dispersal: A Comparison of Natal and Breeding

Groups in Capybaras

INTRODUCTION

Fundamental to the understanding of gene flow and evolution is dispersal. Fully understanding dispersal requires first understanding how individuals choose mates and choose where to reside. In this paper I will examine the forces influencing natal dispersal, the movement of individuals away from their area or social group of birth to their area or social group of breeding, in order to understand the larger pattern of gene flow in a population.

In social species, natal dispersal patterns may result from a trade-off between the benefits reaped from group-living along with the benefits of maintaining adaptive gene complexes on the one hand, and the costs of inbreeding depression and kin competition on the other. For decades researchers have been striving to quantify these costs and benefits and to evaluate which may be the most important in shaping the evolution of dispersal and of social grouping. Understanding the ultimate causes of any behavior begins with examining the consequences of that behavior, both to the individual and as reflected in the population genetics. If dispersers are choosing a group based on some criteria, and not taking the first open and available territory, then it is also reasonable to assume that selection has favored choosing wisely.

Many intraspecific studies have been hindered by the lack of two kinds of comparisons that could provide powerful insights into the evolutionary maintenance of dispersal and philopatry (but see Dobson et al. 1998). First, comparing the reproductive

success of dispersers and philopatric individuals from the same cohort is often missing. This contrast provides tests of the benefits of dispersal movements. Second, it is often difficult to compare the social and ecological environments for philopatric and dispersing individuals. This contrast could provide information about environmental conditions that are most important to individuals, whether they move to a new home range or remain in their present one. In the current study, the limited number of philopatric males allows a preliminary comparison to dispersed males. The social environment of dispersers and philopatric individuals was compared elsewhere (Chapter 3) and revealed differences in levels of agonism. Young males destined to disperse were more aggressive in their native group and actively avoided adult conspecifics, presumably avoiding potential aggression.

In this paper I will compare natal social groups with post-dispersal groups, both in social and ecological terms, in an effort to quantify consequences and elucidate potential ultimate causes of dispersal in capybaras (*Hydrochoerus hydrochaeris*). Five common hypotheses for the selective forces leading to dispersal are inbreeding depression, competition for resources, competition for mates, avoidance of kin competition, and habitat variability (Clobert et al. 2001; Bowler and Benton 2005). Each of these hypotheses leads to predictions for an individual's choice of breeding group. Thus, by comparing the natal and breeding groups, one can identify potential applicable hypotheses suitable for further experimental study.

The inbreeding avoidance hypothesis is one of the most often cited mechanisms for the evolution of dispersal, despite the difficulty in isolating it as the sole mechanism (Moore and Ali 1984). This hypothesis contends that philopatry puts an animal at the risk of mating with close kin, specifically the opposite sex parent or siblings. Sex-biased

dispersal will reduce that risk and the sex at greatest risk should disperse. In polygynous mammals we would expect the males to disperse (Greenwood 1980). It is important to remember that the role of dispersal in effectively reducing inbreeding depression does not in itself cement it as the selective force driving its evolution. In other words, the reduction of inbreeding depression could be a consequence or by-product of selection on another mechanism.

The inbreeding avoidance hypothesis makes three distinct assumptions. First, inbreeding is deleterious by reducing offspring fitness and increasing offspring mortality (i.e., inbreeding depression). This could result from an increase in homozygosity (Templeton and Read 1994) and expression of deleterious alleles (Charlesworth and Charlesworth 1987). Second, there must be a strong selective force, one that outweighs the cost of dispersal. And third, there must be no other, more efficient mechanism for avoiding mating with close relatives. In other words, kin recognition, promiscuity, and extra-group copulations would be insufficient to avoid such matings. Given all these conditions, this hypothesis makes three predictions. One, dispersal will be differential among the sexes (as is seen in many, if not most, polygynous mammals). Two, the least likely to benefit from kin selection will be the sex that disperses, although predicting which sex will disperse may be difficult. For example, in cheetahs the males defend the territories and the females disperse. In lions, the females breed cooperatively and the males disperse (although sometimes in sibling pairs working together.) The final prediction is that juveniles will disperse even if there is no dominant individual (of the same sex) in the natal group to expel them. In terms of current behaviors, this hypothesis would also predict sensitivity to opposite-sex kin such that dispersers should emigrate

more frequently or at younger ages from natal groups with more first and second-order kin.

