Causes and consequences of sexual dimorphism in mandrill (*Mandrillus sphinx*) feeding and spatial behavior.

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March 2023

A thesis submitted for the degree of

Doctor of Philosophy

Faculty of Natural Sciences

The University of Stirling

UNIVERSITY of STIRLING

Summary Abstract

Sexual dimorphism is a widespread phenomenon, the origins of which have long intrigued evolutionary ecologists. Classic evolutionary theory attributes the evolution of sexual dimorphism to sexual and fecundity selection, that arise due to sex differences in optimal reproductive strategy. However, cross-species comparative analyses have found mixed support for sexual and fecundity selection as drivers of dimorphism. Other hypotheses may therefore be required to explain the full diversity of sexual dimorphisms found in nature.

One alternative is the evolution of sexual dimorphism via ecological causation. This thesis explores the possibility of ecological causation of sexual dimorphism, with a particular focus on mandrills (*Mandrillus sphinx*). Mandrills are the most sexually dimorphic primate, with males over three times larger than females, possessing 45 mm canines and displaying extravagant red, blue, and violet ornamentation on their faces and rumps. Males also abandon social groups outside of the breeding season, foraging and travelling separately to females, which could suggest an ecological component to mandrill dimorphism.

One of the key predictions of the ecological causation hypothesis is that greater sexual dimorphism should be associated with greater ecological divergence between males and females. In Chapter 2, I conducted a meta-analysis of 163 species to examine associations between sexual dimorphism and ecological sex differences, measured using stable isotopes. Across species, greater size dimorphism was associated with greater sex differences in trophic level. Chapter 2 thus supports a key prediction of the ecological causation hypothesis and suggests that the strength of relationships between sexual dimorphism and ecology may be underappreciated.

Mandrills are challenging to study in the wild, due to the dense forests in which they are found. I therefore applied research tools that avoided the need to directly observe individuals, to study the socioecology of males and females and investigate the possibility of ecological causation of mandrill dimorphism. In Chapter 3, I analyze the contents of 4024 mandrill fecal samples, collected over an eight-year period, in conjunction with eight years of fruiting phenology data. I find that mandrills are primarily frugivorous, with consumption of fruit tracking phenological patterns of fruit production. The focal group also demonstrated high

dietary flexibility, consuming animal prey, leaves, crushed seeds, and other plant fibers when fruit availability was low.

However, because male mandrills spend much of year solitary, the feeding niche information gained from Chapter 3 largely relates to females. To investigate sex differences in feeding niche, I therefore applied stable isotope analysis to mandrill hairs. In Chapter 4, I detail the results of a diet-switch experiment, that quantified mandrill hair growth rates, isotopic tissue turnover times and isotopic tissue-diet discrimination factors. This experiment showed that stable isotope analysis of mandrill hairs can reveal dietary information on wild mandrills at a temporal resolution of 5.5 days and allowed the stable isotope ratios of wild mandrills to be correctly adjusted for accurate dietary inference.

In Chapter 5 I applied stable isotope analysis to the hairs of wild male and female mandrills. I found that the diets of individual male mandrills were more consistent than individual females, who instead showed more dietary variation, at the individual level. This result suggests that individual male mandrills had more consistent access to preferred resources than individual females, and therefore that males experience differing levels, or outcomes, of resource competition. Males may therefore seasonally leave mandrill social groups to avoid resource competition.

In Chapter 6, I used GPS collars to examine sex differences in mandrill spatial behavior. I found that, during the breeding season, male habitat selection, home-range size and Brownian motion variance was similar to females, but distinct from females during the non-breeding season. These results indicate that collared males were not always within the social group during the non-breeding season. Furthermore, during the non-breeding season, males travelled shorter distances, at slower speeds, compared to the breeding season. Males therefore appeared to expend less energy on travel during the non-breeding season, suggesting that male mandrills may also leave groups to reduce energetic expenditure.

The results of Chapters 5 and 6 suggest that ecological factors compel male mandrills to abandon social groups outside of the breeding season. However, the intensity of sexual selection on male traits may be increased as a result of this behavior, as males must establish dominance and attract unfamiliar females when they re-join social groups to breed. An interaction between sexual and ecologically mediated selection may therefore offer the most complete explanation of why mandrill dimorphism is so extreme.

Declaration of authorship

I, Joshua T Bauld, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of the work carried out in collaboration with others.

Signed…………………….

Date……………………….

Acknowledgements

Firstly, my deepest thanks to my team of supervisors - Luc Bussière, Katharine Abernethy, Jason Newton, David Lehmann, and Isabel Jones - whose support and mentorship have made my PhD such a valuable experience. Thank you all for your insight, knowledge, patience, and most of all for the time you’ve committed to guiding me through my thesis.

Next, I want to express my gratitude to the many SEGC field scientists whose work has allowed this thesis to be written. Particular acknowledgement must go the Animal Capture Unit - David Lehmann, Lisa-Laure Nindiwe Malata, Brigitte Moussavou, Michel Louis Halbwax, Edmond Dimoto, Arthur Dibambou, Loic Makaga and Josué Edzang Ndong – for their dedication to the mandrill collaring program. I would also like to thank the team of phenology observers - Caroline Tutin, Katharine Abernethy, Lee White, Edmond Dimoto and JT Dikangadissi, Richard Parnell, Liz Williamson, Rebecca Ham, Patricia Peignot and Ludovic Momont – whose work over many years has greatly impacted the inferences in the chapters that follow. Most of all I would like to thank Loic Makaga and Edmond Dimoto for their committed support and guidance in the field.

I am extremely grateful to the International Center for Medical Research in Franceville, for allowing me to carry out research at their facility. Special mention must go to Barthélemy Ngoubangoye, Thierry A. Tsoumbou, Cyr I. Moussadji-Kinga and the animal care staff of the Primate Center for their collaboration and allowing me access to their animals.

I would like to thank the IAPETUS Doctoral Training Partnership, UK, the National Agency for National Parks (ANPN), Gabon and the National Environmental Isotope Facility, UK for funding my PhD.

Finally, but most importantly, thank you to my parents Tracy and Richard, to Mama and to my sister Lucy, for your support and encouragement from the very beginning.

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Chapter 1: General Introduction

1.1 Background

Sexual dimorphism describes differences between males and females in traits such as size, shape, coloration, scent, and behavior (Andersson, 1994; Mori *et al.*, 2017). Sexual dimorphism is pervasive across species and incredibly diverse, for example, males are the larger sex in most mammals (Weckerly, 1998), whereas female anglerfish (*Ceratias holboelli*) are around 500 000 times heavier than males (Bertelsen, 1951). Some dimorphic traits seem clearly related to each sex's reproductive role, such as the elaborate plumage of male birds-of-paradise (Paradisaeidae), whereas others appear connected to each sex's ecology, as in the beaks of Caribbean hummingbirds (*Eulampis jugularis*) (Temeles *et al.*, 2000). Explaining this diversity has been a longstanding goal of evolutionary ecology but debate as to the origins of sexual dimorphism still persists (Shine, 1989; Wyman *et al.*, 2013).

This thesis investigates the possible ecological causes and consequences of sexual dimorphism, with a particular focus on mandrills (*Mandrillus sphinx*). Mandrills display extraordinary sexual dimorphism in traits such as body size and ornamentation (Darwin, 1871; Abernethy and White, 2013; Setchell, 2016), as well as an unusual social structure and mating system, involving groups of several hundred animals (Abernethy *et al.*, 2002; Hongo *et al.*, 2016). Why the dimorphism and social behavior of mandrills has evolved to become so extreme is, however, an open question. Mandrills are also vulnerable to extinction, primarily due to habitat loss and climate change, and improved knowledge of the species' understudied ecology is essential to improving its conservation prospects (Abernethy and Maisels, 2019).

Mandrills have historically proven difficult to study in the wild, due to the dense nature of their forest habitat and the challenge of habituating groups of several hundred animals. As a result, in this thesis I use fecal and stable isotope analysis, alongside GPS collars, to study the feeding and spatial behavior of both sexes. These techniques allow ecological data to be gathered from unhabituated animals, by sidestepping the need to directly observe their behavior. Using these data, I consider the impacts of group size on the ecology of each sex, and whether ecological factors like feeding competition and energetic costs may have contributed to the evolution of sexual dimorphism in mandrills.

1.2 The evolution of sexual dimorphism.

Much of the theory explaining the evolution of sexual dimorphism stems from the Darwin-Bateman Paradigm (Dewsbury, 2005). Darwin (1871) observed that one sex, most often males, competes for mating opportunities with the more discriminating sex in terms of mating partner, most often females. The mechanism behind this sex difference in mating strategy was proposed by Bateman (1948), who suggested that male *Drosophila* flies were able to enhance their reproductive success through additional matings, whereas females were not.

Sex differences in optimal mating strategy are rooted in anisogamy, defined as sexual reproduction involving the fusion of gametes that differ greatly in size. In the context of anisogamy, males are defined as the sex with smaller gametes and females as the sex with larger gametes (Lehtonen *et al.*, 2012). It is these sex differences in gametic investment that initially impose differing constraints on the reproductive success of each sex: males invest less energy to produce many small sperm, and are primarily limited by the number of eggs those sperm are able to fertilize, and females invest more energy into producing fewer large eggs, and are usually limited by investment into gamete production (Wade, 1979). Males may therefore compete directly amongst each other for access to females (and their gametes) or compete indirectly to attract receptive females (and their gametes) (Andersson and Iwasa, 1996; McCullough *et al.*, 2016). The selection that arises from this competition for access to mates and their gametes is termed sexual selection (Shuker and Kvarnemo, 2021). To compete for matings, males may evolve larger body size or exaggerated weaponry (Lindenfors *et al.*, 2002; Bro-Jørgensen, 2007). In addition, males may evolve ornaments or courtship displays that signal their quality to females (Emlen *et al.*, 2012; Mitoyen *et al.*, 2019). Sexual selection is often considered to be the only robust theory for explaining the evolution of exaggerated ornaments and weaponry (Parker and Pizzari, 2015).

In contrast to sexual selection, fecundity selection considers traits that affect gamete production (Pincheira-Donoso and Hunt, 2017). Darwin (1871) originally formulated the ‘fecundity advantage hypothesis’ to explain female biased size dimorphism, proposing that increased size may facilitate the production of greater numbers of gametes by females. Fecundity selection has received a great deal of empirical support, with larger body size often being associated with increased egg production in various invertebrates and ectothermic vertebrates (Head, 1995; Prenter *et al.*, 1999; Cox *et al.*, 2003; Dugo-Cota *et al.*, 2022). However, in mammals, larger female body size is associated with slower life histories and greater energetic costs of reproduction (Lindenfors *et al.,* 2007). Thus, it has been suggested that larger size may incur fecundity costs in female mammals and that fecundity selection could promote sexual size dimorphism in mammals by constraining female body size (Cassini, 2017).

The general framework of sexual selection acting on males, and fecundity selection on females, has proven useful in explaining the origins of sexual dimorphism, but other factors are also relevant (Fairbairn *et al.,* 2007; Dugo-Cota *et al.,* 2022). Sexual selection may act on females (Clutton-Brock 2009) and fecundity selection on males (Pincheira-Donoso and Hunt, 2017). For example, female dance flies (*Rhamphomyia longicauda*) possess sexually selected ornaments designed to attract male mating partners (Murray *et al.* 2018). Moreover, in polygamous *Syngnathus* pipefish, which exhibit male pregnancy, male morphology appears to be influenced by fecundity selection (Wilson, 2009). Comparative analyses have also found sexual and fecundity selection to be modestly and inconsistently associated with sexual size dimorphism, suggesting that their effect on dimorphism may vary substantially taxa (Cox *et al.,* 2007; Janicke and Fromonteil, 2021). Consideration of a wider range of evolutionary mechanisms, including those mediated by ecology rather than reproduction, may thus be required for a full understanding of how sexual dimorphism evolves (Krüger *et al.,* 2014; Littleford-Colquhoun *et al.,* 2019).

In cases of sexual dimorphism in traits relevant to ecology, such as body size or feeding morphology, selection mediated by ecology is especially likely to be relevant to species' evolution (Selander, 1966; Hendrick and Temeles, 1989; De Lisle and Rowe, 2015). Such ecological sexual dimorphisms were noted by Darwin (1871) as being "connected with different habits of life, and not at all, or only indirectly, related to reproductive functions" (p. 254). Three main processes have been put forward for ecologically mediated natural selection to produce sexual dimorphism. The first is the dimorphic niches hypothesis, which predicts that intrinsic differences between the sexes in nutritional or energetic requirements may favor the evolution of different optimal phenotype in males and females (Lande, 1980; Slatkin, 1984). The dimorphic niches hypothesis is supported by evidence that the fitness of males and females is optimized by divergent nutritional intakes, suggesting that the sexes can differ in intrinsic requirements (Hunt *et al.,* 2004; Maklakov *et al.,* 2008). The second is the bimodal niches hypothesis, which suggests that the sexes may have similar ecological needs, but that two distinct phenotypes may exist with the ability to meet those needs, with each sex potentially evolving to either phenotype (Schoener, 1969; Slatkin, 1984). There appears to be less support for the bimodal niches hypothesis in the literature (but see Schoener, (1977)) and evidence of differing nutritional optima between the sexes also discredits a hypothesis that requires the sexes to have similar ecological needs.

The third proposal, and perhaps the most studied, is the ecological character displacement hypothesis (Slatkin, 1984; Li and Kokko, 2021). Under this hypothesis, disruptive selection resulting from frequency-dependent competition for resources is predicted to favor the evolution of ecological sexual dimorphism that lowers competition for the resource (Cooper *et al.,* 2011). Disruptive selection may arise when a quantitative trait affects use of a continuously varying resource. For example, birds may feed on a continuum of seed sizes, the consumption of which is influenced by bill size. Initially, in a normally distributed population, the fitness of individuals with intermediate sized bills may be highest, if medium seeds are the most common resource. However, as individuals with intermediate sized bills become more frequent in the population, the availability of medium seeds will fall. The relatively high availability of small and large seeds may then favor individuals with small or large bills, that specialize on these resources, as these individuals will experience lower feeding competition and have the highest food intake. Disruptive selection arises once the fitness of individuals with medium bills falls below the fitness of individuals with small or large bills. Selection will then favor the evolution of two distinct phenotypes and, if each sex evolves towards a particular bill size, an ecological sexual dimorphism (Martin and Pfennig, 2009).

Modelling work has successfully demonstrated that ecological character displacement between sexes, mediated by resource competition, can produce sexual dimorphism (Slatkin, 1984; Bolnick and Doebeli, 2003; Li and Kokko, 2021). De Lisle and Rowe (2015) have also demonstrated the process experimentally, by showing that the fitness of individual salamanders, that display sexual dimorphism in feeding morphology and resource use, is highest when competing for resources against individuals of the opposite sex.

A limitation of models for ecological character displacement between sexes is that they do not include a justification for why an ecological sexual dimorphism should evolve, instead of ecological speciation or two ecologically distinct morphs containing both sexes (Bolnick and Doebeli, 2003). A combination of evolutionary processes may therefore provide the most likely scenario for explaining the evolution of ecological sexual dimorphism (De Lisle, 2019). For example, sexual or fecundity selection may produce an initial dimorphism, say in body size, and if disruptive selection on size arises, each sex will already be biased to evolve towards each end of the phenotypic spectrum. Similarly, if sex differences in nutritional requirements result in dimorphic niches, and frequency-dependent competition for resources arises, males and females may again be expected to respond in divergent manners, if their sex-specific nutritional optima impact foraging decisions. For example, De Lisle (2023) found that, after only three generations, *Drosophila melanogaster* evolved greater sexual dimorphism in dietary preference under high resource competition, but not under low resource competition. After three generations, females and males from the high competition treatment fed on greater proportions of yeast solution and sucrose solution, respectively. This result suggests that inherent sex differences in nutritional requirements, related to the reproductive roles of each sex, led to divergent responses by males and females to resource competition (De Lisle, 2023).

Ecological causation has often been regarded as a less parsimonious explanation for the evolution of sexual dimorphism, and of minor importance, compared to sexual or fecundity selection (Shine, 1989; Blanckenhorn, 2005). However, the abundance of examples of ecological dimorphism found in the literature (Temeles, *et al.* 2000; Pearson, *et al.* 2002; Box 2, De Lisle, 2019; Bauld *et al.,* 2022, this thesis), alongside the modelling and experimental work outlined above, make a compelling case for the evolution, or exaggeration, of sexual dimorphism by ecological processes. The primary goal of this thesis is thus to investigate the possibility that the sexual dimorphism of mandrills could have been enhanced by ecologically mediated selection, not directly related to the reproductive roles of males and females.

1.3 Study Species: Mandrills

1.3.1 Phylogeny and Biogeography

Mandrills are among the largest cercopithecine primates and located in West Central Africa (Abernethy and White, 2013). Their range extends from southern Gabon, through Equatorial Guinea and southwestern Republic of Congo, to the Sanaga river in Cameroon (Abernethy and Maisel, 2019); to the north of which their congener drills (*Mandrillus leucopheus*) are present (Gadsby *et al.,* 2019). The eastern distribution of mandrills is largely limited by the Ivindo and Ogooué rivers, though mandrills have twice been observed in northern Democratic Republic of Congo, but never east of the Congo river (Fay, 1989; Allam *et al.,* 2016; Abernethy and Maisel, 2019). The Ogooué river divides mandrills into two genetically distinct northern and southern populations, occupying northern Gabon, Cameroon and Equatorial Guinea versus southern Gabon and Democratic Republic of Congo, respectively (Telfer *et al.,* 2003).

The genus *Mandrillus* is placed within the African Papionines (subtribe: Papionina), that also contains baboons (*Papio* spp), terrestrial mangabeys (*Cercocebus* spp), arboreal mangabeys (*Lophocebus* spp), geladas (*Theropithecus* spp) and kipunjis (*Rungwecebus* spp). Body size differences between genera initially led to taxonomic confusion, with the small-bodied mangabeys and large bodied mandrills, drills, baboons, and geladas considered as two distinct groups (Pugh and Gilbert, 2018). The result was that mandrills were initially characterized as “forest baboons” (Hoshino, 1984; 1985; Feistner, 1989). However, molecular work indicated that mandrills, drills, and terrestrial mangabeys were a distinct phylogenetic group, more distantly related from baboons and arboreal mangabeys (Harris, 2000). A *Mandrillus-Cercocebus* clade was further supported by morphological analyses, showing that both genera possessed dental and forelimb morphology adapted to consumption of hard foods and foraging in leaf litter (McGraw and Fleagle, 2006).

1.3.2 Socioecology

Knowledge of wild mandrill behavior has historically proven difficult to obtain, due to the challenges of studying unhabituated primates in the dense forests of Central Africa (Brockmeyer *et al.,* 2015; Hongo *et al.,* 2016). Following the early characterization of mandrills as baboons, one male units, containing a single adult male and a few females, were initially thought to be the basic component of mandrill societies (Jouventin, 1975; Hoshino *et al.,* 1984). However, subsequent investigations identified a matrilineal structure to mandrill social groups, alongside female philopatry and male dispersal (Setchell, 2000; Abernethy *et al.,* 2002; Charpentier *et al.,* 2007; 2012; 2020). In addition, numerous studies have demonstrated marked seasonal variation in the proportion of adult males present in mandrill groups, as well as the existence of solitary males throughout the mandrill range, making a social structure based around adult males unlikely (Abernethy *et al.,* 2002; White *et al.,* 2010, Brockmeyer *et al.,* 2015; Hongo *et al.,* 2016). The majority of males only enter mandrill groups when the number of fertile females is high, which occurs during the dry season, allowing females to time most birthing, lactating and infant carrying with the subsequent wet season and high food availability (Abernethy *et al.,* 2002; Hongo *et al.,* 2016; Dezeure *et al.,* 2022). Hongo *et al.* (2014) also found that groups traveled with sub-adult and adult males close to the front, with females and dependent infants closer to the rear and unaccompanied by males, further discrediting the one male unit hypothesis. Mandrill social groups are therefore considered to follow a multi-male multi-female structure (Abernethy *et al.,* 2002; Brockmeyer *et al.,* 2015).

Early studies of mandrill also underestimated the size of mandrill groups, termed ‘hordes’. Using observational methods, groups were estimated to be between 15-95 (Hoshino *et al.,* 1984) and 150 individuals (Tutin *et al.,* 1997). These low estimates were likely due to the challenge of observing an entire mandrill group within forest habitats and because hordes often display fission-fusion behavior, resulting in variable sub-group sizes (White *et al.,* 2010). However, using films of forest gap crossings, Abernethy *et al.* (2002) counted a mean horde size of 620 (range = 338- 845) individuals. More recent genetic work suggested an effective population size of 1000 individuals for the same horde (Guibinga Mickala *et al.,* 2020), backed up by a recent field count of 1250 individuals in the horde (David Lehmann, personal communication). Mandrill hordes are therefore among the largest social groups seen among non-human primates (White *et al.,* 2010).

Mandrills are found almost exclusively within forest habitats, though they may occasionally cross savannas (White, 2007; Brockmeyer *et al.,* 2015). The sizes of mandrill home-ranges were also underestimated by early observational approaches, at between 30-50 Km^2 (Jouventin, 1975; Hoshino *et al.,* 1984; Harrison, 1988). However, using radio-telemetry, White *et al.* (2010) estimated a home-range of 182 Km^2, containing 89 Km^2 of forest. Mandrills thus exploit some of the largest home-ranges of any non-human primate, which is expected given the extreme biomass of a mandrill horde (Clutton-Brock, 1977; White *et al.,* 2010).

The distances traveled by mandrill hordes are usually higher each day during periods of fruit abundance than during periods of scarcity, suggesting fruit availability drives mandrill movement (Hongo *et al.,* 2022). Furthermore, space use is often uneven, as would be expected for a primate mainly consuming fruit resources that are clumped in trees (White, *et al.* 2010). Space use does, however, become more even when fruit availability is low, suggesting movement is influenced by resources that are distributed more ubiquitously in the environment during these periods (Hongo *et al.,* 2018).

Seasonal changes in mandrill space use correspond with observations of mandrill food selection. Fruit is the principal food source for mandrills, though invertebrate and vertebrate prey, leaves, seeds, and other plant fibers are also eaten (Jouventin, 1975; Hoshino, 1985; Lahm, 1986; Harrison, 1988; Rogers *et al.,* 1996; Nsi Akoué *et al.,* 2017). Fruit consumption is highest during the wet seasons when it is most available, with consumption of alternative food types increasing in the dry seasons, when fruit consumption falls (Tutin *et al.,* 1997; Hongo *et al.,* 2018).

1.3.3 Mandrill Sexual Dimorphism

Mandrills are the most sexual dimorphic species among primates (Darwin, 1871; Dixson *et al.,* 2005). Male mass is approximately three times that of females, with males weighing 28.9 Kg (range = 24.5 - 36.0 Kg) and females weighing 9.8 Kg (range = 8.0 - 13.5) (David Lehmann, *unpublished data*). Much of what we know about mandrill sexual dimorphism and behavior comes from a semi-free ranging colony of a few hundred animals, held in a multi-hectare, naturally forested enclosure in Franceville, Gabon (Feistner *et al.,* 1992). Data on these animals has proven highly informative for suggesting the possible functions and drivers of mandrill dimorphism. However, some caution may be needed when translating these results to wild groups, until further research is completed. For example, the behavioral function of mandrill coloration may well be conserved in captivity, but the ability of dominant males to dominate paternity might be exaggerated, compared to the wild.

In semi-free ranging groups, males with larger testes and higher plasma testosterone levels are larger in mass and heavier males attain higher dominance ranks than smaller males (Wickings and Dixson, 1992; Setchell *et al.,* 2008). Males also possess red sexual skin on their faces and genitals (Setchell, 2005). The brightness of red coloration in males is again associated with larger testes, higher testosterone levels and rank attainment (Wickings and Dixson, 1992; Setchell and Dixson, 2001; Setchell *et al.,* 2006). The association between brightness and testosterone suggests that red coloration may be an honest indicator of androgen levels and fight readiness, thus acting as a badge of status (Setchell *et al.,* 2008). Indeed, males of similar brightness are less aggressive between each other, than to duller males (Setchell and Wickings, 2005). Females also display a preference for more brightly colored males, meaning that red skin may also act as a signal of male condition to females (Setchell, 2005).

The red skin on the faces of males is also accompanied by blue paranasal swellings, formed from an enlarged maxillary ridge. The size of these paranasal swellings increases allometrically with male body size, suggesting that they constitute an honest signal of size and fitness (Klopp *et al.,* 2012). Furthermore, brighter blue swellings contrast more strongly with red sexual skin and increase the contrast of male facial displays against foliage (the typical background in mandrill habitat). The most dominant males are those with the highest color contrasts between red skin, blue paranasal swellings, and foliage, again consistent with the hypothesis that facial displays are a badge of status (Renoult *et al.,* 2011).

Mandrills are also sexually dimorphic in terms of canine length, with males averaging 45 mm and females 10 mm canines. Males with canines shorter than 30 mm rarely breed and sires have longer canines than non-sires, implying that longer canines may be a sexually selected weapon in mandrills (Leigh *et al.,* 2008). Both sexes possess sternal glands for scent marking, but the chemical profiles of these scents are distinguishable between the sexes and relate to age and dominance rank in males only (Setchell and Dixson, 2001; Setchell *et al.,* 2010). In addition, scent marking behavior is most prevalent in dominant adult males, suggesting that scent marking is another way in which males communicate their dominance status (Setchell *et al.,* 2010; Vaglio *et al.,* 2015).

Like many other cercopithecines, female mandrills display sexual swelling around estrous and the shape of these swellings may contain information about female quality (Setchell and Wickings, 2004; Huchard *et al.,* 2009). During the breeding season, males are observed to mate-guard females with sexual swellings (Dixson *et al.,* 1993). Mate-guarding by males is biased towards females with higher major histocompatibility complex (MHC) diversity and MHC variants of higher quality (Setchell *et al.,* 2016). Males also preferentially mate-guard high ranking or parous females over low ranking or nulliparous females (Setchell and Wickings, 2006). Dominant males are the most successful in mate-guarding, resulting in a positive association between mate-guarding and paternity, alongside assortative mating, in which the highest ranking males mate more often with the highest quality females (Setchell *et al.,* 2005; Setchell and Wickings, 2006).

The result of mate-guarding by dominant males, in semi-free ranging groups, is high reproductive skew among males, that is not replicated among females (Wickings *et al.,* 1993; Wickings, 1995). In semi-free ranging groups, reproductive skew falls as the number of tumescent females increases (Charpentier *et al.,* 2005), thus reproductive skew may be lower in wild groups, where dominant males probably maintain less control. However, mature males also mate-guard females with sexual swellings in the wild (Hongo *et al.,* 2016) and so some reproductive skew is likely to persist in wild mandrill groups.

The evidence described here suggests a sequence of effects, whereby the development of male secondary sexual traits (larger mass, red sexual skin, blue paranasal swellings, powerful scent glands, long canines) influences rank attainment and female preference, which in turn facilitate successful mate guarding by large, dominant, and brightly ornamented males, who then obtain a higher share of paternity. It is also notable that the sexual dimorphism of mandrills develops due to bimaturism, with males investing at least three or four more years than females towards growth and maturation (Setchell *et al.,* 2001; Dirks *et al.,* 2020). Females also reproduce for the first time approximately four years earlier than males (Wickings and Dixson, 1992; Setchell *et al.,* 2002). Higher reproductive skew and longer maturation periods among males, alongside lower age at first reproduction and longer reproductive lifespans for females, are all strong evidence that sexual selection has had a substantial role in the evolution of mandrill dimorphism (Setchell *et al.,* 2005; Setchell, 2016).

Sexual selection is expected to arise when spatial aggregation of fertile females in space allows individual males to monopolize paternity (Emlen and Oring, 1977; Cassini, 2020a). Female primates are expected to form groups, and thus spatially aggregate, as an anti-predation strategy (Sterck *et al.,* 1997). The frugivorous diet of mandrills, coupled with seasonality in fruit availability throughout their geographic range (Hongo *et al.,* 2018; Bush *et al.,* 2020), also means that fertile females are temporally clustered.

The seasonal timing of cyclical biological events, such as fruit production, is termed phenology (Lieth, 1974). In tropical forests, the phenological cycles of fruiting trees are controlled by numerous variables, including temperature, rainfall, and solar radiation (Borchert, 1983; Reich and Borchert, 1984; Butt *et al.,* 2015; Potts *et al.,* 2020). Across African forests, annual phenological cycles of flowering and fruiting are most frequent, leading to seasonality in fruit availability (Chapman *et al.,* 1999; Bush *et al.,* 2017; Adamescu *et al.,* 2018). Seasonal changes in fruit availability influence many aspects of primate behavior, such as social structure (Asensio and Korstjens, 2009; Aguilar-Melo *et al.,* 2019) and reproductive phenology (Koenig *et al.,* 1997; Matthews *et al.,* 2021).

The consequence of fruiting phenology for mandrills is that females time birthing and lactation with annual peaks in fruit availability. As a result, receptive fertile females are clustered in time during the longer annual dry season (Hongo *et al.,* 2016; Dezerure *et al.,* 2022). The large size of mandrill hordes means that the number of spatially and temporally clustered fertile females is uncommonly high for a primate species (Abernethy *et al.,* 2002). The potential for males to monopolize females is therefore exceptional in mandrills, which should result in stronger sexual selection and has almost certainly contributed to extreme dimorphism in mandrills.

1.3.4 A role for ecological causation?

However, the frugivorous diet and large group sizes of mandrills also have consequences that could, theoretically, exaggerate dimorphism through ecologically mediated selection. In tropical forests, tree species are often aggregated in space, with areas surrounding individual trees containing above average densities of conspecifics (Hubbel, 1979; Condit *et al.,* 2000). Tree species may aggregate depending on habitat conditions, if species are best adapted to particular topographies, light conditions, soil types or nutrients (Itoh *et al.,* 1997; John *et al.,* 2017; McFadden *et al.,* 2019). Alternatively, tree distributions may be influenced by seed dispersal mechanisms, leading to lower aggregation among animal dispersed species than those dispersed by wind or explosively dehiscing capsules (Seidler and Plotkin, 2006). This spatial aggregation of tree species results in fruit being clumped into patches within forests, the distribution of which influences primate diets, habitat selection and daily path lengths, among other aspects of behavior (Stevenson *et al.,* 2000; Aristizabal *et al.,* 2019).

The clumping of fruit resources results in within-group feeding competition, the intensity of which increases with group size (Sterck *et al.,* 1997). The uneven nature of mandrill space use indicates that clumping of fruit influences their movement and large horde sizes mean feeding competition is likely to be high (White *et al.,* 2010; Hongo *et al.,* 2018). Heavier male mandrills might be expected to easily exclude females from feeding patches, as is seen in gorillas (Watts, 1985). However, travel by mandrills within their home-range tends to be along the ground and feeding often takes place in trees (Hoshino *et al.,* 1984; Lahm, 1986). Males could therefore be disadvantaged during feeding competition because climbing should be more costly for heavier animals (Pontzer, 2016). For example, the large size of male gorillas appears to hinder them in reaching arboreal feeding sites (Remis, 1995). Thus, large group size likely produces high feeding competition in mandrills, which may be especially costly for males.

Larger groups of frugivorous primates are also expected to travel further each day between patches of clumped fruit resources (Chapman *et al.,* 1995). Indeed, mandrills travel further during periods of fruit abundance (Hongo *et al.,* 2022), which also coincide with lower numbers of tumescent females (Abernethy *et al.,* 2002; Dezeure *et al.,* 2022). Thus, the periods of greatest energetic expenditure on travel for males, if they are within a horde, coincides with the period when reproductive opportunities are most infrequent. The high body mass of males may also make traveling alongside the horde more challenging than for females (Hongo *et al.,* 2016). This challenge could arise because of trade-offs between the energy an organism expends on body maintenance, which is higher for larger animals, against energy that may be spent on locomotion (Boratyński*,* 2020). Furthermore, during the breeding season males are mate-guarding, fighting and produce grunting displays for approximately 12 hours per day (Abernethy *et al.,* 2002; Hongo *et al.,* 2016). Probably as a result of these behaviors, the breeding season is associated with elevated fecal glucocorticoid metabolites, parasite load, oxidative and nutritional stress in males (Setchell *et al.,* 2010; Beaulieu *et al.,* 2014; Oelze *et al.,* 2020).

High feeding competition, in which males may be disadvantaged, coupled with greater costs of travel and mating competition may well explain observations that male mandrills leave hordes outside of the breeding season (Abernethy *et al.,* 2002; Hongo *et al.,* 2016). However, the resulting seasonal influx of males during the breeding season has two consequences for the mandrill mating system. Firstly, the hierarchy among males is unstable, meaning males must fight to establish dominance when they enter a horde to breed (Smit *et al.,* 2022). This increase in intra-sexual mating competition could explain why mandrill size and canine (i.e. weaponry) dimorphism is so extreme. Secondly, males must obtain mating opportunities in the absence of long-term social relationships with females (Abernethy *et al.,* 2002). The need to court unfamiliar females in a dense habitat implies high inter-sexual mating competition, which could be responsible for the intensity of male ornamentation and grunting vocalizations. Thus, the temporary nature of male horde membership could result in stronger sexual selection and extreme dimorphism in mandrills, compared to primate species with more stable group structures. If resource competition and travel costs are responsible for males leaving mandrill hordes, ecologically mediated selection may be said to have acted to exaggerate mandrill dimorphism, by selecting for male social behavior that subsequently increases sexual selection.

To demonstrate that resource competition and travel costs compel males to leave social groups, sex differences in feeding and spatial behavior must be quantified. However, as the above discussion of mandrill socioecology demonstrates, obtaining accurate data on wild mandrill behavior via observational methods is extremely challenging. The challenge is especially great for solitary male mandrills, which are rarely observed beyond short sightings, and so their behavior is essentially unknown. One solution to the challenge of observing unhabituated wild animals is to study their ecology using remote tracking devices and stable isotope analysis (Cooke *et al.,* 2004; Crawford *et al.,* 2008; Handcock *et al.,* 2009).

Stable isotope analysis has been successfully used to investigate numerous features of primate ecology, including feeding competition (Dammhahn and Kappeler, 2010; Flores-Escobar *et al.,* 2020), nutritional stress (Oelze *et al.,* 2020), habitat segregation (Schoeninger *et al.,* 1997; Carter and Bradbury, 2016) and meat consumption (Oelze *et al.,* 2011). Stable isotope analysis works by quantifying the ratios of heavy to light stable isotopes in animal tissues, which reflect the ratios of the foods they have consumed (Crawford *et al.,* 2008). For example, nitrogen isotope ratios ($^{15}N/^{14}N$) reflect the trophic level at which an animal feeds (Hobson and Welch, 1992). Conversely, carbon isotope ratios ($^{13}C/^{12}C$) in terrestrial ecosystems reflect the plant species that an animal, or its prey, have eaten (Codron *et al.,* 2007).

For primates that are difficult to observe, stable isotope analysis of hairs is particularly useful. Because keratin is metabolically inert, the isotope ratios of hairs remain unchanged after growth (McHuron *et al.,* 2016). The linear nature of hair growth in turn means that variation, or a lack thereof, in isotope ratios along the length of a hair record temporal changes in diet (Cherel *et al.,* 2009). A single sample of hair thus contains long-term information about the feeding niche of an individual, overcoming the need for repeated observations of feeding behavior (Oelze, 2016). Analyzing the stable isotope ratios of mandrills hairs will thus allow the feeding niches of males and females to be contrasted and the impact of feeding competition on each sex to be explored.

GPS collars allow the movement of primates to be tracked in challenging conditions that prevent direct focal follows (Dore *et al.,* 2020). By repeatedly recording the locations of an individual, aspects of spatial behavior such as home-range size and habitat selection can be studied (Pebsworth *et al.,* 2012; Anderson *et al.,* 2017). Investigating the locations, home-ranges and habitat choices of male and female mandrills will reveal whether males are more likely to be found outside of the horde during the breeding season, as is expected based on observational studies. Furthermore, fitting GPS collars allows the travel distances and speeds of tracked primates to be quantified (Klegarth *et al.,* 2016; Bracken *et al.,* 2022). These measures will uncover whether males expend less energy on travel during the non-breeding season, when they are expected to be solitary.

1.4 Thesis Aims

In this thesis I am to: 1) Explore whether ecologically mediated selection may have a more general role in the evolution of sexual dimorphism than is currently appreciated; 2) Expand our knowledge of mandrill socioecology, by examining the feeding and spatial behavior of a wild horde living in a relatively intact habitat, largely free of human disturbance over the past 40 years; improved knowledge of mandrill socioecology will also inform ongoing conservation efforts throughout mandrill range; 3) Assess the possibility that ecologically mediated selection is partially responsible for the exaggeration of sexual dimorphism in mandrills.

Chapter 2: Can diet niche partitioning enhance sexual dimorphism?

A key expectation of hypotheses predicting that sexual dimorphism can evolve via ecologically mediated selection is that greater sexual dimorphism should be associated with larger ecological sex differences. In Chapter 2 I therefore conduct a meta-analysis investigating the strength of associations between sexual size dimorphism and isotopic (ecological) differences between males and females. I also consider the impact of species mean size, dietary class, and gape limitation on the strength of associations between dimorphism and isotopic sex differences, as each of these factors may be expected to influence the ecological relevance of size dimorphism. I then discuss whether the meta-analytic results imply a strong or a weak role for ecologically mediated selection in the evolution of sexual dimorphism.

Chapter 3: Rare long-term data reveal the seasonal dietary plasticity of mandrills (*Mandrillus sphinx*) in response to fruiting tree phenology.

Studies of primate feeding strategies are optimized by long-term data that allow the impact of between year variation in food availability to be accounted for. In Chapter 3, I use eight years of data on mandrill diets and tree phenology, to study the impact of fruit availability on mandrill food selection. Using generalized additive models, I explore seasonal patterns in the consumption of major food types and which foods may constitute important fallback foods. I then quantify which fruit genera are consumed most frequently as a function of availability and discuss why certain fruits may be preferred over others. These results are then discussed in terms of why mandrill feeding strategies and preferences may have arisen.

Chapter 4: Investigating stable isotope turnover and discrimination in mandrill (*Mandrillus sphinx*) hairs with a diet-switch experiment.

Stable isotope analysis is best applied using species-specific knowledge of the relationship between diet and tissue stable isotope ratios. In Chapter 4, I quantify the most important variables for applying stable isotope analysis to mandrill hair samples. Knowledge of hair growth rates and tissue turnover times allow isotope data obtained from hairs to be placed in time, increasing their ecological relevance. Tissue-diet discrimination factors allow the typical enrichment between the diet and tissue isotope ratios of an animal to be accounted for, which is essential for estimating diet composition from tissue stable isotope ratios. I then consider the validity of the diet-switch results within the context of other controlled feeding studies of primates and mammals.

Chapter 5: Stable isotope data suggest an association between extreme sexual dimorphism and resource competition in mandrills (*Mandrillus sphinx*).

Niche divergence between sexually dimorphic males and females raises the possibility that ecologically mediated selection has influenced the evolution of sexual dimorphism. In Chapter 5, I analyze the stable isotope ratios of mandrill hair samples, to examine sex differences in isotopic niche at the levels of sex and individual. Analyzing sex-level differences in isotopic niche reveals whether mandrill dimorphism is associated with dietary divergence between males and females. Examining individual-level niches facilitates assessment of the impact of resource competition on the diets of individual males and females. Findings are discussed by considering whether resource competition may push male mandrills to leave hordes outside of the breeding season.

Chapter 6: Sexual dimorphism in mandrill (*Mandrillus sphinx*) spatial behavior. A role for travel costs in the evolution of sexual dimorphism?

Sexual dimorphism in primates is usually assumed to result from sexual selection. However, males and females that differ markedly in body size may experience differing energetic constraints on space use. In Chapter 6, I use data obtained from direct observational follows and GPS collars to quantify sex differences in seasonal patterns of home-range use, daily path length and travel speeds. More similar home-range use by each sex during the breeding season, and divergence during the non-breeding season, would suggest that collared males left the focal horde outside of the breeding season. If this is accompanied by shorter daily path lengths and slower speeds for males during the non-breeding season, male mandrills may leave social groups to reduce the energy they expend on travel when reproductive opportunities are infrequent. I discuss the results within the context of Chapter 5 and other recent data on the body condition of adult male mandrills, to consider whether ecologically mediated selection has impacted the evolution of extreme dimorphism in mandrills.

Chapter 2: Can diet niche partitioning enhance sexual dimorphism?

A version of this chapter has been published as:

Bauld, J.T., Abernethy, K.A., Newton, J., Lehmann, D., Jones, I.L. and Bussière, L.F., 2022. Can diet niche partitioning enhance sexual dimorphism?. Ecology and Evolution, 12(12), p.e9599.

JB, KA, JN, DL, IJ, and LB conceived the research question and study design. JB conducted the data collection. JB performed analyses and wrote the manuscript drafts with guidance from KA, JN, DL, IJ, and LB. All authors contributed critically to each draft and the published version formatted for this thesis.

2.1 Abstract

Classic evolutionary theory suggests that sexual dimorphism evolves primarily via sexual and fecundity selection. However, theory and evidence are beginning to accumulate suggesting that resource competition can drive the evolution of sexual dimorphism, via ecological character displacement between sexes. A key prediction of this hypothesis is that the extent of ecological divergence between sexes will be associated with the extent of sexual dimorphism. As the stable isotope ratios of animal tissues provide a quantitative measure of various aspects of ecology, we carried out a meta-analysis examining associations between the extent of isotopic divergence between sexes and the extent of body size dimorphism. Our models demonstrate that large amounts of between-study variation in isotopic (ecological) divergence between sexes is nonrandom and may be associated with the traits of study subjects. We, therefore, completed meta-regressions to examine whether the extent of isotopic divergence between sexes is associated with the extent of sexual size dimorphism. We found modest but significantly positive associations across species between size dimorphism and ecological differences between sexes, that increased in strength when the ecological opportunity for dietary divergence between sexes was greatest. Our results, therefore, provide further evidence that ecologically mediated selection, not directly related to reproduction, can contribute to the evolution of sexual dimorphism.

2.2 Introduction

2.2.1 Sexual dimorphism

Classic evolutionary theory posits that anisogamy, or variation between males and females in gametic investment, causes sex differences in optimum life history and reproductive strategy (Andersson, 1994; Lehtonen *et al.*, 2016). Evolution toward these sex-specific optima ultimately produces phenotypic differences between males and females, known as sexual dimorphism (Parker and Pizzari, 2015). One frequently observed sex difference is sexual size dimorphism in which the mean body size of one sex exceeds that of the other (Fairbairn *et al.*, 2007). Size dimorphism is typically predicted to arise via sexual selection when the reproductive success of one sex is limited by mating opportunities, and large size allows individuals of that sex to increase their matings. For example, the biggest male southern elephant seals (*Mirounga angustirostris*) are the best able to monopolize females at breeding colonies (Le Boeuf *et al.*, 2019). Alternatively, or additionally, size dimorphism may be favored by fecundity selection, when one sex's reproductive success is limited by gamete production and gamete production relates to body size, such as in emydid turtles (Emydidae), in which larger females produce more eggs and are therefore more fecund (Stephens and Wiens, 2009). It is this traditional view that size dimorphism is primarily attributable to reproductive differences, which is best evidenced and dominates scientific literature and consensus (Blanckenhorn, 2005).

However, as far back as Darwin's discussions of their “habits of life” (Darwin, 1871, p.254), authors have noted that sexual dimorphisms can relate not only to each sex's reproductive success but also to their respective ecologies (Shine and Goiran, 2021; Temeles *et al.*, 2000; Wasiljew *et al.*, 2021). Divergence of the sexes along various biotic and abiotic niche axes (e.g., temperature, diet, habitat) should facilitate intersex niche partitioning, which may covary with sexual dimorphism in traits relevant to ecology (Butler *et al.*, 2007; Herrel *et al.*, 1999). For example, in the seabird *Sula nebouxii*, larger females dive deeper and feed on larger prey than their male counterparts (Zavalaga *et al.*, 2007).

Such ecological sexual dimorphisms could arise as an indirect, ecological consequence of dimorphism due to reproductive differences, or directly via ecological causation. An example of ecological dimorphism arising as an apparent consequence of reproductive differences can be found in mouthbrooding cichlid fishes. In species in which only one sex carries out mouthbrooding, sex differences in diet also arise as a consequence of distinct reproductive roles, as the mouthparts involved also influence foraging (Ronco *et al.*, 2019). Ecological sexual dimorphisms arising as a consequence of reproductive differences are often considered the most parsimonious explanation for their existence (De Lisle, 2019; Shine, 1989).

2.2.2 Ecological character displacement between sexes

Theoretical work also suggests, however, that ecological sexual dimorphisms can arise solely from ecologically mediated natural selection if frequency-dependent competition for a resource produces disruptive selection. Under these circumstances, the sexes could evolve toward distinct phenotypes, which maximize resource acquisition, by facilitating divergence along niche axes (Slatkin, 1984). This process of ecological character displacement between sexes is analogous to that between nascent species and offers an alternative evolutionary outcome to frequency-dependent resource competition (Bolnick and Doebeli, 2003).

One issue with theoretical models of ecological character displacement, however, is the lack of an a priori justification for character displacement between sexes, as opposed to random subsets of populations (Bolnick and Doebeli, 2003). As a result, an integrated view of reproductive competition and ecological character displacement provides the best model for the evolution of ecological sexual dimorphisms (De Lisle, 2019, 2021). From this perspective, initial phenotypic divergence and/or differing ecological optima between the sexes may usually arise due to anisogamy and reproductive differences (Maklakov *et al.*, 2008; Schärer *et al.*, 2012). For instance, reproductive differences may create sex differences in nutritional optima, leading to divergent foraging decisions and resource allocation (Morehouse *et al.*, 2020; Raubenheimer and Simpson, 2018). These initial differences may then be acted upon by disruptive natural selection, such that the observed differences between sexes emerge through both sexual and ecologically mediated selection. For example, intra-specific reversals in the direction of python (*Morelia spilota*) size dimorphism track interpopulation differences in mating systems, but the degree of size dimorphism relates to available prey sizes (Pearson *et al.*, 2002).

The ecological character displacement hypothesis for sexual dimorphism is perhaps best evidenced by a series of experiments by De Lisle and Rowe (2015) in which male and female salamanders (*Notophthalmus viridescens*) were placed in semi-natural mesocosms, at various competitor densities. In this species, sexual dimorphism in body size and feeding morphology corresponds to sex differences in diet and microhabitat; meaning females may compete more strongly with other females and males with other males. In De Lisle and Rowe's study, growth rates were lower in high-density mesocosms, suggesting that competition impacts fitness for which growth rate is a proxy. Furthermore, females grew faster in mesocosms with a male-biased sex ratio. Females, therefore, had higher fitness when alongside a greater proportion of male competitors, with which they should compete for less, suggesting that sexual dimorphism somewhat reduced competition. Given such evidence, it is conceivable that ecologically mediated selection can play a role in the evolution of ecological sexual dimorphisms.

2.2.3 How important is ecological character displacement?

An outstanding and unresolved question concerns the importance, across taxa, of ecologically mediated selection for creating diversity in sexual dimorphisms. Here we address this question by investigating general associations, across species, between size dimorphism, and ecological divergence in trophic level and basal carbon resources. A central tenet of the ecological character displacement hypothesis is that the degree of dimorphism should scale positively with the degree of ecological divergence between sexes (De Lisle and Rowe, 2015). It, therefore, follows that more sexually dimorphic species should generally show greater ecological divergence than less dimorphic species. Of course, associations between dimorphism and ecological sex differences would not necessarily indicate causation because dimorphism in any individual species may have arisen via ecological causation or as an indirect consequence of reproductive differences. Associations would, however, be consistent with predicted outcomes of ecological character displacement working in isolation or reproductive differences creating the opportunity for disruptive ecologically mediated selection and would suggest a stronger relationship between sexual dimorphism and ecology than previously appreciated.

Ecological divergence related to size dimorphism could be exhibited by sex differences in ecological mean if, for example, dimorphism impacts the prey available to each sex, leading them to feed, on average, at different trophic levels (Mills *et al.*, 2021). Furthermore, sexual size dimorphism could lead to sex differences in ecological variation via numerous mechanisms. For example, the larger sex may be more variable if large size confers access to a greater range of resources (Voigt *et al.*, 2018) or the smaller sex more variable if they are competitively subordinate (Wan *et al.*, 2013). We therefore examine associations between size dimorphism and ecological differences in foraging between males and females, measured using stable isotope analysis. Stable isotope analysis is a common technique for analyzing foraging ecology and we outline our rationale for why it is appropriate for quantifying sex differences in feeding below. Our investigation uses a meta-analytic approach, synthesizing previously published stable isotope data on vertebrates, with a global geographical scope.

2.2.4 Stable isotope ecology

Over recent decades, stable isotope analysis has become an effective tool used for investigating animal ecology (Hobson, 1999; Hobson and Welch, 1992; Swan *et al.*, 2020). Because the ratios of naturally occurring stable isotopes vary in the foods animals consume, and these ratios are incorporated into animal tissues during formation, much can be revealed about an animal's ecology by analyzing stable isotope ratios in its different tissues (Ponsard and Arditi, 2000). Different isotopic systems provide alternative information about the animal from which they are sampled (Newton, 2016), such that ratios of nitrogen stable isotopes ($\delta^{15}N$, see Methods for an explanation of δ notation) vary with trophic levels (Caut *et al.*, 2009) and ratios of carbon-stable isotopes ($\delta^{13}C$) vary with food chain basal resource (Farquhar *et al.*, 1989; Yoneyama *et al.*, 2010). For example, relative ^{15}N-enrichment of polar bears compared with seals indicate polar bears occupy a higher trophic level (Hobson *et al.*, 2002) and $\delta^{13}C$ can distinguish the diets of zebras and giraffes that feed on C4 and C3 plants, respectively (Codron *et al.*, 2006). Combined stable isotope ratios of animal tissues thus allow inferences about the individual niche, meaning ecological differences can be quantified at various levels, including niche differences between males and females, with the greater sex differences in stable isotope ratios taken to indicate more ecological divergence (Foote *et al.*, 2012; Lehmann *et al.*, 2015).

