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Climatic variables are strong predictors of allonursing and communal nesting in primates

by

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Submitted in partial fulfillment
of the requirements for the degree of
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ABSTRACT

Allomaternal care (AMC) is widespread throughout the primate order, with nearly 75% of primate taxa exhibiting some form of AMC. Previous studies of primate AMC have primarily focused on the benefits received from it (e.g., increased infant survival, learning to mother, or improved kin relationships). Our study examined how ecology can influence cooperation and whether energetic costs from AMC are outweighed through increased survival in seasonal and unpredictable environments (e.g. low rainfall, high seasonality, or high variability). Therefore, we tested if increased environmental seasonality and stochasticity will drive certain behaviors especially with cooperative behaviors often linked to arid environments.

Here, we used published data from 91 primate species to ask whether specific AMC behaviors were prevalent in more harsh, unpredictable climates. These AMC behaviors included allonursing, communal nesting, provisioning, babysitting, and carrying. Predictor variables included temperature and precipitation (mean, variation, and seasonality), diet, habitat diversity, mating seasonality, and mating style. We used Phylogenetic Generalized Least Squares (PGLS) to assess which environmental factors could predict AMC behaviors. We found that species inhabiting more seasonal and variable environments were significantly associated with communal nesting ($p=0.004$). While species inhabiting areas with low rainfall, high seasonality and low habitat diversity were strongly associated with allonursing ($p=0.014$). Babysitting, provisioning and carrying did not have significant climatic predictors, which was different from our expected results. However, our results suggest that environmental variables are good predictors of allonursing and communal nesting in primates and can impact variation in AMC behaviors.

INTRODUCTION

Allomaternal care (AMC) is a term often used to describe the care an infant receives from an individual other than its genetic mother, which includes paternal care (Koenig 2017; Burkhardt et al. 2009). It is also considered allomaternal care if a behavior is directed towards the mother, but still benefits the infant (Gilchrist 2007). It is represented throughout the animal kingdom to varying degrees (e.g., 9 % of birds: Rubenstein & Lovette 2007; <1 % of fishes: Desjardins et al. 2008; 0.1 % of social insects: Keller & Chapuisat 2017; Korb et al. 2012; 2 % of mammals: Briga et al. 2012; Isler & van Schaik 2012), though it is thought to have originated as many as 200 million years ago with the evolution of the earliest mammals (Eggert 2017; Konner 2018). AMC is thought to be the evolutionary precursor to cooperative breeding, which is a more derived form of AMC that evolved in select species that include callitrichids and humans (Tecot & Baden 2015). Behaviors that make up allomaternal care can be broken up into several forms of: babysitting, allonursing, carrying, provisioning, protection, communal nesting (Isler & van Schaik 2012).

Benefits of AMC

AMC has a myriad of benefits to mothers and their offspring; however, AMC studies generally investigate it from the point of view of the care provider. Previous studies on mammals suggest that females of cooperative breeders typically have shorter inter-birth intervals and larger litters than non-cooperative ones (Lukas & Clutton-Brock 2012). It has been found that cooperative breeding in birds and mammals can increase the parent's reproductive success as the number of helpers increased (Emlen 1991). Through "load lightening" helpers can reduce the workload of parents, which increases their chance of survival (Crick 1992). In species like

meerkats and rodents, AMC is thought to provide load reduction for the mothers; for example, allonursing often benefited the helper's relationship with the group and showed evidence of shortening the lactation period for the mother, which is strenuous (Isler & van Schaik 2012). Additionally, communal nesting in rodents has been argued as means to defend young against infanticide, and other females can help protect them against any nest intruders (Komdeur et al. 2008). Among birds AMC sometimes comes in the form of communal nesting, which will often start with the building of physical structures that provide thermoregulatory benefits or reduces the risk of predation (van Dijk et al. 2013). Birds show a lot of evidence for AMC behaviors as 852 species of birds were inferred to have some form of cooperative breeding and 150 species that exhibit it sometimes (Cockburn 2006). Parents and offspring of birds can benefit from AMC because insulated nests and helpers will slow down the egg-cooling rates when parents are not there, which will reduce the energetic cost of parents to reheat the eggs (van Dijk et al. 2013). The main benefit for any animal receiving AMC is thought to be increased survival rate for parent and infants, because mothers may gain energetically which will have reproductive advantages or provide opportunity for increased feeding time for the mother (Ross & MacLarnon 2000).

Some perceived benefits that primate helpers receive by participating in allomaternal care is practice for motherhood, increased breeding opportunities, and increased favor from other group members especially if there is dominance in a group (Williams et al. 1994; Lehman and Keller 2006; Hrdy 2016). Some forms of AMC can help alleviate the burden on the mother, for example babysitting can allow the mother to increase foraging time although babysitters may lose a lot of weight in the process (Clutton-Brock et al. 1998). Some patterns that birds with AMC behaviors, like the long-tailed tit (*Aegithalos caudatus*) have are to delay independent

breeding to help the dominant individuals, and therefore pool resources to raise infants which will provide increased favor for the helper and may decrease energetic load on the mother (MacColl et al. 2002). Additionally, we will often see AMC behaviors like provisioning, babysitting, or carrying the infants from adult males typically when parentage is certain (e.g., mongoose lemurs, red-bellied lemurs, tamarins, siamangs). Bonobos chimpanzees, and capuchins, although not dependent on AMC as an infant care strategy will occasionally share food and display more cooperative behavior than most primates, which all aids in increasing survival for the mothers and infants (Burkhart et al. 2009). Other examples are when the reproduction of subordinate females are suppressed to assist the dominant females infant, these examples show that various benefits and costs to the mother, infant, and the helper will depend on the species (Tecot & Baden 2015).