Although competition for resources and mates can be viewed in terms of their immediate motivation for individuals to disperse, both the resource-competition hypothesis and the local mate competition hypothesis are generally discussed in terms of their role in the evolution of dispersal. If dispersal is a response to competition, the reproductive success (i.e., number of offspring per individual) of dispersers should rival that of non-dominant non-dispersers because the competition has been alleviated by the dispersal event. Since subordinate males are not likely to have much mating success, the reproductive success of a male must be measured as lifetime fitness and requires long-term study. The extent to which the dominant male monopolizes the breeding in a group is currently under investigation (Herrera, pers comm.) Several behavioral studies have shown that subordinate males do attempt mating, but their reproductive success is not known (Herrera 1992, Salas 1999, Bedoya 2007, Chapter 2, this dissertation).

The resource competition hypothesis (Greenwood 1980, Moore and Ali 1984) builds on the benefits brought by philopatry and familiarity with the natal area in terms of ability to exploit local resources. In polygynous species, females may be more affected by this because they are mainly responsible for rearing the young and thus are under stronger selective pressure to find resources to support those young (Favre *et al.* 1997). In most monogamous species, however, males help rear the young and defend sufficient resources to attract a female and should therefore be more philopatric. Thus, this hypothesis also predicts male-biased dispersal in polygynous mammals and female-

biased dispersal in monogamous mammals. Indeed, capybaras are polygynous and males are the dispersing sex (Chapter 2).

Because larger social groups will result in increased competition for limited resources, this hypothesis would also predict greater likelihood of dispersal as density increases. Some empirical studies have found that the number of dispersers is positively correlated with population density, particularly for many species of cricetid rodents that undergo population fluctuation and multi-annual cycles (Gaines and McClenaghan 1980). If resource competition is the driving force, one would expect the breeding group to be smaller than the natal group, not necessarily in terms of absolute numbers of individuals, but in terms of their density (as long as resources are evenly distributed).

The resource of interest may be attractive and receptive mates, rather than food or territories. The local mate competition hypothesis (Dobson 1982) builds on the observation that philopatry induces competition for mates among kin, which bears both direct and indirect fitness costs. The sex with the highest reproductive potential should suffer more from competition, and so should disperse more. This hypothesis therefore predicts that, in polygynous species, males should be the dispersing sex, while no difference in dispersal among sexes is expected in monogamous species. In terms of dispersers choosing a breeding territory, one would predict that the breeding territory would have a more favorable sex-ratio than the natal territory. In species with dominance hierarchies in the dispersing sex, having fewer members of that sex should be an attractive characteristic of a breeding group.

The final selective force proposed for dispersal involves the type of habitat variability. In spatially variable environments, models generally suggest that selection

should favor philopatry, or reduced dispersal (Johnson and Gaines 1990), without distinction between the sexes unless there is differential use of the habitat. In habitats where the variation is spatially uncorrelated, temporal variation in patch carrying capacity should select for dispersal (McPeck and Holt 1992). Dispersal in the case of temporal variation enhances the likelihood of finding a suitable location as the quality of the present location deteriorates over time (reviewed in Wiens 2001). Because this variability must be evaluated over large spatial and temporal scales, this hypothesis was not evaluated by this study.