2.2.5 Is size dimorphism associated with isotopic sex differences?

Because stable isotope data tend to be reported reasonably consistently across taxa, compared with other measures of diet, the considerable stable isotope ecology literature provides an opportunity to investigate cross-species associations between sexual dimorphism and ecological (isotopic) sex differences. Our study achieves three main aims. First, using meta-analytic models, we quantify between-study variation in isotopic sex differences in the stable isotope literature and the fraction of this variation constituting heterogeneity (I^2). In the context of meta-analysis, heterogeneity describes the amount of observed between-study variation in effect size that is due to nonrandom variation in true effect size, as opposed to random sampling variation (Borenstein *et al.*, 2017). As a consequence, heterogeneity also indicates the fraction of between-study variation that may be explained by predictor variables, such as the traits of study subjects.

Second, having discovered substantial heterogeneity among studies, we next investigate how much heterogeneity in isotopic sex differences can be explained by size dimorphism. We use meta-regression models including size dimorphism as a predictor variable, to examine associations with isotopic sex differences, and interpret the strength of associations as an indicator of the amount of heterogeneity in ecological sex differences that are explained by sexual dimorphism.

We use size dimorphism as a predictor variable in our analyses despite our interest in its response to certain ecological contexts. Our choice is primarily pragmatic: the diversity of the stable isotope literature means we can readily compute effect sizes using means, errors, and sample sizes for isotopic data of both sexes in many species. In contrast, body size data are most commonly available as mean values, and therefore more suitable as a predictor variable. Our choices also moderate the sensitivity of our meta-analyses. Stable isotopes may not capture all ecological differences between sexes; for example, male and female birds may feed on different seeds, which would not manifest as trophic level differences. Similarly, the sexes may differ in trophic structures and feed on different diets, while being the same body mass, which would be missed by our measure of size dimorphism. However, our sacrifice of some of this detail allowed us to maximize the taxonomic scope and therefore the generality of our results. It also means that our meta-analyses are conservative in nature and that associations between sexual dimorphism and ecological sex differences may be stronger than we detect here.

2.2.6 How important is the ecological context?

Our final aim was to examine whether associations between sexual dimorphism and ecological sex differences are modified by the ecological context. We first test whether species' dietary class and/or mean species size modify relationships between size dimorphism and isotopic sex differences. Dietary class may modify the impact of size dimorphism on isotopic sex differences because species consuming different diets vary in their ecological flexibility. For example, omnivores by definition feed at more trophic levels than herbivores, which could create more opportunity for size dimorphism to exert an influence on the trophic level of each sex. Mean species size (defined here as the mean of males and females) may influence the effect of size dimorphism by causing between-species differences in resource access, which may then impact how size dimorphism affects resource use within species. For example, if size affects the maximum prey size available to each sex, size dimorphism may have a greater impact on smaller species that are already more limited concerning the size of their prey. Conversely, the greater absolute size of larger species may mean proportional size differences between males and females have more impact on their respective interactions with other food web members. We quantify the potential influence of species' dietary class and mean size by including them as additional predictor variables, alongside size dimorphism, in meta-regression models.

Another possibility is that size dimorphism has the greatest ecological impact on carnivores that are gape-limited, meaning they can only consume prey smaller than themselves (Shine, 1991; Shine *et al.*, 2003). For example, in an aquatic food chain formed of gape-limited fish, each species can consume all species smaller than itself, but no species the same size or larger. A trophic level should therefore closely track body size, with the largest fish at the highest trophic level. If a fish species in such a food chain were size dimorphic, the larger sex would have greater access to larger, higher trophic level prey, than the smaller sex, resulting in a difference between males and females in the maximum possible trophic level. As optimal foraging theory predicts that predators often feed preferentially on larger prey, due to greater energetic returns per prey item (Dodrill *et al.*, 2021; Stephens and Krebs, 1986), the larger sex in a dimorphic gape-limited fish would be predicted to feed at a higher trophic level. Conversely, non-gape-limited predators and scavengers, such as cats, can consume prey orders of magnitude larger than themselves, which may minimize any impact of size dimorphism on the trophic levels of each sex. Therefore, we investigate whether gape limitation strengthens associations between size dimorphism and isotopic sex differences. We do this using a meta-regression on a data set constrained to fish and snake species, which are presumed to be able to feed solely by swallowing whole prey and thus considered gape-limited. The predictions from this model are then compared with those from a model containing all other carnivores in our data set, to assess whether the effect of size dimorphism on trophic sex differences is greater in gape-limited carnivores.

2.3 Methods

Our meta-analytic approach and reporting were completed with reference to the guidelines laid out by O'Dea *et al.* (2021).

2.3.1 Data collection

We collated peer-reviewed literature available in the Web of Science Core Collection. The stable isotope literature is large, with the search term “stable isotope” returning ~76,500 studies at the time of writing. To constrain the search, we combined the following specific terms, using the default publication year range of 1900–2020, on 10/11/2020: Isotop* Nich; Isotop Nich* Male; Isotop* Nich* Female; Isotop* Nich* Male Female; Isotop* Nich* Sex Diff*; Isotop Nich* Dimorph; Isotop Dimorph*.

Our searches returned 3489 studies, which we placed into a spreadsheet to highlight duplicates for manual removal. Removing duplicates resulted in 2807 studies for the title and abstract screening. At this stage, we made the decision to constrain our analysis to the nitrogen and carbon stable isotope systems, due to the relatively small number of studies using other systems that were returned by our search terms. We also rejected studies during the title and abstract screening if they did not use bulk stable isotope analysis, used samples of human, museum, archeological or palaeontological origin, were review, comment, or method papers, or if the animals sampled were not wild, not adults, not vertebrates or if data were not available for both sexes.

We then searched the remaining 1279 studies using the ctrl + F search function and, separately, the terms “sex”, “male” and “female”, excluding studies if they contained none of these terms, under the assumption that they did not contain stable isotope ratios for each sex and, if at least one term was present, checking for the presence of the required data. Additional reasons for exclusion were if the full text was inaccessible without purchase or contacting authors, presented incomplete data (mean, error, or sample size missing), was not in English, or was a paper correction.

We then attempted to extract data from the remaining 210 studies. Additional reasons for exclusion at this stage were if raw data were presented as images with >50 rows, if data were from an earlier study already included or if data extraction from figures was not possible. We extracted data from figures using a mouse pointer to individually select data points from an image of the figure, with the image calibrated to the axis values from the original figure; therefore, too much point overlap made this process inaccurate, because not all points could be selected for inclusion. The entire process provided 173 studies in which mean, standard deviation, and sample sizes for each sex were presented in the manuscript, or could be calculated from raw data, or could be taken from model outputs, or extracted from figures (Figure 2.1). We collected data for any vertebrate species, from any global location and, if stable isotope ratios for each sex were presented for more than one tissue type, we entered each tissue as a separate row in our database.

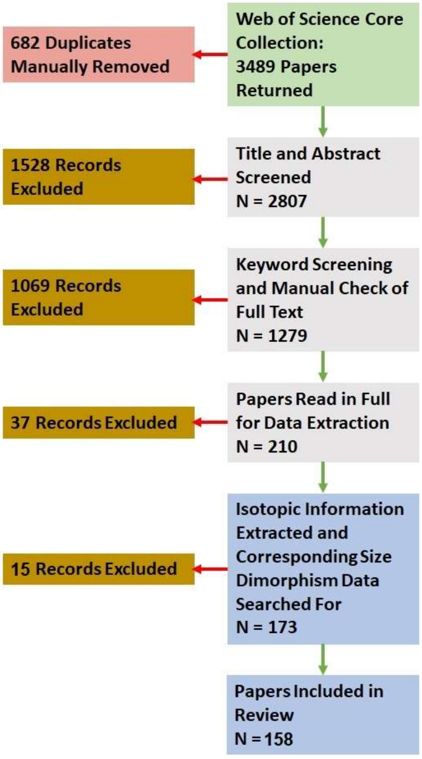


Figure 2.1. Our sequence of study collation, screening, and data extraction, alongside the number of studies excluded at each stage and included in the final analysis.

2.3.2 Effect size choice and calculation

All the stable isotope data we collected were presented in permil units (‰). Permil units describe enrichment or depletion of heavy isotopes, relative to international standards, which exist for nitrogen, carbon, and all other commonly used systems in stable isotope analysis. For example, the standard for nitrogen stable isotope ratios is atmospheric nitrogen (air). The relative enrichment or depletion is expressed using delta (δ) notation, such that

$$\partial = \frac{(R_{sample} - R_{standard})}{R_{standard}}$$

where R_{sample} equals the isotope ratio of the sample and $R_{standard}$ equals the isotope ratio of the standard (McKinney *et al.*, 1950) where R = heavy isotope/light isotope, for example, $^{15}N/^{14}N$. Thus, a positive δ value indicates enrichment in the heavier isotope (in this case ^{15}N) and a negative value indicates isotopic depletion of the sample, relative to the international standard. When comparing two sampling units, such as sex, a more positive (or less negative) value for one sex indicates enrichment in the heavy isotope relative to both the standard and the other sex. It is this difference between sexes in isotopic enrichment that we have used to calculate the effect sizes in our meta-analysis.

All studies from which we extracted data expressed stable isotope data in permil units, therefore further standardization of effects sizes was not necessary (Nakagawa and Cuthill, 2007; Nakagawa and Santos, 2012). We calculated mean differences between male and female stable isotope ratios as the raw mean difference between isotopic means of each sex, as found in each study. We calculated these with a positive mean difference indicating that males were ^{15}N- or ^{13}C-enriched compared with females and a negative mean difference indicating females were isotopically enriched compared with males. For example, a positive δ^{15}N mean difference indicates that males feed, on average, at a higher trophic level.

Regarding meta-analyses of variation, two effect size measures are often recommended in the fields of ecology and evolution, which are the log Variability Ratio (lnVR) and the log Coefficient of Variation Ratio (lnCVR; Senior *et al.*, 2020). lnCVR has the advantage of allowing for mean–variance relationships in effect sizes (i.e., an increase in variance with mean value; Senior *et al.* 2016): our data did not show any evidence of such relationships (Appendix 1). In addition, because lnCVR accounts for variation in mean value by expressing absolute variation as a proportion of group mean, sex differences in isotopic variation could actually be misrepresented through this standardization. For example, if one sex is twice as enriched relative to the international standard as the other and shows twice as much variation, lnCVR would express this as an equal variation. Conversely, as lnVR is calculated using the raw variation values for each group, with no accounting for mean values, the more enriched sex would also be shown to be twice as a variable, more accurately representing each sex's ecology. We, therefore, selected lnVR as our effect size metric for sex differences in variation.

Finally, we selected mass dimorphism (kg) as our measure of size dimorphism, as this measure was most readily available for the highest number of vertebrates, allowing the taxonomic scope of our analysis to be as wide as possible. Body masses for each sex were established using web searches, prioritizing data from peer-reviewed scientific studies, followed by published books and, if necessary, taxon-specific websites. As reliable body mass data could not be obtained for all species, the number of studies in the analysis was reduced to 158. A list of data sources used in our meta-analyses is provided in the Data Sources section.

2.3.3 Model choice and structure

All models used complete case analysis, meaning rows containing missing data for predictor variables or effect sizes (dependent variables) were removed from the analysis. We used multilevel meta-analytic models to quantify the amount of between-study variation that exists for each isotope and effect size and how much of this variation constitutes heterogeneity, as opposed to random sampling variation. We then used multilevel meta-regression models to investigate whether the heterogeneity found could be explained by our predictor variables. To investigate the relationship between sexual dimorphism and ecology, we examined the strength of associations between size dimorphism and sex differences in isotopic mean and variance for carbon and nitrogen.

To examine whether ecological context can modify the relationship between dimorphism and ecology, we ran meta-regressions using sex differences in mean nitrogen isotope as the response variable, with additional predictor variables, dietary class, and mean species size, included alongside size dimorphism. Dietary class constituted a categorical variable with three levels: carnivore, omnivore, and herbivore. Mean size was a continuous variable, calculated by averaging the male and female mass data used for calculating size dimorphism. We ran models including dietary class and mean size separately and together, with and without all combinations of two- and three-way interactions. Three-way interactions were theoretically justified because, if mean species size could modify the effect of size dimorphism on the trophic level, this modification may be more apparent in species with more inherent trophic flexibility, such as omnivores, than those with less, such as herbivores. In addition, the sample size was large enough that the number of parameters to be estimated with three-way interactions did not prevent models from converging. The best models were identified using AICc scores, with lower scores taken to indicate better models (Arnold, 2010).

Initially, we only considered a modifying effect of dietary class on nitrogen mean sex differences because carbon sex differences did not exhibit a significant association with size dimorphism across our entire data set. However, this could be expected to exclude herbivores, which likely feed at only one trophic level, from showing an association. We, therefore, conducted an additional model examining whether dietary class modified the association between size dimorphism and sex differences in mean carbon stable isotope ratio. This model balances our analyses because carbon isotopes in terrestrial systems are primarily influenced by plant photosynthetic mechanisms and therefore represent a niche axis along which the sexes could more easily diverge in herbivores.

As a final test of the association between size dimorphism and ecological sex differences, we quantified the effect of gape limitation by running two meta-regressions including only size dimorphism as a predictor variable and limiting the data sets to gape-limited and non-gape-limited carnivores, in which size dimorphism may have differing impacts on sex differences in trophic level.

Residuals of all models were approximately normally distributed; thus, no data transformations were used.

2.3.4 Random effects

In all the above multilevel models, we included study identity and species as random factors, to account for random sampling variation at both these levels and to adequately account for pseudoreplication, since we potentially considered measures for several tissue samples from the same specimens. We also included phylogeny as a random factor, to account for relatedness between the species included in our data set, following the method of Sanchez-Tojar *et al.* (2020).

2.3.5 Publication bias and sensitivity analysis

Scientific literature may be subject to publication bias, whereby favorable results are preferentially published, thus skewing the results of meta-analyses. We produced funnel plots to identify such biases, by visualizing the distribution of published effect sizes and determining whether there are missing observations that might be expected in the literature (based on variation in effect sizes). In addition, biases may arise when research builds upon influential results from poor quality or low power studies, leading to reduced effect sizes through time, as the true effect is quantified with repetition or higher quality studies. To test for such publication bias in isotopic sex differences, we ran meta-regressions using sex differences in isotopic mean and variance, for carbon and nitrogen, as the dependent variable and publication year as the only predictor variable.

The results of meta-analyses may also be sensitive to decisions about the weights assigned to individual studies as well as to high-influence data points (Koricheva *et al.*, 2013). Meta-analytic models usually account for both within-study variance and between-study variance when assigning weights to individual study results. However, when between-study variance is high, within-study variance can be masked when weighting studies, potentially impacting model results. We, therefore, ran additional models using only the inverse of within-study variance to assign study weights, to determine the influence of our choice of weighting parameter. Finally, to analyze the sensitivity of our models to high-influence data points, we completed a leave-one-out analysis, to calculate Cook's distances for each data point and ran additional models with high-influence data points removed. The results of our tests of publication bias, alternate study weighting and sensitivity analysis, alongside justifications for final data inclusion and model choices can be found in the Appendix.

2.3.6 Software

All data processing, analyses, and plotting were completed using R v4.0.2. We used the R package “metaDigitise” v1.0.1 (Pick, Nakagawa and Noble, 2019) for all data extraction from figures and the package “metafor” v.2.4-0 (Viechtbauer, 2010) to calculate all effect sizes and to run all meta-analytic and meta-regression models. Our phylogeny was constructed using the “rotl” v3.0.12 (Michonneau *et al.*, 2016) and “ape” v5.6.2 (Paradis and Schliep, 2019) packages and we calculated the phylogenetic signal with “phylosignal” v1.3 (Keck *et al.*, 2016) and “phylobase” v0.8.1 (Hackathon, 2020). We created all plots using the R package “ggplot2” v3.3.3 (Wickham, 2016) and tables using “flextable” v0.7.3 (Gohel *et al.*, 2020).

2.4 Results

2.4.1 Dataset

Our final database contained isotopic information from 158 studies, covering 163 species. Mammals were the most common taxa (n = 68), followed by birds (n = 60), fish (n = 18), reptiles (n = 17), and a single amphibian. The species with the greatest female-biased dimorphism was the northern map turtle (*Graptemys geographica*), in which females are 10× the mass of males and the species with the greatest male-biased dimorphism was the elephant seal (*Mirounga leonina*), with males seven times larger than females. The number of effect sizes used in the analyses was highest for $\delta^{15}N$ mean sex differences (n = 282), followed by $\delta^{13}C$ mean differences (n = 276), $\delta^{15}N$ lnVR (n = 272), and $\delta^{13}C$ lnVR (n = 266).

2.4.2 Quantifying heterogeneity in between-sex isotopic differences

Between-study variation was found for sex differences in mean $\delta^{15}N$ (trophic level) and $\delta^{13}C$ (food chain basal carbon resource) and sex differences in $\delta^{15}N$ and $\delta^{13}C$ variation (Figure 2.2). The amount of heterogeneity (I^2) was 90.57% and 94.38% for $\delta^{15}N$ and $\delta^{13}C$ mean sex differences, respectively. Such high heterogeneity indicates that almost all between-study variation in effect size is nonrandom and has the potential to be explained by predictor variables. Regarding sex differences in isotopic variation, heterogeneity was 64.2% and 72.83% for $\delta^{15}N$ and $\delta^{13}C$, respectively, indicating that the majority of between-study variation in between-sex differences in an isotopic variation also has the potential to be explained by predictor variables. In the case of nitrogen, one sex was at least twice as variable as the other in 8.5% of cases and for carbon, in 13.1% of cases (Figure 2.2).

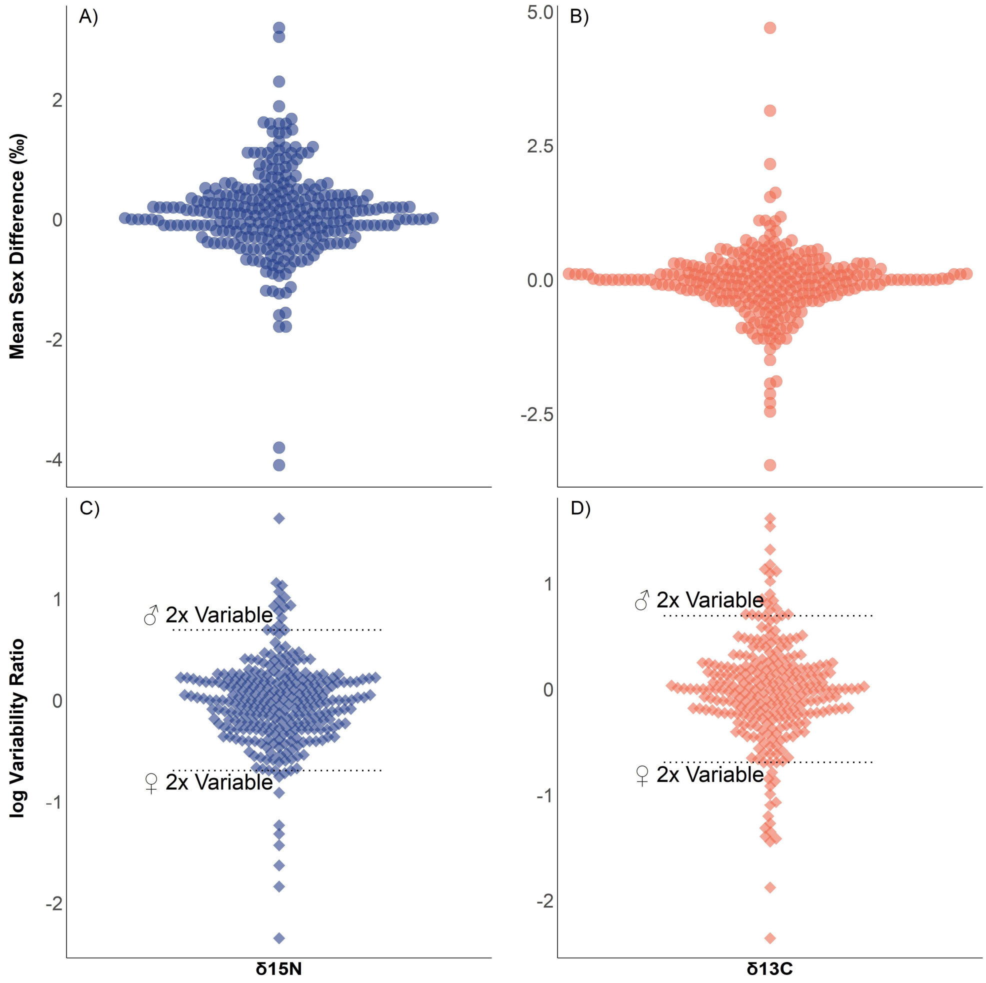


Figure 2.2 Published stable isotope ratio sex differences for nitrogen mean (a), carbon mean (b), nitrogen variation (c), and carbon variation (d). In (a, b), each point represents the raw difference between male and female mean stable isotope ratio, of one tissue of one species. Positive values indicate higher values in males, whereas negative values indicate higher values in females. In (c, d), each point represents the log male:female variability ratio of one tissue, in one species. Positive values indicate males showed more isotopic variation and those above the dotted line indicate that males were more than twice as variable as females. Negative values indicate females showed more isotopic variation and those below the dotted line indicate that females were more than twice as variable as males. X-axes constitute one category, with jitter added to better visualize overlapping observations.

2.4.3 Associations between isotopic sex difference and size dimorphism

Associations between isotopic sex difference and size dimorphism To examine the possibility that size dimorphism relates to ecology, we carried out meta-regressions containing size dimorphism as the sole predictor variable and found modest or nonexistent associations with isotopic sex differences. The estimated effect size of size dimorphism on $\delta^{15}N$ mean difference was significantly positive (mean = 0.126, 95% CI: 0.06–0.19, p = <.001, indicating that a size dimorphism of 100% led to a $\delta^{15}N$ increase of 0.126‰, on average. This effect was modest compared with the variation in isotopic sex differences in our data set (range $\delta^{15}N$ sex difference: −4.1 to 3.2‰). Models of relationships between size dimorphism and $\delta^{13}C$ mean differences, $\delta^{15}N$ variation, and $\delta^{13}C$ variation produced estimate confidence bands that overlapped zero, indicating no significant associations between size dimorphism and these measures of isotopic sex differences. The predictions from these models, alongside their underlying raw data, are visualized in Figure 2.3.

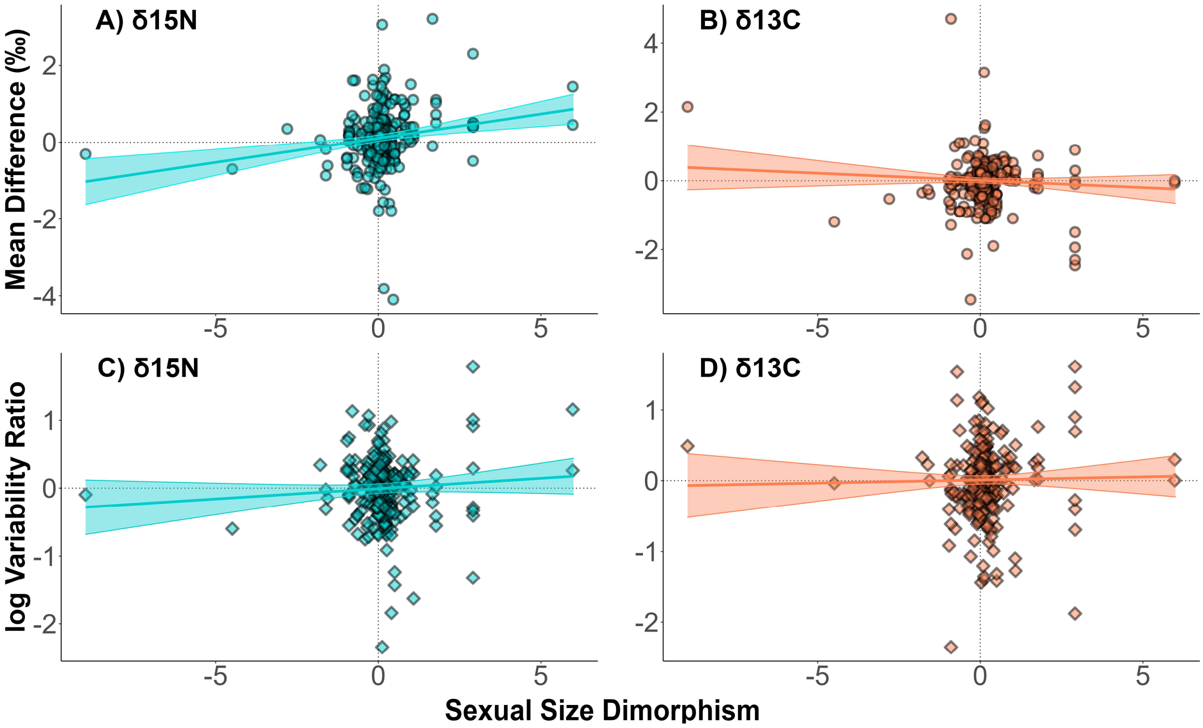


Figure 2.3. The relationship between sexual size dimorphism and stable isotope sex differences in nitrogen mean (a), carbon mean (b), nitrogen variation (c), and carbon variation (d). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains isotopic sex differences.

2.4.4 Quantifying the effects of ecological context

To test the possibility that associations between size dimorphism and feeding vary in strength among ecological contexts, we used meta-regressions to test whether dietary class, mean size, or gape limitation modified the effect of size dimorphism on isotopic sex differences. Model selection using AICc scores indicated that a model containing species mean size and dietary class as predictors of δ^{15}N sex differences, with an interaction between size dimorphism and dietary class, improved model fit (AICc = 512), compared with the size dimorphism-only model above (AICc = 518; Table 2.1). The best model contained an interaction between size dimorphism and dietary class, such that the association between size dimorphism and sex differences in nitrogen mean was statistically nonsignificant in herbivores, significant and moderate in carnivores (0.17, 95% CI: 0.053–0.18, $p < .001$), and significant and strongest in omnivores (0.36, 95% CI: 0.019–0.7, $p = .038$; Figure 2.4). The model also contained a significant effect of mean species size on sex differences in nitrogen mean (0.0000036, CI: 0.00000023–0.0000069, $p = .036$).

Table 2.1. AIC scores for models examining associations between size dimorphism and δ^{15}N mean sex differences in different ecological contexts.

Model Formula	**AIC**
δ^{15}N Mean Sex Difference ~ Size Dimorphism * Dietary Class + Species Mean Size	512.0546
δ^{15}N Mean Sex Difference ~ Size Dimorphism * Species Mean Size + Dietary Class	513.2787
δ^{15}N Mean Sex Difference ~ Size Dimorphism * Species Mean Size	513.8847
δ^{15}N Mean Sex Difference ~ Size Dimorphism * Dietary Class * Species Mean Size	513.8942
δ^{15}N Mean Sex Difference ~ Size Dimorphism * Dietary Class	514.3551
δ^{15}N Mean Sex Difference ~ Size Dimorphism + Dietary Class * Species Mean Size	515.1587
δ^{15}N Mean Sex Difference ~ Size Dimorphism + Dietary Class + Species Mean Size	515.3208
δ^{15}N Mean Sex Difference ~ Size Dimorphism + Species Mean Size	515.9071
δ^{15}N Mean Sex Difference ~ Size Dimorphism + Dietary Class	517.6389

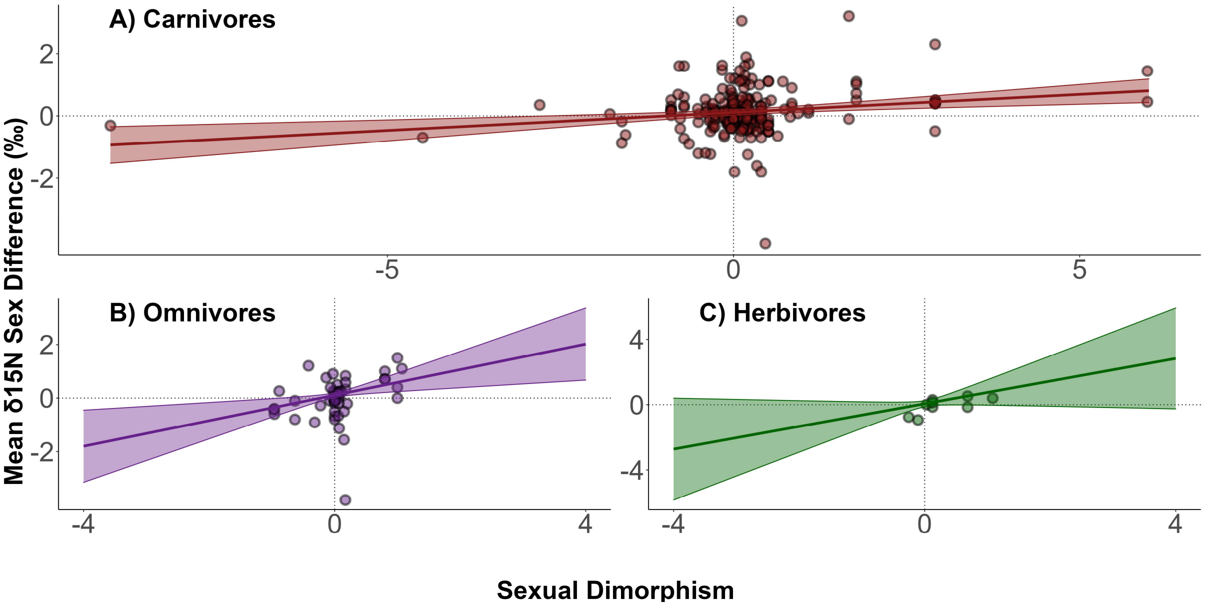


Figure 2.4. The relationship between sexual size dimorphism and mean nitrogen stable isotope ratio sex differences in carnivores (a), omnivores (b), and herbivores (c). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains trophic sex differences in each dietary class.

Regarding sex differences in δ^{13}C, including diet alongside size dimorphism produced results that contrasted with δ^{15}N. In the case of carbon, carnivores and omnivores instead exhibited nonsignificant associations between size dimorphism and isotopic sex differences, whereas herbivores exhibited a significant positive association (0.847, 95% CI: 0.139–1.555, $p = .02$; Figure 2.5).

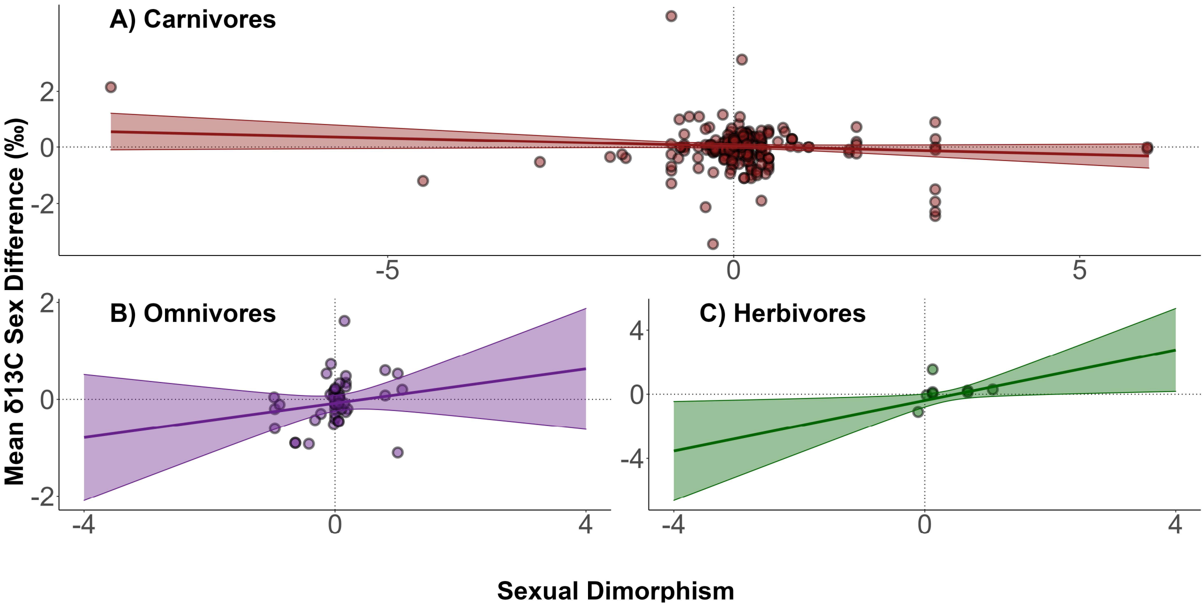


Figure 2.5. The relationship between sexual size dimorphism and mean carbon stable isotope ratio sex differences in carnivores (a), omnivores (b), and herbivores (c). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains trophic sex differences in each dietary class.

Limiting the data set to only gape-limited predators, in which trophic level is predicted to relate more closely to body size, resulting in a 41% increase in the estimated effect of size dimorphism on δ^{15}N mean difference. However, the effect was nonsignificant because of the more modest sample size (0.133, 95% CI: −0.0412 to 0.306, $p = .135$), relative to non-gape-limited (0.094, 95% CI: 0.023–0.17, $p = .01$; Figure 2.6a). Our data set contained local phylogenetic signals for δ^{15}N sex differences in gape-limited predators, with positive phylogenetic signal in snake species (Figure 2.6b), controlling for which weakened the association between size dimorphism and trophic sex differences in gape-limited predators. A nonphylogenetic meta-regression showing a stronger association may be found in Appendix 1.

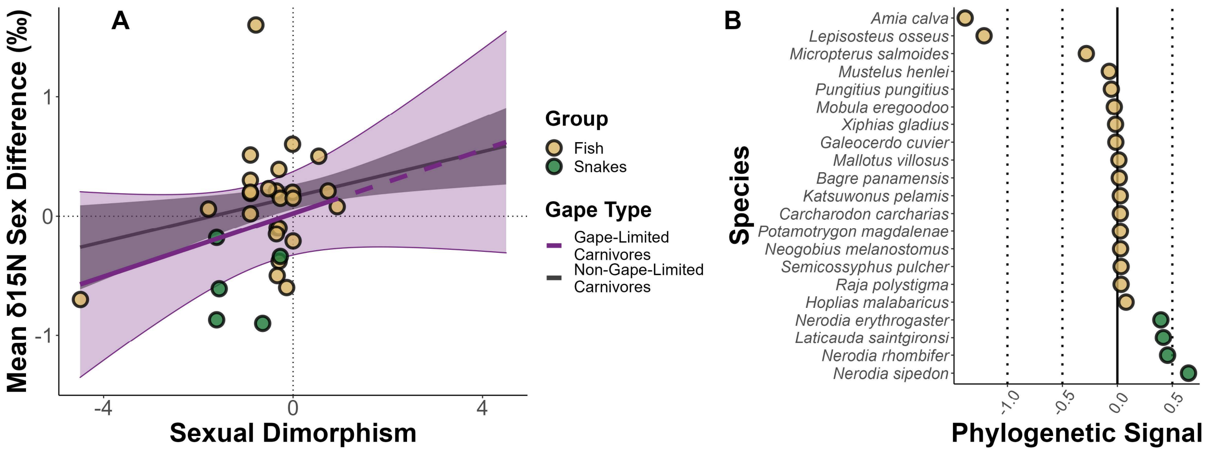


Figure 2.6. (a) The relationship between sexual size dimorphism and mean nitrogen stable isotope ratio sex difference in gape-limited and non-gape-limited carnivores. Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data for gape-limited carnivores, overlaid to assess how well size dimorphism explains trophic sex differences in gape-limited carnivores. Predictions based on gape-limited species are shown in purple (the prediction line is dashed outside the raw data range) and for the non-gape-limited carnivores in gray. (b) Local indicators of phylogenetic association (phylogenetic signal) for mean nitrogen sex differences in gape-limited carnivores.

2.5 Discussion

Using meta-analytical methods, we examined cross-species relationships between sexual size dimorphism and ecological divergence between sexes, measured using stable isotopes. We found that across 166 globally distributed species, size dimorphism was weakly associated with sex differences in mean trophic level ($\delta^{15}N$), but not mean food chain basal resource ($\delta^{13}C$), or variation in either isotope. We also found associations between size dimorphism and isotopic sex differences to be modified by ecological context. The effect of size dimorphism on sex differences in mean trophic level was strongest in omnivores, more modest in carnivores, absent in herbivores, and very modestly affected by species mean size. Dietary class influenced the effect of size dimorphism on sex differences in food chain basal resource in an inverse manner to trophic level, as an association was found in herbivores, but not in omnivores or carnivores. Finally, we found partial evidence that sex differences in trophic level could be more strongly associated with size dimorphism in gape-limited than in non-gape-limited carnivores, as predicted by theory.

2.5.1 Heterogeneity exists in isotopic sex differences

We found heterogeneity in between-sex differences in isotopic mean and variance, for nitrogen and carbon isotopes. Heterogeneity in sex differences for $\delta^{15}N$ and $\delta^{13}C$ indicates nonrandom between-study variation in the extent to which males and females feed at different trophic levels and in different food chains, respectively. Our meta-analytic models, therefore, indicated that large amounts of between-study variation in ecological sex differences may be explained by study-level variables. Though we found some isotopic sex differences to be associated with size dimorphism, which we discuss presently, a large amount of variation was unexplained. Though we found some isotopic sex differences to be associated with size dimorphism, which we discuss presently, a large amount of variation was unexplained. This unexplained variation remains open to explanation by further analyses, some suggestions for which we also outline below. We hope our database provides a useful starting point for further investigations of sexual dimorphism and ecological differences between males and females (Dryad: https://doi. org/10.5061/dryad.k98sf7m99).

2.5.2 Across all species, size dimorphism is associated with sex differences in trophic level, but not food chain basal carbon resources or ecological variability

We found evidence that sexual size dimorphism does, in some instances, scale positively with ecological sex differences. Size dimorphism exhibited a moderate positive association with sex differences in mean $\delta^{15}N$ and thus explained some variation in trophic level differences between males and females. Previous cross-species investigations of the relationship between size dimorphism and $\delta^{15}N$ sex differences have often found inconsistencies, with size dimorphism sometimes relating to trophic differences and sometimes not (Mancini *et al.*, 2013; Phillips *et al.*, 2011). These inconsistencies are likely because the effect is probably modest and may be modified by a wide range of factors, as evidenced by the amount of unexplained variation in our data set. Thus, the size and scope of our analysis is likely the factor that has allowed us to find a clear but moderate effect of size dimorphism on trophic level differences between sexes. No relationships existed between size dimorphism and variation in $\delta^{13}C$ mean sex differences across all species or sex differences in variation in either isotope. Size dimorphism thus does not appear to have a general cross-species influence on sex differences in food chain basal carbon resources or trophic variability. These results conflict somewhat with the conclusions of studies on individual species (Calado *et al.*, 2020; Voigt *et al.*, 2018). It may therefore be the case that size dimorphism is related to sex differences in basal carbon resources and trophic variability in particular species, populations, or contexts, but this association is not sufficiently consistent to covary with sex differences across species.

2.5.3 Associations between size dimorphism and isotopic sex differences are modified by dietary class and gape limitation, but not mean size

We found that ecological context influenced associations between size dimorphism and ecological sex differences. Dietary class modified the effect of size dimorphism on trophic level ($\delta^{15}N$) differences between males and females, with no effect of dimorphism in herbivores, a moderate effect in carnivores, and the strongest effect in omnivores. In contrast, we found an association between size dimorphism and sex differences in food chain basal resource ($\delta^{13}C$) in herbivores, but not in omnivores or carnivores. These results are consistent with our prediction that inherent differences in ecological flexibility might alter the association between size dimorphism and ecology and make sense given the respective feeding niches of the three dietary classes.

As herbivores would be expected to feed exclusively on plants, they should only occupy the position of the primary consumer, leaving little scope for size dimorphism to influence trophic level. Instead, herbivores can more easily diverge along the niche axis related to plant consumption. Because most herbivores in our data set occupy terrestrial habitats, plant consumption is reflected in carbon isotopes in their tissues. Thus, if size dimorphism relates to dietary divergence in herbivores, this divergence seems to arise as sex differences in plant consumption, as opposed to trophic level. For example, stable isotopes suggest that male African elephants (*Loxodonta africana*) consume more grass than females, which may be because larger body size increases food digestive efficiency and food ingestion per mouthful (Shannon *et al.*, 2013).

Carnivores may occupy any position from secondary consumer upwards, meaning each sex could take prey from one or multiple trophic levels, creating some opportunity in carnivores for trophic differences between the sexes to be influenced by size dimorphism. In contrast to the other two groups, omnivores would be expected to consume foods from a minimum of two trophic levels, leading to a greater probability of trophic differences between sexes and the largest opportunity for size dimorphism to influence this difference. This might be why size dimorphism was most strongly associated with trophic sex differences in omnivores in our data set. Sex differences in carnivore and omnivore basal resources may have covaried less with size dimorphism because the basal resources of nonprimary consumers relate not only to their diet but also to the diets of their prey (Codron *et al.*, 2018). Therefore, unless dimorphism produces sex differences in prey access that corresponds to different basal resources, for example, one sex exclusively hunting browsers and the other hunting grazers, a strong association between dimorphism and basal resource sex differences is unlikely. The indirect nature of the relationship between size dimorphism and basal resource in carnivores and omnivores could mean that divergence along this niche axis is less likely to be driven by dimorphism than in herbivores. Together, these results suggest that the association between size dimorphism and ecological sex differences is dependent on the ecological opportunity for feeding differences between males and females.

Our model also contained an independent effect of species mean size on sex differences in trophic levels. However, this effect was multiple orders of magnitude lower than the analytical reproducibility of nitrogen stable isotope analysis. Thus, even though the model estimate was technically positive, we conclude that absolute species size has no meaningful effect on trophic-level sex differences.

Limiting the data set to gape-limited carnivores led to a 41% increase in the effect of size dimorphism on trophic sex differences, compared with non-gape-limited carnivores, though the gape-limited model was nonsignificant. There is substantial evidence available that larger gape increases maximum ingestible prey size and trophic level in fish and snakes (Barnes *et al.*, 2021; Nilsson and Brönmark, 2000; Persson *et al.*, 1996; Webb and Shine, 1993).

Consequently, the larger effect of size dimorphism on trophic sex differences in the gape-limited predators we analyzed could indicate that gape limitation increases the ecological relevance of dimorphism, producing a stronger relationship between dimorphism and ecology. More research is required, however, due to the non-significance of our model. The wide confidence intervals in the gape-limited model may have been due to the small sample size (n = 30) and any potential interaction between gape limitation, size dimorphism, and ecological sex differences should therefore be examined with a larger data set.

An additional possibility is that gape limitation is important to the relationship between size dimorphism and ecological sex differences only when certain conditions are met. There was a phylogenetic signal for trophic-level sex differences in our gape-limited data (Figure 2.6b) and in nonphylogenetic models, the effect of size dimorphism in gape-limited predators was significant and substantially greater than when controlling for phylogeny (Appendix). It could be the case that the phylogenetic random effect captured differences between species in the niches or food webs to which they have adapted. If gape limitation is to produce trophic sex differences in a species, then body size must relate to the trophic level in the prey of that species, in order for higher trophic level prey to be accessible to only the larger sex. This condition may not hold true in all taxa or food webs, and this wider context may need to be considered when investigating the influence of gape limitation on associations between sexual dimorphism and trophic sex differences.

In summary, we found the extent of size dimorphism to be associated with the extent of ecological sex differences, an association that increased in strength when the ecological opportunity for trophic variation was greatest and potentially when size dimorphism was more ecologically relevant. Our results are consistent with both a potential role for ecological character displacement in enhancing sexual dimorphism or for ecological sex differences to arise due to reproductive differences. However, as the associations we found were generally modest, they support previous predictions that the role of ecological character displacement is relatively minor (De Lisle and Rowe, 2015; Fairbairn, 1997) and suggest that size dimorphism produced via reproductive differences is not a powerful driver of feeding differences between males and females.

2.5.4 Future Research Directions

Several questions arise from our meta-analysis that should form the subject of future work. First, the results of our analysis on gape limitation were uncertain and the apparent influence of phylogeny on our results could suggest that the relevance of gape limitation is species or niche specific. Future analyses could therefore examine the impact of gape limitation on ecological sex differences with a greater sample size and taxonomic scope than used presently. For example, a recent analysis found a positive relationship between gape size and fruit size consumed in frugivorous birds (McFadden *et al.*, 2022), and including similar data in future analyses could allow the importance of gape limitation to ecological sex differences to be generalized across a wide range of species and niches.

As our results suggest a relationship between sexual dimorphism and ecology but do not distinguish between reproductive differences and ecological character displacement as driving that relationship, the next major question concerns their relative importance as evolutionary mechanisms. A weak role for ecologically mediated selection implies that sexual and fecundity selection are the main drivers of sexual dimorphism. However, a recent analysis found that size dimorphism was only weakly associated with sexual selection across species, leading the authors to suggest that "alternative mechanisms such as ecological character displacement may be crucial to understand the full diversity of [size dimorphism] in animals" (Janicke and Fromonteil, 2021). Considering our own results, alongside their conclusion, we suggest that a future priority should be the incorporation of sexual, fecundity, and ecologically mediated selection into single cross-species analyses, to quantify their relative importance to the evolution of size dimorphism.

Our analyses support an association but suggest the cross-species patterns may be modest. Why would ecological character displacement be a weaker selective force than other drivers of sexual dimorphism? One possibility is that the frequency-dependent nature of resource competition means that the strength of competition falls as the sexes phenotypically diverge (De Lisle and Rowe, 2015). Alternatively, divergence from the species mean phenotype, while alleviating resource competition, may itself entail fitness costs that eventually exceed those of competition for resources (Bolnick and Doebeli, 2003; Slatkin, 1984). Either possible scenario may place an upper limit on the extent to which ecologically mediated selection can drive character displacement between sexes. Therefore, establishing the mechanistic limitations on ecological character displacement between sexes should also become the focus of future investigations, most likely via modeling and experiment.

A final question is what additional variables could be included in future analyses, to explain the considerable variation in ecological sex differences? Our analyses have highlighted that high amounts of between-study variation in our data remain unexplained, providing opportunities to use our database to investigate additional drivers of ecological differences between males and females. Importantly, isotopic values for an animal's tissues may be affected by many factors, such as body size, body condition, diet quality, and ontogenetic growth (Carleton and Martinez del Rio, 2010; Lecomte *et al.*, 2011; Wolf *et al.*, 2009). Sex differences in any of these variables could potentially influence sex differences in isotopic signals and influence cross-species isotopic comparisons. However, their impact is often species-specific, so a comparative synthesis of the sort we have conducted would require species-level data to become widely available across many taxa.

In relation to why ecological sex differences evolve, nutritional requirements are one potential avenue of investigation. Males and females may target distinct sets of resources in order to meet sex specific nutritional needs, such as lactation or sexually selected signals (Harrison *et al.*, 2017; Thompson, 2013). These differences may influence foraging and other aspects of behavioral ecology (Morehouse *et al.*, 2020). As stable isotopes in animal tissues vary with the foods animals consume, the sex differences in isotope ratio we have observed may illustrate how males and females target distinct resources, to fulfill their own sex-specific nutritional requirements. Future investigations could therefore seek to quantify the strength of associations between-sex differences in nutritional requirements and stable isotope values, which could contribute greatly to our understanding of ecological differences between males and females.

2.6 Acknowledgements

We would like to thank two anonymous reviewers and the editors for their useful feedback on this manuscript. This work was funded by the Natural Environment Research Council, UK

[NERC IAPETUS DTP (NE/L002590/1)]. IJ was supported by a UKRI Future Leaders Fellowship (MR/T019018/1).

2.7 Appendix

2.7.1 Mean-Variance Relationships

Calculating effect sizes that quantify variation differences between groups, such as sex, may be impacted by mean–variance relationships. These describe an increase in variance with an increase in mean and may adversely influence the outcome of meta-analyses. We, therefore, plotted the relationship between raw isotopic mean and standard deviation, alongside linear regressions, to investigate the presence of mean–variance relationships in our data. We found no evidence for mean–variance relationships in female nitrogen (Figure A2.1a), male nitrogen (Figure A2.1b), female carbon (Figure A2.1c), or male carbon (Figure A2.1d).