Variation in AMC

Despite the many benefits of AMC, the occurrence, frequency, and types of AMC are varied (See Table 1 for examples). Parents living in groups may receive benefits from AMC such as respite from caregiving duties, have more efficient foraging, reduced need for vigilance, shorter interbirth intervals, adoption of infants in case of death and reciprocal benefits between mothers and helpers (Mann & Smuts 1998). Often the variation in AMC behavior is referred to as facultative, which is behavior that can but does not always occur or it is referred to as obligate care, which is when there is an expectation for a certain behavior to occur (Baden & Tecot 2015).

Among some obligate cooperative breeders, like the African wild dog (*Lycaon pictus*), banded mongoose (*Mungos mungo*) and the dwarf mongoose (*Helogale parvula*) it was found

that group size and subordinates that can help with infant care have become necessary prerequisites to aid their survival (Komdeur et al. 2008). The evidence that increased group size influences the frequency of AMC and fitness of the group are found to be similar in birds as facultative cooperative birds were more likely to return and help groups that had close relatives and thus expected to show greater levels of AMC (Clutton-Brock 2002). In an example of obligately cooperative birds and mammals, helpers are usually relatives of dominant breeders who haven't left the group, or individuals who failed to breed and return to assist kin (Clutton-Brock 2002; Komdeur et al. 2008). Obligate and facultative care is often defined as regular or opportunistic, and in a study on 217 South African birds it was found that habitat could also predict frequency of AMC behaviors (duPlessis et al. 1995). Obligate helpers were more likely found in savanna habitats with predictable seasonal peaks, while facultative species were found in more unpredictable environments (duPlessis et al. 1995).

Provisioning by individuals other than the mother is seen most frequently in carnivora and primates, in carnivora help varies from protection, provisioning, pup retrieval, babysitting and allonursing (mostly among pinnipeds) (Isler & van Schaik 2012). In other species AMC is rarer, for example out of 38,000 known spider species under 25 are known to exhibit sociality (living communally) with evidence of AMC (Salomon & Lubin 2007). The social spider (*Stegodyphus dumicola*) has 40% of the females reproducing, that will also participate in cooperative care with virgin helpers (although they are less involved in brood care and more in prey attack) through eggsac tending, regurgitation feeding and matriphagy, which is when mothers are consumed by offspring (Junghanns et al. 2017).

It also appears that cooperative breeding in birds has evolved more frequently in altricial than precocial lineages (Ligon & Burt 2004). Cooperative breeding was found to be rare in

clades with precocial young (4% of 789 species) and more common among those with altricial young (11% of 7698 species). In a bird study focusing specifically on a seasonal environment (South Africa) rather than globally of facultative versus obligative cooperative breeding, it was found that facultative species would often nest on the ground and mostly had precocial young, which is a different result from Ligon & Burt's study (2004) (du Plessis et al. 1995). Extended parental care is thought to facilitate AMC although it is not as clear in mammals, which are thought to be influenced by the need for help feeding offspring in altricial compared to precocial species (Scheiber et al. 2017). Among primates it was found that species (especially within New World monkeys), which provided more AMC had a greater shift toward altriciality (Isler & van Schaik 2012). Elephants and ungulates however, were found to be unable to shift toward altriciality because of predation risk, which may be why altriciality is often associated with rates of protection and AMC (Isler & van Schaik 2012).

Table 1 List of the pros of AMC for mothers and infants in diverse taxa

Pros of AMC	Description	Example Species	Source
Respite from caregiving duties	Mothers can reduce their energetic load from infant care through assistance and have more time to rest, socialize or travel	Spectral tarsius (<i>Tarsius spectrum</i>), <i>Callithrix kuhlii</i>	Gursky 2000, Fite et al. 2005
More efficient foraging	Babysitting or helpers provisioning for infants; mothers can spend more time obtaining food and increasing their own chance of survival	Ruffed lemurs (<i>Varecia variegata</i>), Acorn woodpecker (<i>Melanerpes formicivorus</i>), Allodapine bee (<i>Exoneura bicolor</i>)	Baden et al. 2013, Koenig et al. 2016 Bull and Schwarz 1997
Reduced need for vigilance	Living in groups with communal care increases chances of survival through lowering predation risk and infanticide through guarding and babysitting.	Bottlenose dolphins (<i>Tursiops truncatus</i>), cichlid fish (<i>Neolamprologus pulcher</i>), Social spider (<i>Stegodyphus dumicola</i>), Allodapine bee (<i>Exoneura bicolor</i>)	Mann & Smuts 1998, Bergmuller et al. 2005, Salomon & Lubin 2007 Bull and Schwarz 1997
Increased infant survival	Infant survival success can be higher with cooperation from others through babysitting, communal nesting, etc.	Ruffed lemurs (<i>Varecia variegata</i>), Bottlenose dolphins (<i>Tursiops truncatus</i>), Florida scrub jays (<i>Aphelocoma coerulescens</i>)	Baden et al. 2013, Mann & Smuts 1998, Mumme 1992
Interbirth interval decreased and faster postnatal growth	Reducing the energetic strain of infant care and more opportunities to forge grants mothers more resources to reproduce faster, can also reduce risk of predation	Callitrichid primates, Prairie vole (<i>Microtus ochrogaster</i>), Florida scrub jays (<i>Aphelocoma coerulescens</i>)	Mitani & Watts 1997 Solomon 1991, Mumme 1992
Thermal benefits	Huddling can decrease the amount of energy needed to keep infants warm, and aid in increased survival	Meadow voles (<i>Microtus pennsylvanicus</i>), Acorn woodpecker (<i>Melanerpes formicivorus</i>)	Komdeur et al. 2008 Du Plessis 1994
Adoption	In a communal care setting adoption of infant can occur if mother dies, especially if there is high kin relatedness in group	Common voles (<i>Microtus arvalis</i>), social eumenid wasp (<i>Zethus miniatus</i>)	Boyce & Boyce 1988 West Eberhard 1975