Capybaras (*Hydrochoerus hydrochaeris*) are excellent subjects for studying dispersal because of their large body size (large enough to observe from a distance) and social organization. They are terrestrial, diurnal, territorial, and highly social and polygynous, allowing for capture in groups of large numbers. In addition they disperse several kilometers from their natal ranges (Herrera 1992, Salas 1999, Chapter 3 this dissertation). Although they have been locally extirpated from some areas, capybara densities are high in some private ranches of the *llanos*, the seasonally flooded savannas of northern South America. Furthermore, previous studies suggest that capybaras may represent a textbook example of behavioral variation that warrants conservation as its own form of biodiversity. “If the objective is to conserve the evolutionary potential of populations, the process of underlying environmentally-determined behavior patterns must be conserved as well” (Buchholz and Clemmons 1997).

The dispersal patterns and social structure of capybara groups point to certain ultimate hypotheses for dispersal. Dispersal in capybaras is strongly male-biased, with most males emigrating from their natal group prior to breeding for the first time (Chapter

2). Adult, established group members show a strict linear dominance hierarchy in males (Herrera 1986). These two factors suggest that mate competition is important and may be the most powerful selective force for dispersal. If that is the case, then one would further expect that dispersed males would select breeding territories with favorable male-female ratios, or at least more favorable than the natal territory. Also, one would expect that social groups with fewer adult males than the natal territory would mean fewer males ahead of the immigrant in the queue for dominance. By comparing these factors between natal and breeding territories, the current study will help us further understand which selective forces may have shaped the dispersal pattern we see in capybaras.

METHODS

Study Species

Capybaras (*Hydrochoerus hydrochaeris*; formerly known as *Hydrochaeris hydrochaeris*, ICZN 1998.) are large (~50kg) caviomorph rodents that live in groups averaging around 10 individuals with large variation in group size (approximately 4 to 40 individuals; Herrera and Macdonald 1987). These groups are stable, i.e. membership remains more or less unchanged for over a year, with each group consisting of a dominant male, several females, their young and one or more subordinate males (Herrera and Macdonald 1987). At El Frio ranch in Venezuela, these subordinate males were proper group members, as opposed to 'floaters', for at least two years (Herrera 1986). A rigid dominance hierarchy is evident among the males, with the dominant individual being larger and obtaining significantly more matings than subordinates (Herrera and Macdonald 1989). The subordinate males apparently queue for dominance (Herrera and Macdonald 1993), with age being the only significant correlate with dominance (as

opposed to size or aggressiveness; Salas 1999). The mating system is polygynous and there may be a certain degree of cooperative breeding, in the sense that young are maintained in 'creches' and lactating females nurse both their own young and other young in the group (Macdonald 1981; Salas 1999).

Capybaras live in non-overlapping territories defended by all adult group members, including subordinate males (Herrera 1986, Herrera and Macdonald 1989, 1993). A territory typically includes a grazing patch, bush or shade, and a section of a pond or river (Herrera and Macdonald 1989). In the dry season, the scarcity of water can lead groups to congregate at water holes in groups of up to 100 individuals with little aggression (Herrera 1992). The availability of a water source appears to be very important in that it is used for predator avoidance, for wallowing, for temperature regulation, and for mating (Herrera 1986, 1992). Some researchers describe capybaras as the hippopotamus of the New World (Salas 1999), filling the niche of the large, semi-aquatic herbivore. Since the availability of these water sources varies across sites, it may be expected that territorial spatial relationships and population densities also vary between sites and could have consequences for dispersal patterns.

Two previous studies have examined the dispersal of capybaras and revealed possible variation or condition-dependent patterns. Based on research conducted at Hato El Frio, approximately 60 km from the site of the current study, Herrera and Macdonald (1987) proposed that dispersal might occur in groups consisting of both males and females. Anecdotal evidence suggested a scenario wherein a subordinate adult male is joined by several yearlings to form a new group with the adult male as the dominant individual (Herrera and Macdonald 1987, Herrera 1992). In a mark-recapture study,

Herrera (1992) found no sex-bias in dispersal. On the other hand, research conducted by Salas (1999), at the site of the current study, showed that all males dispersed as juveniles while only 25% of females dispersed, with most females remaining philopatric (Salas 1999). These results from El Cedral are more typical of the male biased dispersal found in most mammals (for reviews see Michener 1983, Shields 1987, Chepko-Sade and Halpin 1987). Furthermore, most sub-adult males in this system were solitary, comprising a floater population that was not observed in the El Frio study nor in the current study. The presence of floaters may be an indication of saturation, but this can not be confirmed. The current study found significant male-biased dispersal, with 20 of 23 juvenile males dispersing and none of 26 juvenile females of the same cohort dispersing (Chapter 2).