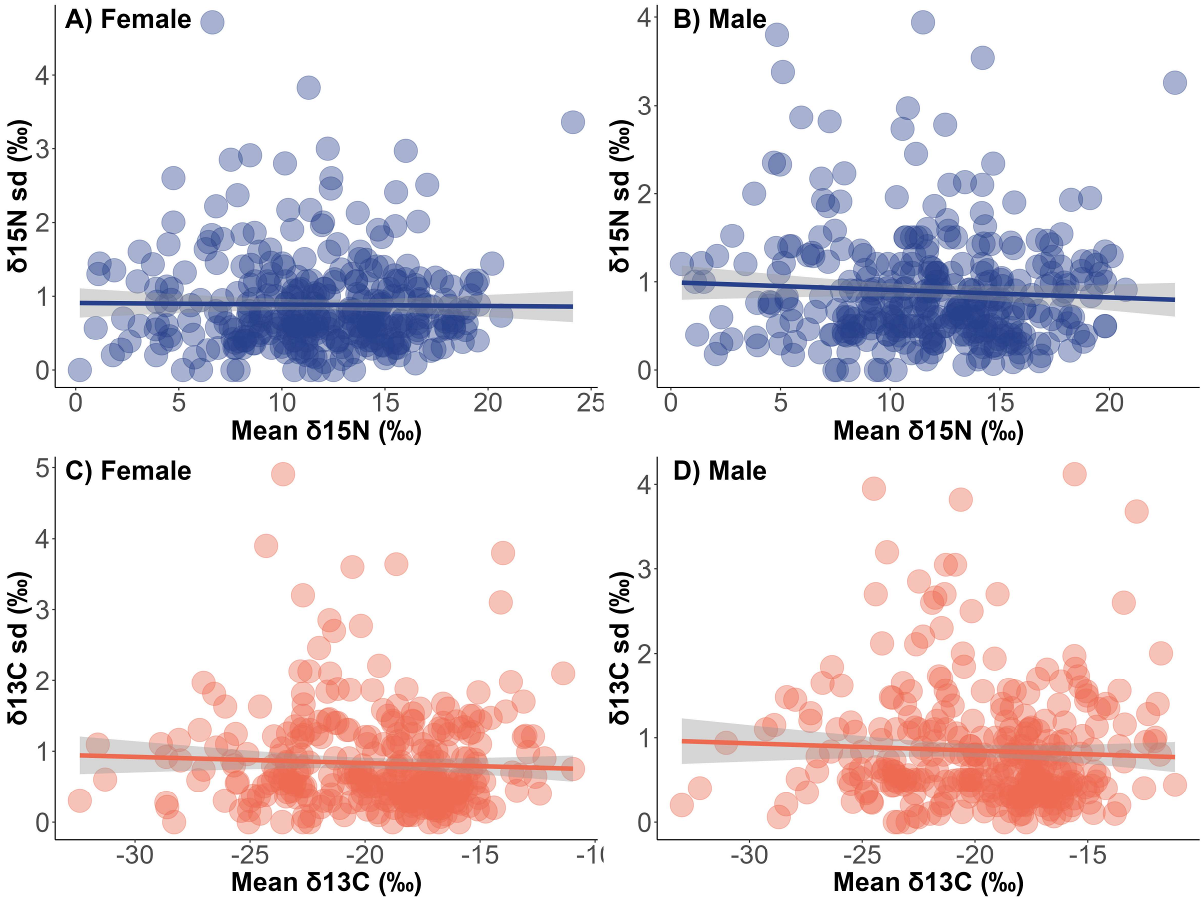


Figure A2.1. Mean–variance relationships in female nitrogen(a), male nitrogen (b), female carbon (c), and male carbon (d).

2.7.2 Publication bias

Publication Year

As one possible identifier of publication bias is a reduction of effect sizes through time, we completed meta-regressions with publication year as the sole predictor variable. We found no effect of publication year on the magnitude of published sex differences in isotopic mean or variation, for either nitrogen or carbon isotopes (Table A2.1).

Table A2.1. Effect of publication year on sex difference in mean and variation, for nitrogen and carbon.

Isotope	**Measure**	**Effect of Publication Year**	**Standard Error**	**Confidence Limit Lower Bound**	**Confidence Limit Upper Bound**	***p***
Nitrogen	Mean Difference	-0.0010	0.0100	-0.0221	0.0202	0.9270
Nitrogen	Variation	-0.0035	0.0066	-0.0164	0.0095	0.6010
Carbon	Mean Difference	0.0066	0.0081	-0.0094	0.0225	0.4195
Carbon	Variation	-0.0094	0.0073	-0.0237	0.0049	0.1979

Funnel plots

Funnel plots can be used to investigate possible publication bias by illustrating asymmetries in published effect sizes, which would suggest particular results are favorably published. Such biases in published literature would influence the outcome of meta-analyses, by skewing summary effect size estimates toward the favored outcome. We, therefore, produced funnel plots displaying published effect sizes for sex differences in nitrogen mean (Figure A2.2), nitrogen variation (Figure A2.3), carbon mean (Figure A2.4), and carbon variation (Figure

A2.5). In all four cases, our plots displayed a fairly even distribution in study outcomes, suggesting that publication bias is not prominent in the literature we have examined.

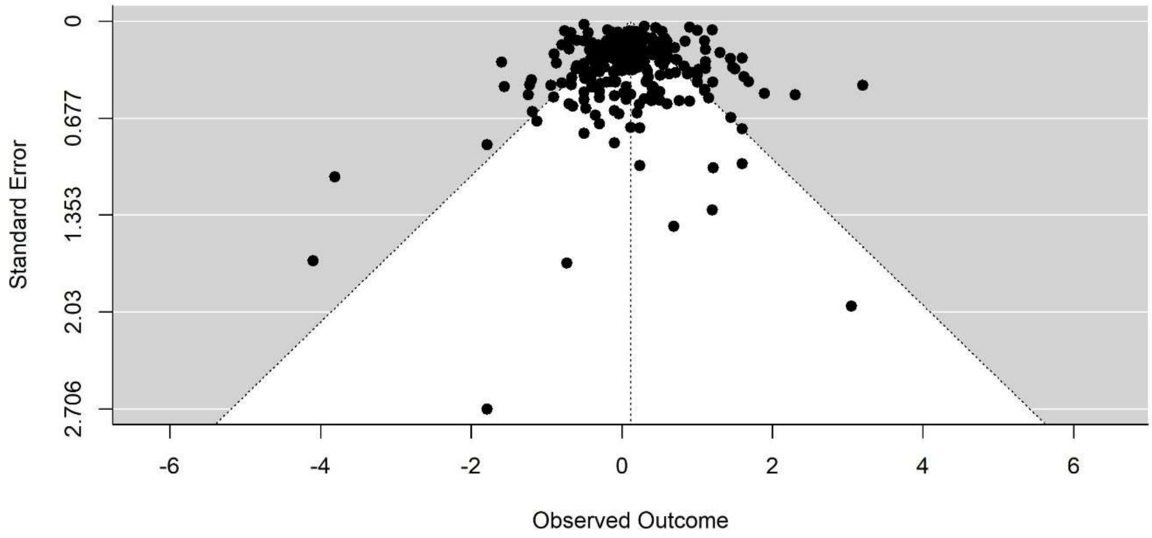


Figure A2.2. Distribution of published sex differences in nitrogen isotope means.

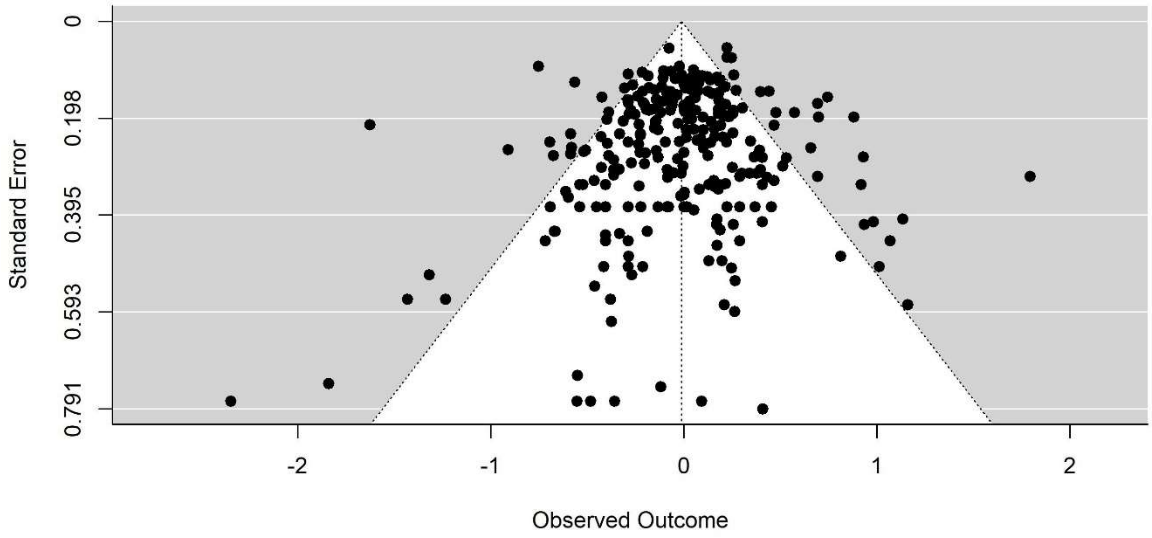
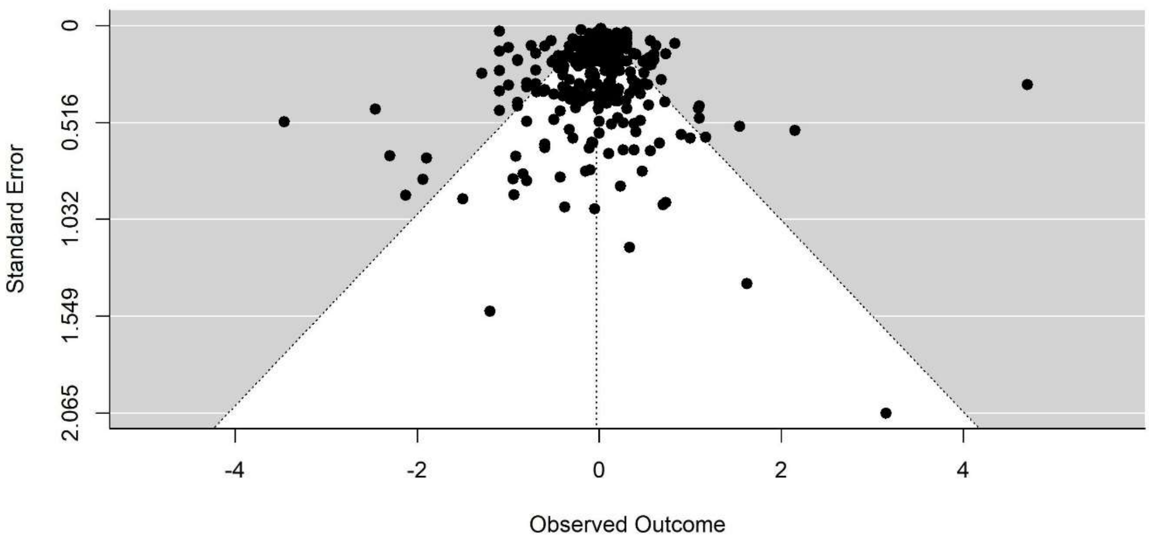
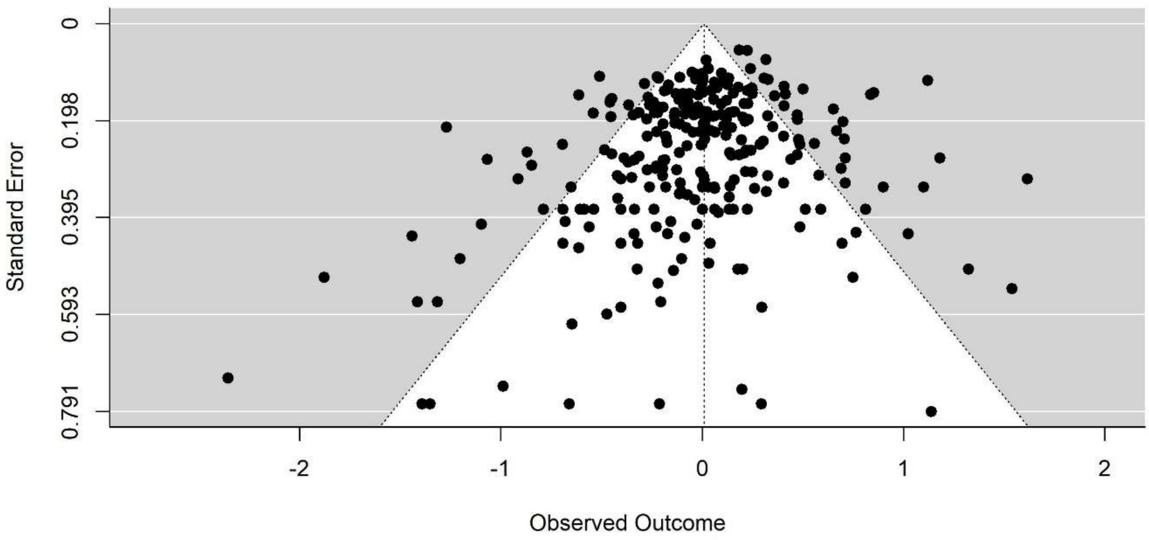


Figure A2.3. Distribution of published sex differences in nitrogen isotope variation.



1209 *Figure A2.4. Distribution of published sex differences in carbon isotope means.*



1210 *Figure A2.5. Distribution of published sex differences in carbon isotope variation.*

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2.7.3 Gape limitation: non-phylogenetic models

When not controlling for phylogeny the effect of size dimorphism in gape-limited predators was statistically significant and almost double that of non-gape-limited carnivores (Figure A2.6).

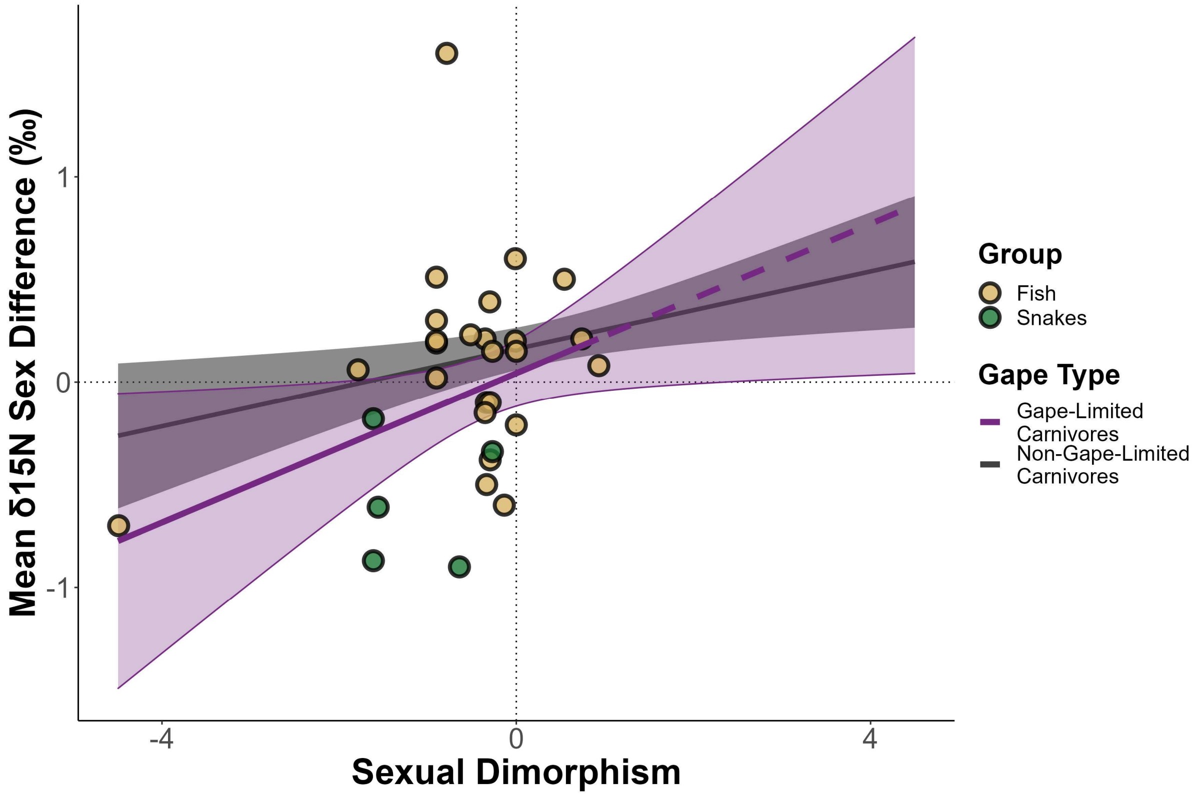

Figure A2.6. The effect of size dimorphism in gape-limited predators (purple) and non-gape-limited carnivores (gray) when not controlling for phylogenetic relatedness between species.

2.7.4 Effect of study weighting method

The weight given to individual effect sizes can alter the outcome of meta-analyses. As our analysis consisted of meta-regressions, including the random factors “paper number,” “species,” and “phylogeny,” each effect size used as a response in our analysis was weighted accounting for within-study variance, heterogeneity between studies, species, and phylogenetic relatedness, and covariance between these random factors. Thus, our models assumed differences between studies and species in the true isotopic difference between sexes. However, high heterogeneity, which was present in our data, can mask within-study variance. It is therefore recommended to also conduct models weighting studies solely by the inverse of within-study variance, to examine the impact of weighting method on model predictions and, therefore, the conclusions of the meta-analysis.

Regarding the relationship between-sex differences in nitrogen mean (trophic level) and size dimorphism, our results were not robust to changing the weighting method, as the confidence interval for the estimated effect of size dimorphism on trophic sex differences overlapped zero (Table A2.2). Our qualitative conclusion would therefore have changed with the alternate weighting, to state that size dimorphism is unrelated to trophic differences between sexes. However, as this weighting method does not account for between-study and between-species heterogeneity in trophic sex differences, we believe it to be inappropriate. The diversity of species investigated by the studies we have meta-analyzed, and the consequent diversity of our analysis, mean assuming a universal difference in sex differences in trophic level is clearly erroneous. We are therefore skeptical of the conclusion this weighting method produces and are more confident in the original model included in the main text.

When weighting by the inverse of within-study variance in the model examining the effect of size dimorphism on sex difference in nitrogen variation (Table A2.3), carbon mean (Table A2.4), and carbon variation (Table A2.5), our qualitative conclusions remained the same.

When including dietary class and mean size alongside size dimorphism, as predictors of sex differences in nitrogen mean, the effect of mean size (which was effectively zero) was absent and the effect of size dimorphism was absent in all dietary classes when weighting by the inverse of within study variance (Table A2.6). Our results in models examining gape-limited (Table A2.7) and non-gape-limited carnivores (Table A2.8) were also not robust to alternate weighting. Finally, the effect of size dimorphism on sex differences in carbon mean sex differences was also statistically nonsignificant when using the alternate weighting method (Table A2.9). However, for the same reasons outlined above, we are more confident in the original models included in the main text.

Table A2.2. Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.046	0.091	0.51	0.61
Size Dimorphism	summary	0.1	0.062	1.63	0.1

Table A2.3. Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen variation, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	-0.0071	0.041	-0.17	0.86
Size Dimorphism	summary	0.039	0.03	1.35	0.18

Table A2.4. Output of fixed effects model examining the effect of size dimorphism on sex differences in carbon mean, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	-0.051	0.11	-0.58	0.62
Size Dimorphism	summary	0.14	0.08	1.84	0.066

Table A2.5. Output of fixed effects model examining the effect of size dimorphism on sex differences in carbon variation, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.044	0.039	1.13	0.26
Size Dimorphism	summary	0.030	0.033	0.91	0.36

Table A2.6. Output of fixed effects model examining the effect of size dimorphism, dietary class and species mean size on sex differences in nitrogen mean, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.21	0.076	2.76	0.0059

Size Dimorphism	summary	0.059	0.06	0.99	0.32
Herbivore	summary	-0.71	0.3	-2.38	0.017
Omnivore	summary	-0.53	0.28	-1.89	0.059
Mean Size	summary	0.00000097	0.0000027	0.37	0.71
SSD:Herbivore	summary	0.65	0.55	1.19	0.23
SSD:Omnivore	summary	0.38	0.27	1.43	0.15

Table A2.7. Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, in gape-limited carnivores, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.11	0.2	0.55	0.59
Size Dimorphism	summary	0.11	0.16	0.73	0.47

Table A2.8. Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, in non-gape-limited carnivores, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.23	0.087	2.6	0.0094
Size Dimorphism	summary	0.054	0.066	0.82	0.41

Table A2.9. Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, in non-gape-limited carnivores, weighting studies only by the inverse of within-study variance.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.030	0.07	0.43	0.67
Size Dimorphism	summary	0.087	0.074	1.14	0.26
Herbivore	summary	-0.89	0.3	-3.01	0.0026
Omnivore	summary	-0.086	0.28	-0.31	0.76
Size Dimorphism:Herbivore	summary	1.3	0.47	2.8	0.0051
Size Dimorphism:Omnivore	summary	0.28	0.21	1.33	0.18

2.7.5 High leverage data points

The outcome of meta-analyses may also be adversely impacted by outliers/high leverage data points that skew model estimates. We therefore used Cook's leave-one-out analysis to identify high leverage data points that may have an unduly large effect on our models. Several approaches are possible for identifying data points as high leverage based on Cook's scores, and we chose to assign those with a Cook's score over three times the mean score, for data points in a given model, as potentially high leverage. We found this approach to be the most conservative, by identifying the highest number of points as possibly high leverage. We then removed these data from the models for which they may be high leverage and re-ran each model.

In models examining only the effect of size dimorphism on sex differences in nitrogen mean (Table A2.10), nitrogen variation (Table A2.11), carbon mean (Table A2.12), and carbon variation (Table A2.13), removing high leverage data points did alter estimated effect sizes but did not change the qualitative conclusions we could draw from the models. When including dietary class and species mean size as predictors, alongside size dimorphism, the effect sizes changed (Table A2.14), but our qualitative conclusions did not. In models analyzing the impact of size dimorphism on sex differences in nitrogen mean in gape-limited (Table A2.15) and non-gape-limited carnivores (Table A2.16), removing high leverage data points also did not change our qualitative conclusions. Finally, when removing high leverage data points from the model examining the effect of size dimorphism and diet on sex differences in carbon mean sex differences, the effect of size dimorphism in herbivores was no longer significant (Table A2.17). This is likely because of the small sample size of herbivores in our data set, rather than an indication that any points should be removed.

Table A2.10. Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.076	0.039	1.95	0.051
Size Dimorphism	summary	0.2	0.053	3.57	0.00036

Table A2.11. Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen variation, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	-0.012	0.029	-0.43	0.67
Size Dimorphism	summary	-0.0048	0.033	-0.15	0.88

Table A2.12. Output of meta-regression model examining the effect of size dimorphism on sex differences in carbon mean, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.022	0.03	0.74	0.46
Size Dimorphism	summary	0.063	0.039	1.63	0.1

Table A2.13. Output of meta-regression model examining the effect of size dimorphism on sex differences in carbon variation, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	-0.0027	0.027	-0.1	0.92
Size Dimorphism	summary	0.031	0.028	1.11	0.27

Table A2.14. Output of meta-regression model examining the effect of size dimorphism and dietary class and species mean size on sex differences in nitrogen mean, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.1	0.044	2.35	0.019
Size Dimorphism	summary	0.18	0.051	3.45	0.00055
Herbivore	summary	0.032	0.46	0.069	0.95
Omnivore	summary	-0.097	0.11	-0.9	0.37
Species Mean Size	summary	0.0000064	0.0000025	2.62	0.0088
Size Dimorphism: Herbivore	summary	0.15	0.64	0.24	0.81
Size Dimorphism: Omnivore	summary	0.44	0.23	1.93	0.054

Table A2.15. Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, in gape-limited carnivores, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.066	0.15	0.45	0.66
Size Dimorphism	summary	0.025	0.096	0.26	0.79

Table A2.16. Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, in non-gape-limited carnivores, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.12	0.054	2.19	0.029
Size Dimorphism	summary	0.19	0.077	2.53	0.011

Table A2.17. Output of meta-regression model examining the effect of size dimorphism and dietary class on sex differences in carbon mean, with high leverage data points removed. Output of meta-regression model examining the effect of size dimorphism and dietary class on sex differences in carbon mean, with high leverage data points removed.

Term	**Type**	**Estimate**	**Standard Error**	**Statistic**	***p***
Intercept	summary	0.014	0.036	0.38	0.7
Size Dimorphism	summary	0.028	0.043	0.66	0.51
Herbivore	summary	0.45	0.49	0.91	0.36
Omnivore	summary	-0.11	0.086	-1.28	0.2
Size Dimorphism: Herbivore	summary	-0.41	0.9	-0.46	0.65
Size Dimorphism: Omnivore	summary	0.29	0.19	1.51	0.13

Chapter 3 Rare long-term data reveal the seasonal dietary plasticity of mandrills (*Mandrillus sphinx*) in response to fruiting tree phenology.

The research was conceived by Joshua Bauld, David Lehmann, Katharine Abernethy, Luc Bussière, Jason Newton and Isabel Jones. Data collection was conducted by Katharine Abernethy and the SEGC field scientists. Joshua Bauld carried out data analysis, with guidance from Luc Bussiere and David Lehmann. Joshua Bauld wrote the chapter with guidance from David Lehmann, Katharine Abernethy, Jason Newton, Luc Bussière and Isabel Jones.

3.1 Abstract

Understanding primate dietary plasticity may give insights into trait evolution and resilience to environmental change. Here we investigate the feeding ecology of mandrills (*Mandrillus sphinx*), a species that forms groups of close to 1000 individuals, which presumably impacts feeding ecology by creating exceptionally high feeding competition. Mandrills are also threatened by habitat loss and climate change and a full understanding of their dietary plasticity is essential to ongoing conservation efforts. Evidence suggests that mandrills are highly generalist feeders, able to consume a wide range of resources to make up shortfalls in fruit availability. However, a lack of long-term data on fruit production within the mandrill geographic range means that it is unknown whether the flexible feeding strategies observed previously are stable over multiple years. We combined two rare datasets comprising eight years of fecal collections and fruit availability observations to assess the dietary flexibility of mandrills in response to seasonal variations in fruit production in Lopé National Park, Gabon. We found fruit to be the most frequently consumed resource and that fruit consumption covaried positively with fruit availability, peaking during periods of fruit abundance. Mandrill dietary diversity increased during periods of fruit scarcity, through greater consumption of animal prey, leaves, seeds, and other plant fibers. These results demonstrate that mandrills are primarily frugivorous, but that they are also highly flexible feeders, able to respond to temporal variation in fruit production over several annual cycles. In addition, we found mandrills to vary in the extent to which they preferred different fruit taxa. Lipid-rich oil palm (*Elaeis guineensis*) fruits were by far the most frequently consumed resource and may

constitute a keystone resource to mandrills in the study site. Our results may be used to initiate future study of mandrill nutritional ecology, as well as inform ongoing conservation efforts throughout mandrill range countries.

3.2 Introduction

Diet has long been a focus of primatological research (Lambert and Rothman, 2015), because of its relevance to topics such as species coexistence (Houle *et al.,* 2006), space use (Hanya *et al.,* 2004; Zhang *et al.,* 2021), life histories (Borries *et al.,* 2011) and morphological trait evolution (Regan *et al.,* 2001; Onstein *et al.,* 2020). Furthermore, habitat destruction and climate change are intense conservation challenges for primates, many species of which are at high risk of extinction (Pacifici *et al.,* 2017; Bernard and Marshall, 2020). Investigating dietary flexibility could provide insights about primates' resilience to change and identify the most (and least) effective conservation strategies (Harcourt *et al.,* 2002; Nowak and Lee, 2013). A greater understanding of wild primate diets may also inform the ongoing debate about optimal human nutrition (Milton, 2000; 2003; Alt *et al.,* 2022).

Long term behavioral and habitat data are key to a full understanding of primate ecology and evolution (Chapman *et al.,* 2017; Melin *et al.,* 2020). In the case of diet, long-term data facilitate inferences about feeding ecology that account for inter-annual changes in variables such as food availability (Chapman *et al.,* 2002; Zhou *et al.,* 2009; Erhart *et al.,* 2018). In this study, we use rare multi-year datasets on diet and fruit production to investigate the feeding ecology of mandrills *(Mandrillus sphinx*), by analyzing seasonal changes in diet across eight annual cycles. We focus on mandrills because their large social groups (Abernethy *et al.,* 2002) and extreme sexual dimorphism (Setchell, 2016) may greatly impact dietary plasticity at the individual and group level.

3.2.1 The Influence of Phenology

One of the major influences on primate diets is seasonal variation in food availability (van Schaik *et al.,* 1993; Peres, 1994; Tuyisingize *et al.,* 2022). The seasonal timing of biological events, such as fruit production, is termed phenology (Lieth, 1974), which in tropical trees is influenced by temperature and rainfall (Reich, 1995; Mendoza *et al.,* 2017; Potts *et al.,* 2020). Frugivorous primates rely on fruit as their principal food source and, as a result, typically exhibit seasonal dietary variation in response to phenological cycles of fruit production (Guo *et al.,* 2007; Chancellor *et al.,* 2012; Butt *et al.,* 2015; DeLuycker, 2021). The taxonomic diversity and abundance of fruit may, however, vary between years because the fruiting phenology of different tree species can follow annual, sub- or supra-annual cycles (Bush *et al.,* 2017; Adamescu *et al.,* 2018). As a consequence, our primary goal was to describe average seasonal changes in mandrill food selection across multiple years, that may have varied in exactly which fruit species were available.

Fluctuations in fruit abundance result in periods of scarcity through the year, and during these times, frugivorous primates are expected to exhibit dietary and behavioral flexibility to make up any nutritional shortfalls (Tutin *et al.,* 1991). Possibilities include switching to other food types, such as leaves or invertebrates, feeding on more consistently available, but lower quality fruits (Hill, 1997; McConkey *et al.,* 2002; Clink *et al.,* 2017), foraging over larger areas (Nagy-Reis and Setz, 2017), or reducing group or party size, to exploit smaller food patches (Tutin and Fernandez, 1993). 'Preferred' food types may therefore be identified as those for which consumption covaries positively with availability (Leighton, 1993). In contrast, 'fallback' foods can be considered as alternative food types, the consumption of which covaries negatively with the consumption of preferred resources (Wrangham and Marshall, 2007). This switching to alternative resources may furthermore be accompanied by an increase in dietary diversity, as primates attempt to make up the nutritional shortfalls of alternative food sources (Lambert and Rothman, 2015).

In addition to assessing which fallback foods are consumed, knowledge of which fruits are selected during periods of abundance is also necessary for understanding frugivore feeding strategies (Leighton, 1993; Doran-Sheehy *et al.,* 2009). Fruits which are consumed in greater amounts as a function of availability may be considered 'preferred' and those consumed less as a function of availability may be classified as 'avoided' (Russo *et al.,* 2005). A robust understanding of how primate diets vary in response to phenology is an important first step to understanding their feeding strategies (Chapman *et al.,* 2002). For example, some foods may be targeted because of their macronutrient contents (Conklin-Brittain *et al.,* 1998) and some may be avoided due to containing plant defensive compounds (Masette *et al.,* 2015).

3.2.2 The Influence of Resource Competition

Primate food selection may also be affected by within- or between-species resource competition. The socioecological model for primate group formation suggests that females form groups as an anti-predation strategy, but that this aggregation of animals in space produces feeding competition (Wrangham, 1980; van Schaik, 1989). The intensity of feeding competition is then in turn influenced by the distribution of resources and group size, and can occur both within and between groups of conspecifics (Sterck *et al.,* 1997). Scramble competition, in which individuals (or groups) compete to be first to arrive at clumped resources, may arise once individuals form groups and increase in strength as group size increases (Miller *et al.,* 2020). Feeding competition can alternatively take the form of contest competition, whereby dominant animals (or groups) exclude others from a resource (Scarry *et al.,* 2013). Within- and between-group feeding competition in turn means that even when resource availability is high, preferred resources may still be less accessible to some individuals (or groups), impacting their food selection. For example, high-ranking chimpanzees have been observed to monopolize the most nutritious fruits at the tops of trees, at the expense of subordinate individuals (Houle and Wrangham, 2021).

Feeding competition may also occur between different species, impacting the food selection of primates living in multi-species assemblages. For example, chimpanzees have been observed to exclude subordinate species from fruit trees (Houle *et al.,* 2010). Species may also avoid competition by segregating habitats in time or space. For example, pitheciine monkeys are thought to have evolved to feed on immature fruit, to access seeds earlier than other species (Ledogar *et al.,* 2013). Similarly, primate assemblages may split habitats by height (Sushma and Singh, 2006) or feed in separate habitats during periods of resource scarcity (Wahungu, 1998). The result of between-species competition is that sympatric frugivorous may exhibit dietary distinction even during periods of fruit abundance and consume different fallback foods during periods of scarcity. Consideration must therefore be given to the fact that frugivorous primates usually live in groups and alongside other frugivorous species, leading to competition for high value resources, when investigating how food selection varies in response to phenology.

3.2.3 Mandrill Ecology

Mandrills are a particularly interesting species in which to study the relationship between tree phenology and diet, because they exhibit several exceptional traits relevant to food selection. Though classified as frugivores, mandrills consume a remarkably wide range of foods, including vertebrate and freshwater prey (Jouventin, 1975; Hoshino, 1985; Harrison, 1988; Norris, 1988; Rogers *et al.,* 1996). Mandrills also live in the largest known social groups, termed ‘hordes’, of any non-human primate (620+/-166, range 340-845; Abernethy *et al.,* 2002). Such large group sizes likely result in high levels of within-group feeding competition and rapid rates of patch depletion. Consequently, mandrills also occupy the largest total home-ranges documented in any wild primate (182 km^2) and travel costs are likely exceptionally high for individuals living in mandrill hordes (White *et al.,* 2010). These socioecological traits are coupled with the most extreme size dimorphism seen in primates and extravagant facial adornments on male animals (Darwin, 1876; Setchell, 2016). Furthermore, the geographic range of mandrills overlaps with those of numerous other primate species and high biomass frugivores, such as forest elephants (*Loxodonta cyclotis*) and red river hogs (*Potamochoerus porcus*) (Tutin *et al.,* 1997). Individual mandrills must therefore cope with high levels of feeding competition, to consume a diet that provides sufficient energy to sustain extensive travel, with nutritional requirements also potentially differing between sexes, due to extreme dimorphism.

Periods of fruit scarcity may hamper the ability of individual mandrills to consume sufficient resources. Previous investigations have documented that when fruit availability is low, mandrill feed on a variety of fallback foods, with a consequent increase in dietary diversity (Nsi Akoué *et al.,* 2017; Hongo *et al.,* 2018). Tree phenological cycles and fruit availability may vary between years, however, and so whether this feeding strategy remains consistent over several annual cycles is an open question, unanswered primarily due to a lack of long-term data on either tree phenology or mandrill diets (White, 2007; Hongo *et al.,* 2018).

In this study, we investigate mandrill feeding strategies using a rare eight year dataset on mandrill diets, obtained from fecal samples gathered over an eight-year period in Lopé National Park, Gabon. We analyze these data in conjunction with a long-term (1986-present) tree phenology dataset, one of only 12 available in Africa (Adamescu *et al.,* 2018) and the only one within the known geographic range of mandrills. The Lopé phenology dataset indicates that fruit abundance varies seasonally, with fruit production peaking in the two wet seasons (Feb-May and September-November) and falling in the two dry seasons (June-August and December-January) (Bush *et al.,* 2017). This fluctuation in fruit availability has previously been observed to influence the diets of primates living within the park (White *et al.,* 1994; Tutin *et al.,* 1997). However, the exact timing and duration of each season, as well as the total amount of fruit produced, may vary between years (Tutin *et al.,* 1991). By combining the fecal and phenology datasets we are therefore able to build upon prior investigations with an analysis of mandrill feeding strategies that account for long-term variation in tree phenology and fruit availability.

To investigate mandrill diets we analyzed 4024 fecal samples, collected between September 1996 and October 2004, from which we recorded the major food types consumed and identified plant tissues to species level, where possible. Using these data, we first set out to describe our study horde’s diet in terms of preferred food types, use of fallback foods and seasonal changes in food type diversity. Mandrills also appear to prefer some fruits over others during periods of abundance (White, 2007, Nsi Akoué *et al.,* 2017). We therefore also examined whether particular fruits were consumed more frequently as a function of availability, suggesting they are preferred foods, and explored why preferences may exist in terms of maximum tree height and nutritional contents. We were interested in the impact of maximum tree height on the frequency at which fruit genera were consumed, because a negative association could suggest that mandrills avoid foraging in tall trees or are excluded from the tops of trees by other frugivorous species. Similarly, we wanted to examine the relationship between nutritional contents and consumption frequency to try and elucidate the mechanisms driving mandrill food selection.

3.3 Methods

3.3.1 Study site

Our study was carried out in Lopé National Park, located in Gabon (-0.2N, 11.6E), Central Africa (Figure 3.1). Lopé National Park covers an area of 4964 Km^2 which is mostly old growth Guineo-Congolian evergreen tropical rainforest, but contains a dynamic forest-savanna mosaic landscape covering approximately 10 % of its northern area (Figure 3.1). This mix of savanna and gallery forests is bordered to the north by the Ogooué (the second largest river in the Congo-Ogooué basin). Our 182 km^2 study area, based on the area used by mandrills in Abernethy *et al.* (2002), is situated within the savanna forest matrix and adjacent continuous forest (Figure 3.1). The dominant type of vegetation at the continuous forest edge in this area is 'Marantaceae forest', which is a young secondary forest with a dense herbaceous understory, dominated by plants of the families Marantaceae and Zingiberaceae. Gallery forest fragments that extend out from the main continuous forest-block into the savanna typically form along small riverbeds and have sparse ground vegetation of lianas and small shrubs. Plant species assemblages and compositions differ between gallery forests, forest fragments and continuous forest (see White, 1994; White and Abernethy, 1997, Tutin *et al.,* 1997, Léal, 2004; Ukizintambara *et al.,* 2007; White, 2007). Notably, the gallery forests have a history of anthropization over several hundred years, that included the planting of oil palms (*Elaeis guineensis*) (Maley and Chepstow-Lusty, 2001; Bostoen *et al.,* 2013). Lopé National Park receives on average 1466+/- 201mm of rain per year; which falls within two distinct time-windows; the long rainy season runs from February to May, and the shorter rainy season from September to November. The short dry season takes place from December to January while the longer dry season occurs from June to August (White 1994, Bush *et al.* 2020).

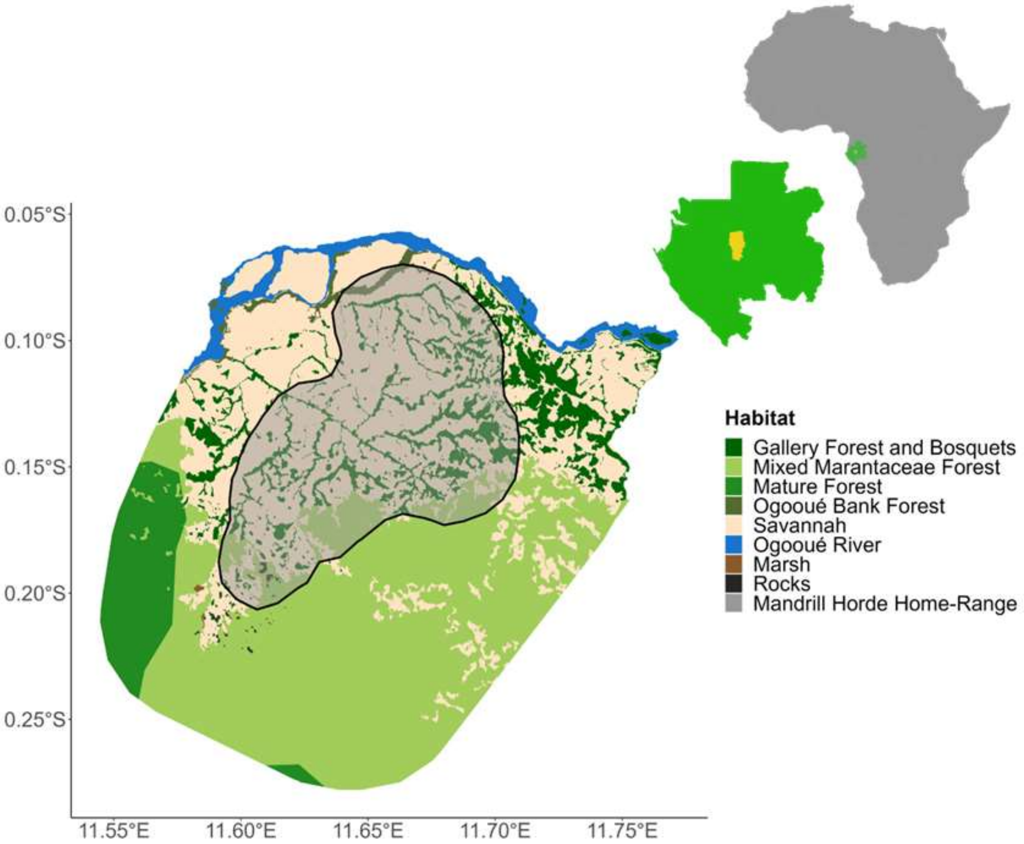

Figure 3.1. The location of Lopé National Park in Gabon, Central Africa, and the distribution of habitats in the study site, with the home-range (90% kernel density isopleth) of the focal horde overlaid (data from White et al., 2010).

3.3.2 Study Population

Our study population consisted of a mandrill horde, usually numbering between 600-800 individuals, though temporary extreme counts of as many as 1350 individuals have been recorded in the past, when two hordes meet (Abernethy *et al.,* 1997). The group exhibits fission-fusion dynamics during periods of low food availability (White, 2007), meaning that the number of individuals varied considerably throughout our eight-year study period, with a recorded range of 340-845 for subgroups (Abernethy *et al.,* 2002). Consequently, the level of within-group feeding competition may have varied throughout the sampling period, potentially impacting food selection. In addition, adult males often leave the horde outside of the breeding season, but even when present, the proportion of adult and sub-adult males has never been observed to exceed 12% (Abernethy *et al.,* 2002) and so our fecal samples were mostly sourced from adult females and juveniles of both sexes. Our analysis of mandrill diets thus largely corresponds to permanent horde members and fewer adult males.

3.3.3 Fecal Collection and Analysis

To investigate seasonal changes in mandrill food selection, we collected 4024 fecal samples over 8 years and 2 months, between September 1996 and October 2004. For all feces collections, the mandrill group being sampled was identified as being all or part of the two hordes known to use the study area, using radiotelemetry to identify the presence or absence of collared individuals (see Abernethy *et al.*, 2002; White, 2007). Only fresh dung (10 minutes to 5 hours old) was collected, to minimize loss of material to fecal predators. When a dung pile was found, the entire fecal pellet was collected into a plastic ziplock bag and conserved at ambient temperature until analysis. Collections were made weekly on a predetermined day to prevent bias to collections in more accessible habitats and to ensure an even representation throughout the year. When logistical constraints prevented collections being made on the determined day of the week, efforts were continued to contact the group and samples were obtained as soon as possible after this date.

Identification of dietary items was made within 3 days of collection to ensure that constituent parts were recognizable and had not been degraded. Analysis of constituent parts followed the protocol established at SEGC by Tutin and Fernandez (1993) for analysis of ape dung. We used 1 mm mesh brass soil sieves to separate the matrix with running water and retain identifiable undigested components. Cleaned dung components were identified to plant part and species as far as possible, using the herbarium and reference collections of seeds curated at SEGC (White and Abernethy, 1997). Where species level identification was not possible, plant genus, plant family or finally ‘component type’, for example ‘unknown stems’ or ‘plant fiber’, classifications were made. Animal and insect remains could rarely be classified beyond Order level (e.g., mammal, reptile, insect, mollusk), however where possible a more precise taxon was noted.

3.3.4 Descriptive Analyses of Food Types and Plant Taxa

To analyze seasonal changes in consumption of major food types, we classified identified foods into one of seven categories. The whole seeds, pulp, skins and fibers of identified fruit species were pooled as ‘Fruit’; leaves from monocotyledonous plant species were clustered as ‘Monocot Leaves’; dicotyledonous leaves were categorized as ‘Dicot Leaves’; chitin from insects, hair, bone and other vertebrate or invertebrate remains were grouped as ‘Animal Parts’; pieces of mushroom were categorized as ‘Fungus’; seeds that showed clear evidence of seed predation (rather than fruit consumption and seed dispersal) were marked as ‘Crushed Seeds’; and unidentified fibers or plant material, pieces of bark, twigs and pieces of wood were termed ‘Other Fiber’.

Alongside seasonal changes in consumption of each food type, we also aimed to analyze seasonal changes in diet breadth. Here, we define ‘diet breadth’ as the count of different non-fruit categories, plus the count of distinct fruit genera present in a fecal sample. We then define ‘fruit breadth’ as the count of distinct fruit genera present in a fecal sample. We can therefore compare changes in diet breadth and fruit breadth throughout the year, to describe temporal variation in the contribution of fallback (i.e. non-fruit) foods to mandrill diet breadth. To classify different plant taxa within the fruit breadth variable, we grouped different tree species to the Genus or Family level, because species level identifications were not always possible. For example, for *Uapaca* sp., there are three species, *U. heudeleotti*, *U. paludosa* and *U. guineensis* present in the study area and their seeds are difficult to reliably tell apart, especially when damaged. This grouping resulted in a loss of some dietary resolution, but allowed us to maximize the sample size for characterizing the phenology of food items in mandrill dung.

Throughout our analyses of seasonal variation in food selection and diet breadth we focus on the presence versus absence of food items, rather than quantifying the amount of each in fecal samples. This is partly because comparisons of quantities across items is difficult (e.g., for fruits with dramatically different seed sizes), but also because fecal pellets represent only the undigested fraction of food and could therefore easily misrepresent food selection or underestimate unidentifiable remains (Tutin and Fernandez, 1993).

3.3.5 Fruit Availability

To facilitate comparisons between fruit consumption and fruit availability, and thus identify preferred or avoided fruit taxa, we calculated fruit availability using data on tree fruiting phenology, tree abundance and tree size. Tree phenology has been monitored in Lopé National Park since 1986 to present. Field researchers use binoculars to record canopy cover of immature and mature fruits, rating coverage on a 9 nine point scale from 0, for no coverage, to 4, for complete coverage (Tutin *et al.,* 2017; Bush *et al.,* 2018). Stem density (stems ha^{-1}) and mean diameter at breast height (cm) (converted to radius) measures were taken from existing census data for each of the four major forest types in the study area (White 1994; Cardoso *et al.* 2020). Phenology data were available for 30 species, in 23 of the 53 genera found in mandrill feces and we obtained a subset of the data available for these species; that matched the date range of the fecal sampling. We then calculated monthly fruit availability scores (FAS) for each species, following the method of Cardoso *et al.* (2020):

$$\text{FAS} = p \times c \times d \times r^2$$

where p is the proportion of a species bearing fruit in any given month; c is the mean proportion of the canopy of each species covered by mature fruit; d is the mean stem density of a species across all census plots in a habitat type; and r is the mean radius at breast height of a species across all census plots in a habitat type. Monthly FAS were calculated for each species in each habitat type and then multiplied by the total area of each habitat within our study area. FAS for each species, in each habitat were then summed, to produce a measure of the total monthly availability of each fruit species, across our study site. Thus, we produced measures of fruit availability that could be compared directly to the frequency at which fruiting taxa appeared in mandrill fecal samples, which were also collected on a monthly basis. In cases where FAS were calculated for multiple species in the same genus, we summed the FAS for all species in a genus, so that our measure of fruit availability matched the taxonomic resolution of our fecal dataset.

3.3.6 Statistical Analyses

Fecal sampling events occurred across all four seasons (long wet, long dry, short wet, short dry), but to raise temporal resolution we focused instead on the day of year on which each sample was collected (e.g. January 1st = Day 1). This allowed us to estimate changes in prevalence at finer temporal scales than those available when considering seasons as discrete periods. To quantify how the probability of occurrence of major food types varied through time we fitted a generalized additive mixed model (gamm) with a logit-link function and binomial error structure using the 'mgcv' package v1.3.89 (Wood, 2017) in R v4.1.3 (R Core Team, 2022). Gamm models make no assumptions about the functional form of a curve, but rather allow us to estimate the curvature best supported by the data. We included a smoothing term for day of year as a fixed factor and food type as a categorical fixed factor, to describe the effect of day of year on binomial presence of each food type in the diet; without fitting a global effect for day of year across food types. We also allowed the curve for each food type to have its own wiggliness, meaning the curve shape could vary between food types, to accurately describe temporal patterns of dietary presence for individual food types (equivalent to Model I in Pedersen *et al.,* (2019)). Day of year was specified as a cyclic cubic regression term to ensure that the intercepts for early January and late December aligned. We also included random intercepts for year as an additional smoother, so that the curves describing the frequency at which each food type appeared in mandrill diets accounted for differences between years in mandrill feeding. Our model structure therefore tends to penalize differences between sampling years, in proportion to the difference between each year and all other years. Smoothing parameter estimation was conducted using restricted maximum likelihood (REML).

To analyze whether mandrills compensate for low fruit availability by consuming alternate resources, we modeled temporal changes in diet breadth (count of distinct food types and fruit genera in a fecal sample) and fruit breadth (count of different fruit genera in a fecal sample) using Poisson gamms, with a log-link function, including day of year as a fixed effect and random intercepts for year. To test whether consumption of fallback foods was statistically associated with fruit consumption, we compared the proportion of fecal samples containing non-fruit food types when fruit was present or absent, using chi-squared tests.

To assess evidence of preference by mandrills for certain fruit genera, we used a binomial generalized linear mixed model, with consumption of fruit as the dependent variable and scaled fruit availability (without mean centering) as the independent variable. A positive relationship between fruit availability and consumption would suggest that mandrills consume more fruit when it is most available, whereas no association between fruit consumption and availability would imply that fruit is not a preferred resource of mandrills. Similarly, relative differences in the strength of relationships between availability and consumption of different fruit genera would also imply differences in the extent to which they are preferred or avoided by mandrills. Therefore, we also included a random slopes argument in this model, allowing the relationship between availability and consumption to differ between fruiting genera, interpreting steeper positive slopes as an indication of greater preference by mandrills. The model containing random slopes for each genus was compared to one containing random intercepts and a fixed effects only model using AIC and the model with the lowest AIC taken as the preferred model (Burnham *et al.,* 2011).