Play (for infants)	Playing is a social activity that is thought to benefit the infant in their development.	Bottlenose dolphins (<i>Tursiops truncatus</i>), Slender loris (<i>Loris ardigradus</i> and <i>L. lydekkerianus</i>), Spectral tarsiers (<i>Tarsius specrum</i>), Humans (<i>Homo sapiens</i>)	Mann & Smuts 1998, Nekaris 2003, Gursky 2000 Goldstein 2012
Reciprocal benefits	Benefits are exchanged reciprocally from helper to mother. Mother's benefits are often grooming or petting for access to infants.	Patas monkey (<i>Erythrocebus patas</i>), Tufted capuchin (<i>Cebus apella nigritus</i>)	Muroyama 1994, Tiddi et al. 2010

Variation in primate AMC

In primates, AMC is widespread across the order (Tecot et al. 2012); however, variation in the types and amount of AMC is high and – with the exception of humans and callitrichines – AMC is facultative (reviewed in Tecot & Baden 2018). With increased research, we now know that nearly 75% of primates display some form of AMC, with 61% of strepsirrhines and 76% of haplorrhines (including humans) showing it in some variation (Tecot & Baden 2015). In an Order with such high incidence of AMC and with demonstrable benefits of these care behaviors, this begs the question of what factors drive the occurrence, frequency, and form of AMC in primates. Among members of the primate order humans and callitrichids (marmosets and tamarins) seem to rely most heavily on non-maternal investment, leading to the convergent evolution of a highly derived form of AMC called cooperative breeding (Burkart et al. 2009).

Among the primates that exhibit AMC the behaviors can be divided into babysitting, thermoregulation/nesting, provisioning, carrying, and allonursing. In primates AMC has been related to faster neonatal growth rates, earlier age at weaning, and shorter interbirth intervals, as well as higher infant survival (Mitani & Watts 1997; but see Tecot et al. 2012). In infant-sharing

species, like langurs mothers allow other females (typically close kin) to carry infants up to 50% of the daylight hours, which gives mothers more time to forage for food increasing their chance of survival (Hrdy 2005). Females in Old World monkeys and apes as well as both sexes in New World monkeys are noted to have a desire to handle, inspect or interact with infants, however the limiting factor for this behavior is whether the mother allows access to other females (Hrdy 2005). Until recently AMC was thought to be absent in strepsirrhines but now it's found that even nocturnal, solitary and pair-living cheirogaleids will display AMC behaviors (Tecot & Baden 2015). This contrasts with other species such as rhesus macaques and chimpanzees who will often refuse access to handling infants. Though the mothers of these species sometimes allow other AMC behavior to occur that is more indirect like provisioning for the infants (Hrdy 1977). Allomaternal care may also increase infant survival rate, which we see evidence of in Lemurs who live in highly seasonal environments that have increasing environmental impacts due to fragmentation of the forests (Tecot et al. 2012).

Justification for including environmental variables

Despite an increasing interest in primate AMC, environmental variables are rarely considered in studies investigating mechanisms driving AMC. There have been studies on the influence of climatic variation on mammalian life histories, however most often these studies focus on litter size, body mass, weaning, or gestation (Tokolyi et al. 2014; Lukas & Clutton Brock 2017). Studies on birds reveal that cooperative breeders occurred in both stable and unstable, as well as seasonal and aseasonal environments (Arnold & Ownes 1998; Ford et al. 1988, Rubenstein & Lovette 2007). It was found that rainfall typically affects food availability, so cooperative breeding mammals have been found to cope better with resource uncertainties

during droughts (Lukas & Clutton-Brock 2017). We currently do not know how AMC is related to environmental factors in primates, although it was found that animals with cooperative care are usually found in hot and unpredictable environments (Cornwallis et al. 2017). Since primates are more restricted in their global geographical range in comparison to birds, a study assessing precipitation, temperature as well as unpredictability and seasonality across many years for primates might generate different results.

AMC has received more attention on how it impacts mother and infant survival rate however, it's still not clear why certain AMC behaviors are preferred over others and whether environment is linked to that. The "hard life hypothesis" is centered on the idea that cooperative breeding, or in our case AMC, may buffer against harsh conditions. This hypothesis is best supported by bird studies, showing that increase of offspring led to more alloparents, and thus a higher provisioning rate under more harsh conditions influenced by low grass cover or low rainfall (Guindre-parker & Rubenstein 2018). It is relevant to examine primate AMC because no other study has conducted a thorough analysis of frequency of AMC and environmental conditions, even though it's clear that primates have higher rates of AMC behavior in comparison to other mammals (Tecot & Baden 2015). Although there have been studies analyzing cooperative care among birds and their environment (Jetz & Rubenstein 2011) and another looking at brain size, fertility and AMC frequencies (Isler & van Schaik 2012). Being able to reproduce successfully is crucial to the continued existence of a species, which is why examining how breeding and infant care strategies are impacted by the environment are crucial to better understand a species ability to survive in the future.