Study Site

Hato El Cedral is located approximately 200 km west of San Fernando, Apure State, and covers close to 50,000 hectares. A population of approximately 10,000 capybaras comprising several hundred social groups is distributed throughout the ranch, although groups tend to concentrate around large, permanent water bodies, particularly in the dry season (Macdonald 1981). The large size of the ranch and lack of fencing low enough to restrict capybara movement allow for studies under natural conditions but without the impact of poaching by humans (Ojasti 1991; E. Herrera, pers. comm.). The core study area was in the approximate center of the ranch, such that dispersing individuals were more likely to settle within ranch boundaries post-dispersal and thus be identifiable.

The ranch is located in the seasonally flooded savannas (*llanos*) of Venezuela. Despite the apparent flatness of the land, there are three distinct kinds of terrain, differing

in their height, soil and vegetation cover. Highest are '*bancos*', banks of former rivers or parts thereof, usually covered in tall grasses or bushes. The '*bajios*' comprise some 75% of the landscape and are covered in short, highly palatable grasses. And the lowest lands, '*esteros*', are swamps, ponds and lakes, many of which dry up completely in the dry season. Isolated patches of woodland are also scattered around the ranch and gallery forests line the major rivers. Banks and woodlands are usually not flooded, while *bajios* tend to be covered by a few centimeters of water except in the height of the dry season. Many private ranches, including El Cedral, manipulate the water levels with dykes, keeping some areas with water year-round and draining others for cattle.

Capture and Identification

Individuals were captured using traditional local methods: chasing from horseback and lassoing. Due to the scattering effect of this method, it was not possible to mark entire social groups. A total of 290 individuals were captured and tagged and an additional 8 individuals were identified by some natural scar or obvious feature. Once captured, individuals could be restrained by hand for marking and morphometric data collection, which took no more than a few minutes and was done at the site of capture. Each animal was weighed and marked with one tag in each ear. Tags had unique numbers and were of varying colors to facilitate identification from a distance. Several measurements and ear notch tissue samples were also collected for a related study. Each individual's sex was determined with palpation of the gonads. Approximate age was determined by weight for those individuals less than 35 kg (see Table 1 for details; Ojasti 1973). All others were classified as adults but more precise age estimates for adult live individuals are not currently available.

Thirteen Social groups were chosen for focal observation because they contained at least three marked juveniles and they were reasonably accessible. Initially the groups were located along an east to west dirt road. Each group had from 3 to 17 individuals marked. For several days following the marking procedure, group location and composition were noted to ensure that membership had stabilized following the disturbance of capture.

Behavioral Observations

Behavior observations were conducted from April through June 2004 and from April 2005 through June 2006, for a total of 1180 hours. On average, each focal group was observed for 74 hours. The openness of the terrain made it possible to observe the entire social group at once, with the exception of individuals that might be hiding under bushes, where the social behaviors of interest were unlikely to take place due to lack of space. Each observation session began by recording group location, using a Garmin 12XL Global Positioning System, compass, and digital range-finder to calculate the coordinates of the approximate center of the group.