We next wanted to examine whether maximum tree height and fruit nutritional contents (protein, carbohydrates, fat, water, fiber, tannins, or phenols) were associated with the frequency at which different fruits were consumed. To do so, we ran separate generalized linear mixed models, with tree height or each nutritional trait as a continuous independent variable, random intercepts for each fruit genus and the binomial presence of each genus in mandrill feces as the dependent variable. We took maximum tree height data from the primary vegetation guide for Lopé National Park (White and Abernethy, 1997) or online databases of plant traits and nutritional data from Rogers *et al.* (1990).

Finally, we aimed to test whether the seed sizes of fruit influenced the rate at which they appeared in mandrill feces. We categorized seed sizes as “very small”, “small”, “medium”, “large” and “very large” based on scaled illustrations in White and Abernethy (1997) and analyzed differences in the frequency at which fruit with different seed sizes were consumed, using a generalized linear mixed model. Seed size was included as a categorical independent variable, fruit genus as a random effect and the binomial frequency at which fruit genera appeared in feces as the dependent variable.

For all models, we visually inspected diagnostic plots to ensure good model fit and adherence to model assumptions. We also explored the sensitivity of our gamms to the number of smoother knots, k, using the *gam.check* function. For a few models, the default number of smoothers suggested the possibility of underfitting. However, increasing k did not reveal patterns that altered our interpretation and so, for simplicity and consistency, we present fitted values for curves from models with k = 10 for fixed effects and k = 9 for the random effect of year.

3.4 Results

3.4.1 Major food types consumed

We grouped the foods that mandrills consumed into 7 categories: fruit, animal parts (including vertebrates and invertebrates), dicotyledonous leaves, monocotyledonous leaves, crushed seeds, fungi, other fibers (including non-fruit fiber and wood). The mandrills consumed a minimum of 67 different plant species, which is a conservative estimate, as not all samples could be identified to species level and many of the families and genera identified have multiple representatives within the horde's home-range (Table A3.1).

Fruit was the most frequently consumed food type, based on binomial presence versus absence, present in 84.8% (95% CI: 83.7-85.9) of fecal samples. The second most frequently consumed food type was animal parts (75.1%, 73.7-76.4), followed by dicotyledonous leaves (51.1%, 49.6-52.7), other fibers (50%, 48.4-51.5), crushed seeds (42.4%, 40.9-44), fungi (11.3%, 10.3-12.3) and monocotyledonous leaves (9.3%, 8.5-10.2) (Figure 2.2).

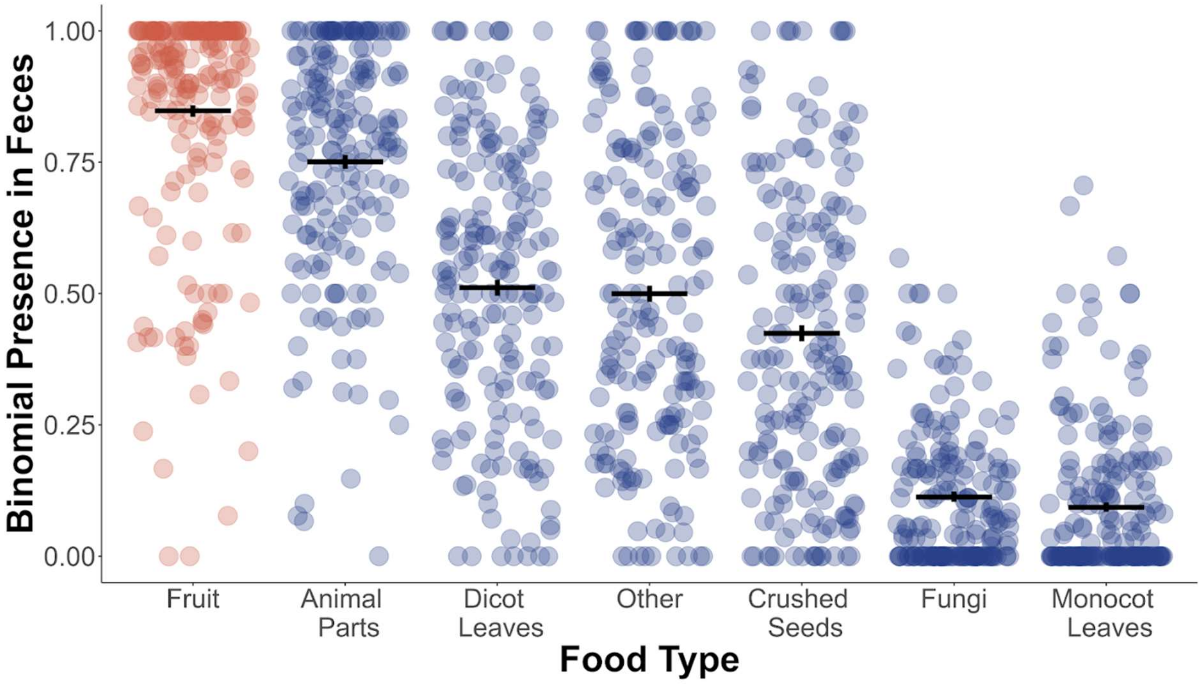

Figure 3.2. Consumption of major food types by the focal horde, across all fecal samples (n = 4024). Data points represent an individual day of the year (n = 192) on which feces were sampled. The position of points on the y axis indicates the proportion of individuals to have consumed each resource on a given day of the year, averaged across all sampling years, and based on binomial presence versus absence. Horizontal lines indicate the proportion of all fecal samples containing a given food type and vertical black lines indicate the 95% binomial confidence intervals around those proportions.

3.4.2 Seasonal patterns of food type consumption

A generalized additive model indicated that consumption frequency of all major mandrill food types was associated with Day of Year (Figure 3.3; Table A3.2). Fruit consumption peaked during the two wet seasons (Figure 3.3: Fr), whereas some alternative food types showed inverse trends compared to fruit, with crushed seeds, dicot leaves and other fibers all exhibiting two peaks in the dry seasons, when fruit consumption was lowest (Figure 3.3: DL, O, CS). Consumption of animal parts appeared somewhat independent of fruit consumption. Peaks in animal consumption were present at the end of the long wet season, when fruit consumption began to decline, but also at the beginning of the long wet season, when fruit consumption was increasing, as well as during the short wet season, when fruit consumption was relatively high (Figure 3.3: AP). Consumption of monocot leaves and fungi had two small peaks in the wet seasons (Figure 3.3: Fu, ML).

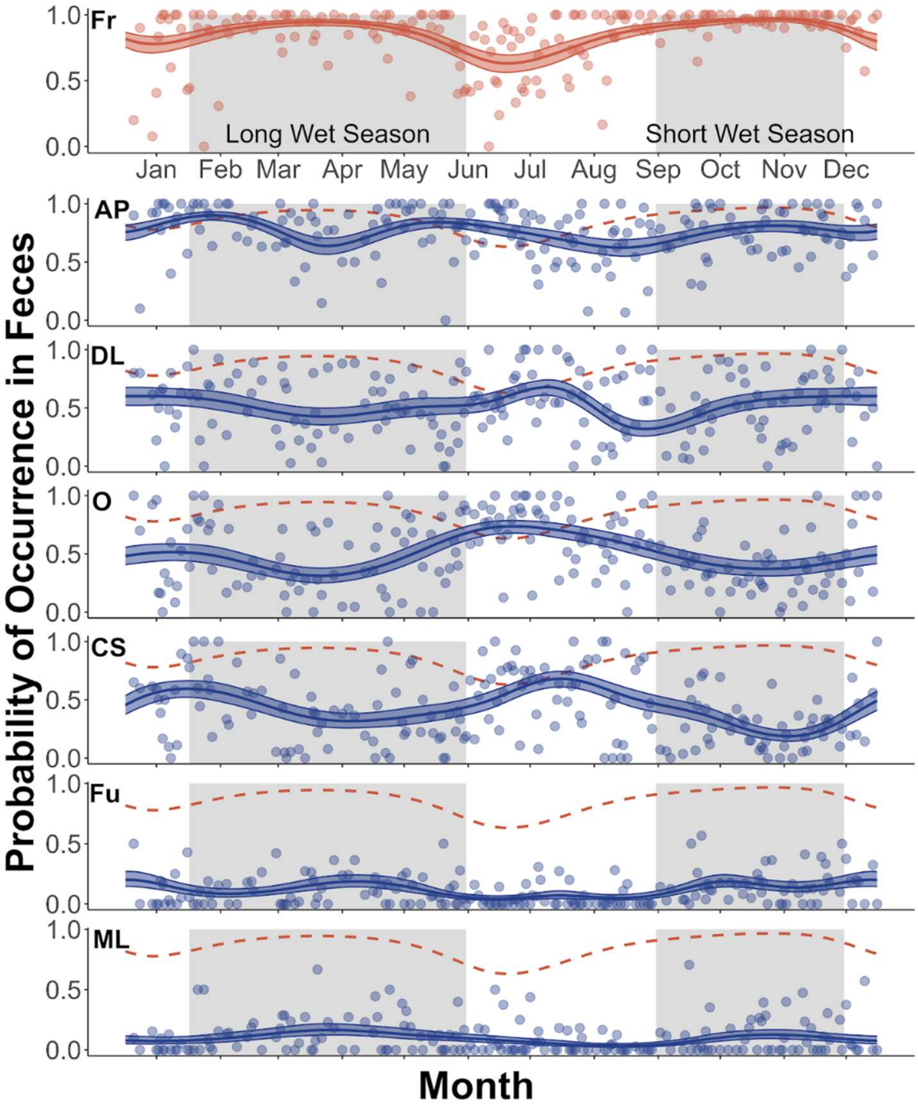

Figure 3.3. Generalized additive model examining the effect of Day of Year on consumption of major mandrill food types (Fr = Fruit, DL = Dicot Leaves, Fu = Fungi, O = Other, ML = Monocot Leaves, CS = Crushed Seeds, AP = Animal Parts). Solid lines indicate the predicted binomial probability of a given food type being found in a fecal sample, on a given day of the year. Ribbons indicate the 95% confidence interval around the predicted binomial probability. The model output is displayed over raw data to visualize the relationship between consumption and day of year. Each data point represents one sampling day (n = 192), and their position on the y axis indicates the proportion of fecal samples (total n = 4024) on that day containing a given food type, averaged across all sampling years, and based on binomial presence versus absence. Dark and light shaded areas are indicative of wet and dry seasons, respectively. Dashed red lines illustrate the predicted binomial probability of a fecal sample containing fruit, for comparison to other food types.

To measure diet breadth, we summed the number of items in a fecal sample belonging to different fruiting genera and to the alternative food type categories used above (e.g. 1x *Dialium sp*., 1x *Uapaca* sp., 1x dicot leaf, 1x animal part, equals a diet breadth of four). Generalized additive models revealed that the overall diet breadth of mandrills remains consistent throughout the year, with any one fecal sample containing four different items, on average (Figure 3.4A; Table A3.3). To measure fruit diet breadth, we summed the number of different fruiting genera present in a fecal sample (e.g. 1x *Dialium sp*., 1x *Uapaca sp*. equals a fruit diet breadth of two). In contrast to diet breadth, fruit diet breadth was observed to fluctuate, peaking at roughly two genera of fruit in an average fecal sample in the two wet seasons, and falling in the dry seasons; especially the long dry season during which an average fecal sample was expected to contain only about one distinct fruit genus (Figure 3.4A; Table A3.4). Consumption of animal parts, crushed seeds, dicot leaves and other fibers was negatively associated with the consumption of fruit. In contrast, there was no evidence that consumption of monocot leaves and fungi was associated with fruit consumption (Table 3.1, Figure 3.4B).

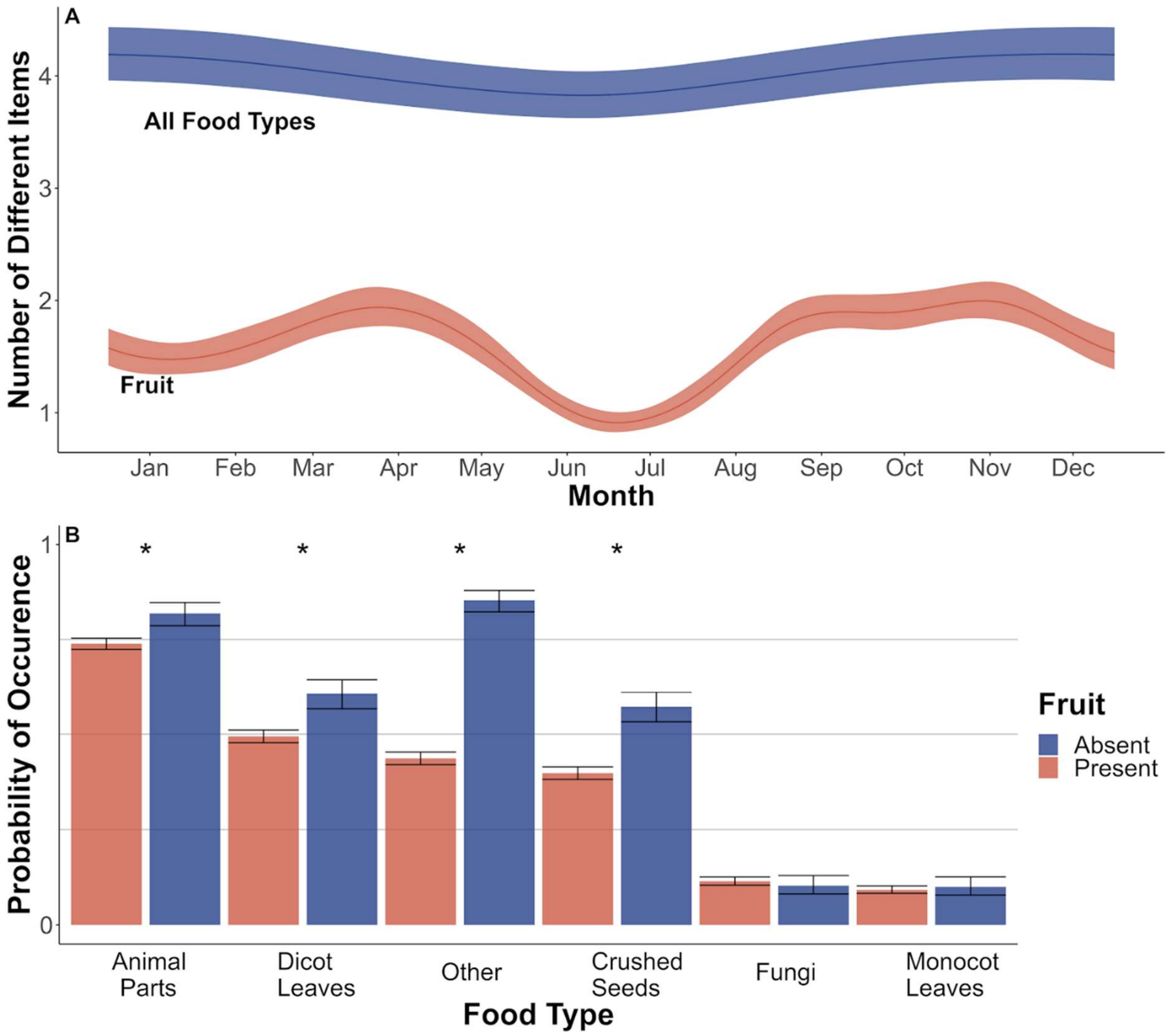

Figure 3.4A. Generalized additive models illustrating the relationship between Day of Year and overall dietary breadth (number of different fruit genera plus different items from other food types) and dietary fruit breadth (number of different fruit genera) across 4024 fecal samples. Lines indicate the predicted number of different food or fruit types being found in a fecal sample, on a given day of the year (Day 1 = January 1st). Ribbons indicate the 95% confidence interval around the predicted numbers of different items. B. The binomial presence of major food groups in fecal samples also containing fruit and those in which fruit was absent. Bar height indicates the proportion of samples containing a food type, and error bars show the 95% confidence intervals around those proportions (fruit present n = 3412, fruit absent n = 612). Asterisks indicate statistically significant differences in the probability of food types occurring in the diet when fruit is present or absent, as indicated by chi-squared tests.

Table 3.1. Results of chi-squared tests examining differences in binomial presence of mandrill food types in fecal samples, when fruit is present or absent in the sample.

Type	Fruit	Proportion	95% CI Lower Bound	95% CI Upper Bound	*p*
Animal Parts	Present	0.74	0.72	0.75	<0.001
	Absent	0.82	0.79	0.85	
Dicot Leaves	Present	0.49	0.48	0.51	<0.001
	Absent	0.61	0.57	0.64	
Fungi	Present	0.12	0.1	0.13	0.41
	Absent	0.10	0.08	0.13	
Monocot Leaves	Present	0.09	0.08	0.1	0.6
	Absent	0.10	0.08	0.13	
Other	Present	0.44	0.42	0.45	<0.001
	Absent	0.85	0.82	0.88	
Crushed Seeds	Present	0.40	0.38	0.41	<0.001
	Absent	0.57	0.53	0.61	

3.4.3 Fruit preference

We found fruit genera to appear in the diet at various frequencies (Figure 3.5). A generalized linear mixed model revealed a positive association between fruit availability and fruit consumption by mandrills, across all genera tested (Table 3.2). Based on AIC scores, a model containing random slopes, that allowed the relationship between availability and consumption to vary between fruiting genera, was preferred (AIC = 16375) over models containing only random intercepts (AIC = 17360) or only fixed effects (AIC = 25127). The random slopes for each genus are displayed in Figure 3.6, and indicate that despite the overall positive association across all genera, there was substantial variation among taxa in the extent to which mandrill consumption covaries with availability. Furthermore, the most favored genera were not always the most frequently consumed. For example, *Vitex sp.* were the most preferred genera, indicated by the steepest positive slope between availability and consumption, but were present in less than 5% of fecal samples. On the other hand, *Uapaca sp.* were present in over 30% of fecal samples, but only the sixth most preferred of the genera analyzed. In another comparison, *Detarium sp.* exhibited the weakest relationship between availability and consumption frequency and *Pentadesma sp.* the fifth strongest relationship, though both genera were present in less than 0.1% of fecal samples.

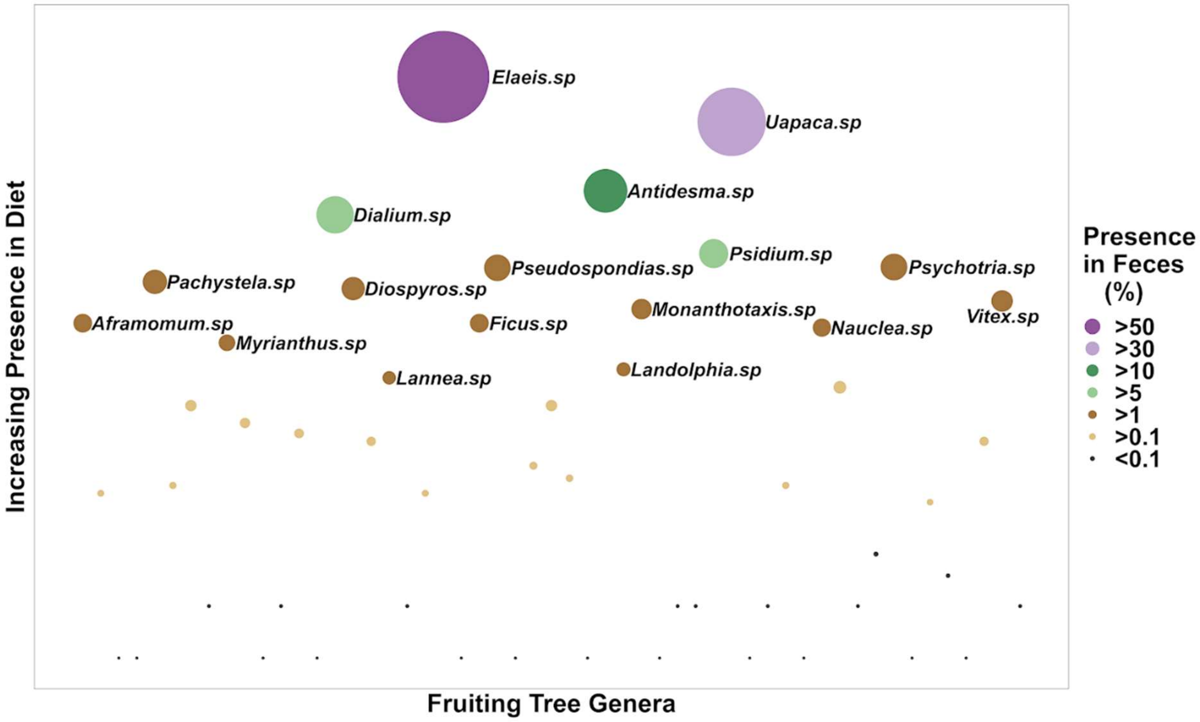

Figure 3.5. Fruit genera consumed by mandrills, ranked by proportional presence in all 4024 fecal samples. Each point represents a single genus, sized according the proportion of fecal samples in which a genus was present, dispersed arbitrarily on the x axis to avoid overlaps and ordered on the y axis by proportional occurrence in feces (log transformed).

Table 3.2. Summary of generalized linear mixed model examining the relationship between fruit availability and consumption by mandrills, with random slopes for each tree genus.

		Estimate	Standard Error	*z*	*p*
Fixed Effects					
Intercept		-5.38	0.37	-14.53	<0.001
Scaled Fruit Availability Score		2.36	1.17	2.018	0.0436
Random Effects					
Genus	Random Intercept Variance	3.69			
Genus	Scaled Fruit Availability Score Variance	93.12			

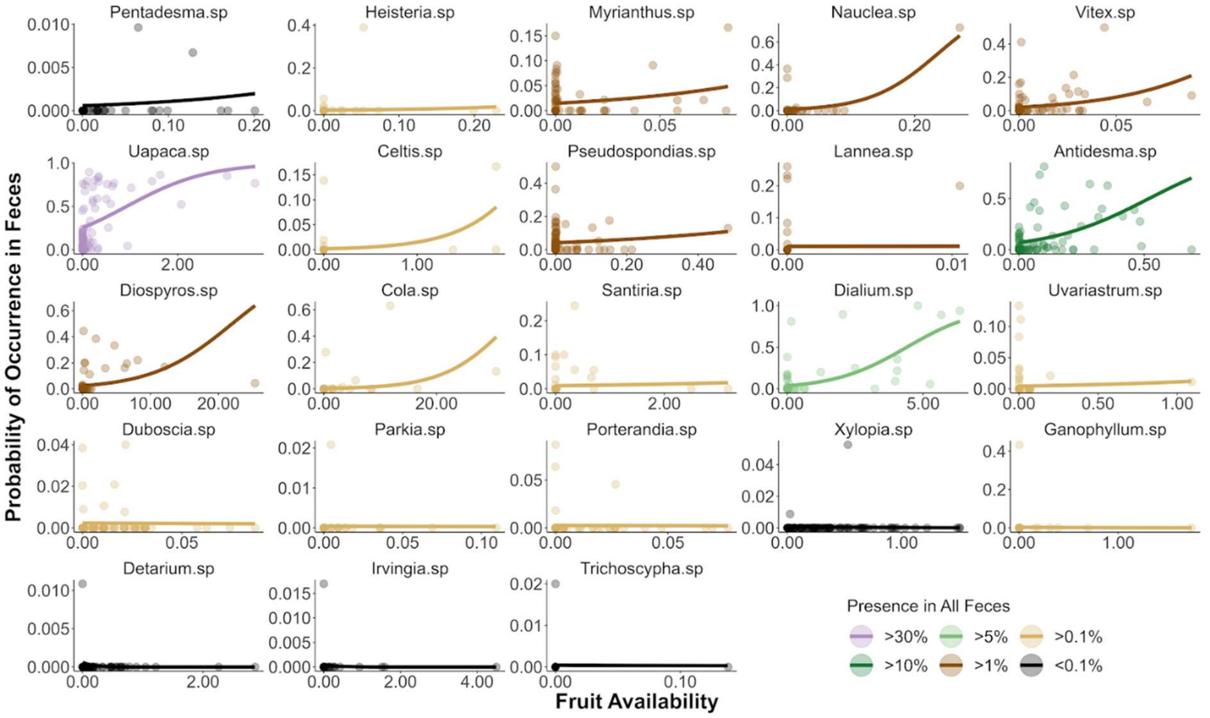

Figure 3.6. The relationship between fruit availability and consumption of fruiting genera by mandrills. Random slope predictions from a generalized linear mixed model are shown over the observed fruit availability range for each genus. Points represent distinct sampling months (n = 83), and their position on the x and y axes indicate the scaled fruit availability and proportion of fecal samples (total n = 4024) containing a fruit genus during that month, respectively. Scales differ between facets to avoid compressing data for genera with lower availability. Intercepts of some species are > 0 because these fruits were consumed on the ground after the ripe fruit our phenology monitoring detects in canopies were no longer available. Effect sizes increase row-wise from left to right, with Vitex.sp exhibiting the largest and Detarium.sp the smallest.

We used generalized linear mixed models to examine whether maximum tree height, fruit nutritional contents or seed size influenced mandrill fruit consumption. The association between tree height and fruit consumption was statistically significant and negative [-0.048, 95%CI: -0.086 - -0.011, p = 0.011] (Figure 3.7), while the association between fruit lipid contents and consumption was statistically significant and positive [0.072, 95%CI: 0.015 -

0.13, p = 0.014] (Figure 3.8). However, the association between lipid content and consumption appears to rely on a single high influence species of fruit: removing *Elaeis sp.* (oil palm) from the data set resulted in no statistically significant relationship between lipid content and fruit consumption. Associations between fruit consumption and contents of protein, carbohydrates, fiber, water, phenols, and tannins were not statistically significant (all p > 0.09). The model examining the relationship between seed size and the frequency at which fruit genera were consumed suggested that seed size was not influential, as there were no significant differences between the consumption frequencies of different seed size categories (Table 3.3).

Table 3.3. Summary of generalized linear mixed model examining the relationship between seed size and fruit consumption by mandrills.

<table>
<tr><th colspan="3">Estimate</th><th>Standard Error</th><th><i>z</i></th><th><i>p</i></th></tr>
<tr><th colspan="6">Fixed Effects</th></tr>
<tr><td colspan="2">Intercept</td><td>-5.27</td><td>0.51</td><td>-10.44</td><td><0.001</td></tr>
<tr><td colspan="2">Seed Size: Medium</td><td>-0.26</td><td>0.51</td><td>-0.52</td><td>0.61</td></tr>
<tr><td colspan="2">Seed Size: Small</td><td>0.31</td><td>1.03</td><td>0.30</td><td>0.77</td></tr>
<tr><td colspan="2">Seed Size: Very Large</td><td>-3.44</td><td>2.23</td><td>-1.54</td><td>0.12</td></tr>
<tr><td colspan="2">Seed Size: Very Small</td><td>-0.06</td><td>1.02</td><td>-0.06</td><td>0.96</td></tr>
<tr><th colspan="6">Random Effects</th></tr>
<tr><td>Genus</td><td>Random Intercept Variance</td><td colspan="4">4.57</td></tr>
</table>

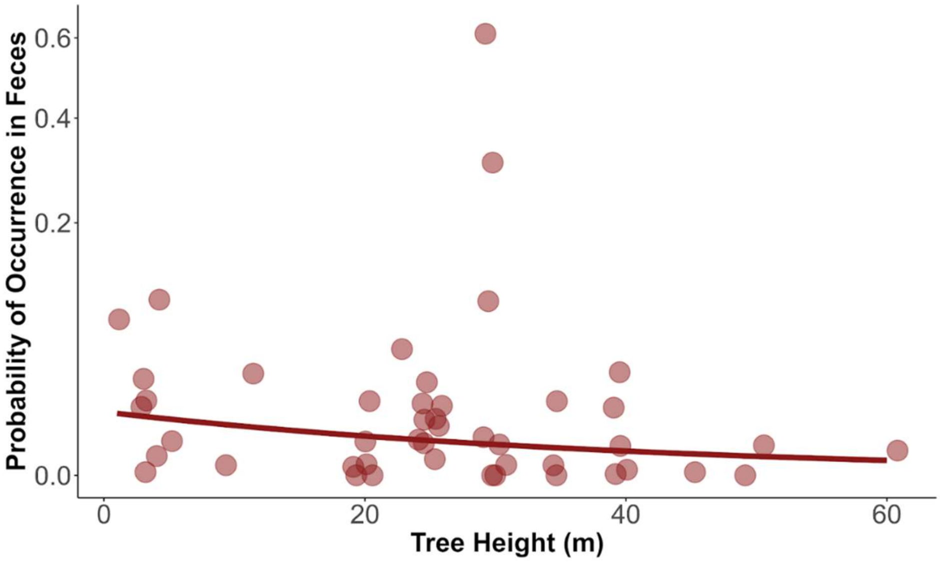

Figure 3.7. The relationship between maximum tree height and fruit consumption by mandrills. Points represent a single fruiting tree genus and their position on the x and y axes indicate the maximum height of each genus in the dataset and proportion of all 4024 fecal samples in which each genus was present, respectively. The line displays the predicted probability for trees of a given height being present in a mandrill fecal sample, based on a generalized linear mixed model. The y axis has been square root transformed and a jitter added to the data to better display overlapping points.

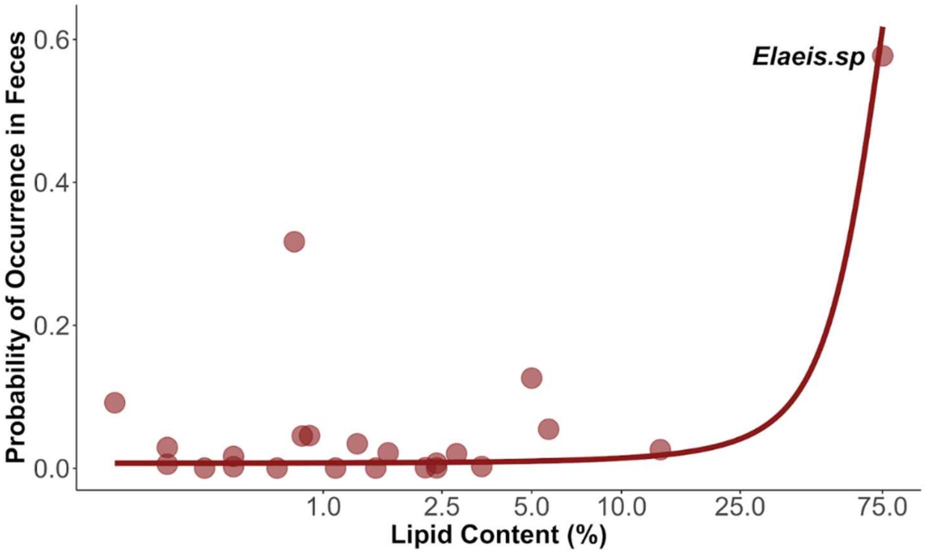

Figure 3.8. The relationship between fruit lipid content and consumption by mandrills. The x axis has been log^{10} transformed to spread clustered data at lower values. Points represent a single fruiting tree genus and their position on the x and y axes indicate the mean lipid content of fruits of each genus in the dataset and proportion of all 4024 fecal samples in which each genus was present, respectively. The line displays the predicted probability for trees with a given lipid content being present in a mandrill fecal sample, based on a generalized linear mixed model. Removing Elaeis sp. (oil palm) from the data set resulted in no statistically significant relationship between lipid content and fruit consumption.

3.5 Discussion

Using rare, long-term data on mandrill feeding ecology and African tree phenology (Tutin *et al.,* 2017), we found that mandrills are highly frugivorous and that fruit consumption tracked availability. With generalized additive models, we also revealed that mandrills maintain a consistent diet breadth throughout the year, in spite of fluctuating fruit availability, via fallback food consumption of certain categories of dietary items. Finally, we found variation between fruiting genera in the extent to which they are preferred by mandrills, at least insofar as consumption covaries with availability.

3.5.1 Mandrill Diet

Fruit was the most frequently present food type in mandrill fecal samples (Figure 3.2) and it exhibited two annual consumption peaks, corresponding to the wet seasons, when fruit availability is highest (Figure 3.3). Similarly, we found strong positive covariance between fruit availability and fruit consumption (Table 3.2). Together these results indicate that fruit was the most preferred resource of our focal horde. In contrast, consumption of animal parts, dicot leaves, crushed seeds and other fibers tended to peak when fruit consumption was relatively low (Figure 3.3). The fact that mandrills displayed a consistent diet breadth throughout the year, despite fluctuating fruit consumption, confirms that increased dietary diversity occurred on a seasonal basis, when fruit consumption fell (Figure 3.4A). Furthermore, we found that consumption of animal parts, dicot leaves, crushed seeds, and other fibers covaried negatively with fruit consumption (Figure 3.4B). These four food types therefore appear to constitute important fallback foods for mandrills, on which they feed to make up for seasonal falls in fruit availability. Consumption of fungi and monocot leaves instead peaked during the two wet seasons (Figure 3.3), but the frequency of their consumption was lower than other fruit alternatives and not significantly related to fruit consumption (Figure 3.4B). These results are evidence that when alternate food types are available alongside fruit, they are not frequently consumed, further supporting that fallback foods are primarily consumed due to a lack of fruit. The only apparent exception to these trends is animal parts, consumption of which peaked during three periods: once at the end of the long wet season, when fruit consumption declined, but also at the beginning of the long wet season as fruit consumption increased, and during the short wet season, when fruit consumption was relatively high (Figure 3.3). Animal parts may thus also constitute an important and preferred resource of mandrills.

Our results corroborate those of previous investigations indicating that mandrills are frugivorous omnivores, whose diets exhibit seasonal responses to fruiting tree phenology (Rogers *et al.,* 1996; Hongo *et al.,* 2018). Given the eight-year time period during which our data were collected, the large number of dietary samples, and a robust measure of fruit availability (Bush *et al.*, 2017, 2018, Cardoso *et al.*, 2020), our results provide an atypically robust reflection of the diet of the focal horde. In turn, the general between-study consistency in mandrill diets, across multiple locations (Jouventin, 1975; Lahm, 1986; White *et al.,* 2010;

Nsi Akoue *et al.,* 2017; Hongo *et al.,* 2018), supports their classification as highly generalist frugivore-omnivores. Further study using advanced techniques, such as stable isotope analysis (Crowley, 2012) or metagenomics (Srivathsan *et al.,* 2016) may prove useful for identifying the full taxonomic diversity of mandrill diets, or for describing the impacts of extreme dimorphism and group size on mandrill feeding ecology. For example, species such as *Pentaclethra macrophyla* are known to be eaten by the focal horde, but the large seeds could not be identified in fecal samples, because they are crushed during mastication.

3.5.2 Mandrill Nutritional Strategy

The feeding strategies employed by primates are thought to have evolved to allow sufficient micro- and macro-nutrients to be obtained from their habitat (Felton *et al.* 2009a). For example, spider monkeys (*Ateles chamek*) and chimpanzees (*Pan troglodytes*) appear to prioritize protein intake, balancing their consumption of carbohydrates and lipids accordingly (Felton *et al.,* 2009b; Uwimbabazi *et al.,* 2021). Conversely, mountain gorillas (*Gorilla beringei*) living in a protein rich habitat, target foods allowing energy intake to be maximized through sugars (Ganas *et al.,* 2008; Rothman *et al.,* 2011). To our knowledge no formal analyses of mandrill nutritional ecology are available, and so we also explored whether the preferences of our focal horde were related to fruit nutritional contents.

Our data indicated that some fruit were consumed more than others as a function of availability (Figure 3.6), suggesting preference by the focal horde for certain fruit genera (Hongo *et al.,* 2018). These preferences are likely to be driven by the nutritional contents of particular fruits (Felton *et al.,* 2009a; 2009b). However, in our analyses of the relationship between fruit nutritional contents and consumption, we found a statistically significant association only between lipid content and consumption frequency. An association between fruit lipid content and consumption suggests that energy intake plays an important role in determining mandrill food selection. The significant association we found, however, was driven largely by consumption of oil palm fruits, which were by far the most frequently consumed resource (Figure 3.5) and contain 75% lipids. Such high consumption frequencies of palm fruits suggest that these are a keystone resource to mandrills in our study site, as for primates throughout Africa (Ornstein *et al.,* 2020).

Unfortunately, we did not have abundance data for palm fruits, but palms are known to fruit year-round in the study site (White, 2007). Oil palms may therefore comprise an energy source to our focal horde that is consistently available throughout the year. If energy from palm fruits is targeted to a greater degree, year round availability of lipid rich fruits may explain why we found no meaningful association between carbohydrate content (an alternate source of energy) and fruit consumption. More specifically, an abundance of available lipid rich palm fruits may have reduced the need for mandrills to pursue caloric intake in the form of carbohydrates.

We also did not find an association between fruit protein content and consumption frequency. A low influence of protein content on mandrill fruit selection could arise because fruits are typically low in protein, compared to other food items that primates feed on (Rothman *et al.,* 2014). Thus, individuals in the focal horde may not have selected fruits due to protein content, because they gain more substantial amounts of protein from other food sources. For example, invertebrates are often a key component of primate diets and can contain higher amounts of protein than other food types, such as fruit (Rothman et al. 2014). High nutritional value of invertebrates, in terms of protein content, may explain our finding that mandrills frequently consume animal parts when fruit availability is high. Indeed, animal prey often contributes a substantial amount of protein to primate macronutrient intake (O'Malley and Power, 2014; Bryer *et al.,* 2015). The quantitative contribution of animal prey to the diet of mandrills, both in terms of consumption volume and nutritional intake, may therefore be more substantial than our presence versus absence approach has revealed here. Future work to quantify the amount of animal prey consumed my mandrills would be useful and may demonstrate that animal parts are not simply a fallback food, but a preferred resource, potentially due to the need for high protein intake.

We did not find statistically significant relationships between fruit consumption and contents of fiber, water, tannins, or phenols. We therefore did not find evidence of factors outside of macronutrients, such as plant secondary compounds, affecting fruit selection by mandrills. The consumption of fruit containing defensive compounds may form a part of mandrills' extremely generalist feeding strategy if they are less selective than other primates in terms of fruit quality. Alternatively, nutritional data on a greater range of fruit species may be needed to further examine the effect of secondary compounds. We only had nutritional contents data for a subset of the fruit genera consumed by our focal horde, and it would therefore be useful to increase the taxonomic coverage of our dataset, to carry out a more complete analysis of the nutritional ecology of the focal horde. It would also be interesting to compare the nutritional ecology of mandrills in different locations or habitat types, to examine the effects of the presence or absence of particular resources, such as oil palms (Hongo *et al.,* 2018). Nutritional analyses may also reveal the potential fitness consequences of obtaining preferred versus fallback foods and give insights into morphological trait evolution and the resilience of mandrills to environmental change.

3.5.3 Feeding Competition

The numbers of mandrills present in a horde, the highest of any non-human primate (Abernethy *et al.,* 2002) mean that the food demands of a single group are extraordinarily high. The biomass of the mandrill horde is around 4852 kg (White *et al.*, 2010), roughly equivalent to the average group biomass for forest elephants at the site (4876 kg; White, 1994) and close to twelve times the group biomass for the largest frugivorous primate, the lowland gorilla (414 kg; White, 1994). These high food demands, as well as rapid rates of patch depletion are the most likely explanation for mandrills also exploiting the largest home-ranges observed in wild primates (White *et al.,* 2010). It is also probably the case that the dietary generalism documented here and elsewhere (Hongo *et al.,* 2018) is, in part, an adaptation to extreme group sizes. We have documented that the diversity of food types eaten by mandrills increases when fruit availability is low. This ability to switch resources in response to a lack of fruit likely carries over to when individual animals are unable to access fruit in feeding patches. Thus, dietary generalism may allow individuals to continue to intake resources even when they lose out during scramble competition within a mandrill horde. Mandrills are also the most sexually dimorphic primate (Setchell, 2016) and sex differences in diet have been observed in other study sites, such as males consuming more hard foods than females (Nsi Akoue *et al.,* 2017; Percher *et al.,* 2017). Therefore, it could also be the case that mandrill dimorphism facilitates some degree of niche differentiation between sexes, that helps to alleviate feeding competition in large social groups.

Mandrills must also cope with interspecific feeding competition. In Lopé, mandrills coexist with several other frugivores (11 other monkey species, chimpanzees, gorillas, red river hogs, and forest elephants) and our focal horde's dietary niche may be influenced by feeding competition and resource partitioning among species. Segregating habitats by height is one way in which coexisting frugivores may attempt to alleviate feeding competition (Sushma and Singh, 2006). Mandrills are often considered semi-terrestrial primates, as opposed to purely arboreal, because they forage mostly, but not exclusively, at ground level (Hoshino, 1985). However, the negative association we found between maximum tree height and fruit consumption was relatively weak (Figure 3.7) and so does not suggest that tree height greatly limits mandrill access to certain fruits or that arboreal habitats are avoided. Notably, oil palm and *Uapaca.sp* are medium sized trees (within our sample) and their fruits were more frequently consumed than any others. Furthermore, because we found only a modest effect of maximum height, and most trees are necessarily shorter than the species maximum height, it is very unlikely that mandrills are limited in terms of foraging height throughout most of their habitat.

Rogers *et al.* (1996) found high levels of leaf litter disturbance when following a mandrill horde at Lopé, suggesting substantial amounts of ground level food was eaten. Consumption of fallen fruit and seeds at ground level most likely explains why we often observed consumption of fruit species when our phenology data indicated zero availability in the canopy (Figure 3.6). Our focal horde also exploited a 182 km^2 home-range during the same time period as feces were collected (White *et al.,* 2010). This estimate is much larger than those for sympatric frugivores at other sites in Central Africa, such as forest elephants at 75 km^2 (Blake *et al.,* 2008), gorillas at 38 km^2 (Sanz, 2004) and chimpanzees at 18km^2 (Cipolletta, 2004). Extreme fruit scarcity in 2004, the final year of fecal sample collection, also resulted in group-fissioning by the focal horde, with sub-groups breaking away from the horde to forage in other areas of the home-range (White, 2007). High mobility and social plasticity, alongside the dietary generalism documented here and by others (Rogers *et al.,* 1996, Nsi Akoué *et al.,* 2017; Hongo *et al.,* 2018) may all play a role in allowing mandrills to coexist with many competing species. Examining the exact nature of feeding competition (and facilitation) between sympatric frugivores in Gabon would be another interesting avenue for future study.

3.5.4 Mandrill Conservation

Evaluating the resilience of mandrills to environmental change is necessitated by their classification as Vulnerable on the IUCN Red List, with habitat degradation from climate change one of the threats identified (Abernethy and Maisels, 2019). The high social and dietary plasticity of mandrills may be a response to the extreme variation in resource availability in West Central Africa over the past millennia (Maley, 1996; White, 2001). Dietary flexibility, in the form of resource switching, could therefore confer some level of resilience to climate change-induced falls in fruit production (Korstjens and Hillyer, 2016). However, mandrill hordes are so large, with an approximate biomass of 4.1 tons (derived from Abernethy *et al.*, 2002) that availability of alternative foods may be limited. At our study site, climate change over the past three decades has resulted in a 1°C rise in temperature, alongside a 300mm fall in annual rainfall and a longer dry season (Bush *et al.,* 2020b). Consequently, fruit availability has fallen dramatically at Lopé in the last 30 years (Bush *et al.,* 2020a).

For comparison, forest elephants, the largest mammal found at Lopé and also a frugivore, have a comparable mean group biomass of around 4.8 tons (White, 1994). A comparison of recent and historical elephant fecal samples from Lopé indicated that elephants are consuming less fruit and much greater quantities of low-quality, fibrous plant tissues in 2022 than they did in 1990 (Tejler *et al.,* unpublished data). This shift in diet, likely a response to lower fruit availability, has been linked to increased seasonal emaciation of elephants documented at Lopé (Bush *et al.,* 2020), suggesting that elephants have been unable to maintain the nutritional quality of their diet faced with current levels of tree productivity. As our fecal data were gathered between 1996-2004, they could provide a useful baseline for comparison to newer data, to examine whether the Lopé mandrills' diet has changed in the intervening 20 years. Contemporary data could highlight whether mandrills are consuming the same fruits as before, or whether they are having to consume fruit which we found to be less preferred. Additionally, repeating our analysis could indicate whether temporal consumption of fruit has remained consistent, or if fallback foods are forming a greater part of present day mandrill diets.

An understanding of mandrill resilience to environmental change is crucial not only to protect mandrills, but also to conserve forests throughout their range. Our study has highlighted that mandrills primarily consume fruit, which likely means they play crucial functional roles, including as seed dispersers and predators. We found that mandrills consumed fruit with a range of seeds sizes at similar frequencies. However, forest elephants in Gabon have been found to consume whole seeds up to 21 cm in diameter (Feer, 1995), which is a great deal larger than the seeds of any fruit genus that appeared in mandrill fecal samples. Different frugivores may therefore act as seed dispersers for distinct assemblages of fruiting trees and, given that mandrill home-ranges are so large compared to many sympatric frugivores, they may play a unique functional role as seed dispersers within Central African forests. In addition, the importance of invertebrate foods we have documented means that mandrills also influence the wider food web, by impacting invertebrate communities and the trophic interactions those species are involved in.

Our detailed analysis of how environmental parameters are influencing mandrill dietary strategies reflect the importance of this species within forest phenology and trophic structure, as well as its vulnerability to oncoming climate-driven environmental changes. For a species with such a restricted global distribution, this is of importance to international assessments (IUCN Red List) of the species' conservation priority.

3.6 Appendix

Table A3.1. All plant taxa identified in mandrill feces. The lowest taxonomic level identified in each family is highlighted in bold. Where a genus was only represented by a single species in Lope National Park, this species was taken as present in the diet. Where no members of a genus or family were identified to species level, the genus or family was taken as present in the diet. This resulted in a minimum dietary diversity of 67 identified plant taxa and a maximum dietary diversity of 119 plant taxa, if all species of each family found in mandrill feces were assumed to be eaten. In addition to these 119 taxa, species known from observational data to be consumed by the horde are highlighted in red, meaning the total diversity of taxa consumed by mandrills is higher than we found through fecal analysis.

Family	**Genus**	**Species**
Zingiberaceae	*Aframomum*	***sericeum,*** *longipetiolatum*, *leptolepsis*
Annonaceae	*Annonidium*	***Floribundum***

Euphorbiaceae	*Antidesma*	***venosum, vogelianum***
Lauraceae	*Belschmeidia*	***Fulva***
Ochnaceae	*Campylospermum*	*Elongatum*
Zingiberaceae	*Costas*	*afer*
Ulmaceae	*Celtis*	***tessmannii***
Vitaceae	*Cissus*	***dinklagei***
Rutaceae	*Citrus*	***limonum***
Sterculiaceae	*Cola*	***lizae***
Olacaceae	*Coula*	***edulis***
Euphorbiaceae	*Croton*	***mubango***
Leguminosae	*Cryptocephalum*	***staudtii***
Leguminosae	*Detarium*	***macrocarpum***
Leguminosae	*Dialium*	***lopense, pachyphyllum,*** *guineense, dinklagei, soyauxii*
Ebenaceae	*Diospyros*	***dendo, manni, polystemon, zenkeri***
Euphorbiaceae	*Discoglypremna*	***caloneura***
Sapotaceae	*Donella*	***ogowensis***
Tiliaceae	*Duboscia*	***macrocarpa***
Arececeae	*Elaeis*	***guineensis***
Annonaceae	*Enantia*	***chlorantha***
Moraceae	***Ficus***	*barteria, carica, cyathistipuloides, elasticoides, kimuenzensis, mucuso, ovata, polita, recurvata, subsagittifolia, sur, thonningii, variifolia*
Sapotaceae	*Gambeya*	***subnuda***
Sapindaceae	*Ganophyllum*	***giganteum***
Clusiaceae	*Garcinia*	***gnetoides, ovalifolia***
Olacaceae	*Heisteria*	***parvifolia***
Acanthaceae	*Hypoestes*	*verticullaris*
Irvingiaceae	*Irvingia*	***gabonensis***
Irvingiaceae	Klainedoxa	*gabonensis*
Apocynaceae	*Landolphia*	***incerta, jumellei, manni***
Anacardiaceae	*Lannea*	***welwitschii***
Rubiaceae	*Massularia*	*acuminata*
Leguminosae	***Millettia***	*barteri, griffoniana, laurenti, manni, sanagana, versicolor*
Annonaceae	***Monanthotaxis***	*congolensis, diclina, klainii*
Annonaceae	*Monodora*	***angolensis***
Moraceae	*Musanga*	***cecropioides***
Moraceae	*Myrianthus*	***arboreus***
Lecythidaceae	*Napoleonaea*	***vogelii***
Rubiaceae	***Nauclea***	*didderichii, latifolia, pobeguinii, vanderguchtii*
Olacaceae	***Ongokea***	*gore*
Sapotaceae	*Pachystela*	***brevipes***
Leguminosae	***Parkia***	*bicolor, filicoidea*
Passifloraceae	*Paropsia*	*grewiodes*
Mimosaceae	*Pentaclethra*	*macrophylla*

Clusiaceae	*Pentadesma*	***butyracea***
Rubiaceae	*Polycoryne*	*fernandensis*
Rubiaceae	*Porterandia*	***cladantha***
Anacardiaceae	*Pseudospondias*	***longifolia, microcarpa***
Myrtaceae	*Psidium*	***guineensis***
Hypericaceae	*Psorospermum*	*febrifugum*
Rubiaceae	***Psychotria***	*penduncularis, venosa, voegliana*
Myristicaceae	*Pycnathus*	*angolensis*
Zingiberaceae	***Renealmia***	*cincinnata, macrocolea*
Humiriaceae	*Sacoglottis*	*gabonensis*
Burseraceae	*Santiria*	***trimera***
Flacourtiaceae	*Scottellia*	***coriacea***
Olacaceae	*Strombosiopsis*	***tetrandra***
Apocynaceae	***Strychnos***	*congolana, malacoclados*
Dilleniaceae	*Tetracera*	*podotricha*
Mimosaceae	*Tetrapleura*	*tetraptera*
Moraceae	*Treculia*	***africana***
Meliaceae	*Trichillia*	*prieureana*
Anacardiaceae	***Trichoscypha***	*abut, acuminata, anomala*
Euphorbiaceae	*Uapaca*	***guinensis, heudelotii,*** *paludosa, togoensis, vanhouttei*
Annonaceae	*Uvaria*	***versicolor***, *scabrida, klaineana, psorosperma*
Annonaceae	*Uvariastrum*	***pierreanum***
Verbenaceae	*Vitex*	***doniana***
Annonaceae	*Xylopia*	*aethiopica, hypolampra, parviflora,* ***quintasii,*** *staudtii*
Cyperaceae	*Bulbostylis*	*densa, laniceps*
Cyperaceae	*Cyperus*	rotundus, sphacelatus
Cyperaceae	*Eleocharis*	variegata
Cyperaceae	*Fimbristylis*	pilosa
Cyperaceae	*Kyllinga*	echinata
Cyperaceae	*Rhynchospora*	corymbosa
Cyperaceae	*Scleria*	boivinii
Marantaceae	*Marantochloa*	cordifolia, filipes, purpurea
Marantaceae	*Megaphrynium*	macrostachyum, velutinum
Marantaceae	*Haumania*	liebrechtsiana
Marantaceae	*Hypselodelphys*	violacea
Marantaceae	*Sarcophrynium*	spp.
Marantaceae	*Trachyphrynium*	braunianum
Graminae		spp.