Correlates of AMC- What predicts AMC behaviors

Some studies suggest that allomaternal care is a survival mechanism that evolved in response to harsh or unpredictable circumstances often through environmental conditions like low rainfall, or social conditions like inexperience in motherhood (Hrdy 2005). AMC in birds is thought to be a risk aversion strategy as helpers will prevent starvation for nestlings (through provisioning), increase clutch success, prevent depredation during harsh conditions, and allowing more clutches to be laid during good years, which can extend the breeding season (Rubenstein 2011). Recent comparative analyses in birds often link cooperative breeding with environments characterized by unstable food availability, and that helpers at the nest can reduce reproductive failure in harsh years (Griesser et al. 2017; Jetz and Rubenstein 2011; Cockburn 2006). Moreover, recent comparative analyses have shown that AMC in birds and mammals occurs more frequently in unpredictable environments, such as those with low annual rainfall and high stochasticity through time (Guindre-parker & Rubenstein 2018).

Temperature can be an influential factor in predicting AMC behaviors particularly, communal nesting; by huddling, cold stressed animals are able to decrease the amount of food needed to maintain body heat thus increasing their survival rate (Springer et al. 1981). Similarly, meadow voles will huddle together in the winter and then raise their first litters in a communal nest for reproductive and thermal benefits until the outside temperature reaches a certain level (Komdeur et al. 2008). A study on Seychelles warblers showed that during a shortage of breeding opportunities typically due to limited habitat space or quality resulted in facultative cooperative breeding and would revert to independent breeding once higher quality territories became available (Komdeur et al. 2008). Jetz and Rubenstein's (2011) research on environmental uncertainty and cooperative breeding in birds found a strong relationship between fitness and living in

unpredictable environments, as well as a weak but significant correlation for cooperative breeders to have a wider diet range than non-cooperative breeders.

Environmental stress is a condition that affects the well-being and performance of an organism by reducing its fitness and is thought to drive adaptations over time (Kamilar & Beaudrot 2018). With the increasing amount of environmental stochasticity given the overwhelming evidence for human induced climate change, it is imperative that we examine how animals will respond to shifts in temperature and rainfall patterns (Tokolyi et al. 2014). Environmental variables have been shown to have important influences on behavior and physiology (Isler & van Schaik 2012; Lukas & Clutton-Brock 2017). In African mole rats, for example, AMC behaviors are associated with arid environments and unpredictable rainfall (Faulkes et al. 1997). Also, some seasonal breeders (e.g., camelids) adjust their reproductive patterns in accordance with rainfall seasonality and nutrition (Moreira & Rodrigues 2016). There is also increasing evidence that stressors like high temperatures, food and water access can influence the hypothalamic-pituitary-gonadal axis, thus compromising female functions as well as male semen quality (Moreira & Rodrigues 2016). Species most at risk are endemic to the tropics and who are restricted in their ranges due to the extent of human development (Jetz et al. 2007). Abiotic stress relating to variables like temperature and precipitation generally impact cold-blooded organisms rather than warm-blooded animals, however animals that live in the tropics have narrower tolerances because it tends to vary less in climate (Davies & Buckley 2012; Kamilar & Beaudrot 2018). Thus, primates are more likely to be affected than other mammals because most generally live in tropical environments often with restricted ranges (Kamilar & Beaudrot 2018).

Seasonality tends to increase with latitude because of annual variation in temperature and the environmental variability can have complex, even contrasting effects on life history traits, depending on adult or juvenile mortality (Tokolyi et al. 2014). Examining habitat and variability in rainfall and temperature can yield more accurate information of what is expected in the region versus the variability. Among some bird studies we see that cooperative breeding is associated with low mortality, increased sedentariness, lower latitudes, and decreased environmental fluctuation (Arnold & Owens 1998). In one study on the social system (cooperative versus non-cooperative) and preferred habitat type (savanna versus non-savanna) of African starlings it was found that although no cooperative breeders were found in the desert, which contained the greatest climatic variation, cooperative breeding was positively associated with semiarid savanna habitats that were highly seasonal and unpredictable (Rubenstein & Lovette 2007). The presence of non-breeding helpers has also been associated with low annual rainfall, suggesting that aridity may predict the distribution of cooperative breeding in mammals, and that mammals will have multiple breeding attempts per year (Lukas & Clutton-Brock 2017). This differs from birds which breed more seasonally, occupy warm (rather than cold in mammals) temperature localities, and longevity is related to group formation (Arnold & Owens 1998; Downing et al. 2015; Lukas & Clutton-Brock 2017).

Jetz and Rubenstein (2011) conducted a study on 95% of the world's bird species to identify how the environment influences cooperative breeding. They refer to uncertainty as climatic variation, and it was hypothesized to impact behavior, morphology, and physiological traits. They found that among and within year variation in precipitation positively affected cooperative breeding, while cooperative breeding was slightly negative for among-year temperature variation, within-year temperature variation wasn't affected (Jetz & Rubenstein

2011). In a study on mammals it is suggested that aridity predicts distribution of cooperative breeding, and that mammals are likely to have multiple breeding attempts year-round (Lukas & Clutton-Brock 2017). This differs from birds which breed more seasonally, occupy warm (rather than cold in mammals) temperature niches, and longevity is related to group formation (Arnold & Owens 1998; Downing et al. 2015; Lukas & Clutton-Brock 2017). We attempt to look at these differences in temperature and precipitation to see if there is any significant relation to certain allomaternal care behaviors (Isler & van Schaik 2012; Jetz & Rubenstein 2011; Lukas & Clutton-Brock 2017).

Aims and Objectives

The objectives of this study are threefold (1) Examine the association between climatic factors and AMC behaviors in primates; (2) Compare our results to bird studies (particularly Jetz & Rubenstein 2011) that suggest aridity and climate variability are predictors of AMC; and (3) Compare our results to studies that examined other aspects of AMC and cooperative breeding evolution in primates and other mammals.