Two methods were used for documenting social behavior: focal individual observations and focal group observations. Focal *individual* observations were conducted for each marked animal for 10 minutes, noting nearest neighbors, all occurrences of social behaviors, and event behaviors such as scent marking. During focal *group* observations, all occurrences of social interactions involving a marked individual were documented for all individuals in the group noting general age class and sex (if possible) for any un-marked participants. Interactions between two unmarked individuals were noted on an opportunistic basis. For every behavior several parameters were noted: date,

time, initiator, recipient, behavior, outcome (e.g., of a fight), and any additional behaviors of relevance. A 'courtship' was re-classified as a 'mating' if the male mounted the female more than 4 times. This is also the definition used by Salas (1999) and is based on previous data that at least 7 mounts are required for ejaculation (Ojasti 1973, Salas 1999). The detailed ethogram was modified from several previously published ethograms for this species (Herrera 1986; Salas 1999). Table 1 lists the social behaviors and definitions relevant to this study.

Detecting Dispersal

For the purposes of this study, natal dispersal is defined as the movement of individuals away from their natal area or social group to the area or social group where breeding first takes place (Clobert *et al.* 2001). This species' high levels of sociality and territoriality led me to define dispersal by establishment in a new social group, rather than by spatial location or absolute distance moved. Although successful breeding (i.e., paternity) could not be determined in this study, the group where a male first attempted to court a female was classified as his breeding group. Searches of the study area to detect dispersers were conducted at least once per week, more frequently when an individual had recently disappeared from a group. The road and trail system of the ranch allowed for fairly extensive searching from a vehicle and was aided by ranch workers who covered even more ground on horseback.

For the remainder of this paper, individuals that were marked as juveniles and eventually dispersed will be referred to as 'dispersers', including when examining their behavior prior to dispersal. Individuals that were marked as juveniles and were later defined as philopatric will be referred to as 'philopatric individuals'. Data on dispersers

are compared pre- and post-dispersal while data on philopatric individuals are compared pre-and post- age of dispersal (15 months). Because all dispersers were males and only two philopatric males provide enough behavioral data for consideration, the confounding variable of gender is ever-present in these analyses and their interpretation. Only disperser males and philopatric females yield enough data to analyze statistically, while philopatric males are considered separately and subjectively.

Many juveniles that were marked either disappeared or lost their ear tags, so that they could not be classified as either ‘dispersed’ or ‘philopatric’. These individuals were excluded from analysis. Although individuals that were initially captured and marked as subadults or adults could not be classified as philopatric or disperser, they allowed me to identify the partner of social interactions with the focal individuals.

Territories

Evaluating the territories of social groups was done qualitatively with respect to the amount of shade or vegetative cover, water, and dry ground. Each territory was searched as thoroughly as possible at least once during each season: the height of the dry season, the height of the wet season, and the transitions between them. Each one was classified as good, fair, or poor with regard to each parameter and relative to the other surrounding territories. For example, a “good” territory had enough vegetative cover to allow all group-members to be under shade during the afternoon while a “poor” territory left most group-members exposed to the sun. In addition, some social groups entirely switched their territorial boundaries during the wet season, returning to their original dry season territory the following year. This movement was used as an indication that each

sub-territory alone did not hold sufficient resources year-round and was considered a territory quality indicator.

Overall territory size could not be determined in the absence of radio-telemetry data for most groups. However, because a road served as both an observation transect and a patch of valuable dry ground during the wet season, the width of the territory along this transect was used as a surrogate for size. This was also used as the denominator in the density calculations. The number of individual members of a group was calculated in several ways: the average number of adults seen at any one time; the maximum number of adults ever seen at one time; the average number of males; and the maximum number of males.

Data Analysis

Statistical analyses were performed in SPSS v15. Due to small sample sizes and non-normality of data, nonparametric tests were used most often unless otherwise noted. In some cases, samples were too restricted to warrant statistical analysis, but are compared qualitatively.

RESULTS

Comparing social group sizes revealed differences between natal groups and breeding groups. Using territory width as a rough index of territory size, dispersers did not tend to move to territories of a different size (Wilcoxon Signed Ranks Test, $p > .05$). Neither did they go to territories with a lower density of capybaras, whether density was calculated with the average number of adults present or the maximum number of adults present. The average number of adults in natal territories = 47 and 46 in breeding groups. The maximum number of adults in natal territories was 13 and 12 in breeding groups.