Table A3.2. Summary of generalized additive model examining the effect of Day of Year on consumption of major mandrill food types.

Component	**Term**	**Estimate**	**Standard Error**	***t***	***p***
Parametric Coefficients	Intercept	1.19	0.12	9.93	<0.001
	Crushed Seeds	-1.49	0.05	-29.41	<0.001
	Dicot Leaves	-1.11	0.05	-22.32	<0.001
	Fruit	0.82	0.07	12.35	<0.001
	Fungus	-3.33	0.07	-49.97	<0.001
	Monocot Leaves	-3.53	0.07	-50.48	<0.001
	Other	-1.15	0.05	-22.85	<0.001
Component	**Term**	**Effective Degrees of Freedom**	**Reference Degrees of Freedom**	***F***	***p***
Smooth Terms	s(DayofYear): Animal Parts	7.73	8	139.45	<0.001
	s(DayofYear): Crushed Seeds	7.68	8	320.47	<0.001
	s(DayofYear): Dicot Leaves	7.82	8	141.43	<0.001
	s(DayofYear): Fruit	7.35	8	331.32	<0.001
	s(DayofYear): Fungus	7.74	8	100.63	<0.001
	s(DayofYear): Monocot Leaves	6.33	8	66.50	<0.001
	s(DayofYear): Other	6.32	8	323.30	<0.001
	s(Year)	7.81	8	140.09	<0.001
Adjusted R^2: 0.33, Deviance Explained: 0.27					

Table A3.3. Generalized additive model examining the relationship between day of year and overall diet breadth of mandrills.

Component	**Term**	**Estimate**	**Standard Error**	***t***	***p***
Parametric Coefficients	Intercept	1.39	0.025	55.86	<0.001
Component	**Term**	**Effective Degrees of Freedom**	**Reference Degrees of Freedom**	***F***	***p***
Smooth Terms	s(DayofYear)	2.58	8	41.88	<0.001
	s(Year)	6.94	8	48.91	<0.001
Adjusted R^2: 0.051, Deviance explained: 0.0526					

Table A3.4. Generalized additive model examining the relationship between day of year and breadth of fruit species consumption by mandrills.

Component	**Term**	**Estimate**	**Standard Error**	***t***	***p***
Parametric Coefficients	Intercept	0.433	0.030	14.41	<0.001
Component	**Term**	**Effective Degrees of Freedom**	**Reference Degrees of Freedom**	***F***	***p***
Smooth Terms	s(DayofYear)	7.19	8	403.49	<0.001
	s(Year)	6.14	8	26.78	<0.001
Adjusted R^2: 0.124, Deviance explained: 0.115					

Chapter 4: Investigating stable isotope turnover and discrimination in mandrill (*Mandrillus sphinx*) hairs with a diet-switch experiment.

Joshua Bauld, David Lehmann, Jason Newton, Luc Bussière and Katharine Abernethy conceived the research. Mandrill tissue samples were obtained by Joshua Bauld, Barthélemy Ngoubangoye, Thierry A. Tsoumbou and Cyr I. Moussadji-Kinga. Laboratory analysis was conducted by Joshua Bauld and Jason Newton. Data analysis was carried out by Joshua Bauld, with guidance from Luc Bussière. Joshua Bauld wrote the chapter, with guidance from Luc Bussière, Jason Newton, David Lehmann, Katharine Abernethy, and Isabel Jones.

4.1 Abstract

Stable isotope analysis of animal tissues can provide ecological insights, such as levels of niche overlap and the timing of nutritional stress. However, stable isotope analysis is optimized by species-specific knowledge of the relationship between diet and tissue stable isotope ratios and these data are unavailable for many species of primate. We aimed to address this by studying the incorporation of stable isotopes into the hairs of mandrills (*Mandrillus sphinx*), during a diet-switch that altered the isotopic signal of the diet fed to captive mandrills. We quantified the time taken for the stable isotope ratios of mandrill mustache hairs to express the diet-switch, finding the lag time of the hair nitrogen isotope signal to be 23 days and that of hair carbon to be 38 days. We also measured the growth rates of five mandrill hair types, which revealed variation between hair types, with growth rates ranging from 10.7 mm month^{-1} to 16.4 mm month^{-1}. Finally, after mustache hairs had reached or approached equilibrium with dietary nitrogen and carbon, we calculated tissue-diet discrimination factors for each isotope ratio. Hair-diet discrimination was 3.1 ‰ for $\delta^{15}N$ and 2.8 ‰ for $\delta^{13}C$. Our results increase the analytical precision of future investigations of primate stable isotope ecology.

4.2 Introduction

The ratios of stable isotopes in animal tissues are often analyzed to investigate aspects of animal ecology (Ben-David and Flaherty, 2012). Isotopes are atoms of the same element with different numbers of neutrons. The ratios of stable isotopes in animal tissues reflect those of the diet an animal has consumed, as the atoms from food form the building blocks of animal tissues (Sulzman, 2007). This biochemical relationship between animal diets and tissues means inferences can be made about animal feeding ecology from tissue stable isotope ratios (Newton, 2016).

In animals, the conversion of dietary protein to amino acids and carbohydrates tends to favor excretion of ^{14}N and uptake of ^{15}N (Kelly, 2000). Consequently, animal tissues are usually ^{15}N-enriched compared to the foods an animal has eaten, meaning the ratio of ^{15}N:^{14}N rises (Post, 2002; Rioux *et al.,* 2020). Nitrogen stable isotope ratios have therefore proven useful in delineating trophic relationships among individuals and species in the same food web (DeNiro and Epstein, 1981; Hobson and Welch, 1992; Forero *et al.,* 2005; Hoondert *et al.,* 2021). Carbon stable isotope ratios in terrestrial ecosystems are largely influenced by photosynthetic mechanisms, with C4 plants relatively ^{13}C-enriched compared to C3 plants (Farquhar *et al.,* 1989; Zhou *et al.,* 2022). These isotopic differences between plants in turn influence the carbon isotope ratios of their consumers, meaning carbon stable isotope ratios can distinguish, for example, browsing versus grazing herbivores and which of these prey types are predated by carnivores (Voigt *et al.,* 2013; Malindie *et al.,* 2020). Ratios of sulfur stable isotopes in plants largely reflect local geology meaning that, when spatial variation in geological sulfur ratios is present, sulfur isotope ratios in animal tissues may be used to track movement (Richards *et al.,* 2003; Kabalika *et al.,* 2020).

This range of potential ecological information has made stable isotope analysis a useful tool in primatology (Sandberg *et al.,* 2012; Tsutaya *et al.,* 2022). For example, past studies have used the stable isotope ratios of primate tissues to draw inferences on subjects ranging from social dynamics (Oi *et al.,* 2021) and meat consumption (Oelze *et al.,* 2011), to species coexistence (Flores-Escobar *et al.,* 2020) and nutritional stress (Oelze *et al.,* 2020). The wide range of questions that may be addressed using stable isotope analysis means that application of the technique to primatology will likely continue to expand, especially for investigating species which are challenging to study through direct observation (Crowley *et al.,* 2016).

Primate hair is a particularly useful tissue for several reasons (Oelze, 2016). Firstly, the durable structure of keratin, the main protein component of hair, means deterioration and changes in isotope ratios post-sampling are minimal, simplifying sample preservation (Lubec *et al.,* 1987; Saul *et al.,* 2021). Secondly, under certain circumstances, such as when great apes leave night nests, hair may be sampled non-invasively (Wessling *et al.,* 2019; Oelze *et al.,* 2020). Finally, because hair growth occurs over many weeks, sequential isotopic variation between segments of hairs can reveal temporal ecological changes, such as weaning dynamics, within a single animal (Carboni *et al.,* 2022).

To optimize the application of stable isotope analysis to primate hairs, especially when using sequential hair segments, knowledge of species specific hair growth rates, isotopic lag times and tissue-diet discrimination factors are useful. Hair growth rates describe the amount of time taken for an animal to produce hair of a certain length, allowing a date to be ascribed to a given hair segment (Guilfoyle *et al.,* 2022). Isotopic lag times indicate the period required for the isotope ratios in animal hair to reflect a change in diet (Oelze, 2016). Previous studies have used the term tissue turnover time to describe the time taken for hair to reflect a change in diet, which is the term used for metabolically active tissues, such as blood (Tieszen *et al.,* 1983). However, hair is a metabolically inert tissue and the time taken for hair to reflect dietary changes represents a delay in hair expressing isotopic turnover in the metabolically active tissues that feed hair follicles, as opposed to true turnover within hair keratin (Ayliffe *et al.,* 2004; Rode *et al.,* 2016). We are therefore following the terminology of Oelze (2016) and using isotopic lag time to describe the time taken for hair stable isotope ratios to express a change in diet. Discrimination factors describe the typical magnitude of isotopic enrichment between animal food and tissue, which must be accounted for to accurately reconstruct diet composition from stable isotope data (Post, 2002; Pearson *et al.,* 2003; Cherel *et al.,* 2005).

These species-specific measures are generally investigated using experiments with captive animals (Martinez del Rio, 2009). Regarding non-human primates, past studies have investigated stable isotope dynamics across several species and tissues (Reitsema, 2021; Nakashita *et al.,* 2013; Macharia *et al.,* 2014; Tsutaya *et al.,* 2017; Reitsema *et al.,* 2020).

However, a previous review has highlighted the need to expand the range of species covered by captive experiments (Crowley, 2016). To our knowledge, no studies of stable isotope dynamics exist for the African Papionins (Papionina), a sub-tribe containing baboons (*Papio* spp.), geladas (*Theropithecus gelada*), mangabeys (*Lophocebus* spp. and *Cercocebus* spp.), drills and mandrills (*Mandrillus* spp.). Our study aimed to address this by investigating hair growth rates, isotopic lag times and tissue-diet discrimination factors for hair in mandrills (*Mandrillus sphinx*), using a diet-switch experiment. Such experiments involve altering the diet of captive animals, by adding foods of different isotopic composition, to measure the time taken for tissues to reflect the isotopic signal of the new diet.

4.3 Materials and Methods

4.3.1 Ethical Approval

The tissue sampling of CIRMF mandrills for measuring hair growth rates and stable isotope analysis received ethical approval from the University of Stirling, UK (AWERB (19/20) 034).

4.3.2 Study Subjects, Housing and Diet

We conducted our experiment at the International Center for Medical Research in Franceville, Gabon. The center holds a large colony of semi-free-ranging mandrills, established in 1983. The original population consisted of 15 unrelated individuals, with any further changes in population size resulting from natural births and deaths over time. Our experimental group consisted of six male and seven female adult mandrills. One female, however, developed a respiratory infection and did not complete the experiment. Prior to the experiment the mandrills were housed in a 3.5 ha, naturally-forested enclosure where they had access to invertebrates and native plants, most of which use C3 photosynthesis. In addition to these natural foods, the group received bananas and a soy-based cake to provide carbohydrate and protein supplementation.

To complete the diet-switch experiment, our study animals were transferred to a separate enclosure, containing rest sites and enrichment items, but without access to vegetation. In this enclosure the mandrills received the same banana and soy-based cake diet as prior to the experiment. However, the cake was modified for the duration of the experiment by adding blended tuna and maize during production. The soy-based cake was expected to be ^{15}N-depleted compared to the native plants in the mandrills' previous enclosure, because soy is a nitrogen fixing plant and should therefore exhibit a lower ^{15}N:^{14}N ratio than C3 plants (Okito *et al.,* 2004). Maize is a C4 plant and is therefore predicted to be ^{13}C-enriched compared to C3 plants and tuna, as a marine animal, is expected to be ^{34}S-enriched, relative to terrestrial foods (Finucane *et al.,* 2006; Nehlich *et al.,* 2015). The modifications made to the experimental food items were therefore anticipated to produce a depletion in mandrill tissue ^{15}N and enrichment in ^{13}C and ^{34}S.

4.3.3 Tissue Sampling and Hair Growth Measurement

To facilitate transfer between enclosures and tissue sampling, each animal was immobilized using intramuscular injections of ketamine with a Telinject blowpipe, containing the anesthetic Imalgene1000 (10 mg/kg of body weight), under the supervision of vets BN and T-A T. Mustache hairs were sampled by plucking several hairs during transfer to the experimental enclosure, prior to the diet-switch, and on three subsequent occasions for each animal during the experiment. Three to four animals were re-sampled each week during the experiment, to capture the continuous response of hair isotope values to the diet-switch as opposed to sampling all animals on 3 discrete occasions.

We preserved the plucked hair samples in polythene ziplock bags. On the second sampling date of each animal, we shaved a small patch of beard, eyebrow, mustache, occipital and thigh hair and recorded the location of the patch. Then on the third sampling date, we recorded the amount to regrowth of each hair type, to the nearest 0.5 mm. After sampling was complete on each animal's fourth sampling date, they were returned to their original 3.5 ha enclosure.

4.3.4 Stable Isotope Analysis

To analyze the isotopic lag time of mandrill mustache hairs, i.e. the time taken for hairs to isotopically express the diet-switch, we used the hairs plucked on each individuals' final sampling session. Analyzed hairs were therefore sampled during weeks 8-12 of the experiment and, because hair isotope ratios express the diet consumed over the weeks prior to sampling, the entire 12 weeks of the experiment was sampled by our approach. Analyzing multiple hair samples from each animal may have increased the chance of isotopically capturing the diet-switch in each individual, but for economic reasons this was not possible.

Prior to analysis, we cleaned surficial contaminants and lipids from all hair samples using a 2:1 chloroform:methanol solution. All hairs from an individual were allowed to soak for one hour in the solution, before being shaken vigorously and the solution poured away. We then left each sample to dry in an extractor unit. Once dried, we then cut hair into segments for sequential stable isotope analysis. Closest to the follicle, where hairs are thickest, we cut the hairs into 2 mm segments, approximating 5.6 days of hair growth (Results). Matching hair segments, for example, all segments 2-4 mm along each hair, were combined in a single tin cup for weighing and encapsulation. We used between 3-6 hairs per animal to ensure a 2 mm segment met the minimum mass requirement of 0.1 mg (scale readability: ±0.001 mg), combining hairs as needed to analyze several segments per animal. As hairs thinned towards the distal end, the length of segments was increased as required for samples to weigh >0.1 mg. To quantify the isotopic signal of the diet, we freeze dried samples of banana and soy-based cake and prepared samples >0.1 mg and >0.25 mg into tin cups. We used two weights for each sample, as 0.1 mg samples did not contain sufficient sulfur, and 0.25 mg contained too much carbon, for accurate analyses.

We analyzed the stable isotope ratios of nitrogen, carbon and sulfur using a Thermo Scientific™ EA IsoLink™ IRMS System. Stable isotope ratios are expressed as ratios relative to international standards, which are: atmospheric N_2 for nitrogen, PeeDee Belemnite for carbon and Vienna-Canyon Diablo Triolite for sulfur stable isotope ratios. Relative ratios of heavy to light isotopes (e.g. ^{15}N:^{14}N) are expressed using delta notation (e.g. $\delta^{15}N$) and ‰ (permil) units.

During each run of the mass spectrometer, we also ran an internal laboratory standard of hair from a wild mandrill. We found the minimum reproducibility between samples of wild mandrill hair to be 0.10 ‰ for $\delta^{15}N$ and $\delta^{13}C$ and 0.21 ‰ for $\delta^{34}S$.

4.3.5 Statistical Analysis

We modeled hair growth using a linear mixed model with ‘hair type’ as a fixed factor, random intercepts for ‘animal ID’ and ‘weekly hair growth’ as the response variable. We used weekly hair growth in the model because this was the timescale on which growth was measured in the experiment. To generate 95% confidence intervals we bootstrapped the fixed effects for the mixed model, using 1000 replicates. We present the estimate of hair growth on a per month timescale for comparison to other studies, which we produced by dividing the weekly estimates by seven, to calculate daily growth rate, and multiplying this number by 30. We also present the daily growth rates in the results because we used daily growth rates to quantify the growth time of hair segments used during stable isotope analysis.

To analyze isotopic lag time, we first quantified the time taken for a given segment of hair to be grown. We did this by dividing the central measure of a hair segment by the estimated daily growth rate for mustache hairs. For example, the section from 2-4mm is centered on 3mm, therefore the growth time ascribed to that segment is: 3mm/0.357mm day^{-1} = 8.4 days. The growth time for each segment was then subtracted from the sampling date for the relevant animal, to date each segment. We then calculated the time in days between the growth of each hair segment and the diet-switch (range: -79 - +70 days pre- and post-switch). Before conducting statistical analyses, we removed all data from segments of 0-2mm, as these segments include the hair follicle and follicles contain additional tissue types to hair, which may incorporate isotopes at different rates.

To test whether the diet-switch had induced the expected isotope ratio changes in the hairs, we conducted linear models examining the difference in nitrogen, carbon, and sulfur stable isotope ratios between the earliest and most recently grown hair sections of each animal. We then compared the estimated magnitude of change between early and recent segments to the mass spectrometer's minimum reproducibility, to assess whether detectable changes had taken place in each stable isotope ratio, following the diet switch.

Finding that detectable changes had occurred for nitrogen and carbon stable isotope ratios, we estimated the isotopic lag time of mustache hairs for each isotope, using non-linear mixed models. We included tissue stable isotope ratios of hair segments, either '$\delta^{15}N$' or '$\delta^{13}C$', as response variables, 'days' (before or after the diet-switch) as a fixed effect and random intercepts for 'animal ID'. We specified a self-starting four parameter logistic curve that required estimated starting values for the left-hand asymptote (mean hair isotope ratio before the diet-switch), the right hand asymptote (mean hair isotope ratio after isotopic equilibrium), a value for the inflection point of the curve (the x axis value for the midpoint between the two asymptotes) and a numeric scale parameter on the x axis. The model then estimated fitted values for each of these parameters via maximum likelihood ("ML").

We took the fitted value for the inflection point as the estimated half-lives of $\delta^{15}N$ and $\delta^{13}C$. We then calculated the time required for 95% of the total isotopic change within hairs to take place, based on the fitted values from each nonlinear mixed model and took these as the isotopic lag time for each isotope. Using the *getIntitial* function from the 'stats' v4.1.3 (R Core Team, 2022) resulted in stable starting values for the $\delta^{15}N$ model, whereas the suggested starting values for the $\delta^{13}C$ model included a negative half-life estimate. Several iterations, with different starting values, were therefore required to model the isotopic lag time of $\delta^{13}C$ and we selected the model with the lowest AIC (Burnham *et al.,* 2011). To generate confidence intervals for the half-life of each isotope, we conducted re-sampling with replacement, to generate 1000 simulated data sets from our original data. We then ran the same nonlinear mixed model on all 1000 data sets and took the 2.5% and 97.5% quantiles for the estimated inflection point, across all model runs, as the 95% confidence interval for $\delta^{15}N$ and $\delta^{13}C$ half-lives.

To calculate nitrogen and carbon discrimination factors, we used the following equation:

$$\Delta X = \delta_{hair} - \delta_{diet}$$

where ΔX is the discrimination factor for a given isotope, δ_{hair} is the stable isotope ratio of mandrill mustache hairs and δ_{diet} is the isotope ratio of the diet. To calculate δ_{diet}, we first used linear models with either ‘$\delta^{15}N$’ or ‘$\delta^{13}C$’ as response variables and ‘food type’ as a fixed effect, to estimate mean $\delta^{15}N$ and $\delta^{13}C$ of bananas and the soy-based cake. We then assumed a 50:50 intake ratio of each food type, as this was the ratio provided to the animals, to calculate δ_{diet}. As δ_{hair}, we took the predicted ‘$\delta^{15}N$’ or ‘$\delta^{13}C$’ of mandrill mustache hairs for Day 70 of the experiment, from the previous non-linear mixed models. To generate confidence intervals around each estimated discrimination factor, we took the predicted 2.5% and 97.5% quantiles for δ_{hair} on Day 70 of the experiment, from the previously described bootstrapping procedure. We then computed ΔX using the mean, lower bound and upper bound estimates of δ_{hair}, for each isotope.

4.3.6 Software

We complete all analysis in R v4.1.3 (R Core Team, 2022). During analyses we used the ‘lme4’ v1.1-31 package (Bates *et al.,* 2015) for conducting linear mixed effects models, ‘nlme’ v3.1-161 (Pinheiro *et al.,* 2022) for non-linear mixed effects models, ‘rsample’ v1.1.1 (Frick *et al.,* 2022), ‘boot’ v1.3-28.1 (Canty, 2022), ‘broom.mixed’ v0.2.9.4 (Bolker and Robinson, 2022), ‘purrr’ v0.3.5 (Henry and Wickham, 2022) for bootstrapping and ‘DHARMa’ v0.4.6 (Hartig, 2022) for checking model assumptions. We completed all data wrangling, plotting and produced all summary tables with the packages ‘tidyverse’ v1.3.2 (Wickham *et al.,* 2019), ‘lubridate’ v1.9.0 (Grolemund and Wickham, 2011), ‘ungevis’ v0.1.0 (Wilke, 2022), ‘ggplot2’ v3.4.0 (Wickham, 2016), ‘ggpubr’ v 0.5.0 (Kassambara, 2022)and ‘flextable’ v0.8.3 (Gohel and Skintzos, 2022).

4.4 Results

4.4.1 Hair Growth

Using a linear mixed model, we found growth rates to be similar among beard, eyebrow and mustache hairs and to be slightly higher for occipital and thigh hairs (Table 4.1). Beard hairs grew at a rate of 10.8mm month^{-1} (bootstrap 95% CI: 7.8 - 13.7mm month^{-1}), eyebrow hairs at 10.7mm month^{-1} (4.74 - 16.6mm month^{-1}) and mustache hairs also at 10.7mm month^{-1} (4.77 - 16.6mm month^{-1}). Occipital hairs were the fastest growing hairs at 16.4mm month^{-1} (10.5 - 22.3mm month^{-1}) and thigh hairs grew at 13.4mm month^{-1} (7.4 - 19.2mm month^{-1}) (Figure 4.1).

Table 4.1. Monthly and daily growth rates of each mandrill hair type.

Hair Type	**Daily Growth Rate (mm)**	**Lower Bound 95% CI**	**Upper Bound 95% CI**	**Monthly Growth Rate (mm)**	**Lower Bound 95% CI**	**Upper Bound 95% CI**
Beard	0.36	0.26	0.46	10.78	7.8	13.67
Eyebrow	0.36	0.16	0.55	10.68	4.74	16.59
Mustache	0.36	0.16	0.55	10.72	4.78	16.62
Occipital	0.55	0.35	0.74	16.4	10.46	22.3
Thigh	0.45	0.25	0.64	13.36	7.41	19.26

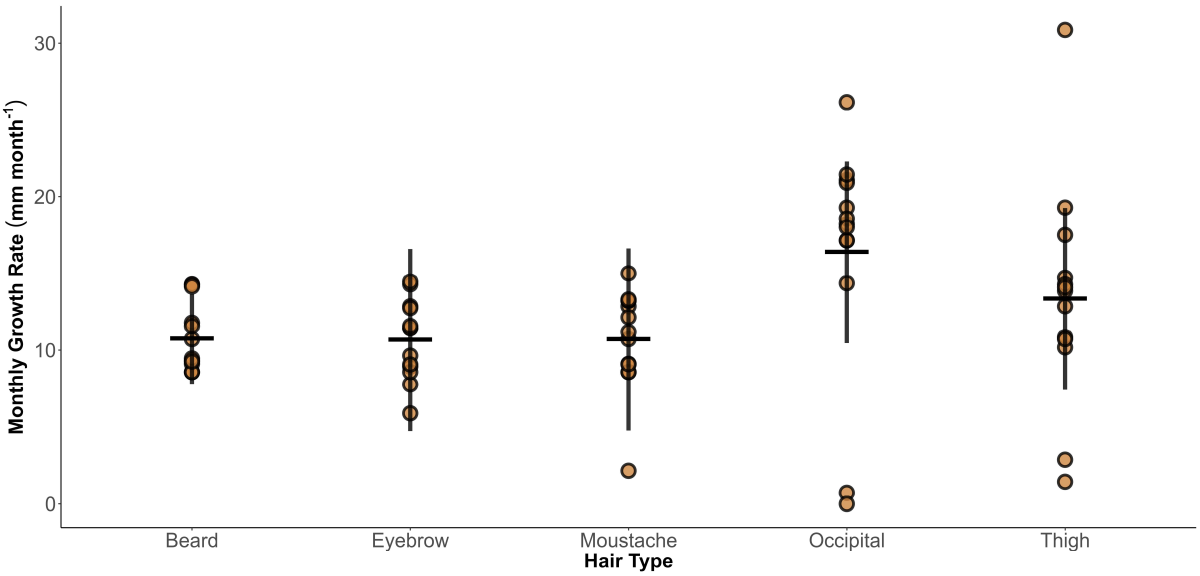

Figure 4.1. Growth rates of five mandrill hair types. Colored points show the observed growth rates of each hair type, in each individual (n = 13). Black horizontal lines display the mean growth rate for each hair type, vertical lines show the 95% confidence interval for the mean estimate, based on 1000 bootstrap replicates.

4.4.2 Isotopic Lag Times

To examine whether the diet switch produced a change in the stable isotope ratios of mandrill hairs, we conducted linear models examining the mean change between each animal's distal hair segment (earliest grown) and the hair segments adjacent to the follicle (recently grown) (Figure 4.2). δ^{15}N exhibited a statistically significant decrease between the earliest and most recent segments (mean = -0.47‰, 95% CI = ±0.39, *p* = 0.026). δ^{13}C showed a statistically significant increase (0.35‰, ±0.21, *p* < 0.01). The change in δ^{34}S between the earliest and most recent hair segments was not statistically significant (-0.0031‰, ±0.09, *p* = 0.97). The minimum reproducibility of our mass spectrometer was 0.1‰ for δ^{15}N and δ^{13}C and 0.21‰ for δ^{34}S. Therefore the predicted changes between early and recent hair segments for δ^{15}N and δ^{13}C exceeded minimum reproducibility and were detectable, whereas the predicted change in δ^{34}S was not.

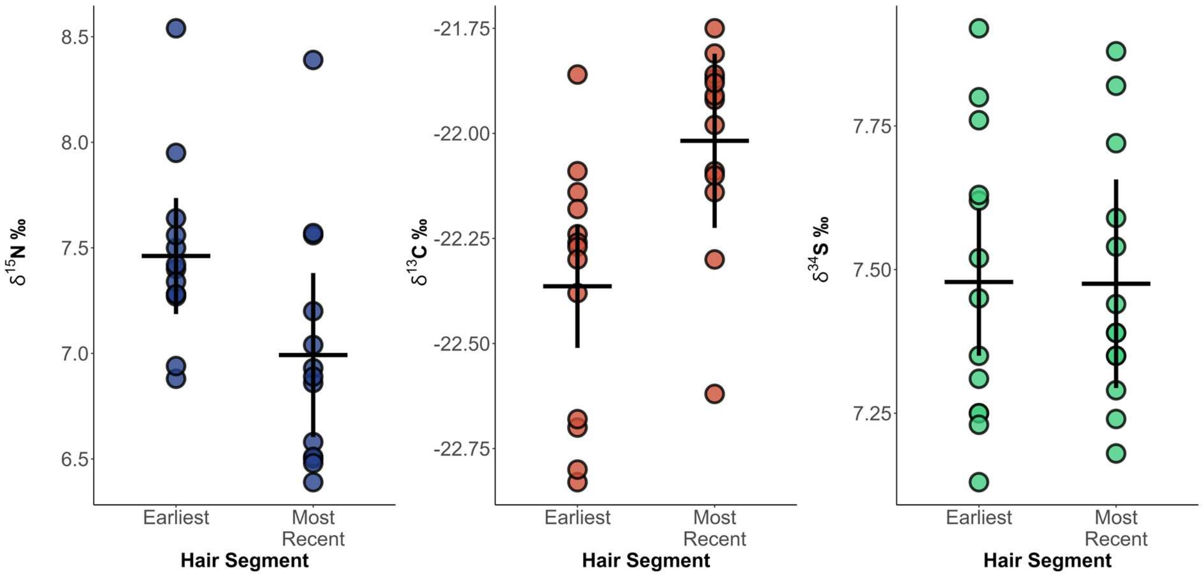

Figure 4.2. Differences in δ^{15}N, δ^{13}C, δ^{34}S between the distal (earliest) (n = 13) and follicle adjacent (most recent) (n = 13) hair segments of each individual mandrill. Black horizontal lines display the mean growth rate for each hair type, vertical lines show the 95% confidence interval for the mean estimate and data points represent the observed isotope ratio of each element, in individual hair segments.

To quantify the isotopic lag time of mandrill mustache hairs, we fitted non-linear mixed models to the sequential δ^{15}N and δ^{13}C hair segment data. We did not attempt to quantify the isotopic lag time of δ^{34}S, as our previous analysis suggested that no detectable change in δ^{34}S had taken place. We found the isotopic lag time for δ^{15}N to be shorter than δ^{13}C, with the model estimating a δ^{15}N half-life of 9.95 days (bootstrap 95% CI: 2.31 - 14.6 days) (Table 4.2; Figure 4.3). Isotopic equilibrium between mandrill mustache hairs and dietary nitrogen, taken as the time required for 95% of the total isotopic change was 22.5 days. The isotopic lag time for δ^{13}C was approximately double that of δ^{15}N, with the δ^{13}C half-life estimated to be 22.7 days (bootstrap 95% CI: -7.39 - 34.8 days) (Table 4.3; Figure 4.4). Isotopic equilibrium between mandrill mustache hair and dietary carbon was predicted to be reached after 38.1 days.

Table 4.2. Model summary for the non-linear mixed effects model analyzing the relationship between days before or after the diet switch and mandrill mustache hair nitrogen stable isotope ratio.

Estimate		**Standard Error**	**df**	***t***	***p***
Fixed Effects					
Isotope Ratio Pre-Diet Switch	7.57	0.14	124	53.5	<0.001
Isotope Ratio Pre-Diet Switch	6.96	0.15	124	45.8	<0.001
Half-life	9.95	1.91	124	5.2	<0.001
Scale Parameter	3.67	1.55	124	2.3	0.0197
Random Effects					
Isotope Ratio Pre-Diet Switch		Variance	0.18		
Isotope Ratio Post-Diet Switch		Variance	0.28		
Residual		Variance	0.084		

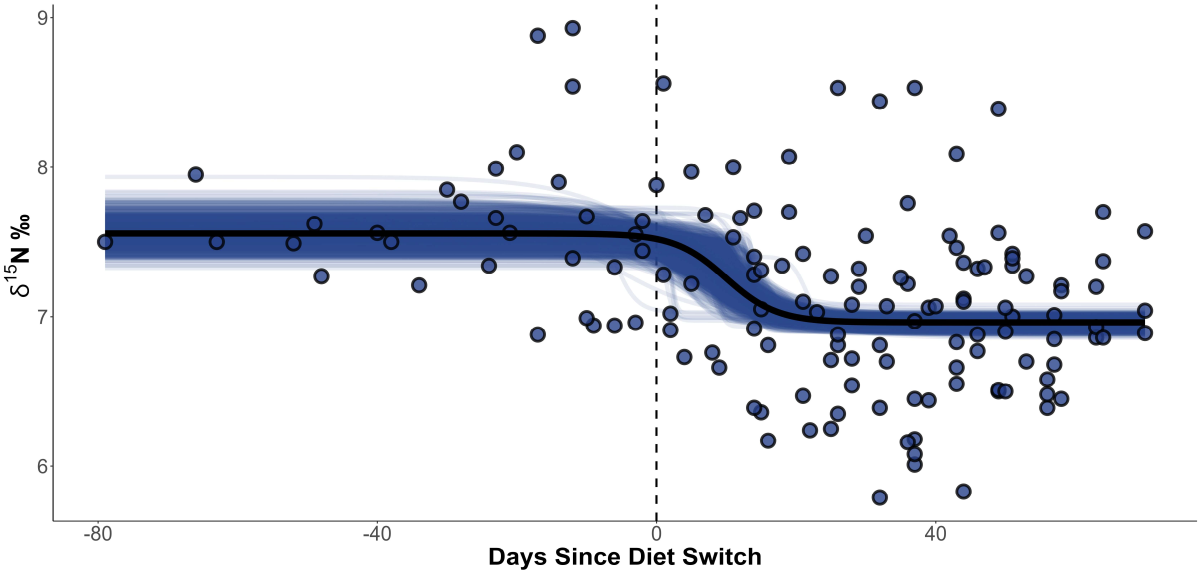

Figure 4.3. The relationship between days before or after the diet-switch and mandrill mustache hair δ^{15}N. The solid black line displays the population level prediction of nitrogen isotopic lag time and the blue lines illustrate uncertainty around that prediction, based on 1000 bootstrap replicates. Data points are raw stable isotope ratio data for each hair segment used in the analysis (n segments = 140, n individual mandrills = 13).

Table 4.3. Model summary for the non-linear mixed effects model analyzing the relationship between days before or after the diet switch and mandrill mustache hair carbon stable isotope ratio.

	Estimate	**Standard Error**	**df**	***t***	***p***
Fixed Effects					
Isotope Ratio Pre-Diet Switch	-22.2	0.068	124	-325.1	<0.001
Isotope Ratio Pre-Diet Switch	-22.0	0.082	124	-269.8	<0.001
Half-life	22.72	4.23	124	5.4	<0.001
Scale Parameter	-5.7	3.5	124	-1.63	0.1
Random Effects					
Isotope Ratio Pre-Diet Switch		Variance	0.068		
Isotope Ratio Post-Diet Switch		Variance	0.048		
Residual		Variance	0.029		

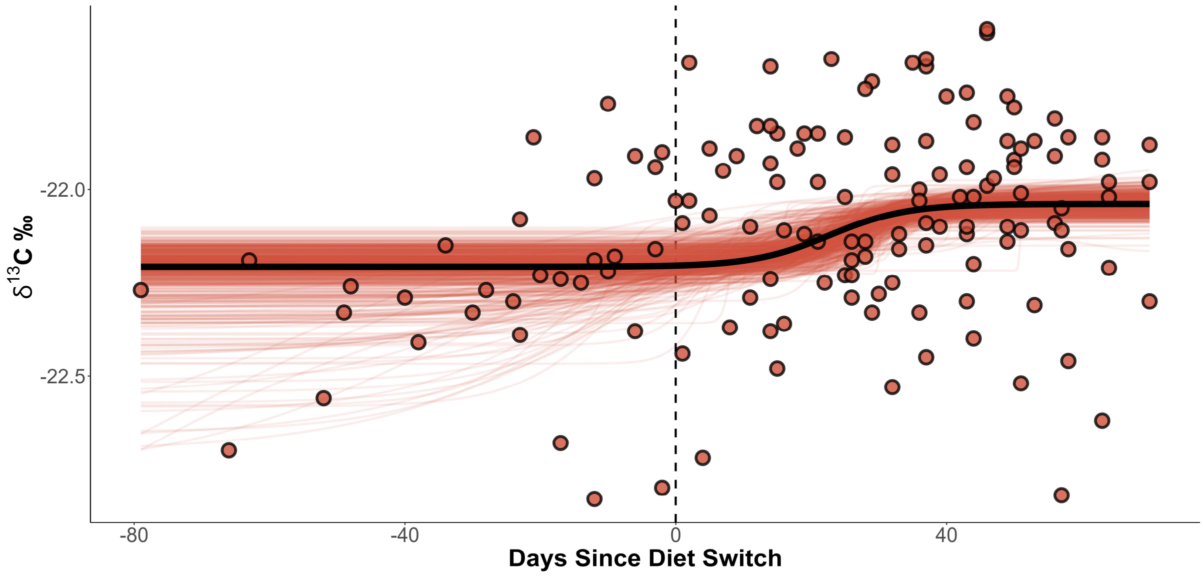

Figure 4.4. The relationship between days before or after the diet-switch and mandrill mustache hair δ^{13}C. The solid black line displays the population level prediction of carbon isotopic lag time and the orange lines illustrate uncertainty around that prediction, based on 1000 bootstrap replicates. Data points are raw stable isotope ratio data for each hair segment used in the analysis (n segments = 140, n individual mandrills = 13).

4.4.3 Hair-Diet Discrimination Factors

To calculate discrimination factors we calculated the isotope ratio difference between δ_{hair} on Day 70 and δ_{diet}. Based on our estimates of isotopic lag times, mandrill mustache hairs should have been in equilibrium with dietary nitrogen before Day 70, but slightly short of equilibrium with dietary carbon. However, hair $\delta^{13}C$ at Day 70 was likely to be very close to the eventual asymptotic value at which equilibrium would have been reached (Figure 4.4). Calculating the difference between δ_{hair} and δ_{diet} resulted in discrimination factors of 3.1‰ (bootstrap 95% CI: 3.04 - 3.17‰) for $\delta^{15}N$ and 2.8‰ (bootstrap 95% CI: 2.76 - 2.86‰) for $\delta^{13}C$.

4.5 Discussion

We set out to quantify growth rates, isotopic lag times and tissue-diet discrimination factors for mandrill hairs, because investigations of stable isotope dynamics within primates are sparse in the literature (Crowley *et al.,* 2016). Our experiment has revealed that mandrill hair growth rates varied between individuals and between body parts, suggesting that hairs should be sampled from the same location on different animals when sampling wild individuals. In our investigation of isotopic lag times for mandrill hairs, we found hair $\delta^{15}N$ to respond faster to the diet-switch, compared to hair $\delta^{13}C$, a result that mirrors other studies (Huelsemann *et al.,* 2009). Finally, we found isotopic discrimination factors between mandrill hairs and diet to be slightly higher for $\delta^{15}N$ than for $\delta^{13}C$, with both isotopes showing a similar magnitude of isotopic discrimination to other studies of captive primates. Our results can be applied to increase the analytical precision of future investigations of primate stable isotope ecology.

4.5.1 Hair Growth

Knowledge of species-specific hair growth rates enhance stable isotope analysis, by allowing the time taken to grow a length of hair to be quantified and, therefore, for individual hair segments to be dated. We found substantial growth rate variation between individuals for all hair types, however, such inter-individual variation is impossible to account for when sampling wild individuals. Our measures of mean growth rate, that account for inter-individual variation, can therefore be applied during future studies of mandrill stable isotope ecology. For example, a 10.7cm length of mandrill mustache hair may be assumed to have taken one month to grow in wild individuals, based on our results. Our results also suggest that researchers should conduct hair sampling on the same body parts across individuals in a single study, to reduce error due to differing growth rates between hair types.

4.5.2 Isotopic Lag Times

Before estimating the isotopic lag time of mandrill mustache hairs, we first examined the isotope ratios of the earliest and most recently grown hair segments, to test whether hair isotope ratios had responded to the diet switch. We found that hair $\delta^{15}N$ and $\delta^{13}C$ both responded to the diet switch, with $\delta^{15}N$ exhibiting a negative change and $\delta^{13}C$ showing a positive change. In contrast, we did not observe a change in $\delta^{34}S$ between the earliest and most recently grown hair segments. A lack of change in $\delta^{34}S$ may have resulted from low isotopic distinction between the experimental diet and the diet consumed by the study animals prior to the diet-switch. An additional possibility is that the isotopic lag time of hair $\delta^{34}S$ is too long to be captured by a 70 day experiment. A slower response of tissue $\delta^{34}S$ has previously been documented in mammals (Bahar *et al.,* 2009). In terms of mammal hairs, it has been hypothesized that $\delta^{34}S$ exhibit a longer lag time because sulfur is contained within the amino acids cysteine and methionine. Cysteine is a non-essential amino acid, meaning it may be synthesized from endogenous sulfur atoms and not only from dietary sulfur, leading to a delay in cysteine $\delta^{34}S$ reflecting a change in diet (Richards *et al.,* 2003). However, because our study animals were semi-free ranging, and their diet was not fully controlled prior to the experiment, distinguishing between these two possibilities was not possible.

Having found hair $\delta^{15}N$ and $\delta^{13}C$ to have responded to the diet-switch, we then estimated the isotopic lag times of both elements. We found the half-life of $\delta^{15}N$ to be approximately 10 days, and for hair nitrogen isotope ratios to be in equilibrium with the new diet after 22 days. Lag times for hair $\delta^{15}N$ are rare in the literature (Oelze, 2016). A previous investigation of a single cow found a half-life of 19 days for hair $\delta^{15}N$, approximately double our own estimate (Schwertl *et al.,* 2003). However, the same study also found hair to reach isotopic equilibrium after the equivalent of two half-lives, matching our results (Schwertl *et al.,* 2003). Similarly, an investigation of shaved rat hairs showed that hair $\delta^{15}N$ had reached equilibrium with a new diet after a maximum of 40 days, implying a half-life and lag time close to our own estimates (Caut *et al.,* 2008).

Regarding the lag time of hair $\delta^{13}C$, our model estimated a half-life of 23 days, approximately double that of hair $\delta^{15}N$ and for isotopic equilibrium to be reached after 38 days. The isotopic lag time of mandrill mustache hair therefore appears similar to that of rats, with Caut *et al.,* (2008) finding that rat hair $\delta^{13}C$ also reached equilibrium after a maximum of 40 days. These results contrast somewhat with Tieszen *et al.,* (1983) who found a hair $\delta^{13}C$ half-life of 47.5 days in gerbils, suggesting some interspecific differences in isotopic lag time for hair tissues. Our results are, however, consistent with studies of human hair, in which $\delta^{15}N$ has also been found to have a shorter lag time than $\delta^{13}C$ (Huelsemann *et al.,* 2009), which could suggest that this is a pattern to be expected in primate hairs.

4.5.3 Hair-Diet Discrimination Factors

When comparing the predicted mean δ_{hair} on Day 70 of our experiment to δ_{diet}, we found discrimination factors for mandrill mustache hairs of 3.1‰ for $\delta^{15}N$ and 2.8‰ for $\delta^{13}C$ Prior investigations of tissue-hair discrimination factors for $\delta^{15}N$ have found values between 2.6‰ in vervet monkeys (*Chlorocebus aethiops sabaeus*) (Macharia *et al.,* 2014) to 3.5‰ in Japanese macaques (*Macaca fuscata*) (Nakashita *et al.,* 2013), with chimpanzees (*Pan trogladytes*) and orang-utans (*Pongo pygmaeus*) in between (Tsutaya *et al.,* 2017; 2021). In terms of tissue-diet $\delta^{13}C$ discrimination factors, published values range between 2.6‰ in orang-utans (Tsutaya *et al.,* 2021) to 3.8‰ in chimpanzees (Tsutaya *et al.,* 2017). Our results are therefore within the ranges so far published for other non-human primate species and will aid future investigations aiming to accurately reconstruct mandrill diets from hair stable isotope ratios.

4.6 Appendix

Figures A4.1 and A4.2 illustrate the nonlinear relationships between days before or after the diet switch and δ^{15}N or δ^{13}C of mandrill mustache hair, for each individual, given between individual differences in random intercept. The predicted slope of each individual is displayed alongside the raw stable isotope ratio of the mustache hair segments from each animal. The plots show that there are differences between animals in the extent to which their data match the population level predictions from the nonlinear mixed models presented in the main text. As our nonlinear models contained random intercepts, these between animal differences are accounted for during model fitting and we therefore believe our results are robust to inter-individual variation in response to the diet-switch. The plots also, however, reveal the main limitation of our study, which is that female mustache hairs are shorter than male hairs, leading to less temporal coverage for each female. An interesting future analysis would be to analyze additional hairs from the females, sampled earlier during the diet-switch experiment, to increase the robustness of our estimates of hair isotopic lag times in mandrills.

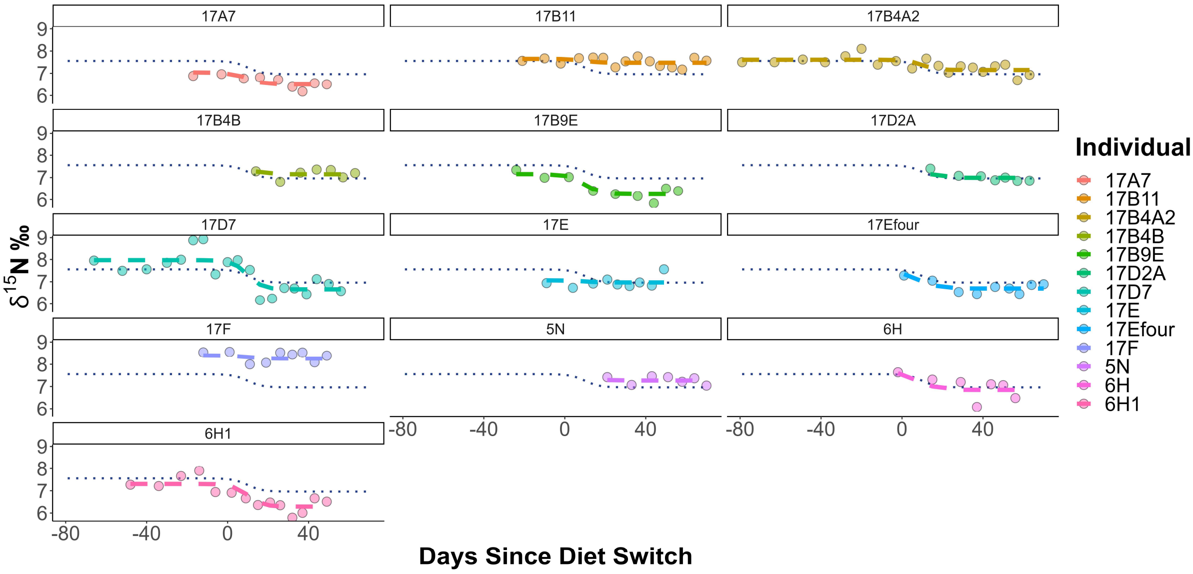

Figure A4.1. The relationship between days before or after the diet-switch and mandrill mustache hair δ^{15}N in each animal, given between individual differences in random intercept. The dotted blue line indicates the population level prediction for δ^{15}N isotopic lag time and the colored dashed lines display the δ^{15}N response of individual mandrills (n = 13) to the diet switch. Colored points display the δ^{15}N of individual hair segments (total n = 140), which differ in number between individuals due to inter-individual differences in moustache hair length.

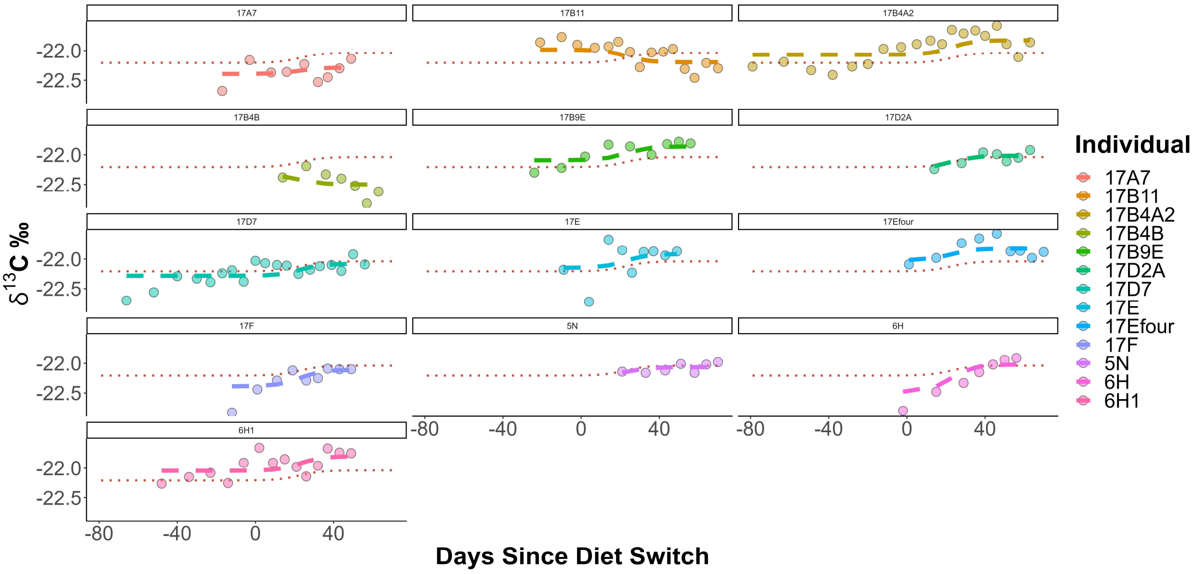

Figure A4.2. The relationship between days before or after the diet-switch and mandrill mustache hair δ^{13}C in each animal, given between individual differences in random intercept. The dotted orange line indicates the population level prediction for δ^{13}C isotopic lag time and the colored dashed lines display the δ^{13}C response of individual mandrills (n = 13) to the diet switch. Colored points display the δ^{13}C of individual hair segments (total n = 140), which differ in number between individuals due to inter-individual differences in moustache hair length.