We expect to see all the AMC behaviors be predicted by unpredictable and highly seasonal environments. We predict allonursing, babysitting, provisioning and carrying to be found in areas with lower rainfall, more habitats and higher temperatures, based on previous results (Lukas & Clutton-Brock 2017) and because these behaviors will help in times of resource scarcity. Since communal nesting depends on huddling we would expect lower temperatures to be a good predictor of it. We don't expect seasonal mating to be significant, because some studies suggest that year-round breeding increases survival in unpredictable environments, which is expected for primates with AMC. Primates with polygamy are expected to be more significant

for AMC behaviors, since there are results from bird and mammal studies that suggest that pair-living is often associated with non-cooperative behaviors (Lukas & Clutton-Brock 2017; Guindere-parker et al. 2018). To evaluate as many species as possible we conducted a meta-analysis of published peer-reviewed articles looking at the various AMC behaviors and climate.

MATERIALS AND METHODS

Data Collection

Climatic, environmental and AMC behavior data were gathered from primary literature for 91 primate species including 34 Platyrrhini, 35 Cattarrhini, 1 Tarsiiformes, 15 Lemuriformes, and 6 Loriformes. The species included in this analysis were selected on the basis of accurate climate and allomaternal care frequency data availability. The variables that were tested were (1) precipitation (2) temperature (3) diet (4) habitat diversity (5) mating system and (6) mating seasonality. Precipitation and temperature were each separated into mean, seasonality, and inter-annual variation. Whenever possible the primate AMC and climate data used in these analyses were taken from published studies on wild primate populations, although some captive studies were incorporated for mating styles.

Allomaternal care was divided into categories: allonursing, communal nesting, babysitting/retrieval, provisioning others, provisioning male, carrying others, and carrying male. The frequency of AMC behaviors incorporated Isler and van Schaik's (2012) method and database. We differed from their study by separating communal nesting from babysitting/thermoregulation into two separate variables. We followed Isler & van Schaik's (2012) paper by assigning frequencies for each allomaternal behavior ranging from 0 to 1.

Communal nesting was the only behavior documented through binary numbers; 0 as not present and 1 as present due to the limited amount of studies on the frequency of communal nesting.

Climatic data was obtained from Tolokyi et al. (2014), which includes data on rainfall and temperature variation from 1961-2009. We accounted for the possible confounding effects of diet by assigning Isler and van Schaik's (2012) diet categorization into numbers 1 (frugivore/folivore/granivore), 2 (frugivore/faunivore/omnivore), 3 (herbivore/folivore), and 4 (carnivore/faunivore/insectivore) for each primate.

Habitat diversity was assessed through Lukas and Clutton-Brock's (2017) method, using the IUCN 13 broad categories for habitat (desert, forest, rock areas, caves and subterranean, savannah, grassland, shrubland, wetlands, coastal, intertidal, neritic, oceanic and artificial). This was used to assess the existence of each primate species in different areas and assign them to various habitats. In case of primates having no listed habitats under the IUCN database, we used the definitions IUCN provides for each category and found it through primary literature.

Seasonal mating is also an important factor to consider because it is typically associated with environmental seasonality. Seasonal mating was documented as binary (0 or 1); non-existing or existing. We described a primate as a seasonal breeder if the mating period was confined to 6 months or less.

There are several studies that discuss the importance of mating systems among fish, social insects and birds suggesting that cooperative breeding may have evolved from species that are socially monogamous and have high levels of kinship with group (Wong et al. 2012; Lukas & Clutton-Brock 2012). In birds it was found that cooperative breeding was associated with mating systems that had low extra-pair paternity and relatedness between offspring and breeding females was high (Cornwallis et al. 2010). Most mammals have polygynous mating systems with

only 5% of mammals being socially monogamous (Lukas & Clutton-Brock 2012). Therefore, we included mating systems as a category to see if allomaternal care was significant for primates that is reflective of results in birds and insects. Mating style was assigned ordinal values ranging from 1-14 that captured mating behavior, which ranged from monogamous, polygynandrous, polygynous, polyandrous, or polygamous mating styles prevalent in each species.

Data Analysis

We conducted all analyses in the R statistical computing environment (Version 3.4.4). First, we conducted a correlation plot for all the independent variables (Diet, Temperature mean/seasonality/variation, Precipitation mean/seasonality/variation, Seasonally mating, Habitat diversity, and Mating system) (See Figure 1). The strength of the correlations are indicated in blue for positive and red for negative. Afterwards, we proceeded to conduct a principal components analysis (PCA) using the `princomp` function in the `psych` package to explore the relationships between the environmental independent variables (diet, mating style and seasonal mating were excluded since they weren't related) and dependent variables separately. The number of components to retain for subsequent analysis was determined with the Kaiser-Guttman rule (factors with an eigenvalue larger than 1). The varimax rotation was used to improve the results from the PCA axes. Two separate PCAs were conducted: (1) environmental factors with habitat diversity (2) allomaternal care variables. Mating style and seasonal mating were grouped together, but since they were only two factors we decided to not use the PCA results and simply leave them as is.

After the PCA we conducted a Phylogenetic Generalized Least Squares Regression (PGLS) test using the `caper` package (Orme et al 2012). The package `ape` (Popescu et al. 2012)

was used to match the species to the tree in the dataset and caper package was used to fit models that control for phylogenetic relationships. The phylogenetic relationships were analyzed by using the 10k trees database against the three allomaternal care PCA results. Finally, we conducted an Akaike Information Criterion (AICc) using the “dredge” function in the MuMIn package in R (Barton 2018) and then conducted conditional average models. We considered models with a delta AICc less than 2 (Burnham et al. 2011) to represent statistically equivalent models. After the initial analysis we used the model averaging function to summarize the predictor variables in the top models.