However, natal territories did have more males than breeding territories – measured by maximum number of males present at any one time (Wilcoxon Signed Ranks Test, $p = .034$, Figure 1). However, this difference was not significant when measured as average males present (Wilcoxon Signed Ranks Test, $p > .05$).

Most dispersers moved to social groups with either better shade or cover or no change from their natal group. Only two of nine dispersers went to a group with less shade. No other patterns emerge from the comparisons of available water during the dry season, dry land during the wet season, or tendency to need to move locations between seasons.

Unfortunately, limitations of this study preclude continued behavioral observations after individual dispersers immigrated into a new group. Thus, the age at first successful mating or mating attempt is not known. However, courting behavior did reveal some interesting differences between philopatric and dispersing males. At least one philopatric male mated in his natal group at approximately 15 months, but it was with a subadult female, not an adult. Another young male of approximately the same age mated with a subadult female, but it was not clear that he was philopatric because he was marked at 11 months, which could mean he had immigrated into that group prior to capture and identification. (The youngest confirmed disperser emigrated from his natal group at 9 months (Chapter 2).) Adult females, however, never completed successful mating with philopatric males. They may have been courted, but were either interrupted by another male or the female rejected him herself.

Once in their secondary group, immigrants were seen courting females, but no successful mating occurred until they were with the group several weeks and were at least 18 months old (full adults).

DISCUSSION

The data presented here reveal several patterns with respect to the selection of a social group by dispersing males. Dispersers tend to move to groups that are less dense in terms of adult individuals per unit area. They also select groups with fewer adult males than their natal group. While dispersers appear to prefer some minimal amount of shade or vegetative cover, there is not a clear trend to move to a breeding territory with more shade than the natal territory.

Previous results provide additional background data with which to interpret these results. At least in this study site, dispersal is almost completely male-biased, with no clear cases of natal dispersal by females and only three philopatric males of 23 marked juveniles (Chapter 2). There also appears to be substantial dispersal costs in terms of mortality risk and injury, indicating that the selective advantage for dispersal must be strong enough to overcome those costs.

Inbreeding avoidance hypothesis

The extent to which avoidance of inbreeding is the system of mating in capybaras can not be determined without pedigree data. Thus, evaluating the role of inbreeding depression as a selective force in the evolution of dispersal must be indirect. Some aspects of capybara behavior suggest that mating with close relatives could be avoided without dispersal away from the social group. Although kin recognition has not been examined in this species, the prominent scent marking with both anal scent glands and a

snout scent glands provide a mechanism for recognizing kin, so that close relatives could be avoided, that would be much less costly than long distance dispersal. If capybaras can recognize and avoid mating with close relatives, they could do so despite very short dispersal distances, which average only 1230 meters (Chapter 2). Juveniles appear to be driven to emigrate by the aggression levels of the group, at least in part (Chapter 3). Without this aggression by adults, the young might stay in the group and thus have more opportunity to breed with related females. Finally, the active avoidance of young males by females is ubiquitous. Females avoid reproduction with all young males, whether they are natal males or immigrants. Although their low standing in the dominance hierarchy (Herrera and Macdonald 1993, Bedoya 2007) may be one reason, the result would be avoidance of inbreeding as the system of mating.

Competition

The resource competition hypothesis is supported perhaps in part by the tendency of young capybara males to move to a territory that is neither smaller or more dense than their natal territory. The resource in question is not likely to be food, since capybaras are grazers in grassland with abundant forage during all but the height of the dry season. In examining the characteristics of territories, the only pattern that emerged was the apparent avoidance of areas with little shade, suggesting some minimum amount of shade that is acceptable. But they didn't necessarily move to more favorable shade, suggesting that this is not a limited resource for which they were competing.