Chapter 5: Stable isotope data suggest an association between extreme sexual dimorphism and resource competition in mandrills (*Mandrillus sphinx*).

Joshua Bauld, Jason Newton, David Lehmann, Katharine Abernethy, Isabel Jones and Luc Bussière conceived the research. Wild mandrills were sampled by David Lehmann, Lisa-Laure Nindiwe Malata, Brigitte Moussavou, Michel Louis Halbwax, Edmond Dimoto, Arthur Dibambou, Loic Makaga and Josué Edzang Ndong. Laboratory analysis was conducted by Joshua Bauld and Jason Newton. Joshua Bauld completed data analysis and wrote the chapter with guidance from Jason Newton, David Lehmann, Katharine Abernethy, Luc Bussière and Isabel Jones.

5.1 Abstract

Males and females often display niche divergence that is accompanied by sexual dimorphism in traits that are relevant to ecology, such as body size. Associations between sexual dimorphism and niche divergence suggest that selection mediated by ecology, as opposed to sexual or fecundity selection mediated by reproduction, could be involved in the evolution of sexual dimorphism. Here, we investigate niche divergence between male and female mandrills, which exhibit sexual dimorphism in body size, dental morphology, and social behavior, all of which may influence the feeding niche of each sex. To do so, we apply stable isotope analysis, which quantifies various features of animal niches, such as trophic level or basal carbon resource. We sequentially analyze the stable isotope ratios of mandrill mustache hairs, which allows multiple measures of an individuals' feeding niche to be obtained from a single tissue sample. Pooling all hair samples, we find the isotopic niches of male and female mandrills to be similar in size and to overlap extensively, suggesting dietary similarity at the level of sex. However, when analyzing mandrill isotopic niches at the individual level, we find that males are much less variable within individuals, compared to females. Lower male within individual variance suggests that males consume more consistent diets over time and that males experience different levels, or outcomes, of feeding competition to females. We end by discussing the implications of our results for the possibility that resource competition has shaped the evolution of extreme sexual dimorphism in mandrills.

5.2 Introduction

5.2.1 Ecological Sexual Dimorphism

Studies of animal niches have historically paid little attention to within-species differences among individuals (Bolnick *et al.,* 2003). However, it is increasingly clear that intraspecific niche differences are more common than previously thought (Bolnick *et al.,* 2007; Araujo *et al.,* 2011; Dall *et al.,* 2012). One frequently observed form of intraspecific difference is niche divergence between males and females (Summers *et al.,* 1990; Jones *et al.,* 2020), which may often be accompanied by sexual dimorphism in traits relevant to ecology, such as body size or feeding morphology, known as 'ecological sexual dimorphisms' (Temeles *et al.,* 2000; De Lisle and Rowe, 2015). Ecological sexual dimorphisms may arise because of sex differences in nutritional requirements, sexual selection, resource competition between males and females, or a combination of these factors (Shine, 1989; Kerneleguen *et al.,* 2015; De Lisle, 2023). At present, however, the relative importance of different evolutionary mechanisms, and particularly intersexual resource competition, to the evolution of ecological sexual dimorphisms is unknown (De Lisle, 2019; Janicke and Fromonteil, 2021).

Irrespective of how ecological sexual dimorphisms evolve, associations between sexual dimorphism and intersexual niche divergence suggest an underappreciated relationship between sexual dimorphism and ecology (Chapter 2, Bauld *et al.,* 2022). Intersexual niche divergence may be indicated by sex differences in ecological means: for example, by sex differences in average trophic level (Drago *et al.,* 2015), food quality (Shannon *et al.,* 2013) or space use (Clutton-Brock *et al.,* 1987; Wang *et al.,* 2021).

5.2.2 Variance Component Analysis

Another promising approach to revealing niche differences between sexes is to analyze the variance components of male and female niches (Roughgarden, 1972; de Lima *et al.,* 2019). Higher variance between individuals of one sex would imply that individuals of that sex are more ecologically diverged, relative to individuals of the sex displaying lower between individual variance. Any residual niche variance, unexplained by variance between individuals, may then be assumed to result from niche variance within individuals. Higher residual niche variance in one sex would therefore imply wider, more generalist, individual level niches for that sex, relative to individuals of the sex exhibiting lower residual niche variance (Newsome *et al.,* 2009; Yurkowski *et al.,* 2016). Applying variance component analysis to leopards (*Panthera pardus*), Balme *et al.* (2020) found the niches of individual males to be narrower than individual females, possibly because sexual size dimorphism allows males to consistently access larger prey. Variance component analysis thus provides an opportunity to identify subtle niche differences between males and females and help clarify how ecological sexual dimorphism arises.

Balme *et al.*'s (2020) results, however, required the documentation of over 5000 leopard kills, and observational data on this scale is often difficult to obtain. Stable isotope analysis of animal tissues provides an alternative approach to gathering observational data for measuring the niche width of individuals and sexes (Newsome *et al.,* 2007; Shipley and Matich, 2020). The nitrogen stable isotope ratios ($^{15}N/^{14}N$) of animal tissues tend to vary with the trophic level at which an animal feeds (DeNiro and Epstein, 1981; Hobson and Welch, 1992). In contrast, the carbon stable isotope ratios ($^{13}C/^{12}C$) of terrestrial animal tissues are largely determined by the plants on which they, or their prey, feed on (Codron *et al.,* 2007). This association between animal diet and tissue stable isotope ratios mean that inferences can be drawn about the feeding ecology of animals from the stable isotope ratios of their tissues (e.g. Codron *et al.,* 2006; Lewis *et al.,* 2018). For example, nitrogen and carbon isotope ratios may be considered as axes within Hutchinson's (1957) concept of ecological niches as an *n*-dimensional hypervolume (Bearhop *et al.,* 2004). The stable isotope ratios of animal tissues can then be analyzed in two dimensions, to construct ellipses that represent approximate characterizations of animal feeding niches (Jackson *et al.,* 2011). The ellipses of males and females may then be compared to consider niche overlap or sex differences in niche size (Thompson *et al.,* 2012; Lehmann *et al.,* 2015; French *et al.,* 2018).

In the case of keratinous tissues, like hair or whiskers, dietary isotope ratios are incorporated throughout growth (McHuron *et al.,* 2016). Isotopic variation between sequential segments of linearly growing tissue thus provides a temporally structured record of dietary variation (Cherel *et al.,* 2009). This temporal record means long-term data on the feeding niche of individuals can be obtained from a single sampling event, negating the need for repeated observations of feeding behavior (Oelze, 2016). These data may then be used to conduct variance component analysis on the niches of males and females, such that: isotopic variance between individuals indicates the amount of ecological divergence between members of a given sex and residual isotopic variance, unexplained by variance between individuals, is assumed to result from isotopic variance along the hairs of individuals and is therefore a measure of the niche width of individuals of a given sex (Newsome *et al.,* 2009; Kerneleguen *et al.,* 2012; Yurkowski *et al.,* 2016).

Variance component analysis of stable isotope data has previously been used to investigate ecological dimorphisms in a number of species. For example, similarity in the niche variance components of male and female seals (*Arctocephalus pusillus doriferus*) suggests that resource competition may not be more important than sexual selection to the evolution of size dimorphism in this species (Kerneleguen *et al.,* 2015). In other studies, sex differences in niche variance components have been attributed to restrictions in foraging close to juvenile rearing sites for females, but not males (Elliot Smith *et al.,* 2015; de Lima *et al.,* 2019; de Lima *et al.,* 2022; Franco-Trecu *et al.,* 2022). To our knowledge, no studies examining sex differences in isotopic niche variance components have yet suggested a role for resource competition in driving intersexual niche divergence or accompanying sexual dimorphism. In addition, no prior studies have used stable isotopes to examine sex differences in niche variance components in primates, despite evidence of intersexual niche divergence related to ecological sexual dimorphisms (Pokempner and Kamilar, 2008).

5.2.3 Mandrill Sexual Dimorphism

Among primates, mandrills present a compelling case for a potential relationship between sexual dimorphism and niche divergence. Mandrills are the among the most size dimorphic primates (male mean = 28.9 Kg, female mean = 9.8 Kg, in our focal group, David Lehmann *unpublished data*), with males also possessing extravagantly colored ornamentation and 4.5cm canines (Leigh *et al.,* 2008; Setchell, 2016). In semi-free ranging groups, females preferentially mate with the most brightly ornamented males (Setchell, 2005) and males exhibit a longer maturation period (Setchell *et al.,* 2001), alongside high reproductive skew (Setchell *et al.,* 2005); all of which suggest a role for sexual selection in the evolution of mandrill dimorphism. However, the diets of males, which possess larger jaws and teeth, have been found to include a greater proportion of hard foods than those of females, whereas females consume more invertebrates (Nsi Akoue *et al.,* 2017; Percher *et al.,* 2017). Most males also leave social groups outside of the breeding season, and are solitary for much of the non-breeding season (Abernethy *et al.,* 2002). These studies suggest an ecological component to mandrill sexual dimorphism and the potential for niche divergence between sexes. Niche divergence between males and females could in turn suggest a potential role for sex differences in nutritional requirements or resource competition in the evolution of mandrill dimorphism, alongside sexual selection.

In this study, we aimed to quantify niche differences between male and female mandrills using stable isotopes. We sequentially analyzed the stable isotope ratios of nitrogen and carbon in segments of mandrill mustache hairs, to test the possibility of sex differences in isotopic niche. To facilitate our investigation, we first measured the range of isotopic variation to which mandrills in our study site may be exposed through their diets. To do so, we examined the isotope ratios of mandrill food items, testing whether these differed between food types, seasonally or spatially. These analyses allowed us to contextualize the mandrill stable isotope data, by revealing the factors that may drive individual isotopic variation.

After establishing the possible sources of mandrill isotopic niche variation, we analyzed differences between the isotopic niches of males and females, in terms of size, shape and overlap of their two-dimensional isotopic niche ellipses. A previous analysis of mandrill fecal contents at our study site indicated that females are generalist feeders (Chapter 3). Comparing the isotopic niches of males and females thus allowed us to determine the amount of ecological divergence between males and females and whether males are also generalist feeders, at the level of sex.

Next, we conducted variance component analysis on the isotopic niches of males and females, to describe sex differences in niche variation at the individual level. Using this approach, we able to quantify the amounts of isotopic variation between individuals of each sex, and thus measure the extent of feeding niche divergence between individual males and females. We then took the residual isotopic variance of each sex, unexplained by between individual variance, as a measure of the niche widths, and thus dietary generalism, of individual males and females. Given that males are solitary for much of the year and females are exclusively social (Abernethy *et al.,* 2002), females should experience higher levels of feeding competition and move between feeding patches more regularly (Sterck *et al.,* 1997). We therefore expected males, if solitary and feeding in distinct locations, to exhibit higher between individual isotopic variation and lower residual variation, which would indicate niche divergence between males and narrow individual feeding niches, respectively. This outcome would be consistent with males experiencing lower resource competition and so feeding more consistently that females, due to their solitary foraging strategy. Conversely, we expected females to display lower between individual isotopic variance and higher residual variance, indicating niche similarity between females and wide individual level niches, respectively. This outcome would be consistent with social females moving regularly between patches, because of high rates of patch depletion, and feeding opportunistically, due to high resource competition.

5.3 Methods

5.3.1 Authorization and Ethical Approval

The tissue sampling of mandrills, for stable isotope analysis, was approved by the Centre de la Recherche Scientifique et Technologique (CENAREST), Gabon (AR0036/16) and received ethical approval from the University of Stirling, UK (AWERB (16/17) 39).

5.3.2 Study Site and Population

Our study was carried out in Lopé National Park, located in Gabon (-0.2N, 11.6E), Central Africa. Lope National Park (4964 Km^2) consists mostly of continuous, old growth forest, with savanna and gallery forests covering 10% of its northeast area. In this savanna-forest mosaic, gallery forests, with ground vegetation consisting of shrubs and lianas, spread along waterways throughout the savanna. Rainfall arrives seasonally, within a long (February to May) and a short (September to November) wet season. A long (June to August) and short (December to January) dry season take place between the two wet seasons (White, 1994, Bush *et al.,* 2020). For a more detailed description of the plant diversity in Lopé National Park see White and Abernethy (1997).

Our study focused on a horde of mandrills occupying the forest-savanna mosaic and the northernmost continuous forest (White *et al.,* 2010). Observational counts suggest the horde usually consists of between 600-800 individuals, though counts as high as 1350 individuals have been recorded, when two hordes met (Abernethy *et al.,* 1997). More recent genetic work on the horde suggested an effective population size of approximately 1000 individuals (GuibingaMickala *et al.,* 2022). Most adult males leave the horde during the non-breeding season and during the breeding season adult and sub-adult males have never been observed to make up more than 12% of individuals (Abernethy *et al.,* 2002). As a result, a large number of our mandrill tissue samples were gathered during the breeding season, as conducting sampling during this period increased the chance of targeting adult males. These adult males were unknown as individuals prior to sampling because the horde is not fully habituated. Whether males were social or solitary during the feeding window represented by the isotope data in their mustache hairs was therefore unknown.

5.3.3 Mandrill Food Item and Hair Sampling

We collected samples of mandrill food between February and May 2019, December 2019, and January 2020 and during May 2020. Our samples were therefore sourced during the long wet seasons of 2019 and 2020 and the 2019/20 short dry season, allowing us to test for the presence of seasonal and inter-annual shifts in the Lope National Park isotopic baseline.

The focal horde is known to be frugivorous and so we prioritized collecting samples of fruit from the 15 species most frequently consumed by the horde (Chapter 2). Fruit available below 2 m height was sampled directly from plants, otherwise relatively fresh fallen fruit, free of mold or bite marks, was collected. To ensure that we sampled the entire range of isotopic variation to which mandrills may be exposed through their diet, we also opportunistically sampled other fruit species, young leaves, flowers, seeds, and invertebrates. Sample collection was carried out throughout the horde’s home-range, to ensure any spatial changes in the isotope ratios of mandrill food items were accounted for in our analysis. Each mandrill food sample was placed into a polypropylene centrifuge tube, alongside a small amount of indicating silica gel beads, to facilitate drying. All samples were identified to species level where possible and the corresponding tube labeled, alongside the sampling date. The location (longitude/ latitude) and a description of the microhabitat from which the sample was taken were also recorded. Upon return to the field station, each centrifuge tube was opened and placed into a large, sealed container, alongside a substantial amount of silica gel, to allow each sample to fully dehydrate.

Mandrill mustache hairs were gathered between 11/05/2015 and 14/05/2019. Individual animals were anesthetized using Zoletil (Tiletamine and Zolazepam), administered via a teledart applied with a CO2 Injection Rifle (Daninject JM SP 25). Males received 80 mg Tiletamine and 80 mg of Zolazepam. Females received 25mg of Tiletamine and 25mg of Zolazepam. The age-sex class, weight, and tooth wear (for approximate aging) were recorded for each animal. Mustache hairs were sampled by plucking hair, including the follicle, and stored in polythene zip lock bags. Upon completion of tissue samples (and GPS collar fitting, see Chapter 6), each animal was allowed to recover within a soft bag, then released and visually monitored.

5.3.4 Stable Isotope Analysis

All sample processing and analysis was conducted under laboratory conditions at the Scottish Universities Environmental Research Center, Glasgow, UK. Prior to analyzing the stable isotope ratios of mandrill food items, samples were freeze-dried to remove any remaining water. Samples were then placed into tin cups for weighing (scale readability: ±0.001 mg) and encapsulation. Between freeze-drying, weighing and analysis, all plant tissues were stored in a desiccator, to prevent rehydration and spoiling. We initially carried out work to examine spatial variation in plant sulfur isotope ratios, but because of uncertainty over the period of time hair sulfur isotope ratios take to express a change in diet (Chapter 4), these results are not shown. Plant tissues often contained very low amounts of sulfur and high amounts of carbon, meaning two samples of differing mass were often needed to separately analyze sulfur and carbon isotope ratios. Nitrogen was present in intermediate amounts in plant tissues and so valid results were obtained from analysis of samples weighed for sulfur, of which we analyzed a greater number than for carbon. The sample sizes of plant tissue carbon (n = 264) and nitrogen isotope ratios (n = 496) therefore differ in our results.

To prepare mustache hairs for analysis, hairs from each animal were placed in borosilicate vials containing a 2:1 chloroform:methanol solution and allowed to soak for one hour. After this period, vials were shaken vigorously to remove sediment and lipid contaminants from the hairs. We then left the tube to settle, allowing any lipid to rise to the top of the solution, before disposing of the waste liquid. The vials were then left open in an extractor unit, to allow the hairs to dry.

After drying, we cut hairs into segments, to sequentially analyze variation in stable isotope ratios along the length of each hair. Nearest to the follicle, where hairs are thickest, we cut the hairs into 2mm segments, placing matching hair segments (i.e. all segments from 2-4mm) into a single tin cup for weighing and encapsulation. We used between 3-6 hairs per animal, to ensure that combined samples for each 2mm segment weighed over 100µg, which was the minimum mass required for analytical reproducibility (Chapter 4). As hairs became thinner towards the distal end, it was necessary to increase the length of segments used in each sample to meet the minimum mass requirement.

We carried out stable isotope analysis using a Thermo Scientific™ EA IsoLink™ IRMS System, optimized for sulfur sensitivity. The stable isotope ratios of all samples are expressed using delta (δ) notation (McKinney *et al.,* 1950) and permil (‰) units, relative to an international standard, such that: $^{15}N/^{14}N = \delta^{15}N‰$ and $^{13}C/^{12}C = \delta^{13}C‰$. The international standard for nitrogen and carbon stable isotope ratios are atmospheric ^{2}N and PeeDee Belemnite, respectively.

5.3.5 Statistical Analysis

To understand the factors that could influence isotopic variation in mandrill tissues, we first investigated isotopic variation between mandrill food types and whether the stable isotope ratios of forest plant tissues varied spatially or temporally. We initially used a biplot, with $\delta^{13}C$ on the x axis and $\delta^{15}N$ on the y axis, to graphically explore the clustering of mandrill food items when grouped into 11 categories: C3 Fruit, C3 Leaf, C3 Seed, C3 Bulb, C3 Bark, C3 Sap, C3

Flower, Forest Animal, Savanna Animal, Savannah Plant, Fungi. We then compared the 11 category plot to one with five categories: Forest Animal, Forest Plant, Fungi, Savanna Animal, Savanna Plant, to decide which number of food type categories best described the isotopic clustering of mandrill food items. Using AIC scores (Burnham *et al.,* 2011) we then compared a linear mixed model containing food type categorical fixed factor and random intercepts for food species, to an intercept only model, containing only random intercepts for species, to determine which model best predicted food item δ^{15}N and δ^{13}C.

To examine whether temporal or spatial variation of the isotopic baseline in mandrill habitats existed, we tested the effect of season and sampling location on the isotope ratios of forest plants. Forests are the principal habitat of mandrills and plants are the primary producers in forest habitats, as well as the main food source of mandrills. Therefore, consistent temporal or spatial variation in the isotope ratios of plants would suggest that isotopic baseline shifts occur within mandrill habitats, that would need accounting for when analyzing the isotope ratios of mandrill tissues. To explore the possibility of temporal shifts in isotopic baselines, we ran linear mixed models using season as a categorical predictor of forest plant δ^{15}N and δ^{13}C, with random intercepts for species. We then compared this model to an intercept only model, also containing random intercepts for species, using AIC. To examine the effect of sampling location on forest plant δ^{15}N and δ^{13}C**,** we used linear mixed models containing either latitude or longitude as continuous fixed effects and random intercepts for species. We then graphically compared the predictions of these models to the raw data on which the models were based, to assess the effect size of latitude and longitude relative to the isotopic variation among forest plants.

Before analyzing the isotopic niches of male and female mandrills, we first estimated the positions of each sex within isotopic space, allowing us to compare the isotope ratios of the mandrills we sampled to their food items and other studies of mandrill stable isotope ecology. We calculated mean values for each sex, for both isotopes, and constructed confidence intervals around the means using the 2.5% and 97.5% quantiles of the data for all mandrill hair segments. After estimating means and confidence intervals for each sex, we then adjusted these values by the hair-diet discrimination factors developed in Chapter 4. Discrimination factors describe the typical magnitude of isotopic enrichment between animal tissues and their dietary items, which must be accounted for before making inferences about animal diets from tissue isotope ratios. We then compared these adjusted tissue values to the isotope ratios of mandrill food items to consider the major food types consumed by mandrills in Lopé.

To compare the isotopic niches of males and females, constructed ellipses representing the niche of each sex in two dimensions, with $\delta^{13}C$ on the x axis and $\delta^{15}N$ on the y axis. We compared ellipses constructed with three methods: standard ellipse area (SEA), representing two dimensional standard deviation; standard ellipse area corrected for small sample size (SEA_C); and Bayesian Standard Ellipse Areas (SEA_B), estimated with 10 000 posterior draws (see Jackson *et al.,* 2011). We found all three approaches to be comparable in terms of the estimated niche size of each sex. We therefore chose to use the standard ellipse areas for plotting, as they are convenient to display, and to compare the size and overlap of male and female niches using the Bayesian method, as this approach provides robust estimates of error.

To conduct variance component analysis, we used intercept-only linear mixed models. We ran four separate models analyzing male and female variance in $\delta^{15}N$ and $\delta^{13}C$. The isotope ratios of individual hair segments were included as the dependent variable and random intercepts were included for individual identity. We took the random intercept variance in each model as an estimate of isotopic variance between individual males or females and the residual variance as a measure of isotopic variance within individual of each sex. The sum of both variance components was taken as a measure of the total niche width of each sex, for each isotope (Newsome *et al.,* 2009; Yurkowski *et al.,* 2016).

5.3.6 Software

All statistical analyses were conducted in R v4.1.3 (R Core Team, 2022). All data wrangling, plotting and production of tables was completed using the packages "tidyverse" v1.3.2 (Wickham *et al.,* 2019), "lubridate" v1.9.0 (Grolemund and Wickham, 2011), "ggplot2" v3.4.0 (Wickham, 2016) and "flextable" v0.8.3 (Gohel and Skintzos, 2022). Creation and manipulation of shapefiles and rasters was carried out with the packages "sf" v1.0-9 (Pebesma, 2018), "terra" v1.6-47 (Hijmans, 2022) and "raster" v3.6-11 (Hijmans, 2022b). Stable isotope ellipses were constructed with the package "SIBER" v2.1.6 (Jackson *et al.,* 2011). Linear mixed models were run using the packages "lme4" v1.1-31 (Bates *et al.,* 2015) and "nlme" v3.1-161 (Pinheiro *et al.,* 2022).

5.4 Results

5.4.1 Mandrill Food Stable Isotope Ratios

To contextualize the stable isotope ratios of mandrill mustache hairs, we analyzed the stable isotope ratios of plant and invertebrate foods available in the home-range of our study group. Firstly, to understand how mandrills may be exposed to isotopic variation through the various food types they consumed, we produced biplots displaying the $\delta^{13}C$ and $\delta^{15}N$ ratios of all mandrill food items. Grouping the foods into 11 food types (C3 Fruit, C3 Leaf, C3 Seed, C3 Bulb, C3 Bark, C3 Sap, C3 Flower, Forest Animal, Savanna Animal, Savannah Plant, Fungi) resulted in numerous overlapping pair-wise combinations (Figure A5.1). Instead, grouping food types into five categories (Forest Animal, Savanna Animal, Forest Plant, Savannah Plant, Fungi) produced categories that were ecological meaningful, for example mean forest plant $\delta^{15}N$ was lower than mean forest animal $\delta^{15}N$, though extensive overlap still existed between food types (Figure 5.1). To investigate whether the five food type categories explained isotopic variation between food types, we compared linear mixed effects models containing food type as an independent variable with intercept only models, using AIC. AIC was lower for the food type model both for $\delta^{15}N$ (AIC = 2354.5 for food type model vs. 2387.8 for intercept only model) and for $\delta^{13}C$ (food type model AIC = 1451.3, intercept only model AIC = 1545.4), and so the food type models were taken as the preferred models. Invertebrates from the forest or savanna were ^{15}N-enriched relative to plants and fungi and fungi were ^{15}N-enriched relative to plants (Table 5.1). In addition, invertebrates and plants from the savanna were ^{13}C-enriched relative to invertebrates, plants and fungi from the forest and fungi were ^{13}C-enriched relative to forest invertebrates, which were in turn ^{13}C-enriched relative to forest plants (Table 5.2).

Table 5.1. The effect of food type on mandrill food items $\delta^{15}N$.

		Estimate	**Standard Error**	***t***
Fixed Effects				
Intercept		6.29	0.35	17.92
Savannah Animal		0.53	1.88	0.28
Fungi		-1.50	0.83	-1.79
Forest Plant		-2.65	0.44	-6.01
Savannah Plant		-2.13	1.37	-1.55
Random Effects				
Species	Intercept Variance	2.92		
Residual	Observation Variance	2.46		

Table 5.2. The effect of food type mandrill food items $\delta^{13}C$.

		Estimate	**Standard Error**	***t***
Fixed Effects				
Intercept		-27.29	0.39	-69.53
Savannah Animal		6.59	2.03	3.24
Fungi		1.92	0.91	2.11
Forest Plant		-2.50	0.49	-5.07
Savannah Plant		13.87	1.49	9.34
Random Effects				
Species	Intercept Variance	3.37		
Residual	Observation Variance	3.02		

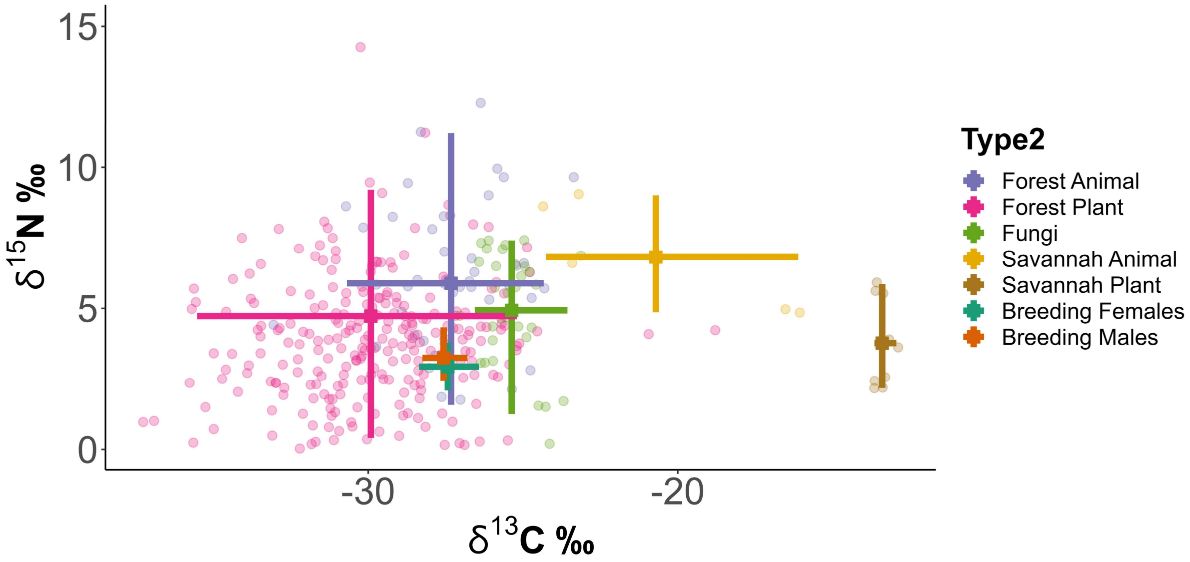

Figure 5.1. Isotopic variation between mandrill food items, when grouped into five categories. Each circular point represents at individual food item sample (forest plant n = 246, forest animal n = 43, fungi n = 32, savannah plant n = 9, savannah animal n = 5). Square points indicate the mean of each food type and colored lines display the 95% confidence interval around the mean, based on the 2.5% and 97.5% quantiles of the raw data in each category. Means and 95% confidence intervals for stable isotope ratios of male (n individuals = 9, n hair segments = 169) and female (n individuals = 12, n hair segments = 108) mandrill mustache hairs are shown for comparison, after adjustment for tissue-diet discrimination factors (Chapter 4).

To quantify the isotopic baseline values for the primary habitat of the focal horde, we fitted intercept only models estimating the mean $\delta^{13}C$ or $\delta^{15}N$ values for forest plant (primary producer) tissues in our study site (Table 5.3; Table 5.4). The mean $\delta^{13}C$ of forest plants was -28.8‰ (95% Confidence Interval: -29.4 to -28.1‰) and the mean $\delta^{15}N$ of forest plants was 3.6‰ (3.1 to 4.1‰). To assess the presence of temporal isotopic baselines shifts in our study area, we assessed whether forest plant isotope ratios varied between the long rainy seasons in 2019 and 2020 and the 2019/20 short dry season. We found the AIC for intercept only models for both $\delta^{15}N$ (AIC = 1,953.7) and $\delta^{13}C$ (AIC = 1,089.0) to be slightly lower than that for models including season as predictors of forest plant $\delta^{15}N$ (AIC = 1,957.4) or $\delta^{13}C$ (AIC = 1,091.2), thus the intercept only models were taken as the preferred models.

To analyze whether the isotope ratios of mandrill food items varied spatially, we conducted linear mixed effects models examining the impact of latitude and longitude on the isotope ratios of forest plants (Table A5.1, A5.2, A5.3, A5.4). Comparing predictions from each of these models against the raw isotope ratios of forest plants indicated that any linear relationships between latitude or longitude and δ^{13}C or δ^{15}N were modest, relative to the total isotopic variation between plants (Figure A5.2, A5.3, A5.4, A5.5). Weak linear relationships imply a lack of isotopic gradients and that isotopic variation is instead spatially heterogeneous (Figure 5.2; Figure 5.3).

Table 5.3. Model estimating mean δ^{13}C of forest plants in Lopé National Park.

		Estimate	**Standard Error**	***t***
Fixed Effects				
Intercept		-29.78	0.35	-85.38
Random Effects				
Species	Intercept Variance	4.94		
Residual	Observation Variance	3.31		

Table 5.4. Model estimating mean δ^{15}N of forest plants in Lopé National Park.

		Estimate	**Standard Error**	***t***
Fixed Effects				
Intercept		3.65	0.24	14.98
Random Effects				
Species	Intercept Variance	2.26		
Residual	Observation Variance	2.54		

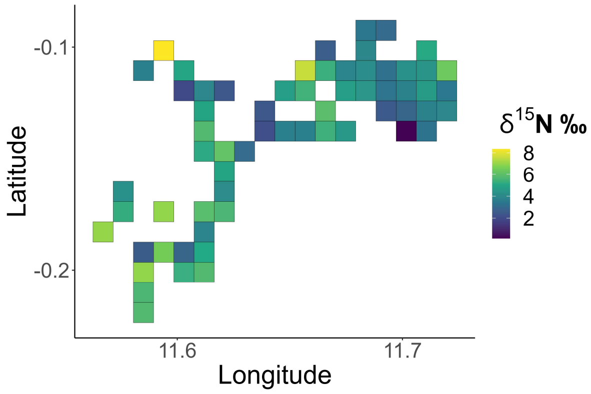

Figure 5.2. Spatial variation in δ^{15}N of mandrill food items (n = 471). Pixels are equal to 1 km^2 and colored according to the mean stable isotope ratio of mandrill food items samples in that pixel (sample sizes vary between pixels).

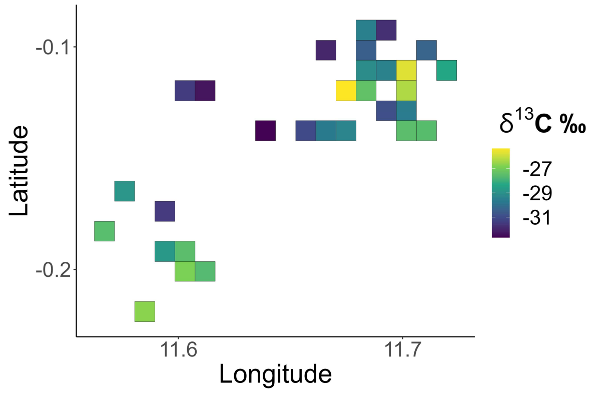

Figure 5.3. Spatial variation in δ^{13}C of mandrill food items (n = 251). Pixels are equal to 1 km^2 and colored according to the mean stable isotope ratio of mandrill food items samples in that pixel (sample sizes vary between pixels).

5.4.2 Mandrill Isotopic Niches

After segmenting mandrill moustache hairs, our final sample sizes included 160 segments from nine individuals and 96 segments from 12 individuals for males and females, respectively. Mean δ^{13}C of each sex was -24.60 ‰ (95% Confidence Interval: -24.90 to -24.30 ‰) and -24.70 ‰ (-25.0% to -24.50 ‰) for females and males, respectively. Mean δ^{15}N was 6.10 ‰ (5.93 to 6.27 ‰) and 6.33 ‰ (6.05 to 6.61 ‰) for females and males, respectively. After adjusting for tissue-diet discrimination factors (Chapter 4), the mean values of male and female mustache hair δ^{13}C and δ^{15}N were in similar locations, relative to mandrill food items (Figure 5.1). Mean $\delta^{13}C_{adjusted}$ of each sex was -27.40 ‰ for females (95% Confidence Interval: -27.70 to -27.10 ‰) and -27.50 ‰ (-27.80 to -27.30 ‰) for males. Mean $\delta^{15}N_{adjusted}$ was 3.00 ‰ (2.83 to 3.17 ‰) and 3.23 ‰ (2.95 to 3.51 ‰) for females and males, respectively.

We compared the isotopic niche areas of both sexes using standard ellipses (SEA), standard ellipses with a correction for small sample size (SEA$_c$) and Bayesian inference (SEA$_B$). We found little difference between ellipse areas estimated by different approaches (Table 5.5). We therefore chose to plot the standard ellipse areas of each sex (Figure 5.4) and to compare the sizes and overlap between the niches of males and females using Bayesian inference. The isotopic niches of female and male mandrills were similar in size and location within isotopic space, but differed somewhat in shape, with the female niche obviously wider on the δ^{13}C axis and male niche slightly wider on the δ^{15}N axis (Figure 5.4). When comparing 10 000 posterior draws for each sexes niche size (SEA$_B$), the isotopic niche of females was larger than that of males in 93.7% of cases (Figure 5.5). Regarding overlap between the ellipses of each sex, the area of overlap covered 82.5% (95% Credible Interval: 68.7-95.9%) of the male niche (Figure 5.6) and 67.2% (53.2-81.3%) of the female niche.

Table 5.5. Isotope niche sizes of male and female mandrills.

Class	**SEA**	**SEA$_c$**	**SEA$_B$**	**SEA$_B$ 95% Credible Interval**
Breeding Females	0.74	0.75	0.73	0.61-0.91
Breeding Males	0.61	0.61	0.60	0.52-0.70

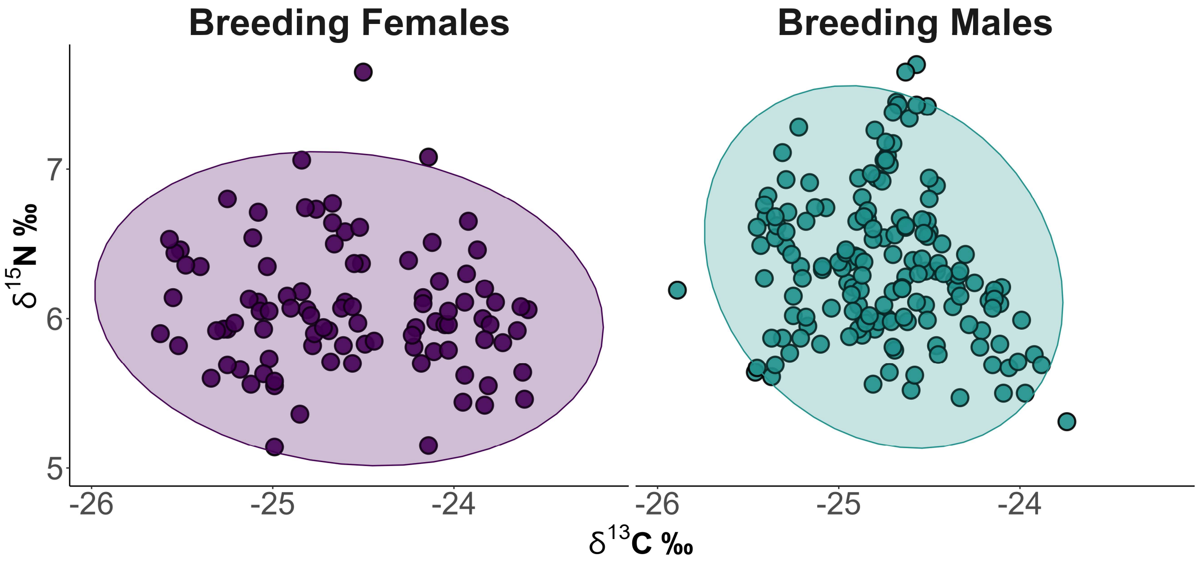

Figure 5.4. Isotopic niches of male (n individuals = 9, n hair segments = 169) and female mandrills (n individuals = 12, n hair segments = 108), based on all hair segments from all individuals of each sex. Each point represents the position in isotope space of each hair segment and standard ellipse areas (SEA) represent the 95% isotopic niche area of each sex, based on those positions.

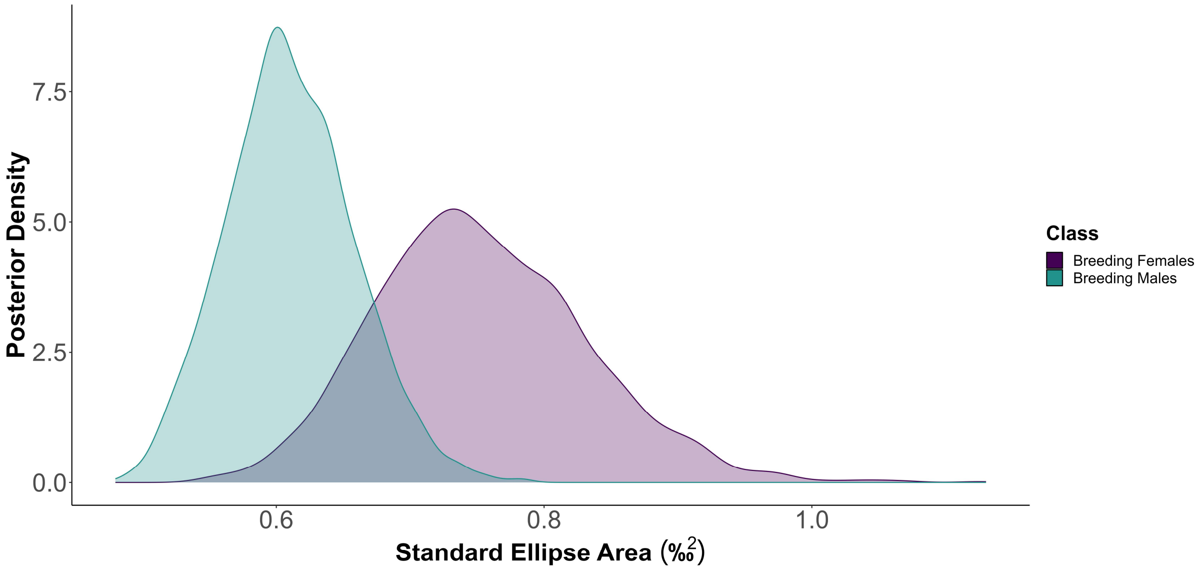

Figure 5.5. Posterior distributions of 10 000 draws for female (n individuals = 12, n hair segments = 108) and male (n individuals = 9, n hair segments = 169) standard ellipse areas, estimated via Bayesian inference (SEA^B), using $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of mustache hair segments.

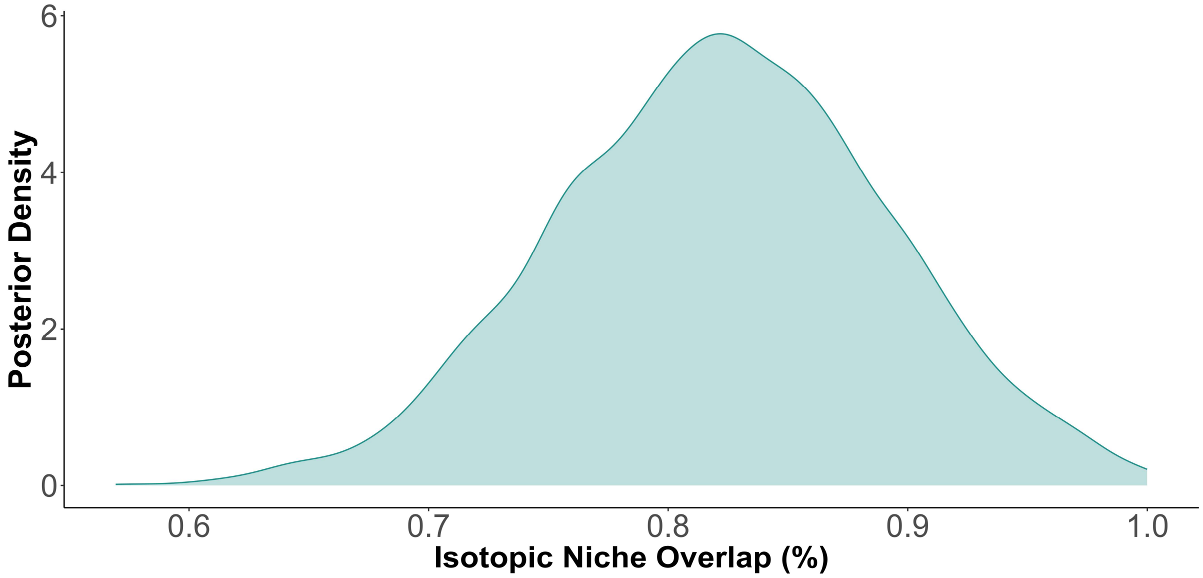

Figure 5.6. Posterior distributions of 1000 random draws for the area of the male (n individuals = 9, n hair segments = 169) ellipse (SEA_B) overlapped by the female (n individuals = 12, n hair segments = 108) ellipse, using $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of mustache hair segments.

5.4.3 Variance Component Analysis

After finding that female and male niches were similar in size and location, we next examined whether the niche variance components differed between the sexes. To explore these differences in the raw data, we first produced biplots displaying the δ^{13}C and δ^{15}N ratios of all mandrill hair segments. Individual males showed substantial clustering within individuals and variation between individuals. In contrast, data for individual females was much less clustered within individuals, suggesting more dietary variation within individuals and less between individuals (Figure 5.7). To confirm these observations, we examined the variance components of the δ^{15}N and δ^{13}C niche of each sex, using linear mixed models. Consistent with the ellipses in Figure 5.4, total δ^{13}C niche width (the sum of random intercept and residual variance) was higher in females than males, whereas total δ^{15}N niche width was higher in males than in females (Figure 5.8).

The niche variance components, in terms of random intercept (between individual) and residual (within individual) variance, also differed between sexes (Figure 5.8). Regarding δ^{13}C, female random intercept variance (0.25 ‰^{2}) was the largest of all variance components and approximately double that of male random intercept variance (0.13 ‰^{2}). Similarly, female δ^{13}C residual variance (0.096 ‰^{2}) was over three times greater than that of males (0.03 ‰^{2}). In contrast to all other niche components, female δ^{15}N random intercept variance (0.08 ‰^{2}) was smaller than male random intercept variance (0.18 ‰^{2}). In terms of residual δ^{15}N variance, female variance (0.12 ‰^{2}) again exceeded male variance (0.08 ‰^{2}). For both δ^{13}C and δ^{15}N, random intercept variance exceeded residual variance in males. In females, random intercept variance exceeded residual variance for δ^{13}C, but for δ^{15}N residual variance exceeded random intercept variance. Summary tables for each variance component model are available in the Appendix (Tables A5.5; A5.6; A5.7; A5.8).

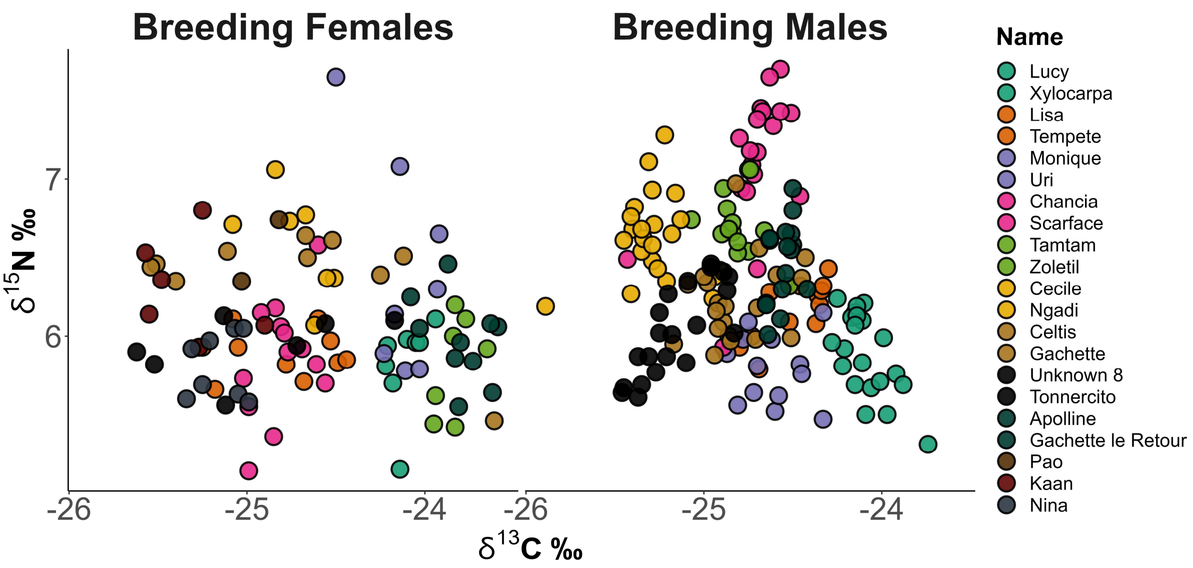

Figure 5.7. $\delta^{13}C$ and $\delta^{15}N$ ratios of all male (n individuals = 9, n hair segments = 169) and female (n individuals = 12, n hair segments = 108) mandrill hair segments. Points represent the position of each hair segment in isotopic space. Points colors correspond to individual mandrills, to illustrate the area of isotopic niche space occupied by each animal.

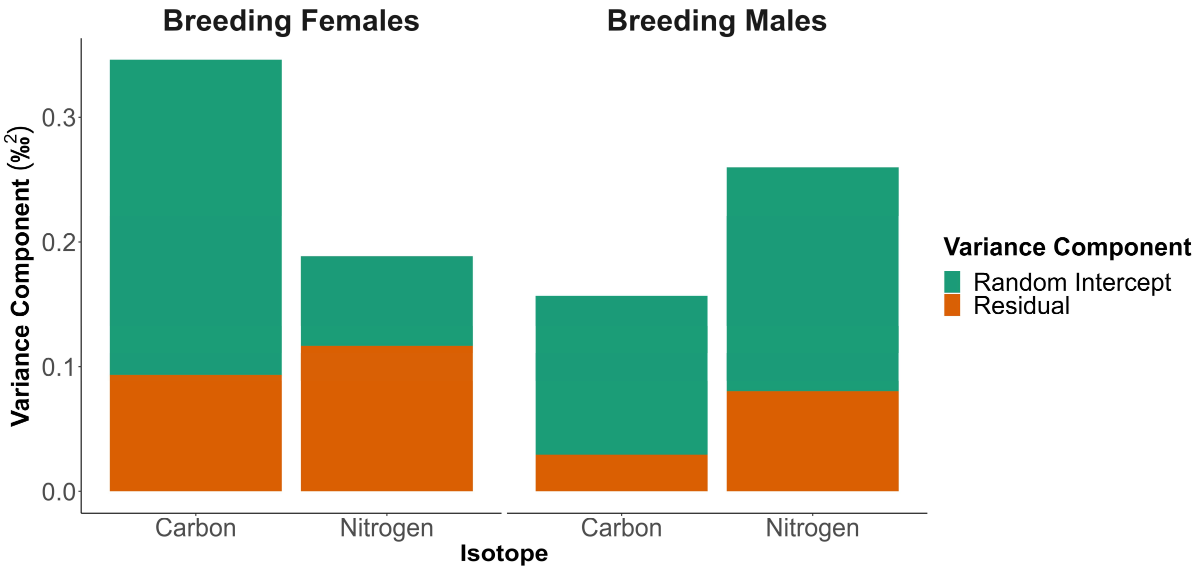

Figure 5.8. Random intercept (between individual) and residual (within individual) $\delta^{13}C$ and $\delta^{15}N$ ratios of male (n individuals = 9, n hair segments = 169) and female (n individuals = 12, n hair segments = 108) mandrill hair segments, estimated via linear mixed models. Y axis units are ‰^{2} as the niche components constitute variance calculated by squaring the standard deviation, which are in ‰ units.