RESULTS

Summary of Statistics

Precipitation and temperature variables correlated strongly with each other in the correlation matrix (see Figure 1), therefore we used a PCA to get orthogonal predictors that could be used in subsequent analyses. The allomaternal care PCA results had three axes out of the seven, which had an eigenvalue greater than 1. AMC1 composed of provisioning male and others, babysitting, carrying male and others which were all greater than 0.70. We see a positive relationship between all of these variables. While AMC2 consisted only of allonursing at 0.96. AMC3 was strongly significant for communal nesting, at 0.95. In these results AMC1 explains 60% of the variance of the data, AMC2 and AMC3 each explain 20% of the variation.

Table 2 Principle Component Analysis (PCA) of AMC behavior variables. Factor loading >0.5 are shown in bold.

	Label	Eigen value	% Var. Expl	Allo-nursing	Communal nesting	Babysitting /retrieval	Provision Male	Provision Other	Carry Male	Carry Other
AMC 1	Assisting infant care	3.41	0.6	0.03	-0.12	0.71	0.92	0.88	0.82	0.72
AMC 2	Allonursing	1.13	0.2	0.96	0.01	-0.22	0	0.14	-0.26	0.28
AMC 3	Communal nesting	1.11	0.2	-0.01	0.95	0.42	-0.15	-0.1	-0.06	-0.01

The PCA of the climatic variables revealed that the first two axes out of the seven had an eigenvalue greater than 1. The variables that loaded most heavily on PC1 (≥ 0.6) is precipitation mean, seasonality, variation and habitat diversity. In PC1 we see that habitat diversity, precipitation seasonality and variation are positively related, however precipitation mean has an inverse relationship with them. PC2 is composed of temperature mean, seasonality, and variability. In PC2 temperature seasonality and variance have a positive relationship while temperature mean is inversely related, which reflects similar results for precipitation in PC1. PC1 explains 37% of the variance in the data and PC2 explains 73%.

Table 3 Principle Component Analysis (PCA) of environmental dependent variables. Factor loading >0.5 are shown in bold.

	Label	Eigen value	% Var. Expl	Temp. Mean	Temp. Seasonality	Temp. Variability	Prec. Mean	Prec. Seasonality	Prec. Variability	Habitat Diversity
PC1	Precipitation and Diversity	2.59	0.37	0.01	0.32	0.26	-0.88	0.87	0.7	0.62
PC2	Temperature	2.55	0.73	-0.92	0.88	0.83	-0.3	0.09	0.37	0.04

Separate PGLS analyses were conducted for the three AMC variables against PC1, PC2, diet, seasonal mating, and mating style. AMC1 was not strongly predicted by any variable. For AMC2 we noticed that PC1(Precipitation and Habitat Diversity) was significant with p-value of

0.014 and the coefficient was positive (0.211+). We noticed that PC2 (Temperature) and Diet had a significant effect on AMC3. PC2 had a p-value of 0.004 and Diet was 0.043 making them the only significant independent variables, and they both had positive coefficients (0.155; 0.338 respectively) for the AMC3 variable. Seasonal mating and mating style didn't have any significant impact on any of the allomaternal care variables.

Table 4 Results from the Phylogenetic Generalized Linear Squares Regression analysis							
			Climate factors from PCA			Covariates	
	df	adjR ²	PC1	PC2	Diet	Seasonal Mating	Mating Style
AMC1	82	-.016	0.4941+	0.216 +	0.8165+	0.9347+	0.2-
AMC 2	80	0.065	0.01409+	0.381-	0.80884-	0.3688+	0.78328-
AMC 3	82	0.115	0.271727+	0.004 +	0.043225 +	0.121857-	0.562771 +

* Numbers in bold have a trait that is significant at the $p < 0.05$ level. +/- sign denote the association with positive or negative.

The modeling conditional average also reaffirmed the results from the PGLS. For AMC1 none of the values were significant, and therefore had no good predictors because the null model (containing on the intercept) was among the best 5 models ($\Delta < 2$). AMC2 was associated with three equivalently good models. We found that after running the importance function for AMC2, PC1 had the highest sum of AICc weights with a value of 0.95. In the AICc model averaged coefficients and conditional averages of PC1 also reflected the PGLS values showing it was the best predictor with a p-value of 0.003 and a positive coefficient. AMC3 had 6 models with $\Delta < 2$. PC2 and Diet had sum of AICc weights of at 0.96 and 0.69, respectively. The model averaged coefficients and the conditional average also showed PC2 and Diet to have significant positive p-values at 0.003 and 0.05 respectively.