Natal territories did have more males than breeding territories, leading us to the mate competition hypothesis. The breeding territories did not have a more favorable sex ratio, but since the dominant male is likely monopolizing access to the females, having

more females would not necessarily improve the mating opportunity of subordinate males. Fewer adult males also mean fewer males ahead of the immigrant in the queue for dominance. The tenure of dominance for males appears to be at least two years (Herrera 1986) and the greatest predictor of dominance is age (Salas 1999). Thus, if the immigrant can gain access to a group with as few adult males as possible and just survive, dominant status should be attainable. One study suggested that while subordinate males may attempt mating, all successful matings (apparent ejaculation) was by the dominant male (Salas 1999). However, the genetic analysis that will provide more conclusive information about paternity in social groups is still in progress (Herrera et al. in prep).

The ability of philopatric males to at least attempt to mate in their natal group suggests a balance of fitness between philopatric males and dispersing males. While the dispersers have the benefit of reduced inbreeding depression in their offspring, reduced competition for mates, and reduced competition with kin, they are subject to the costs of dispersal in terms of injuries and later initiation of breeding. The philopatric males may breed earlier, but risk inbreeding depression in their offspring and are forced to mate with younger females that may not be effective mothers, particularly in light of the risk of infanticide in this species (pers. obs.).

Conclusions

Taken collectively, the current data suggest that competition for mates, perhaps via dominance in a quality territory, is driving dispersal in capybaras. As is often the case, long-term studies comparing the likelihood of philopatric males versus dispersing males to achieve dominance would be ideal. However, if such studies are not feasible,

genetic data on the likelihood of the dominant to father the offspring in the group, combined with population genetic structure, could lead to further insights.

The site-specific potential variation in capybara dispersal suggests either continuing selection on this behavior (Herrera 1992; Salas 1999; Chapter 2) or past selection that favored plasticity. The Herrera population at Hato El Frio showed dispersal by both sexes fairly long-distances, an average of 5.6 km. Both Salas and Congdon report male-biased dispersal (at Hato El Cedral) and relatively common short-distance dispersal. If this variation is an accurate description of genetic dispersal, then these populations could be an invaluable tool for examining the cues and drivers of dispersal. Furthermore, the population studied by Salas (1999) and the current study are separated by just seven years in the same site. The primary difference is the presence of many subadult and adult male ‘floaters’ (not belonging to any social group) in the late nineties and very few floaters seen in the more recent case. These floaters suggest a drive to emigrate from the natal group but lack of drive or inability to immigrate into a breeding group.

The discrepancy between the three studies may be an example of *pre-saturation* and *saturation dispersal*. Saturation dispersal is dispersal of excess individuals, typically young, old or injured and not capable of breeding given the high competition in saturated populations. Dispersal of these individuals is the “safety valve” of the population that alleviates over-populated areas and has been described mainly with reference to small mammals (Lidicker 1975). The population studied by Salas (1999) may have been experiencing saturation of territories, thus contributing to the male ‘floater’ population. Over evolutionary time this may lead to reduced dispersal (Lidicker 1975), but in just five to seven years, the population was reduced by half (MARNR 2007), with annual

harvests, poaching, and recent climate conditions all contributing. Pre-saturation dispersal involves the emigration of individuals that are physically capable of breeding in the natal territory and presumably would if the dominant breeding pairs were removed (Gaines and McCleneghan 1980) and probably applies to the populations studied by Herrera (1992) and Congdon (Chapter 2). Notice that in these latter cases, the driving force is mate competition.

Population genetics in this species, at least in Venezuela, has likely undergone a fairly recent restriction. Because capybaras are a valuable source of protein for people in a struggling Venezuelan economy, once individuals disperse beyond the boundaries of protected areas, they are not likely to survive to reach another population. Hence, gene flow is now restricted to the protected areas and most are not large enough to encompass more than one genetic population. A recent preliminary study in Venezuela revealed historic connection, but recent genetic isolation of three populations (Giselle 2006). Work is ongoing to increase sample size and further examine the population genetics within Venezuela. Future work to include countries where capybaras are commercially managed but not widely hunted will provide valuable comparisons and greatly increase our understanding of the genetic implications of dispersal and its inhibition in this species.