5.5 Discussion

We aimed to investigate whether mandrills exhibit niche divergence between males and females, at the levels of sex and individual, using stable isotope analysis of mandrill mustache hair segments. Our analysis of mandrill food items suggested that, on average, invertebrates were ^{15}N-enriched relative to plants and food items in savannas were ^{13}C-enriched relative to those in forests, though there was substantial variation in each category. Higher isotopic variation in mandrill tissues thus likely indicates greater diversity in food consumption. When analyzing the isotopic niches of male and female mandrills, we found both sexes to be in similar locations within isotopic space, suggesting little dietary niche divergence overall between males and females. However, variance component analysis revealed sex differences in niche variation at the individual level, consistent with males and females experiencing differing levels, or outcomes, of resource competition.

5.5.1 Isotopic Variation in Mandrill Food Items

Before interpreting the stable isotope ratios from mandrill hair samples, it was first important to describe isotopic variation within the study site, to understand the potential sources of isotopic niche variation for individual mandrills (Roberts *et al.,* 2017). Visualizing the isotope ratios of mandrill food items in two dimensions (i.e. δ^{13}C versus δ^{15}N), it was clear that using 11 categories did not lead to obvious clustering within plant parts (Figure A5.1). For example, fruit stable isotope ratios were not obviously distinct from those of leaves, similar to findings at another site in Gabon (Oelze *et al.,* 2014). Splitting the data into five categories (C3 Plants, Forest Animals, C4 plants, Savanna Animals and Fungi) appeared to be a more parsimonious and meaningful way to categorize the samples. Using five categories was preferred to an intercept only model for predicting δ^{15}N and δ^{13}C of mandrill food items, though substantial isotopic variation within categories and overlap between categories remained present in the data (Figure 5.1). These results suggest that inferences about mandrill diets from tissue stable isotope ratios must be limited to a fairly coarse resolution: greater isotopic δ^{15}N and δ^{13}C along the length of a hair may indicate greater variation in trophic level or plant species consumption, respectively.

The mean δ^{13}C of forest plants in Lopé National Park was -29.8‰ (95% CI: -30.4 to -29.1‰), which is similar to Loango National Park, Gabon (−30.5 ±3.5 ‰, Oelze *et al.,* 2014). Furthermore, the mean δ^{15}N of 3.7‰ (3.2 to 4.1‰) for forest plants in Lopé was close to the average for Loango plants (3.3 ± 2.5‰). Thus the isotopic baseline within the home-range of our mandrill horde is similar to those of other primates studied within Gabon, which could facilitate inter-site comparisons.

To test whether temporal isotopic baseline shifts occurred in Lopé, we analyzed differences in forest plant isotope ratios between the 2019 and 2020 long wet seasons and the 2019/20 short dry season. We found that models containing season as an independent variable did not explain forest plant isotope ratios better than intercept only models, suggesting that no seasonal or inter-annual shifts in isotopic baseline took place. We also tested whether simple spatial gradients in δ^{15}N or δ^{13}C were present within the hordes home-range. Each model examining the effect of latitude and longitude on the isotope ratios of forest plant tissues suggested very modest effects, relative to the total isotopic variation we found between plants (Figure A5.2; A5.3; A5.4; A5.5). Isotopic variation in plants was instead spatially heterogeneous (Figure 5.2; 5.3). The lack of consistent spatial or temporal variation of the isotopic baseline in Lopé, compared to isotopic differences between plant species and food types, means we find no reason to systematically account for time and space in our analysis of mandrill stable isotope data. Instead, we can be assured that local variation in isotopic signal is a modest source of error, and may not interfere with the detection of strong patterns related to dietary variation among or within individual mandrills.

5.5.2 Mandrill Isotopic Niches

The mean stable isotope ratios of mandrills in Lopé were remarkably similar to the results obtained by Oelze *et al.* (2020) for mandrill hairs in Lékédi National Park, also in Gabon. The δ^{13}C ratios of Lopé males (-24.73‰, 95% CI: -24.96 to -24.49‰) and females (-24.61‰, -24.90 to -24.31‰) were ^{15}N-enriched by approximately 0.5‰ compared to Lékédi (mean both sexes: -25.1‰). The δ^{15}N values of Lopé males (6.33‰, 6.05 to 6.61‰) and females (6.10‰, 5.93 to 6.27‰) were even closer to values from Lékédi (mean both sexes: 6.0‰) (Oelze *et al.* 2020). The similarity in stable isotope ratios of hairs between Lopé and Lékédi suggest broad consistency in the dietary niches of mandrills between these two sites, as has been found during inter-site comparisons of mandrill diets using observational and fecal contents data (Nsi Akoué *et al.,* 2017; Hongo *et al.,* 2018; Chapter 3). Adjusting the Lopé mandrill data by the appropriate hair-diet discrimination factors for mandrills (Chapter 4) placed both male and female mandrills within the isotopic ranges of Forest Plants, Forest Animals and Fungi in Lopé (Figure 5.1). The isotope ratios of mandrill mustache hairs in our study are thus consistent with previous feeding studies showing that mandrills are omnivorous and feed largely in C3 forest food webs (Nsi Akoué *et al.,* 2017; Hongo *et al.,* 2018; Chapter 3).

The isotopic niches of male and female mandrills were similar in size and location within isotopic space (Table 5.5; Figure 5.4), as well as similar in size to the isotopic niches of other primates (Hermsmeyer, 2019; Flores-Escobar *et al.,* 2020). Previous work has shown that the focal horde are highly generalist omnivores, but with a diet dominated by fruit (Rogers *et al.,* 1996; White, 2007). However, because the number of adult males in the horde is generally less than 12% (Abernethy *et al.,* 2002), knowledge of the feeding niches of mandrills in Lopé is mostly limited to females and juveniles (Chapter 3). Our finding that the isotopic niche of males is 82.5% overlapped by females indicates that, at the level of sex, male and female diets are alike in our study site, as in other locations (Nsi Akoué *et al.,* 2017). The female isotopic niche, however, was larger than the male niche across 93.7% of the posterior draws for each sex's ellipse area, suggesting that females have a slightly wider diet breadth than males. Feeding competition among individuals is expected to increase with group size (Sterck *et al.,* 1997), potentially leading to higher dietary diversity for groups containing more individuals, as individuals must forage more opportunistically. The larger isotopic niche of females, which are permanent horde members, may therefore be a first indication that they experience more feeding competition than males, which are temporary horde members, and often forage alone (Abernethy *et al.,* 2002).

5.5.3 Isotopic Niche Variance Components

To further investigate the possibility that male and female mandrills experience differing levels, or outcomes, of feeding competition, we conducted variance component analysis on the isotopic niches of each sex. Summing the random intercept (between individual) and residual (within individual) variance components revealed that total $\delta^{13}C$ niche width of females was greater than that of males. Conversely, the total $\delta^{15}N$ niche width of males was larger than females. These results mirrored the differing isotopic niche shapes of each sex (Figure 5.4). However, somewhat conflicting with the high overlap between male and female isotopic niches, plotting the individual level raw data showed isotopically clustered males and dispersed females, suggesting niche differences between the sexes at the individual level (Figure 5.7).

The magnitude of $\delta^{15}N$ between individual variance (random intercept variance) was the only variance component found to be larger in males than females. Importantly, the raw data ranges of $\delta^{15}N$ were very similar between sexes (Figure 5.7), suggesting that greater trophic level variance among males is not because large size provides access to higher trophic level prey, as suggested for other dimorphic species (Louis *et al.,* 2021). High $\delta^{15}N$ between individual variance in males may be because they are solitary (Abernethy *et al.,* 2002) and feed in distinct locations to other males and the horde. If the prey present in these locations differ in trophic level, individual males would be expected to feed at different trophic levels for extended periods, leading to larger differences between males in average trophic level, compared to females.

An alternative explanation could be that males specialize on distinct resources, leading to consistent dietary differences between individuals. For example, an adult male has been observed carrying part of a duiker carcass, though whether the mandrill in question made the kill or scavenged the prey is unknown (Jouventin, 1975). However, this explanation seems less likely, as it would require all males to have developed their own foraging or hunting specializations, for the consistent inter-male trophic differences we have found here. The overlap between male and female niches we have found (Figure 5.5), alongside the broad similarity of male and female diets observed by others (Nsi Akoué *et al.,* 2017), indicate that males are generalist foragers, in a similar manner to females. It is thus more probable that the between individual trophic variance of males is due to opportunistic foraging in separate locations that contain distinct prey types.

Somewhat unexpectedly, because all females were within the same horde and often feeding in similar locations, δ^{13}C between individual variance was much greater in females than in males and was the largest of all niche variance components. Thus, plant consumption differed more between individual females than individual males. The large absolute measure of between individual δ^{13}C variance in females suggests that differences between females in plant consumption are consistent over time. Mandrill hordes are formed of philopatric females in a matrilineal and highly nepotistic hierarchy (Setchell, 2000; Charpentier *et al.,* 2022). It is possible that contest competition among matrilines leads to consistent differences between matrilines, and therefore individual females, in resource access over time. In another population, high ranking females have been found to spend less time foraging than low ranking females, implying that resource access is related to hierarchical dominance in mandrills (Dezeure *et al.,* 2022). Alternatively, the reproductive status of individual females may have differed, given that mandrill hordes contain females that are ovulating, pregnant, carrying infants (and therefore lactating), or relatively free of reproductive constraints, in varying proportions throughout the year (Hongo *et al.,* 2016). Lactation is associated with increased energy intake in female primates (Cui *et al.,* 2018), meaning δ^{13}C divergence between female mandrills could have been driven by variation in food selection between females in different reproductive states.

After accounting for between individual random intercept variation, there remained residual variance in each model, which we took to represent within individual isotopic variation (Newsome *et al.,* 2009). Regarding δ^{13}C, female residual variance was over three times larger than male residual variance, suggests that individual females consumed a wider diversity of plant foods than individual males. The same outcome followed for δ^{15}N, for which residual variance was also greater for females than males. Individual females thus also exhibited more trophic level diversity than individual males. Considering residual variance in both isotopes together, these results imply that, over the period of time represented by hair isotope data, female diets were more diverse than male diets, at the individual level. Thus, females exhibited larger isotopic niches at the individual level, whereas male niches were relatively narrow.

The niche width differences between individual males and females may be a consequence of differing levels of feeding competition experienced by each sex. Feeding competition and movement between feeding patches is expected to increase with group size (Sterck *et al.,* 1997, Gillespie and Chapman, 2001) and mandrills live in exceptionally large social groups (Guibinga Mickala *et al.,* 2022). It therefore follows that scramble competition should be high within mandrill hordes and that hordes must regularly move on to new feeding patches. If female mandrills are social and males often solitary (Abernethy *et al.,* 2002), females may experience higher levels of scramble competition and somewhat random resource access. Food selection by individual females may therefore be relatively opportunistic, which would explain high within individual variance in females. In contrast, solitary males should experience lower feeding competition and may be able to remain in the same feeding patches for extended periods, as a single individual should deplete resources at a much slower rate than a large group of animals. Lower feeding competition and longer patch residency times would allow male mandrills to feed more consistently on a narrower range of preferred resources, producing low within individual feeding variance.

5.5.4 A possible role for resource competition in the evolution of mandrill sexual dimorphism?

The sex differences in within- and between-individual niche variation we have documented here are suggestive of an interplay between sexual dimorphism and feeding ecology in mandrills. Sex differences may exist in nutritional requirements (Maklakov *et al.,* 2008) and these have been proposed to explain dietary differences between male and female primates (Rothman *et al.,* 2008). Experimental evidence also suggests that sex differences in nutritional requirements may interact with resource competition to produce ecological sexual dimorphism (De Lisle, 2023). In mandrills, females have been observed to more frequently consume animal prey than males, perhaps because of higher protein requirements (Nsi Akoué *et al.,* 2017). However, the high amounts of overlap between male and female isotopic niches we have found here suggest that any differences in nutritional requirements do not lead to substantial niche divergence between the sexes in mandrills. It is possible that the large size of male mandrills counterbalances the energetic costs of pregnancy and lactation to females, reducing sex differences in nutritional requirements (Key and Ross, 1999). Divergence in male and female nutritional intake may therefore be too subtle to have played a substantial role in the evolution of mandrill sexual dimorphism.

A lot of evidence points towards sexual selection as a driver of mandrill dimorphism (Setchell, 2016). Males are 3.4 times larger than females and possess 45mm canines and colorful ornamentation, with each of these traits influencing male rank attainment or female mate choice (Setchell, 2005; Leigh *et al.,* 2008; Setchell *et al.,* 2008). Males also exhibit high reproductive skew, develop more slowly and first reproduce at an older age than females (Dixson *et al.,* 1993; Setchell *et al.,* 2005; Charpentier *et al.,* 2005). These results are strong evidence that males invest time and energy into the development of secondary sexual traits that maximize mate acquisition, as would be expected under sexual selection. However, sexual dimorphism driven by sexual selection is a common occurrence among primates (Plavcan, 2001) and the unanswered question is why mandrill dimorphism is so extreme. The sex differences in dietary generalism we have found here, more specifically, wider feeding niches in individual females and narrower feeding niches in individual males, may offer some explanation.

Modeling suggests that resource competition between males and females could, in isolation, produce sexual dimorphism (Lande, 1980; Slatkin, 1984; Bolnick and Doebeli, 2003). But perhaps a more likely scenario is that resource competition may act to exaggerate existing sexual dimorphism produced by sexual selection (De Lisle, 2019). For example, the extent of carpet python (*Morelia spilota*) size dimorphism changes depending on the range of prey sizes available in a given location (Pearson *et al.,* 2002). In the case of mandrills, social differences between males and females may explain why individual males exhibited lower within individual isotopic variation than females over time. Seasonal influxes of males into mandrill hordes occur during the breeding season, when the number of tumescent females is highest (Hongo *et al.,* 2016), suggesting that many males are solitary outside of the breeding period. Female primates are proposed to live in groups to reduce individual predation risk (Clutton-Brock and Janson, 2012) and males must therefore forgo this protection when solitary. The relative dietary consistency exhibited by males suggests that lower feeding competition is one of the benefits males gain from leaving hordes, because lower individual level feeding variation implies more regular access to preferred resources. However, leaving hordes means that males are unable to form long-term social relationships with females. Consequently, upon joining the group breeding males must rapidly establish dominance over other males and signal their quality to females, in a dense forest environment (Abernethy *et al.,* 2002). The intensity of intra- and inter-sexual mating competition may therefore be relatively high in mandrills, as a result of males rejoining hordes on a seasonal basis. In this manner, the response of male mandrills to within-group resource competition may have increased sexual selection for large body size, long canines, and colorful ornamentation and explain why mandrill dimorphism is so extreme compared to other primate species.

The sex differences in dietary generalism we have found thus give some indication that sexual selection and resource competition could have interacted to produce extreme sexual dimorphism in mandrills. However, using only stable isotope data, we cannot rule out that the dietary sex differences we have documented are simply ecological consequences of size dimorphism due to sexual selection. For example, sexual selection may have produced large male mandrills that are able to dominate feeding patches whilst in social groups, which would also lead to relatively high isotopic / dietary consistency in males. We cannot exclude this scenario, as we do not know the social status of males prior to capture and hair sampling. One way to address this is to analyze spatial data obtained from GPS collars fitted at the same tissues were sampled. Alongside high feeding competition, another ecological cost to the large size of mandrill hordes is that extensive daily travel is required for horde members to consume sufficient food (White *et al.,* 2010). If daily energetic expenditure on locomotion is greater for large males (Key and Ross, 1999), lower travel costs may be an additional advantage for males that leave mandrill hordes. Analyzing sex differences in home-range use will reveal when and why males leave mandrill hordes and may give more support to a role for ecologically-mediated selection in the evolution of mandrill dimorphism (Chapter 6).

5.6 Appendix

Grouping mandrill food types into 11 categories produced multiple overlapping pair-wise combinations of categories, for example, fruits, leaves and flowers largely overlap each other (Figure A5.1).

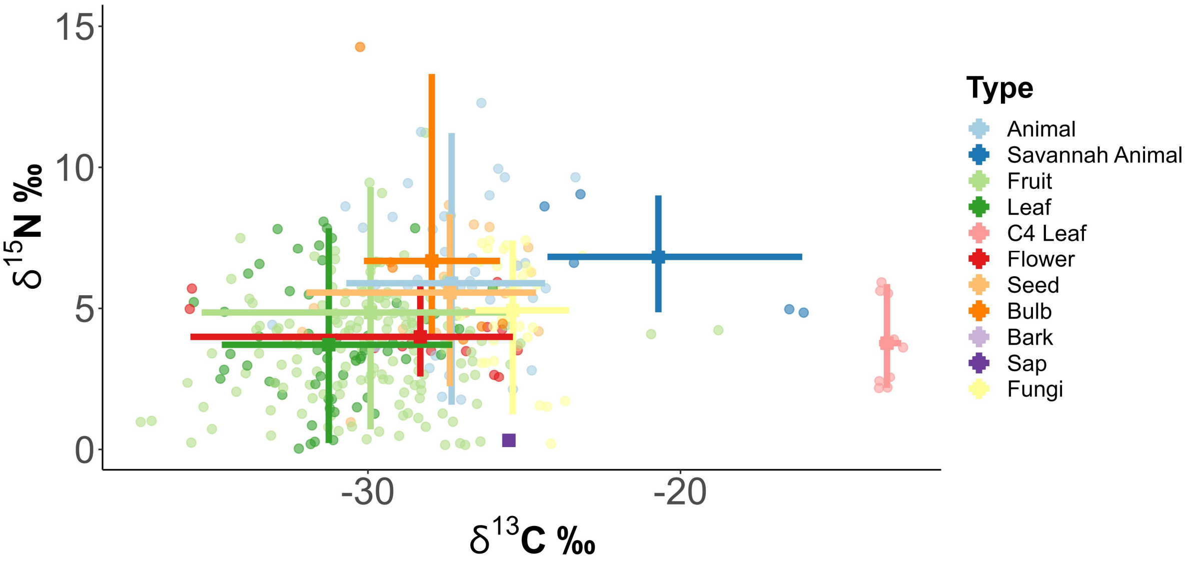

Figure A5.1. Isotopic variation between mandrill food items, when grouped into 11 categories (fruit n = 155, leaf n = 56, seed n = 15, flower n = 15, bulb n = 6, sap n = 1, animal n = 43, fungi n = 32, C4 leaf n = 9, savannah animal n = 5). Each data circular point represents at individual food item sample. Square points indicate the mean of each food type and colored lines display the 95% confidence interval around the mean, based on the 2.5% and 97.5% quantiles of the raw data in each category.

Analyzing linear relationships between longitude or latitude with δ^{13}C or δ^{15}N, did not produce strong linear relationships, relative to the total isotopic variation between samples of mandrill food items. Thus, spatial gradients in the stable isotope ratios of mandrill food items did not appear to exist in the study site (Figure A5.2; A5.3; A5.4; A5.5).

Table A5.1. The effect of latitude on mandrill food item δ^{13}C.

		Estimate	**Standard Error**	***t***
Fixed Effects				
	Intercept	-31.28	0.99	-31.66
	Latitude	-9.64	6.56	-1.47
Random Effects				
Species	Intercept Variance	5.53		
Residual	Observation Variance	3.76		

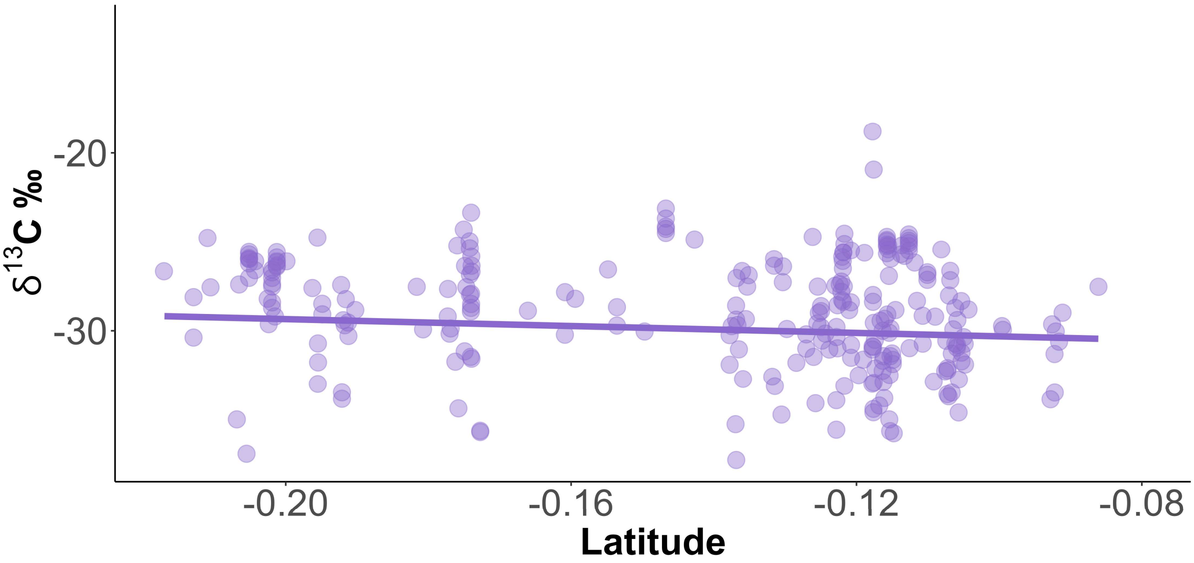

Figure A5.2. The relationship between latitude and δ^{13}C of mandrill food items. Each point represents displays the latitude and isotope ratio of an individual food sample (n = 192). The purple line displays the predicted relationship between latitude and food item δ^{13}C.

Table A5.2. The effect of latitude on mandrill food item $\delta^{15}N$.

		Estimate	**Standard Error**	***t***
Fixed Effects				
	Intercept	4.49	0.51	8.74
	Latitude	7.05	3.15	2.24
Random Effects				
Species	Intercept Variance	2.59		
Residual	Observation Variance	2.19		

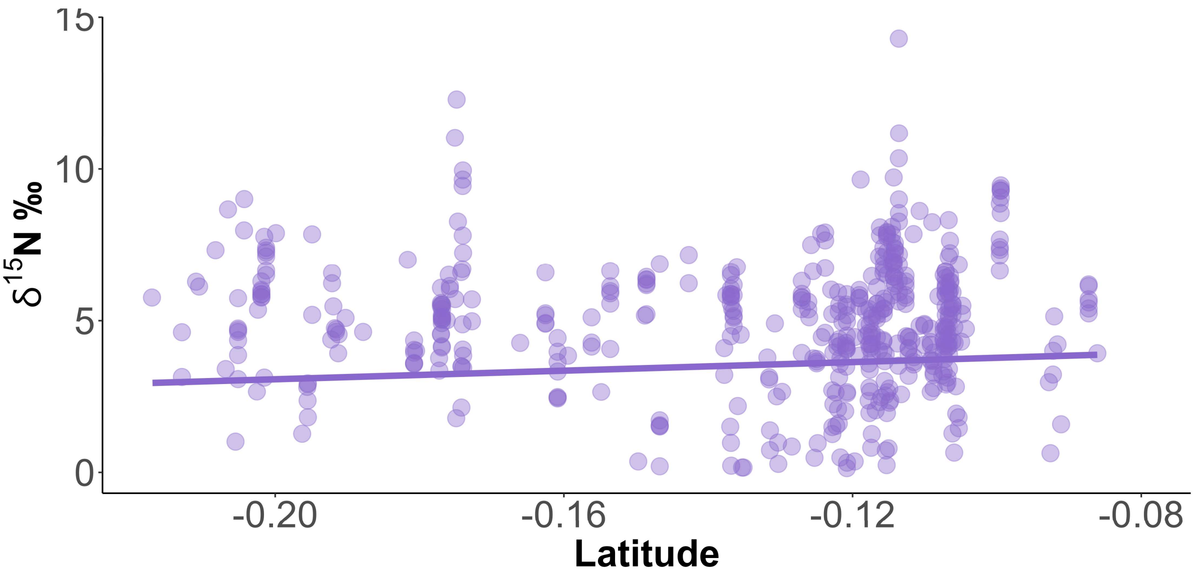

Figure A5.3. The relationship between latitude and $\delta^{15}N$ of mandrill food items. Each point represents displays the latitude and isotope ratio of an individual food sample (n = 424). The purple line displays the predicted relationship between latitude and food item $\delta^{15}N$.

Table A5.3. The effect of longitude on mandrill food item $\delta^{13}C$.

		Estimate	**Standard Error**	***t***
Fixed Effects				
	Intercept	-2.57	49.66	-0.05
	Longitude	-2.35	4.26	-0.55
Random Effects				
Species	Intercept Variance	5.52		
Residual	Observation Variance	3.80		

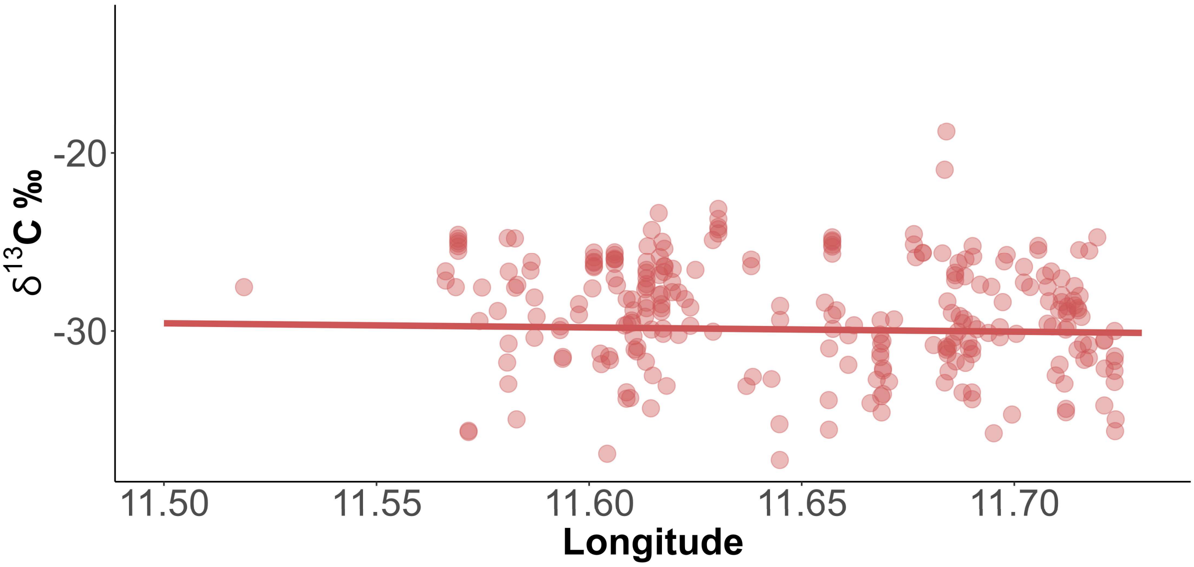

Figure A5.4. The relationship between longitude and $\delta^{13}C$ of mandrill food items. Each point represents displays the latitude and isotope ratio of an individual food sample (n = 192). The red line displays the predicted relationship between longitude and food item $\delta^{13}C$.

Table A5.4. The effect of longitude on mandrill food item δ15N.

		Estimate	**Standard Error**	***t***
Fixed effects				
Intercept		-5.98	22.21	-0.27
Longitude		0.82	1.90	0.43
Random effects				
Species	Intercept Variance	2.32		
Residual	Observation Variance	2.24		

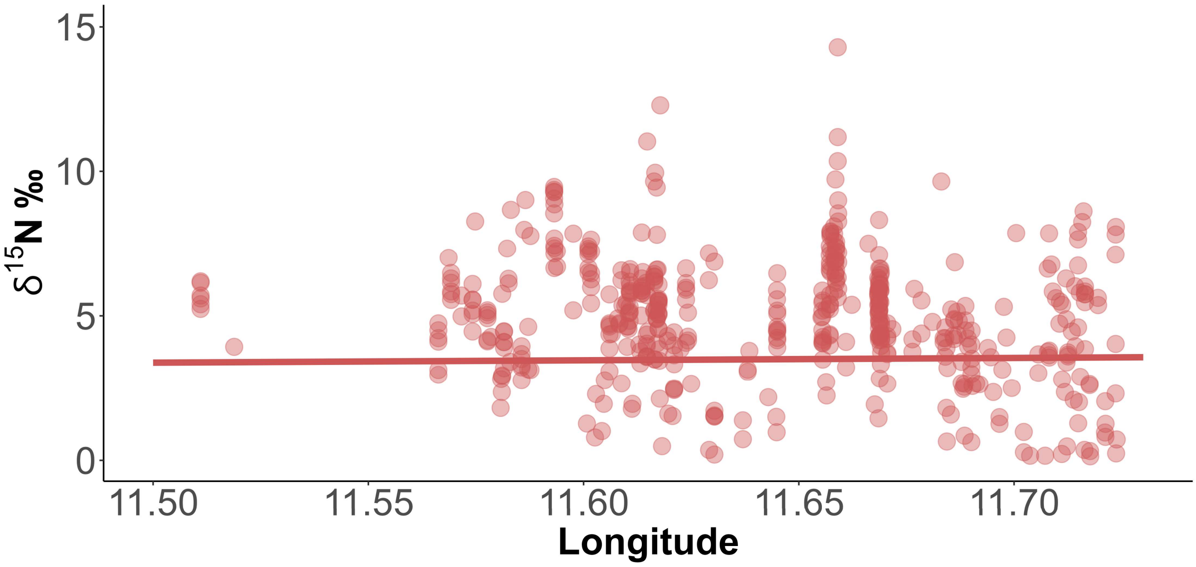

Figure A5.5. The relationship between longitude and δ15N of mandrill food items. Each point represents displays the latitude and isotope ratio of an individual food sample (n = 424). The red line displays the predicted relationship between longitude and food item δ15N.

The following four tables display the summaries of linear mixed models used to conduct variance component analysis on the isotopic niches of male and female mandrills.

Table A5.5. Female δ^{15}N variance components.

		Estimate	**Standard Error**	**df**	***z***
Fixed Effects					
	Intercept	6.10	0.09	84	71.01
Random Effects					
Name	Intercept Variance	0.08			
Residual	Observation Variance	0.12			

Table A5.6. Male δ^{15}N variance components.

		Estimate	**Standard Error**	**df**	***z***
Fixed Effects					
	Intercept	6.33	0.14	151	44.30
Random Effects					
Name	Intercept Variance	0.18			
Residual	Observation Variance	0.08			

Table A5.7. Female δ^{13}C variance components.

		Estimate	**Standard Error**	**df**	***z***
Fixed Effects					
	Intercept	-24.61	0.15	84	-165.10
Random Effects					
Name	Intercept Variance	0.25			
Residual	Observation Variance	0.096			

Table A5.8. Male δ^{13}C variance components.

		Estimate	**Standard Error**	**df**	***z***
Fixed Effects					
	Intercept	-24.73	0.12	151	-206.47
Random Effects					
Name	Intercept Variance	0.13			
Residual	Observation Variance	0.03			

Chapter 6: Sexual dimorphism in mandrill (*Mandrillus sphinx*) spatial behavior. A role for travel costs in the evolution of sexual dimorphism?

Joshua Bauld, Jason Newton, David Lehmann, Katharine Abernethy, Isabel Jones and Luc Bussière conceived the research. Wild mandrills were collared by David Lehmann, Lisa-Laure Nindiwe Malata, Brigitte Moussavou, Michel Louis Halbwax, Edmond Dimoto, Arthur Dibambou, Loic Makaga and Josué Edzang Ndong. Joshua Bauld completed data analysis and wrote the chapter with guidance from Jason Newton, David Lehmann, Katharine Abernethy, Luc Bussière and Isabel Jones.

6.1 Abstract

Larger bodied animals typically occupy wider home-ranges than smaller animals. However, larger animals incur greater energetic costs of body maintenance, which may trade-off against the energy available for locomotion and limit the maximum home-range that an animal can occupy. In species with extreme sexual size dimorphism, this trade-off could place divergent limitations on the maximum home-range size of each sex. Mandrills are the most sexually dimorphic primate, in terms of body size, and the larger males often leave social groups outside of the breeding season, suggesting sex differences in space use. We fitted GPS collars to 12 female and seven male mandrills, to explore possible sex differences in home-range size, habitat selection, Brownian motion variance (a proxy for behavioral state changes), daily travel distance and travel speed. We found home-range size and habitat selection to be similar between the sexes during the breeding season, but to differ during the non-breeding season. In addition, males exhibited lower Brownian motion variance (fewer switches between feeding, resting and travel) during the non-breeding season and a substantial increase during the breeding season. These results suggest that collared males were more often solitary during the non-breeding season and more often social during the breeding season. Males also, on average, traveled shorter distances, at slower speeds, during the non-breeding season, indicating that males expend less energy on travel when solitary. These results suggest that energetic trade-offs have heavily impacted the mandrill mating system and have potentially contributed to the exaggeration of mandrill sexual dimorphism.

6.2 Introduction

Sexual dimorphism is most commonly attributed to sexual selection, but may also be driven by additional evolutionary mechanisms (Shine, 1989; Janicke and Fromonteil, 2021; Chapter 2). For example, modeling and experimental work suggest that sexual dimorphism could also evolve via resource competition and ecological character displacement between sexes (Slatkin, 1984; Bolnick and Doebeli, 2003; De Lisle and Rowe, 2015; Li and Kokko, 2021). Selection mediated by reproduction and ecology need not be considered in isolation, and could even interact to exaggerate sexual dimorphism (Lande, 1980; De Lisle, 2019). Indeed, an interaction between sexual selection and resource competition, but also energetic trade-offs related to locomotion (flight), may best explain body size dimorphism in giant petrels (*Macronectes* spp.), the most sexually dimorphic seabirds (Gonzáles-Solís *et al.,* 2000). Sex differences in energetic trade-offs may therefore be a useful and understudied factor for explaining the existence of sexual dimorphism, particularly in cases of extreme size dimorphism.

6.2.1 Sexual dimorphism and energetic trade-offs

Animal home-range size tends to scale positively with body size (Lindstedt *et al.,* 1986; Tucker *et al.,* 2014; Tamburello *et al.,* 2015). Furthermore, in sexually dimorphic species, the larger sex has often been found to occupy more extensive home-ranges (Mysterud *et al.,* 2001; Ofstad *et al.,* 2016). However, individuals of larger species have higher basal metabolic rates and therefore greater energetic costs of maintenance, alongside higher energetic costs of travel (Taylor *et al.,* 1982; White *et al.,* 2019). Trade-offs may therefore exist between the energy an organism requires for maintenance against the energy available for locomotion, potentially reducing the home-range area that an animal can occupy (Boratyński*,* 2020). In species displaying sexual size dimorphism, it is possible that this trade-off could constrain the maximum home-range of the larger sex, which could suffer higher maintenance costs to trade-off against locomotion. Sex differences in energetic trade-offs could suggest an influence of travel costs on the evolution of sexual dimorphism.

In addition to the energetic costs of movement, home-range use by animals may be influenced by other factors including food distribution (Di Bitetti, 2001), water availability (Gehrt and Fritzell, 1998), and the distribution of rest sites and predators (Coleman and Hill, 2014). In group-living animals, such as primates, group size is also relevant, because groups containing more individuals should deplete feeding patches, such as fruiting tree canopies, faster than small groups (Chapman, 1988). Larger groups may therefore travel further each day in search of food (Stevenson and Castellanos, 2001). The result is a positive relationship between group biomass and home-range size in social animals (Clutton-Brock and Harvey, 1977; Makarieva *et al.,* 2005). Thus, other ecological factors, such as food availability, may need to be accounted for when investigating a potential influence of energetic trade-offs and space use on the evolution of sexual dimorphism.

6.2.2 Mandrill Sexual Dimorphism

Among primates, mandrills (*Mandrillus sphinx*) are the most sexually dimorphic in terms of body size, with males approximately three times heavier than females (male mean = 28.9 Kg, female mean = 9.8 Kg, in our focal group, David Lehmann *unpublished data*). In addition, males possess 4.5 cm canines and brightly colored ornamentation on their faces, rumps, and genitalia (Setchell, 2005; Leigh *et al.,* 2008; Setchell *et al.,* 2008). Though other members of the Papionine lineage exhibit sexual dimorphism in size and canine length, as well as male ornamentation (Bergman *et al.,* 2009; Galbany *et al.,* 2015), mandrill dimorphism, in particular the ornamentation of males, is uniquely extravagant (Darwin, 1871).

Another uncommon aspect of mandrill ecology is the group structure and mating system. Many Papionines, such as macaques (*Macaca* spp.), live in multi-male, multi-female groups, with resident males (Higham *et al.,* 2012). Alternatively, many baboons (*Papio* spp.) live in hierarchical societies, consisting of one-male units, containing a single dominant male and several females (Swedel, 2002; Goffe *et al.,* 2016). Most male mandrills, however, only join social groups during the breeding season, when the number of fertile adult females is highest (Hongo *et al.,* 2016). This seasonal influx of males may intensify sexual selection, and perhaps explain why mandrills are exceptionally dimorphic, because males must rapidly establish dominance and demonstrate their quality to females (Abernethy *et al.,* 2002).

It is currently unknown why male mandrills leave social groups outside of the breeding season, but travel costs relating to their large body size are one possibility (Hongo *et al.,* 2016). Mandrills live in exceptionally large social groups, termed 'hordes', often numbering 600-800 individuals (Abernethy *et al.,* 2002). The biomass of mandrill hordes is thus exceedingly high (approximately 4.9 tons for our focal horde), leading to the largest known home-ranges among non-human primates (>180km^2; White *et al.,* 2010). The extensive travel required to sustain several hundred animals may be impossible for male mandrills to maintain year-round, due to energetic trade-offs between locomotion and maintenance, with a body mass much higher than that of females.

In this study, we aimed to compare male and female spatial behavior during the breeding and non-breeding seasons, to address the question of why males seasonally leave social groups. To do so, we fitted 12 adult female and seven adult male mandrills with GPS collars, to track space use by individuals of each sex between 2017 and 2022. To investigate whether collared males were likely to have left the horde, we analyzed sex differences in home-range use, habitat selection and Brownian motion variance (Horne, *et al.* 2007), during the breeding and non-breeding seasons. If the home-range sizes and habitat choices of males are more similar to females during the breeding season and diverge during the non-breeding season, this would make it unlikely that males exploit the same areas as females outside of the breeding season and imply that they are not with the horde.

Brownian motion variance (σ^2_m) is a measure of the irregularity of animal movements, based on the actual and expected locations of an animal (Horne *et al.,* 2007) and can be interpreted as a proxy measure for the behavioral state of an animal. For example, alternations between resting or feeding and travel between feeding patches would be expected to produce higher motion variance. Mandrills are frugivorous (Rogers *et al.,* 1996; Hongo *et al.,* 2018) and frugivores may exhibit high motion variance when regularly alternating between feeding and searching for new patches of clumped fruit resources. Larger groups of animals should move between patches at higher rates than smaller groups or solitary animals (Stevenson and Castellanos, 2001). Thus, hordes of mandrills would be expected to display higher motion variance than solitary males. If the motion variance of males is more similar to females during the breeding season, but lower during the non-breeding season, this would further indicate that males are not foraging with the horde outside of the breeding season.

We then address the question of why male mandrills may opt to leave hordes outside of the breeding season, in terms of energetic trade-offs. First, using GPS collar data, we analyze seasonal changes in the daily travel distance and speed of both sexes. We expected to find that males travel similar distances to females, at similar speeds, during the breeding season. Conversely, during the non-breeding season, we expected males to travel shorter distances, at slower speeds, which would indicate that they expend less energy on travel when there are few fertile females available. Because GPS data is obtained remotely, we could not be certain that males were solitary or social (hereafter, "group status") on days when they were not observed. We therefore corroborated the data from more recent GPS collars, by analyzing data collected via direct observations between 1998 and 2004 (White, 2007). These data constituted daily path lengths of known individuals, including females, social males, and solitary males. We therefore analyzed the effects of sex and season on the daily path lengths of individuals whose group status was known, to ascertain whether these data produced similar results to GPS data. Furthermore, fruit availability data was available for the time period that focal follows were conducted. We therefore also analyzed the impact of fruit availability on mandrill daily path lengths, to test whether fruit availability had a greater impact on mandrill travel than sex, breeding seasonality and group status.

6.3 Methods

6.3.1 Authorization and Ethical Approval

The collaring of mandrills was approved by the Centre de la Recherche Scientifique et Technologique (CENAREST), Gabon (AR0036/16) and received ethical approval from the University of Stirling, UK (AWERB (16/17) 39).

6.3.2 Study Site and Population

Our study was conducted in Lopé National Park, Gabon (-0.2N, 11.6E). The park is 90% covered by continuous forest, with a forest-savanna mosaic covering 10% of the northern and eastern areas. In the mosaic, savanna constitutes the largest habitat type and is intersected by strips of gallery forest running along waterways. We considered three major habitat types relevant for mandrill habitat selection, given the approximate home-range of the focal horde: continuous forest, gallery forest and savanna. Approximately 1400 mm of rain falls across an annual cycle, which is split into four seasons: a long wet season (February to May), a long dry season (June to August), a short wet season (September to November), and a short dry season (December to January) (White, 1994, Bush *et al.,* 2020). The seasonality in rainfall leads to temporal variation in fruit production, which impacts the diets of primates within the park (Tutin *et al.,* 1997; Chapter 3).

We fitted GPS collars to members of a horde that largely occupies the forest-savanna mosaic (White *et al.,* 2010). The number of individuals in the horde is usually between 600-800, but can rise to over 1000 (Abernethy *et al.,* 2002). Horde size is so variable because the number of older males fluctuates seasonally (Abernethy *et al.,* 2002) and because the group exhibits highly flexible, fission-fusion behavior in response to seasonal changes in fruit production (White *et al.,* 2010). Furthermore, some males may remain within the horde to pursue breeding opportunities that arrive outside of the main breeding season (Hongo *et al.,* 2016). These two factors mean that, when analyzing the spatial behavior of individuals using remotely sensed GPS collar data, the size of (sub-)groups in which females are present and male group status cannot be certain. However, given that male group status is related to seasonal availability of fertile females (Abernethy *et al.*, 2002; Hongo *et al.*, 2016), it is likely that males are more often solitary in the non-breeding season. Similarly, if horde fissioning is related to fruit availability, female (sub-)groups are probably often larger during periods of fruit abundance (White *et al.*, 2010).

6.3.3 Animal Capture and Collar Fitting

We fitted collars to mandrills between 01/08/1998 and 15/11/2022. From 1998 to 2008 these were VHF collars, requiring close (<1km) contact with the animals to verify positions and group compositions. From 2017 onwards, we used GPS collars and remote tracking alongside VHF capabilities. Consequently our data covers multiple seasons and years but, crucially, GPS locations were returned for females and males across 346 and 365 days of the year, respectively, during the 2017-2022 period. Thus, we were able to analyze the relationship between day of year and the spatial behavior of both sexes.

Individual animals were anesthetized using Zoletil (Tiletamine and Zolazepam), administered via a teledart applied with a CO2 Injection Rifle (Daninject JM SP 25). Males received 80 mg Tiletamine and 80 mg of Zolazepam. Females received 25mg of Tiletamine and 25mg of Zolazepam. The approximate age in years, age-sex class and weight were recorded for each animal. A Telonics GPS Iridium collar weighing <3% of animal body mass (a maximum of 5% is recommended for terrestrial primates) was then fitted to each animal. The collars also carried a VHF transmitter for tracking individuals and this was tested before fitting each collar. Once collars were fitted, each animal was allowed to recover within a soft bag, then released and visually monitored.

6.3.5 Focal Follows

To record the daily path length of known individuals, focal follows were carried out between 17/09/1998 and 06/05/2004. Focal follows were conducted by recording the sleeping site of an individual and re-locating the individual the following morning using VHF radiotelemetry. A given individual was followed for the entire day and bearings taken via radiotelemetry to record the location of the individual every 30 minutes. Daily path length was then calculated using the minimum distances through forest habitat, or using a savanna crossing of <180m between half-hourly locations and are therefore conservative estimates. For more details on the calculation of daily path lengths using focal follows see White (2007).

6.3.6 Analyzing Home-Range Use

We analyzed GPS location data using the R Programming Language (R Core Team, 2022) and the ‘move’ v4.1.1 package (Kranstauber *et al.,* 2022). Because the frequency at which successful fixes were obtained varied between individuals, we filtered the data to include only the first fix each day and only fixes obtained before 08:01 am. Our data thus generally corresponds to the daily ‘waking site’ of each individual, or a nearby location in the case of fixes obtained closer to 08:01 am. Using this approach maximized the number of individuals we were able to include in our analysis, but has the disadvantage of quantifying daily distance and travel speed using euclidean distances (rather than travel through appropriate habitats) between waking sites. Mandrill movement may deviate substantially from straight lines between daily locations (White *et al.*, 2010), but we considered it likely that longer estimated euclidean distances between waking sites would generally correspond with greater actual travel distances and speeds. We calculated distances and speeds between daily waking sites using the inbuilt *distance* and *speed* functions from the ‘move’ package.

To calculate home-range size and Brownian motion variance, we fitted dynamic Brownian bridge movement models (Kranstauber *et al.,* 2012), again using the ‘move’ package. These models estimate home-ranges based on conditional random walks between locations and are advantageous over some other home-range estimators because they consider the order and timing of locations, thus accounting for spatio-temporal autocorrelation (Kranstauber *et al.,* 2012). For applying the dynamic Brownian bridge movement models to daily location data, we set the margin to 3, the window size to 7, meaning mandrill movement was modeled based on sequential one week chunks of data (Silva *et al.,* 2020). The location error was set to 5, thus our models assumed that GPS collar location fixes were accurate to within 5m. The extent was set to 0.85 and the dimSize to 1000 though an iterative process, to ensure the map area was large enough to contain each estimated home-range. We estimated home-ranges using subsets of 30 daily locations for each animal. Using 30 day subsets of data allowed us to produce monthly home-range estimates that were reproducible between animals for which we had differing amounts of data. We were also able to produce multiple home-range estimates for males and females in both the breeding and non-breeding seasons, to analyze the effects of sex and season on home-range size. For three mandrills (two females, one male), shorter periods of between 20-30 days were used, to include these individuals in the analysis. Whether or not these individuals were included in the analysis did not change our qualitative conclusions. We took the 95% isopleth of each estimated home-range as the monthly home-range for each animal. The mean day of year for each 30 day period (i.e. the middle day) was used to allocate each home-range estimate to the breeding or non-breeding season. In addition to the order and timing of location fixes, dynamic Brownian bridge movement models utilize an estimate of Brownian motion variance (σ2m) for estimating home-ranges. We therefore extracted the motion variance estimates for each animal to analyze seasonal changes in the frequency of behavioral state changes for males and females.

6.3.7 Statistical Analysis

To analyze seasonal changes in monthly home-range size we used a generalized linear mixed model, with monthly home-range size as the response variable and sex (‘male’, ‘female’), season (‘breeding’, ‘non-breeding’) and their interaction as independent variables. We also included a random intercept for individual identity, to account for individual differences in home-range size.

To analyze temporal variation in habitat selection, we first assigned a habitat type to each daily first GPS collar location, using the *st_within* function from the ‘sf’ package (Pebesma, *et al.* 2018). We then fitted a multinomial generalized additive mixed model, with the binomial presence of individuals in each habitat type as the response variable. As fixed factors, we included a smoother for day of year, habitat type (‘gallery forest’, ‘continuous forest’, ‘savanna’), sex and their interactions. Day of year was included as a cyclic cubic regression term to allow the intercepts for early January and late December to align. Random intercepts for individual identity were also included, to account for differences between individuals in the relationship between habitat selection and day of year. We did not fit a global effect for day of year, instead fitting individual curves for each habitat type, each with their own wiggliness (equivalent to Model I in Pederson *et al.,* 2019). Thus, individual curves were created describing the separate relationships between day of year and selection of each habitat type, by each sex.

To analyze temporal changes in the motion variance, daily travel distance and travel speed of each sex, we also fitted generalized additive models, with each of these variables as a response. Excepting the lack of a fixed factor for habitat type, these generalized additive mixed models were fitted following the same procedure as the model examining habitat selection. For all generalized additive mixed models, restricted maximum likelihood was used to estimate smoothing parameters.

Next, we used a linear mixed model to investigate the effect of sex and season on the daily path lengths of known individuals, recorded using focal follows. Daily path length was included as the response variable and a 'group type' categorical variable describing individual sex, group status and season ('horde member all seasons', 'social male all seasons', 'solitary male breeding season', solitary male non-breeding season') used as a fixed effect. 'Horde member' instead of 'female' was used as a category because one individual was a juvenile male. However, because juvenile males are also permanent horde members, tracking this individual was equivalent to tracking adult female horde members. We also included random intercepts for individual identity to account for individual differences in daily path length.