Table 5 Sum of AICc weights associated with each model					
	Climate factors from PCA			Covariates	
	PC1	PC2	Diet	Seasonal Mating	Mating Style
AMC1	0.28	0.43	0.26	0.26	0.46
AMC2	0.95	0.31	0.26	0.32	0.24
AMC3	0.32	0.96	0.69	0.46	0.28

*Numbers in bold is a significant model, that is >0.6

Discussion

We found that high seasonality and high variability in climate was correlated to both allonursing and communal nesting. It was anticipated to see babysitting, carrying and provisioning be strongly associated with the environmental factors, especially climate unpredictability because of how energetically costly most of these behaviors are. However, none of these variables had any strong predictors. Interestingly, primates that partook in allonursing were strongly correlated to areas with lower rainfall and likely to be found in more than one habitat, but not higher temperatures. Nursing another female's offspring, allonursing, is thought to have evolved from kin selection or reciprocity benefits, which makes it useful in harsh conditions because it increases the fitness of the mother and infant (MacLeod & Lukas 2014). Among rodents that partake in AMC it was found that communal nesting was often associated with colder temperatures and could often be correlated to allonursing since the nest would be shared until spring time (Hayes 2000; Isler & van Schaik 2012). The exception is when rodents are in stressful or low resource environments they may choose not to participate in allonursing

because it wouldn't be advantageous (Hayes 2000). In our study primates involved in allonursing and communal nesting were separated into individual loading factors, and both were more likely to occur with unpredictable or variable precipitation or temperature, respectively, rather than only participating during resource abundance like some facultative rodents (Hayes 2000). Since primates generally don't live in areas with extreme cold temperatures that may be why temperature was not as strong of a predictor for allonursing as it might have been for rodents. This ties in with another study that allonursing is more common when females produce litters and when resources are more abundant labeling it as more opportunistic behavior (MacLeod & Lukas 2014; Lukas & Clutton-Brock 2017). Additionally, a potential explanation for allonursing being correlated with low precipitation and a fluctuating seasonal climate could be associated with periods of low resource availability for primates. Although diet wasn't a strong predictor it's possible that allonursing in our results can be predicted by unpredictable or harsh years, because food resources are limited during arid periods, and thus it increases fitness to partake in this AMC behavior as a group.

Primates that were found in lower temperatures were significantly associated with communal nesting, which is expected due to huddling behavior during nesting and reflective of studies on cooperative breeding in rodents (Hayes 2000). Primates with more protein in their diet also are strongly associated with communal nesting and found to be a good predictor of it. Communal nesting is rather rare among primates however there is a lot of evidence suggesting it increases maternal success, and mothers having more time to forage increased infant survival rate (Baden et al. 2013). This is reflective of our results because lower temperatures and variable climate would increase the stress on the animal, so it would be useful for sharing communal nests to maintain body heat. This is reflective of studies on rodents that participate in communal

nesting during colder temperatures (Hayes 2000). In our research mating style and mating seasonality were found to have no significant effect on predicting AMC behavior, which was unexpected because temperature and precipitation seasonality was significant.

The most in-depth studies comparing cooperative breeding and environmental properties comes from birds, it is useful to use these studies as a comparison to primates, however due to the broad geography of birds and the generally more tropic location of primates there will be numerous differences. In the Jetz and Rubenstein (2011) study it was found that cooperative breeding birds generally had wider diets and lived in more unpredictable environments, which is reflective of our results for primates. In another study allonursing was found to be most common among carnivores that are cooperative breeders (MacLeod & Lukas 2014). In our results allonursing wasn't significant with more protein in the diet of primates with AMC, however communal nesting was found to be.

In Lukas & Clutton-Brock (2017) they found that mammals that were cooperative breeders were found in more environments and that arid environments associated with more group members providing allopaternal care. In their study they also found that cooperatively breeding primate live on average in 1.4 different habitat types and socially monogamous lived in 1.2. In our results we focused on types of AMC behavior frequency rather than a broader category of whether there was cooperative breeding. Our results found a similar answer that cooperative breeders were found in 1.3 different habitats and all the primates that had AMC behaviors were found in 1.6 different habitats. This makes sense because if more primates are found in different habitats within a region we would expect greater variability in weather, which is reflective of the results. Additionally, Lukas & Clutton-Brock (2017) showed that mammals that exhibited AMC were generally found in arid habitats and would breed year-round, in our

results allonursing could be predicted by low rainfall, however breeding year-round wasn't significant in our results.

In Isler & van Schaik's (2012) results from their PCA analysis of primates it was dominated by provisioning, but still included all allomaternal care behaviors other than allonursing which was loaded on a second factor. Our results were similar except after separating communal nesting from babysitting it was our third rotated factor. In their results they found that provisioning and carrying were highly correlated with brain size and fertility, while allonursing was also to a lesser extent. In Isler & van Schaik (2012) they found that allonursing in primates is not another element of helping but rather an independent variable of allomaternal care, which could be linked to relatedness and tolerance of other females. We also find in our study that allonursing is independent (other than communal nesting) compared to the other allomaternal care variables supporting this conclusion.

Limitations

The limitations of this study have to do with the sample size not including all the primates that exhibit allomaternal care. The database was impacted due to the quality of climate data for each species, as well as reliable observations of allomaternal care for all primate species. In addition, some primates are fragmented in different locations and sometimes there is within-group variation where the same species may show variation in allomaternal care behavior or mating style, which is why we chose to assign numerical values to each by assessing the frequency. If we want to understand the variation in AMC behavior more clearly more within-species studies could be valuable in the future. Furthermore, mating style might prove to be a more significant result if there is a better way to categorize the various types among species;

there was a lot of variation when assigning ordinal values. Future studies will benefit from improved allomaternal care frequencies from observations within primate species as well as better climate coverage for the tropical regions.

Habitat diversity attempts to account for the numerous environments that a species can occupy to try to improve the climate data. However, there are sometimes variations of habitat choice within species groups that makes it hard to address in a large primate comparative study. Due to the limited information on climate data and ranges of primates in hard to study areas we tried to include only the primates with the most accurate documentation. The climate data is from 1961-2009, so it would be valuable to incorporate recent climate data with this study to see if recent increased stochasticity on the planet is influencing any primate AMC behaviors. It could also be valuable to have a better way to categorize climatic variation that can be applied in comparative studies concepts like the 'Dual Benefits Framework' (Shen et al. 2017). AMC observation on species can help us improve our understanding on how the environment will impact their behaviors and how same species in different environments may differ.