Table 1. Ethogram and definitions of relevant behaviors and terms for a study of capybara dispersal. A complete ethogram is available upon request to the author.

Two event behaviors are considered different bouts if they are separated by another defined behavior, a change in participant, or at least 5 minutes, unless otherwise noted.

Social Behavior

Court Male closely follows the female with his head held high and his chin close to her rump and mounts less than four times, maybe not at all. Distinguish from ‘mate’. (~Salas 1999)

Mate Male closely follows the female with his head held high and his chin close to her rump. The female lowers her rump and the male mounts her. Male mounts at least four times. Distinguish from ‘court’. (~Salas 1999)

Age Classes

Baby / Infant Socially dependent on mother or females, typically < 4 kg. Field identification: stick closely to female or other babies, ~3 kg or less.

Juvenile Independence to 11.9 months; up to 24.9 kg
Field identification: noticeably / undoubtedly smaller than an adult.

Subadult 12 to 17.9 months; 25.0 to 35.9 kg
Field identification: males have visible testes but no morrillo; females same size as known subadult

Adult 18.0 months and older; 36.0 kg and heavier
Field identification – males have visible testes and prominent morrillo; females are same body size as adult males but with no visible testes and only small morrillo, if any.

Group Membership / Changes

Disperser Individual no longer associates with its natal group and is repeatedly seen outside its natal territory. If that individual engages in courtship or mating in the secondary group, it is considered an immigrant to that group.

Philopatric An individual remains in its natal group until adulthood AND / OR is observed courting or mating in the natal group AND / OR gives birth in the natal territory.

Member An individual is repeatedly seen in only one group, interacts with other group members, and may engage in courtship or mating.

Satellite Group Member An individual repeatedly seen in the territory but rarely observed interacting with other group members. These individuals are often peripheral or at the edge of the group. They are not seen in any other group’s territory (see Floater).

Floater An individual is observed in more than one territory and may interact with members of either territories’ social group.

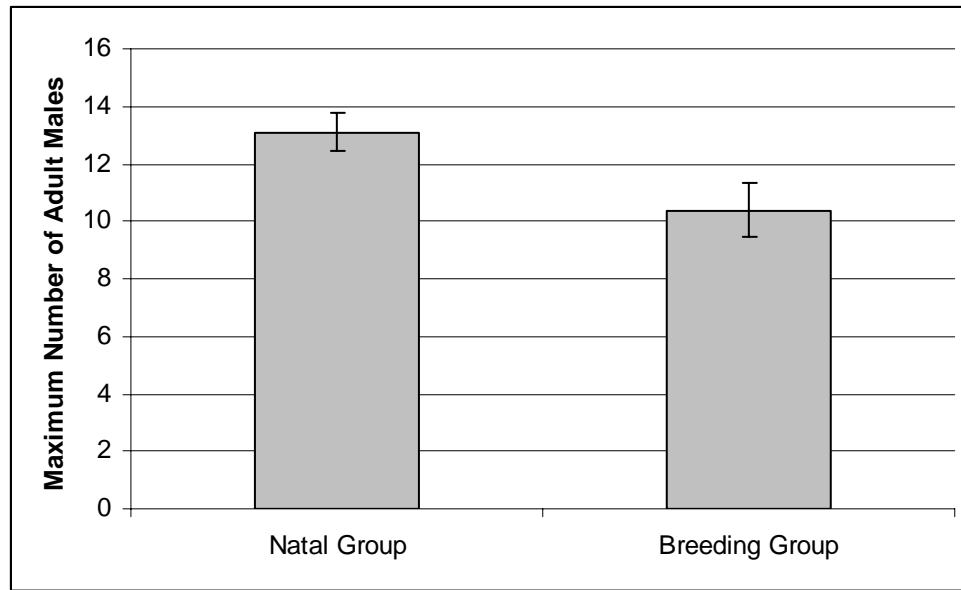


Figure 1. The maximum number of capybara males present at any one time in the natal and breeding groups of dispersers. Mean and standard error are shown.

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