Conclusion

There is a lot of research still emerging regarding AMC behavior in primates. Studies on individual species that analyze the frequency of these behaviors as well as larger sampling will help us improve our understanding and assessment of impact from the environment. It is interesting that only allonursing and communal nursing were more likely to be present in low rainfall and low temperature environments. Both AMC behaviors are less frequent than behaviors like provisioning and carrying in primates, so it's interesting to see how increased unpredictability will impact primates in Madagascar since it has a greater frequency of

communal nesting than other locations globally with primates. As Madagascar is already seasonally variable and with increasing unpredictability on the planet; future studies on lemurs and their AMC frequencies could be very useful in understanding these results further.

Dividing allomaternal care by frequency per primate species against environmental variables is the first study of its kind and future studies with increased information can help us improve our understanding. Adding litter size, reproductive skew and group size might be useful to add into this study to see what else could be a good predictor of AMC especially since Lukas & Clutton-Brock (2017) found evidence that cooperative breeding was strongly associated to polytoccy and aridity. The increasing unpredictability in the climate makes it important for us to assess how animals will react and to see what sort of infant care strategies will be most useful for survival. This study requires further research looking into allonursing and communal nesting in comparison to provisioning, carrying, and babysitting to analyze the variations and patterns of all these behaviors. It will be interesting to see how frequencies of these behaviors may change in the coming years, and how the inclusion of more AMC primates with accurate climate data will improve and add to this research.

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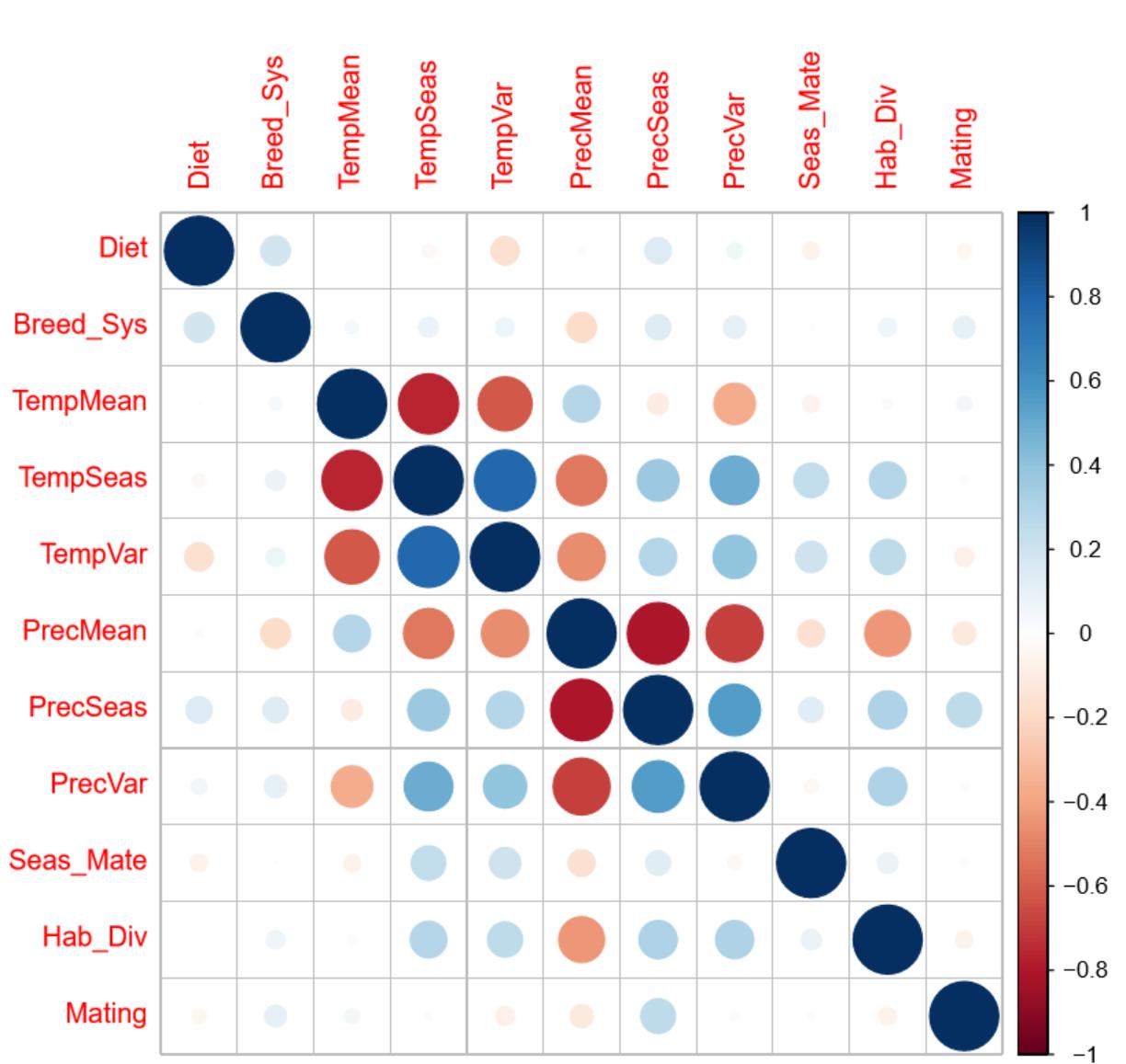
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Appendix

Figure 1 Correlation plot of all the Dependent Variables



* The strength of the correlations are indicted in blue for positive and red for negative.