To investigate whether changes in fruit availability, related to climatic seasonality, was as or more important than breeding seasonality, we also analyzed the impact of fruit availability on daily path lengths. For a detailed description of how fruit availability was calculated, refer to Chapter 3. To analyze the impact of fruit availability, we constructed linear mixed models with daily path length as a response variable, 'group type' as a categorical fixed factor, monthly fruit availability as a continuous fixed factor and random intercepts for individuals. We ran this model with and without an interaction between 'group type' and monthly fruit availability. We also constructed a linear mixed model with monthly fruit availability as the sole predictor of daily path length, with random intercepts for individuals, to examine if fruit availability had an effect of daily path length independent from group type. We compared the four candidate models for explaining variation in daily path length using AIC scores, taking the model with the lowest score as the preferred model (Burnham *et al.,* 2011).

We graphically examined the residuals of all models, to ensure that model assumptions were met. In the analysis of daily path lengths based on focal follows, a gaussian error structure was suitable, with well distributed residuals. For the habitat selection model, a binomial error structure produced an appropriate residual distribution. For models examining temporal changes in monthly home-range size, daily travel distance, travel speed and motion variance, we found a gaussian error structure to be unsuitable. Each of these measures sometimes involved low means that approached the lower bound of displacement (0). Because a gamma distribution is constrained to be positive but can also include continuous (i.e. non-integer) numbers, it closely matches the properties of the data. We therefore specified a gamma error structure, which led to well distributed residuals.

6.3.8 Software

All analyses were completed in R v4.1.3 (R Core Team, 2022). Data wrangling, plotting and production of tables were completed using the packages 'tidyverse' 1.3.2 (Wickham *et al.,* 2019), 'lubridate' v1.9.0 (Grolemund and Wickham, 2011), 'ggplot2' v3.4.0 (Wickham, 2016) and 'flextable' v0.8.3 (Gohel and Skintzos, 2022). Creation and manipulation of shapefiles was conducted using the 'sf' v1.0.9 (Pebesma, 2018) and 'concaveman' v1.1.0 (Gombin *et al.,* 2020) packages. Home-range calculation was carried out with the packages 'move' v4.1.1 (Kranstauber *et al.,* 2022) and 'moveViz' v0.10.5 (Schwalb-Willmann *et al.,* 2020). All statistical models, checks of residuals and predictions were completed with 'boot' v1.3-28.1 (Canty and Ripley, 2022), 'mgcv' v1.8-41 (Wood, 2017), 'glmmTMB' v1.1.5 (Brooks *et al.,* 2017) and 'DHARMa' v0.4.6 (Hartig, 2022).

6.4 Results

6.4.1 The effect of sex on space use

To explore whether male and female spatial behavior varied between the breeding and non-breeding seasons, we examined seasonal changes in monthly home-range size, habitat use and Brownian motion variance. Males appeared to be more spatially similar to females during the breeding season and to use somewhat more distinct areas during the non-breeding season (Figure 6.1). Regarding seasonal changes in monthly home-range size, a generalized linear mixed model (Table 6.1) suggested that male and female home-ranges were similar in size during the breeding season. However, the sexes showed distinct changes in the non-breeding season, with females displaying larger home-ranges and male home-ranges shrinking (Figure 6.2)

Table 6.1. Summary of a generalized linear mixed model examining male and female monthly home-range sizes during the breeding and non-breeding seasons.

		Estimate	**Standard Error**	***z***	***p***
Fixed Effects					
Intercept		0.055	0.007	8.24	<0.0001
Male		0.004	0.010	0.36	0.72
Non-Breeding		-0.018	0.008	-2.26	0.024
Male: Non-Breeding		0.031	0.014	2.27	0.023
Random Effects					
Individual	Intercept Variance	0.000049			

A generalized additive model revealed that male habitat selection was also more similar to females during the breeding season and more distinct during the non-breeding season (Figure 6.3). Females were present almost exclusively within gallery forests throughout the year, with some use of continuous forest during the non-breeding season. In contrast, males showed greater use of continuous forest during the non-breeding season, coupled with a reduction in gallery forest use. As for home-range size, males were much more similar to females during the breeding season and largely used gallery forests. The use of savanna habitats by both sexes was very low and occurred at similar frequencies between the breeding and non-breeding seasons.

The sexes also differed in temporal patterns of Brownian motion variance. A generalized additive model indicated female motion variance fluctuates regularly throughout the year, with peaks in the breeding and non-breeding seasons. Conversely, male motion variance showed a clear peak only during the breeding season (Figure 6.4).

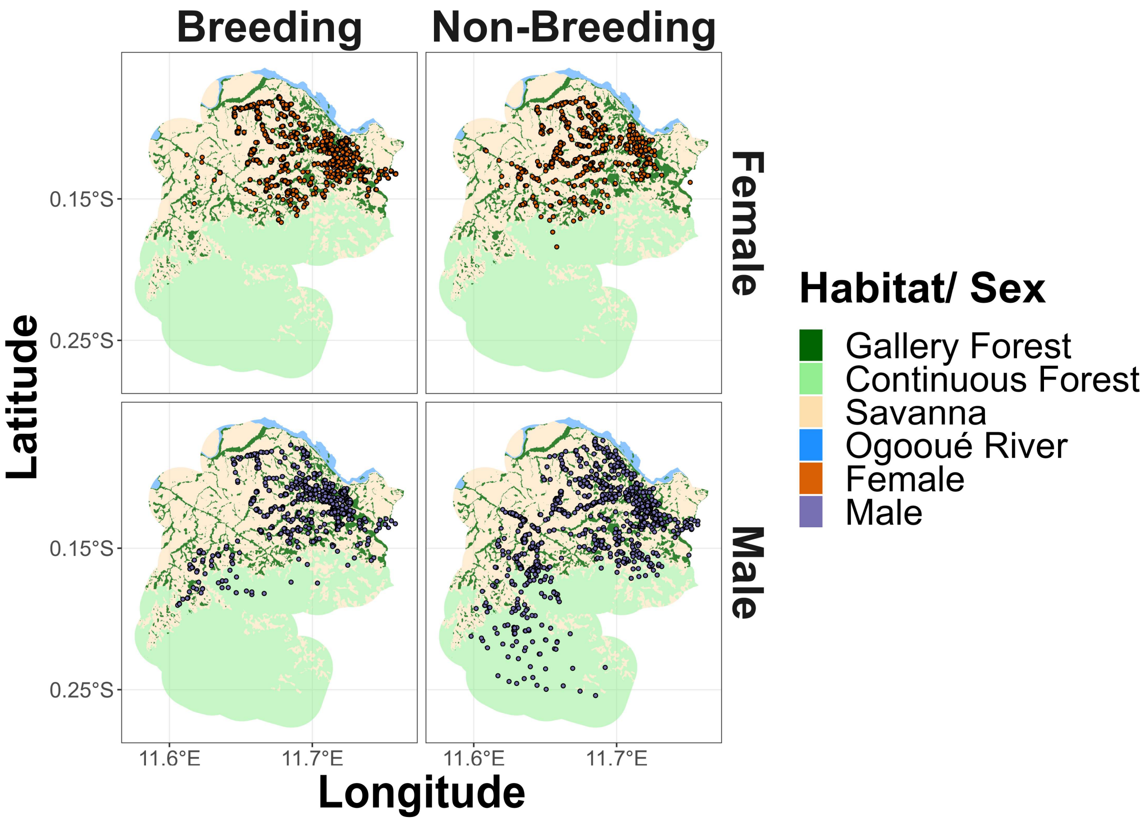

Figure 6.1. Locations of male (n individual = 7, n locations = 1698) and female (n individual = 12, n locations = 1606) mandrills during the breeding and non-breeding seasons. Each point indicates the daily waking site of a collared individual Some points lie outside of the habitat areas, because on some occasions mandrills crossed the Offoué river (distinct from the Ogooué to the north of the park), which is the eastern park boundary.

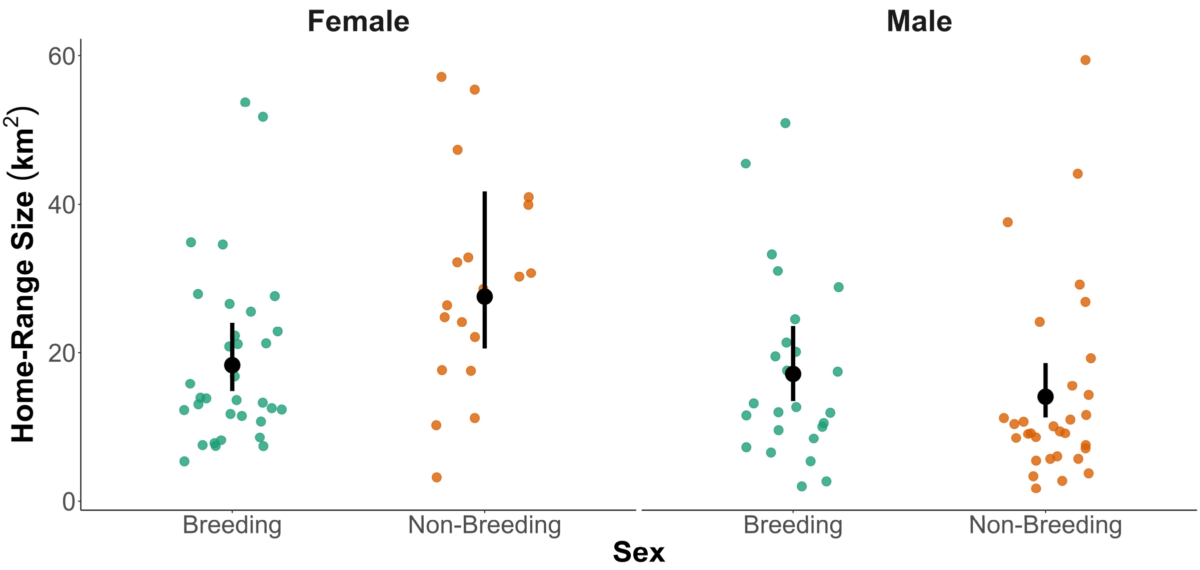

Figure 6.2. Male (n individuals = 7, n home-ranges = 56) and female (n = 12, n home-ranges = 52) home-range sizes during the breeding and non-breeding seasons. Each colored point represents the home-range size of one individual, over one month. Black points represent the mean monthly home-range size for a given group and vertical black lines show the 95% confidence interval around the means.

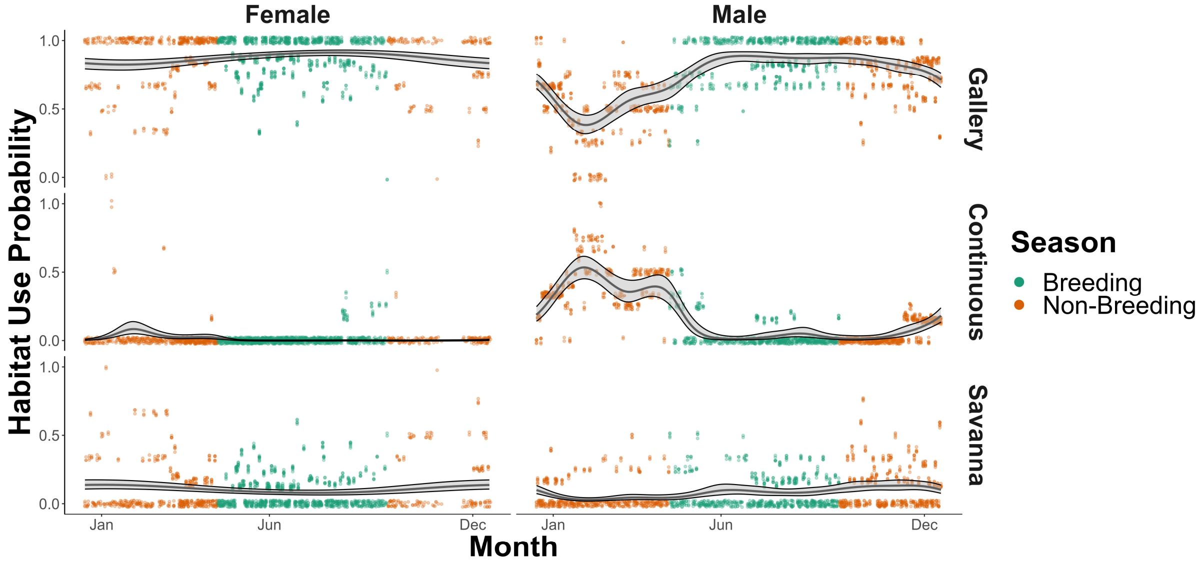

Figure 6.3. Seasonal changes in habitat selection by adult male (n individuals = 7, n locations = 5094) and adult female (n individuals = 12, n locations = 4818) mandrills. Each point represents the first location recorded each day, for a single animal. Grey lines display the predicted likelihood of each sex being present in each habitat type on a given day of the year. Grey ribbons display the 95% confidence interval around that prediction.

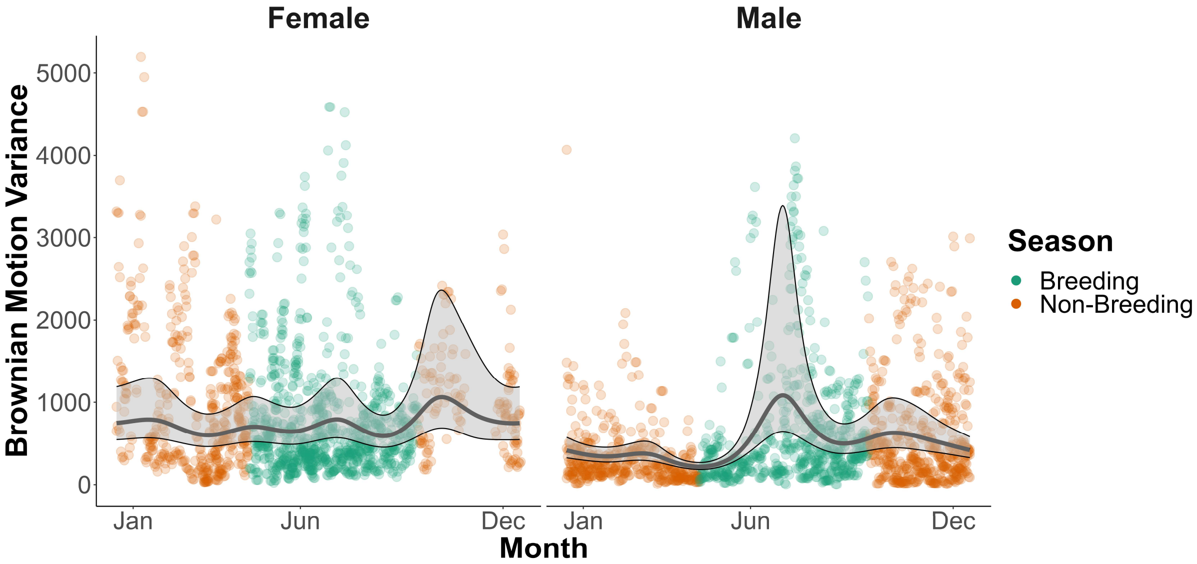

Figure 6.4. Seasonal changes in Brownian motion variance, a measure of the irregularity of space use, of adult male (n = 7) and adult female (n = 12) mandrills. Points represent a single measure of motion variance for a single animal over a three day period (n females = 1548, n males = 1669). Grey lines display the predicted motion variance of each sex on each day of the year. Grey ribbons display the 95% confidence intervals around the predicted motion variance of each sex.

6.4.2 The effect of sex on travel

To investigate potential sexes differences in travel, we compared male and female daily travel distance and speed during the breeding and non-breeding seasons. Generalized additive models suggested that daily travel distance and speed fluctuate aseasonally in females, peaking during both the breeding and non-breeding seasons. However, male daily distance and speed, as for motion variance, showed major peaks during the breeding season (Figure 6.5; Figure 6.6).

Our analysis of GPS collars is limited by uncertainty about the social status of collared males during the period each individual was tracked. This uncertainty means that some males may have been social during the non-breeding season and some solitary during the breeding season. Thus, analyzing male spatial behavior in the context of breeding seasons, as opposed to known group status, is only a proxy measure following general patterns of observed mandrill behavior (Abernethy *et al.,* 2002). A major consequence of this is that the seasonal changes in male home-range size, motion variance, daily distance and speed are likely to be conservative. Had we been able to categorize males as social or solitary, it is likely that associations between group status and movement would be stronger than we have found here.

Because of uncertainty about the group status of males, we supplemented our analysis of GPS data with direct observational data on known individuals, from an earlier time period. Analyzing these focal follows using a linear mixed model (Table 6.2) showed that daily path lengths were similar between permanent horde members (females and juveniles) and social adult males. In contrast, solitary adult males traveled shorter distances than horde members and social males during both the breeding and non-breeding seasons, on average (Figure 6.7). AIC scores suggested that models including monthly fruit availability as a predictor of mandrill daily path lengths were not preferable to models considering only group type (Table 6.3).

Table 6.2. Summary of a linear mixed model examining the effect of group type and season on mandrill daily path lengths.

		Estimate	**Standard Error**	***z***	***p***
Fixed Effects					
Intercept		3,760.35	314.07	11.97	<0.0001
Social Male		343.05	814.64	0.42	0.674
Solitary Male Breeding Season		-1,837.30	852.27	-2.16	0.031
Solitary Male Non-Breeding Season		-2,294.69	926.49	-2.48	0.013
Random Effects					
Individual	Intercept Variance	1206218			
Residual	Observation Variance	3964811			

Table 6.3. AIC scores of models examining the effect of group type and monthly fruit availability on mandrill daily path length.

Fixed Factors	**Random Factors**	**Degrees of Freedom**	**AIC**
Group Type	1|Individual	6	3,916.8
Group Type + Fruit Availability	1|Individual	7	3,917.7
Group Type * Fruit Availability	1|Individual	10	3,922.2
Fruit Availability	1|Individual	4	3,920.2

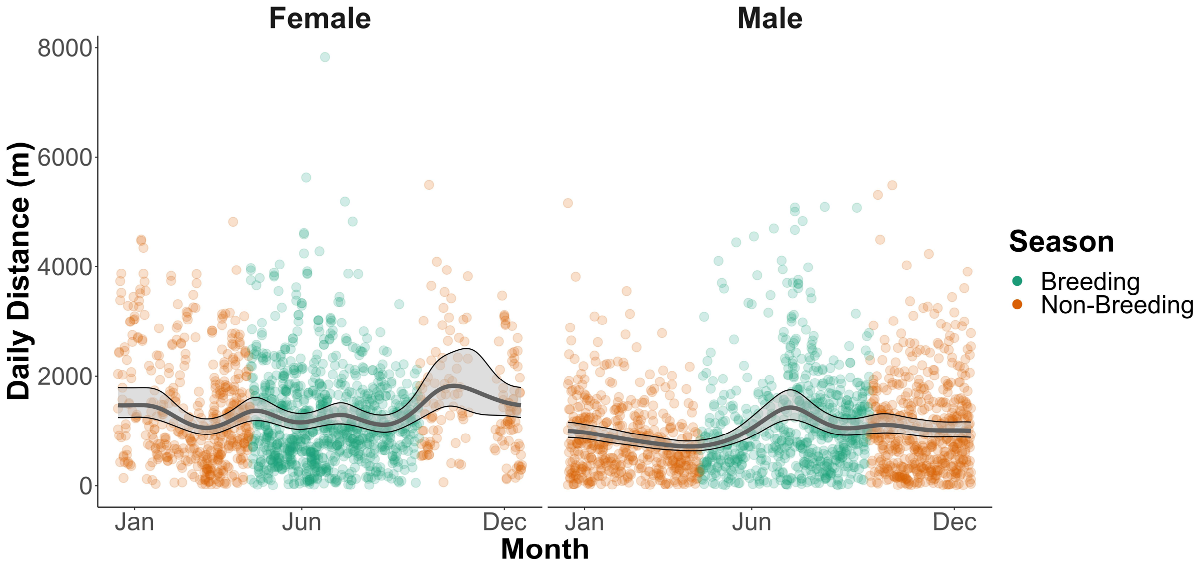

Figure 6.5. Seasonal changes in daily distance, meaning straight line distance between waking sites, of adult male (n = 7) and adult female (n = 12) mandrills. Points represent a single measure of distance travelled in one day for a single animal (n females = 1594, n males = 1693). Grey lines display the predicted daily distance of each sex on each day of the year. Grey ribbons display the 95% confidence intervals around the predicted daily distance of each sex.

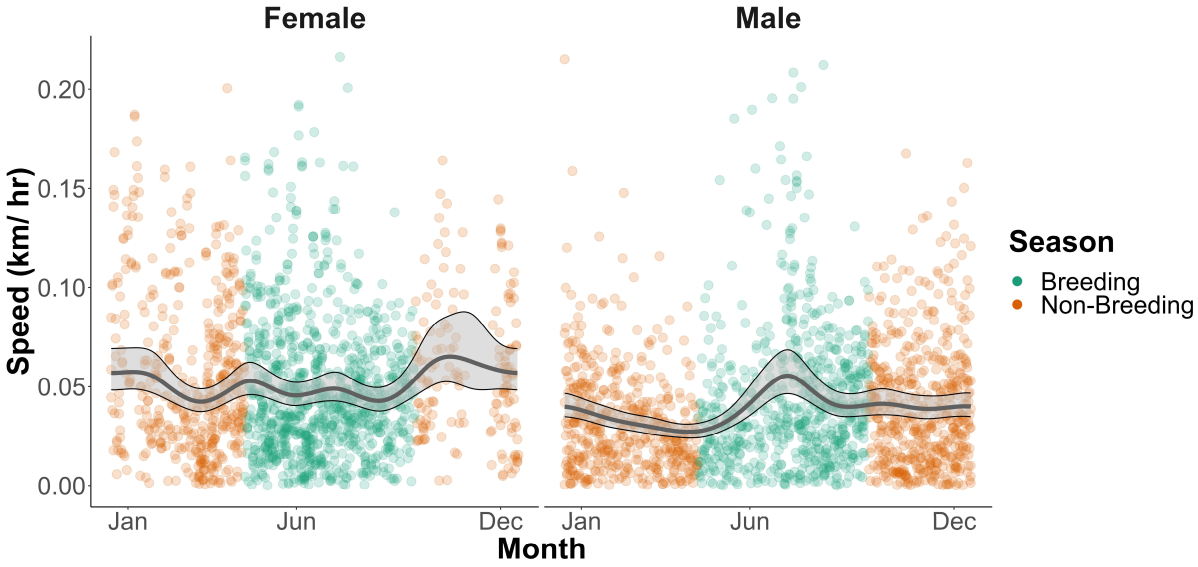

Figure 6.6. Seasonal changes in travel speed, meaning speed between daily waking sites, of adult male (n = 7) and adult female (n = 12) mandrills. Points represent a single measure of travel speed over one day for a single animal (n females = 1594, n males = 1693). Grey lines display the predicted speeds of each sex on each day of the year. Grey ribbons display the 95% confidence intervals around the predicted speed of each sex.

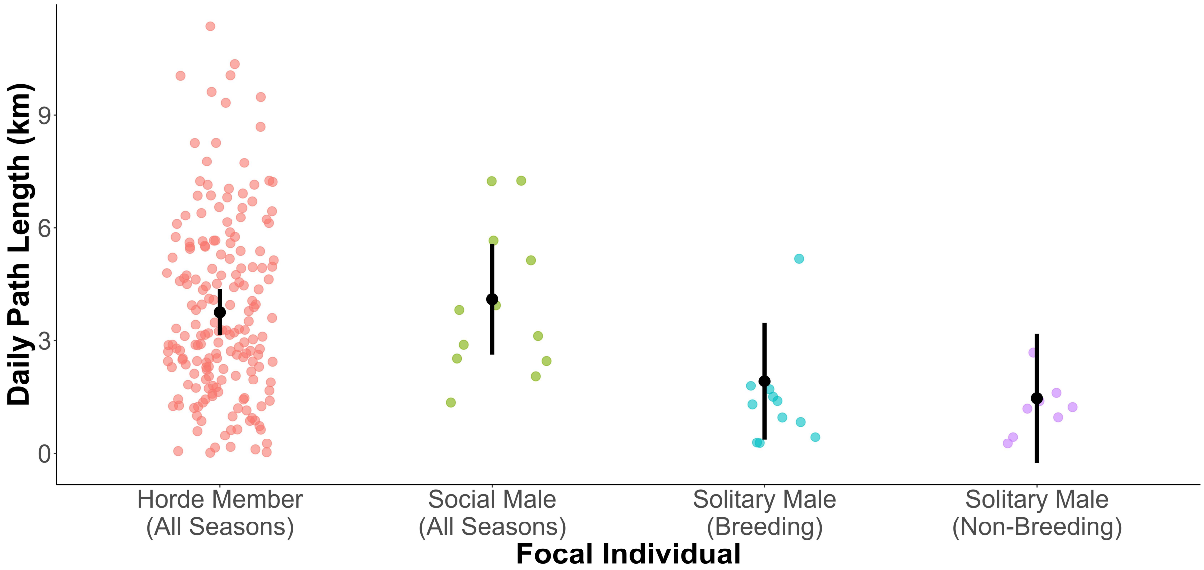

Figure 6.7. Daily path length differences between horde members (n individuals = 23, n daily paths = 184), social males (n individuals = 5, n daily paths = 12), and solitary males the breeding (n individuals = 5, n daily paths = 11) and non-breeding seasons (n individuals = 4, n daily paths = 8). Colored points represent a single measure of daily path length, obtained from a direct focal follow of an individual mandrill from sleeping site to sleeping site. Black points represent the mean daily path length of each group type and black vertical lines display the 95% confidence interval around each mean.

6.5 Discussion

Our study is the first to explore sex differences in mandrill spatial behavior using GPS collars, allowing males to be tracked even when solitary. We reveal clear differences between males and females in patterns of home-range size, habitat selection and space use during the non-breeding season. Conversely, in the breeding season, male spatial behavior is similar to females. During the non-breeding season, males, on average, exploited smaller home-ranges than females, used distinct habitats, and displayed less variable movement. These results imply that males in our study were not permanent members of the focal horde and further evidence that male mandrill group presence varies depending on the availability of fertile females. Furthermore, during the non-breeding season, males exhibited shorter average travel distances and lower speeds, suggesting that males expend less energy on travel during this period. These findings are a first indication that travel costs may influence the mandrill mating system and that energetic trade-offs may be important to the evolution of extreme sexual dimorphism in mandrills.

6.5.1 The effect of sex on seasonal space use.

Information on unhabituated mandrill space use, and particularly by solitary males, has historically proven difficult to obtain because of the dense forests in which mandrills are found (Hongo *et al.,* 2016). We examined sex differences in seasonal habitat selection, monthly home-range size, and Brownian motion variance, using GPS collars, which allowed space use data to be obtained remotely, without carrying out focal follows (Figure 6.1).

Male habitat selection differed from females on a seasonal basis. Throughout the year females were found largely in gallery forests, with only a small amount of continuous forest use in the non-breeding season. It is relevant to note that in the mosaic structure, some forest types may be briefly used simply as a travel corridor through a predominantly savanna area, rather than selected as a preferred choice of forest habitat. Conversely, males increased their use of continuous forest during the non-breeding season and, like females, almost exclusively used gallery forest in the breeding season. Much higher use of continuous forest by males is strong evidence that they, at least sometimes, were not travelling with the horde. It is possible that these males were alongside a sub-group of females containing no collared individuals. But the predicted use of continuous forest by females being minimal for the entire year makes the use of this habitat by uncollared females seem less likely.

The generalized linear mixed model examining the relationship between sex, season and monthly home-range size suggested that male and female home-ranges are similar in size during the breeding season. However, as predicted, male home-ranges shrank during the non-breeding season, whereas female home-ranges became larger. Primate home-ranges are expected to increase linearly with group biomass, and mandrill hordes conform to this expectation (White *et al.,* 2010). So, the fact that male home-ranges were smaller during the non-breeding season suggests that they were in groups of smaller biomass than females during this time, if they were not solitary.

The horde's fission-fusion behavior leads to subgroups containing fewer individuals and hence lower biomass (White, 2007). But fission-fusion by the horde cannot explain relatively small male home-ranges, otherwise the effect of season on male home-ranges would be indistinguishable from that of females. Males could leave the horde and form bachelor groups, with lower biomass and home-range requirements. However, large bachelor groups of multiple mature males have never been observed in mandrills, though a single solitary male may associate with up to three younger males (Abernethy *et al.,* 2002; SEGC, *unpublished data*). Thus, the smaller average home-ranges of males during the non-breeding season strongly suggests that at least some males were solitary, or associated with <5 others, and so required less space than social females.

We also found sex differences in seasonal patterns of Brownian motion variance. A generalized additive model revealed that female Brownian motion variance fluctuated throughout the year, showing multiple peaks in the breeding and non-breeding seasons. However, males showed a clear peak in motion variance during the breeding season. Higher Brownian motion variance indicates fewer regular paths and increased movement, whereas lower values indicate more regular paths and lower movement (Silva *et al.,* 2018). Mandrills are omnivores, with a diet dominated by fruit (Nsi Akoué *et al.,* 2017; Chapter 3), and would therefore be expected to travel most when moving between fruiting trees (Goldsmith *et al.,* 1999). As fruit patches (tree canopies) are of similar sizes larger primate groups should move more regularly between feeding patches than smaller groups (Di Bitetti, 2001). Conversely, solitary males would need to travel in search of new feeding patches less regularly than females. Longer patch residency times would result in less frequent behavioral state changes between feeding and travelling, explaining lower male motion variance in the non-breeding season. Thus, the fact that males exhibited an obvious peak in motion variance during the breeding season is further evidence that they were within larger groups during this time, and either solitary or in smaller groups during the non-breeding season.

The similarity of male habitat selection, home-range size, and motion variance to females during the breeding season, and dissimilarity during the non-breeding season, all strongly suggest that collared males were only temporary horde members. Furthermore, the divergent temporal patterns exhibited by each sex indicates that their space use is governed by different factors. Female mandrill space use is known to be driven by food availability (White, 2007; Hongo *et al.,* 2018). The home-ranges of female mandrills were larger during the non-breeding season, which is also the time of year when fruit availability in highest (Tutin *et al.,* 1997). During periods of fruit abundance, the horde tends to remain as a larger units, whereas during periods of scarcity, the horde may fission into sub-groups (White, 2007). Larger sub-groups likely explain why females used greater areas during the non-breeding season. The fact that males displayed the opposite pattern, with larger home-ranges in the breeding season, implies that male home-range use is not primarily driven by fruit availability and fission-fusion behavior. Our results, alongside those of prior studies (Abernethy *et al.,* 2002; Hongo *et al.,* 2016), indicate that males join the horde during the breeding season. This is most clear when considering that males were often located in the continuous forest during the non-breeding season, a habitat rarely exploited by females. Male space use therefore appears to be driven by the seasonal availability of fertile females, as opposed to fruit availability (Abernethy *et al.,* 2002; Brockmeyer *et al.,* 2015; Hongo *et al.,* 2016).

6.5.2 Males expend less energy on travel during the non-breeding season.

Group membership provides male primates with a number of benefits, including access to mating partners (Plavcan, 2001; Cassini, 2020b) and enhanced predator detection (van Shaik *et al.,* 1983; Matsumoto-Oda *et al.,* 2018). So, if male mandrills are leaving the horde, the loss of female access and predator detection must be offset by the benefits of being solitary. Two generalized additive models indicated that the average daily travel distance and speed of males was lower during the non-breeding season and increased during the breeding season. Energetic expenditure on movement rises with the distance an animal travels (Marcus Rowcliffe *et al.,* 2012) and with the speed at which an animal moves (Taylor *et al.,* 1982). Thus, the lower average daily distances and speeds that male mandrills exhibited during the non-breeding season suggest that they expend less energy on travel during this period.

To confirm that the group status of males is the most likely determinant of their spatial behavior, we analyzed daily path length data for individuals whose social status was known.

A linear mixed model showed that the daily path lengths of social males were similar to permanent members (females and juveniles) of the horde. In contrast, solitary males traveled significantly shorter distances than horde members. Reduced travel by solitary males was consistent whether individuals were tracked in the breeding or non-breeding season.

Including monthly fruit availability in models explaining daily path lengths did not improve the predictive power of the models (Table 6.3). A limited effect of fruit availability on the daily path length of horde members was surprising, given that female space use is influenced by fruit availability in another study site (Hongo *et al.,* 2018; 2022). It could be that our measure of monthly fruit availability, corresponding to the entire study area, was too coarse in resolution to associate strongly with spatial behavior that occurs on more local scales. However, the same fruit availability measure was associated with fruit consumption by the horde, during the same time period that the focal follows were conducted, meaning our measure of fruit availability is associated with the hordes behavior (Chapter 3). Alternatively, flexible social behavior by the horde may explain why fruit availability is a poor predictor of daily path length. While the actual location of mandrill hordes is determined by the distribution of fruit, fission-fusion behavior might allow females to moderate the distances they travel by forming smaller sub-groups. Thus, flexible social behavior could allow hordes to mitigate lower fruit availability, by travelling shorter distances in smaller groups, that deplete patches more slowly. Low explanatory power of fruit availability for male movement, relative to group status, implies that changes in male social behavior is the primary determinant of male daily path length. This analysis of known individuals thus supports our conclusion that male spatial behavior is driven primarily by group membership, as opposed to other factors, such as food availability.

Why should male mandrills need to forgo the benefits of group life to expend less energy on travel, when the relative cost of traveling further or faster tends to be lower for larger animals (Taylor *et al.,* 1982)? This question is especially pertinent given that, after controlling for group size, larger bodied primates tend to have larger home-ranges (Milton and May, 1976). The home-ranges of mandrills are exceptionally large compared to other primates, due to the total biomass of mandrill hordes (White *et al.,* 2010). It may be that the home-ranges of mandrill hordes are so large, and the size differences between males and females so extreme, that the energetic costs of maintenance for males are too high to remain with the horde all year.

This idea is supported by investigations showing that larger animals exhibit higher basal metabolic rates (White *et al.,* 2019) and that these energetic costs may trade-off against the maximum home-range size that an animal can occupy (Boratyński*,* 2020). Furthermore, when male mandrills are courting females, they spend a substantial amount of time mate guarding and fighting other males (Setchell *et al.,* 2005; Setchell *et al.,* 2016). Stable isotope analysis suggests that time devoted to mate guarding produces nutritional stress in males during the breeding season (Oelze *et al.,* 2020). The most dominant males also experience greater oxidative stress than lower ranking males, or females, during the breeding season (Beaulieu *et al.,* 2014). Moreover, in semi-free ranging groups, fecal glucocorticoid metabolites and parasite load are elevated in dominant males (Setchell *et al.,* 2010). As a result, adult males may end the breeding season in poor body condition which, coupled with higher baseline costs of body maintenance, renders them unable to continue to travel alongside the horde. Abandoning the horde and expending less energy on travel may thus form part of a strategy to recoup sufficient body condition to compete for females in the following breeding season.

6.5.3 A role for energetic trade-offs in the evolution of mandrill dimorphism?

We found that, outside of the breeding season, males selected different habitats, used smaller home-ranges, and displayed lower motion variance than females, all of which supports previous studies showing that most males leave mandrill hordes during the non-breeding season (Abernethy *et al.,* 2002; Hongo *et al.,* 2016). The lower average travel distance and speed of males we found in the non-breeding season suggest that lower travel costs may be one of the reasons male mandrills leave social groups. Sex differences in locomotion costs are not commonly invoked to explain the evolution of sexual dimorphism in primates, but have been proposed in other species (Gonzáles-Solís *et al.,* 2000).

Sexual dimorphism is instead generally explained by sexual selection (Andersson, 1994). There is strong evidence for sexual selection in mandrills, in which larger body size, longer canines and brighter coloration are all positively associated to male rank attainment, female preference and reproductive success (Setchell, 2005; Leigh *et al.,* 2008; Setchell *et al.,* 2008). However, if labile traits such as body size and coloration are related to male reproductive success, it is possible that the energy balance of individuals is also a relevant factor. Individuals are expected to devote energy towards reproductive effort only once their basic metabolic requirements have been met (Brown *et al.,* 1993). In social animals, an individuals' ability to meet these requirements may be impacted by within-group feeding competition and the costs of traveling with a group (Markham *et al.,* 2017).

Theory suggests that resource competition can act to enhance sexual dimorphism produced by sexual selection (De Lisle, 2019). Analyzing the same individuals as in this study, Chapter 5 showed that male mandrills are less impacted than females by resource competition. However, the stable isotope analysis used in Chapter 5 could not determine if males avoid resource competition by leaving the horde, or if their large body size allows males to dominate feeding patches within the horde. The spatial analyses presented here suggest that the same males often leave the horde outside of the breeding season, suggesting that the avoidance of feeding competition is what allowed males to exhibit more dietary consistency than females (Chapter 5).

Taken together, the spatial and isotopic analyses of the same males imply that these individuals experience reduced feeding competition and travel costs, as a result of leaving the horde. Solitary males should therefore be able to maintain a more positive energy balance than social males, as result of greater food intake and reduced energy expenditure. Coupled with Oelze *et al.* 's (2020) finding of nutritional stress in actively breeding males, our isotopic and spatial analyses suggest that male energy balance has impacted the mandrill mating system, by driving males to seasonally leave the horde.

The temporary nature of male group presence has two impacts on the mandrill mating system. Firstly, the dominance hierarchies among males are unstable (Smit *et al.,* 2022), meaning males must compete for dominance upon entering the horde. Secondly, males are unable to form long-term relationships with females (Abernethy *et al.,* 2002) and must therefore communicate their quality to females through other means, such as ornaments. Intra- and inter-sexual breeding competition, the two components of pre-copulatory sexual selection, are thus likely to be exaggerated by males entering and leaving the horde, compared to primate species that form more stable societies. Our present results, and those of Chapter 5, suggest resource competition and energetic trade-offs compel males to leave mandrill hordes. These results are supportive of the possibility that ecological factors, unrelated to reproduction, have impacted the mandrill mating system to produce stronger sexual selection and exaggerate sexual dimorphism in mandrills.

Chapter 7: General Discussion

7.1 Background

Determining the origins of sexual dimorphism has been a major focus of evolutionary ecology, yet a complete explanation of how sexual dimorphism evolves remains elusive (Shine, 1989; Wyman *et al.,* 2013). The most widely accepted explanation is that anisogamy leads to sex differences in optimal reproductive strategy (Parker and Pizzari, 2015). These sex differences result in sexual or fecundity selection that may favor sexual dimorphism in morphological or behavioral traits that optimize the reproductive success of each sex (Lindenfors *et al.,* 2002; Mitoyen *et al.,* 2019). However, some sexually dimorphic traits, such as body size, may not only influence the reproductive success of males and females, but also their respective ecologies (Selander, 1966; De Lisle and Rowe, 2015). The existence of ecologically relevant sexual dimorphisms suggests that alternative evolutionary mechanisms, mediated by ecology instead of reproduction, could also produce sexual dimorphism (Slatkin, 1984; De Lisle, 2019). For example, sex differences in nutritional optima, energetic trade-offs, or response to resource competition could favor the evolution of ecological sexual dimorphisms (Gonzáles-Solís *et al.,* 2000; De Lisle, 2023). The notion of sexual dimorphism driven by ecologically mediated selection remains controversial, however, and concrete examples are rare (Li and Kokko, 2021).

This thesis adds to the body of evidence suggesting that selection mediated by ecology could contribute to the evolution of sexual dimorphism, both generally and in mandrills specifically. In the next paragraphs I summarize the sequence of questions and approaches before discussing each of the chapters in more detail. We first used a meta-analytic approach to model cross-species associations between sexual dimorphism and ecological sex differences, measured using stable isotopes. This meta-analysis included data from 158 studies, across 163 vertebrate species with a global distribution, to investigate whether a relationship between sexual dimorphism and ecology could be more general than currently appreciated (Chapter 2; Bauld *et al.,* 2022).

We next analyzed data from eight-years of mandrill fecal collections and fruiting tree phenology, to investigate how mandrill diets vary in response to seasonal variation in fruit production. The multi-year duration of the datasets allowed robust conclusions to be drawn about the feeding niche of mandrills, that provided a strong framework within which to interpret the stable isotope analysis of mandrill tissues (Chapter 3). We also conducted a diet-switch experiment to further strengthen our application of stable isotope analysis to mandrills, by establishing species-specific hair growth rates, isotopic tissue turnover times and hair-diet isotopic discrimination factors (Chapter 4).

We then completed stable isotope analysis of wild, free-ranging mandrill hair segments, to examine sex differences in isotopic niche at the levels of individual and sex. These analyses allowed us to consider whether mandrill dimorphism is associated with niche divergence between wild males and females and whether individuals of each sex experience differing levels, or outcomes, of feeding competition (Chapter 5). Finally, we investigated sex differences in space use, with data obtained from focal follows and GPS collars. Here we explored whether males and females differ in seasonal patterns of home-range use and travel behavior, aiming to determine whether and why most male mandrills leave social groups outside of the breeding season (Chapter 6). Taken together, Chapters 5 and 6 allowed us to consider the extent to which resource competition or energetic trade-offs may have contributed to the evolution of extreme sexual dimorphism in mandrills.

In the following discussion I approach several themes in turn, summarizing the results that are relevant to each theme, before considering the implications of my findings and future research that could be conducted based on my results. Firstly, I discuss the general importance of ecologically mediated selection to the evolution of sexual dimorphism. Next, I consider the consistency of my results with the hypothesis that ecologically mediated selection has influenced the evolution of sexual dimorphism in mandrills. I then examine how the results of the fecal analysis in Chapter 3, and the diet-switch experiment in Chapter 4, facilitated the application of stable isotope analysis to wild mandrills. Finally, I discuss some of the implications of my results for mandrill conservation.

7.2 A general role for ecologically mediated selection in the evolution of sexual dimorphism?

In Chapter 2, we set out to conduct a meta-analysis examining cross-species associations between sexual size dimorphism and isotopic sex differences in vertebrates, to assess the strength of associations between sexual dimorphism and ecological sex differences. Because the nitrogen and carbon stable isotope ratios of animal tissues reflect an individuals' trophic level or basal carbon resource, respectively (Hobson and Welch, 1992; Codron *et al.,* 2007), associations between size dimorphism and isotopic differences between males and females would suggest that sexual dimorphism separately impacts, or has been impacted by, the feeding ecology of each sex.

7.2.1 Summary of Results

Our meta-analytic models revealed that ecological sex differences are widespread, and that between-species variation could relate to explanatory variables, such as the traits of study subjects. We found a modest positive association between size dimorphism and sex differences in trophic level, implying that, across species, greater size dimorphism leads to greater trophic level sex differences, driven by the larger sex feeding at a higher trophic level (Figure 2.3). We also revealed the importance of ecological context on associations between dimorphism and ecological sex differences. Sex differences in trophic level were absent in herbivores, modest in carnivores and strongest in omnivores (Figure 2.4). Conversely, sex differences in basal carbon resources were present in herbivores, but not omnivores or carnivores, thus indicating greater dimorphism is associated with larger sex differences in plant consumption in herbivores (Figure 2.5). We further found that size dimorphism might have a greater impact on sex differences in trophic level in gape-limited predators, in which size may have a greater impact on maximum ingestible prey size and trophic level. However, controlling for phylogeny weakened the association between size dimorphism and trophic level sex differences in gape-limited carnivores (Figure 2.6).

The meta-analysis in Chapter 2 considered sex differences in isotopic mean and variance, but not the isotopic niches of individuals of each sex. When applying stable isotope analysis to mandrills in Chapter 5, we revealed sex differences in isotopic niche at the individual level (Figure 5.7; 5.8), a pattern distinct from the sex level mean and variances analyzed in Chapter 2.

7.2.2 Interpretation and Future Research Directions

Experimental and modelling work has shown that ecological factors can proximately and ultimately affect sexual dimorphism (Slatkin, 1984; Bolnick and Doebeli, 2003; De Lisle and Rowe, 2015; De Lisle, 2023), but the general importance of ecology for explaining variation in dimorphism is a matter of ongoing debate (De Lisle, 2019; Li and Kokko, 2021). The associations we found between size dimorphism and isotopic sex differences indicate a cross-species relationship between sexual size dimorphism and ecological sex differences. Thus, the influence of ecologically mediated selection on the evolution of sexual dimorphism may be greater than currently appreciated. However, the modesty of associations between size dimorphism and trophic level sex differences is also consistent with previous assertions that the role of ecologically mediated selection in driving sexual dimorphism is relatively minor (Fairbairn, 1997; De Lisle and Rowe, 2015). Furthermore, our finding that ecological context modified associations between size dimorphism and ecological sex differences is consistent with arguments that ecological effects on sexual dimorphism are more likely under a limited range of circumstances (Li and Kokko, 2021).

Chapter 2 considered isotopic sex differences, measured as sex differences in isotopic mean or standard deviation. In our analysis of mandrill isotopic sex differences, we found males and females to be very similar in terms of isotopic mean and standard deviation. Mandrill males are about three times larger than females (Abernethy and White, 2013), thus the results of Chapter 5 do not match predictions from Chapter 2, that greater size dimorphism is associated with larger trophic level differences between males and females. Chapter 5 does however, conform with our finding in Chapter 2 of high variation among taxa in the extent to which the sexes differ isotopically.

Our stable isotope analysis of mandrill hairs revealed that, while males and females may be isotopically similar on average, the sexes can differ greatly at the individual level, with individual females more variable than individual males. At present, only a few studies have examined sex differences in individual level isotopic variance (Introduction, Chapter 5). However, as more studies are conducted on this topic, a meta-analysis of associations between sexual dimorphism and individual level isotopic sex differences could be an exciting approach for discovering covariation between sexual dimorphism and intersexual niche divergence.

7.3 Ecologically mediated selection as a cause of mandrill dimorphism.

A great deal of evidence has accumulated suggesting that sexual selection has been an important driver of mandrill sexual dimorphism (Setchell, 2016). However, a number of dimorphic traits in mandrills, such as body size and dental morphology, are ecologically relevant and associated with dietary sex differences (Percher *et al.,* 2017; Nsi Akoué *et al.,* 2017). Furthermore, most male mandrills leave social groups on a seasonal basis, which may intensify sexual selection for large male size and ornamentation (Abernethy *et al.* 2002; Hongo *et al.,* 2016). Thus, an interaction between ecologically mediated selection and sexual selection may best explain why sexual dimorphism is so extreme in mandrills. The primary aim of this thesis was therefore to investigate whether the sex differences in mandrill feeding and spatial behavior were consistent with a role for ecologically mediated selection in the evolution of mandrill dimorphism.

7.3.1 Summary of results related to ecological sexual dimorphism in mandrills

The sexes were in similar positions within isotopic space, with $\delta^{13}C$ means of -24.6‰ and -24.7‰ and $\delta^{15}N$ means of 6.1‰ and 6.3‰ for females and males, respectively. The isotopic niche of male mandrills was 82.5% overlapped by the female isotopic niche and the niches of each sex were similar in size, with the female niche only slightly larger. However, the sexes displayed stark niche differences at the individual level. Regarding both $\delta^{15}N$ (trophic level) and $\delta^{13}C$ (plant diversity), random intercept (between individual) variance exceeded residual (within individual) variance in males. For both isotopes, the female residual (within individual) variance exceeded that of males. Somewhat surprisingly, female $\delta^{13}C$ random intercept (between individual) variance also greatly exceeded male random intercept variance (Chapter 5). We found male habitat selection, home-range size, and Brownian motion variance to differ more from females during the non-breeding season, than during the breeding season. Furthermore, we found that males travelled shorter distances, at slower speeds, during the non-breeding season, compared to the breeding season (Chapter 6).

7.3.2 The importance of ecologically meditated selection to the evolution of mandrill sexual dimorphism and future research directions

The mean position of females within isotopic space suggests that the diet of the females we sampled was omnivorous, as the ranges of both forest plant and forest animal foods contained the female mean, for both isotopes. Females were also positioned entirely within the ranges of forest plants and forest animals and did not overlap with savannah food items (Figure 5.1). Thus, the female isotope data from Chapter 5 is consistent with the fecal data from Chapter 3, indicating that females largely feed on plants and animal prey within C3 forest habitats. The mean position of males within isotopic space was very close to the female mean, for both isotopes (Figure 5.1). Therefore, the diet of males is likely to be similar to that of females.

Fecal analysis also revealed that females are highly generalist feeders (Chapter 3). Thus, we can be confident that the isotopic niche ellipse for females (Figure 5.4) is representative of a generalist feeding niche. The similarity in size between the niche ellipses of both sexes (Figure 5.4), alongside 82.5% overlap of the male ellipse by the female ellipse (Figure 5.5), strongly suggests that males are also generalist feeders, when considering all individuals combined (Chapter 5).

However, when analyzing niche variation at the individual level, the results suggested differing contributions of within and between individual dietary variation to the total niche widths of each sex (Figure 5.7; Figure 5.8). For both isotopes, between individual variance exceeded within individual variance in males (Figure 5.8). Thus, the total niche width of males was explained more by dietary differences between males, than variation in food consumption within individual males. Dietary differences between males may be expected because they spend much of the year solitary (Abernethy *et al.,* 2002), meaning individual males are likely to forage in distinct locations. Thus, differences in food availability between the foraging locations of individual males could explain high between individual isotopic variation (Chapter 5).

After accounting for niche variance explained by random intercepts for individuals (i.e. between individual niche variance), we took the remaining residual isotopic variance as representing within individual feeding variation (Chapter 5). Female within individual variance exceeded that of males for both isotopes (Figure 5.8), suggesting that individual females had more varied diets than individual males, on average. Optimal foraging theory posits that an animals' food choices should be based on the maximum nutritional return that can be made by choosing a given item (Pyke *et al.,* 1977). An animal should therefore opt to feed on preferred resources that provide the highest return on foraging energy investment, given free choice. Thus, higher dietary consistency for individual males implies that the males we sampled had more consistent access to preferred resources than individual females. Conversely, higher within individual variance in females suggests that individual females had more variable diets than individual males. Therefore, some ecological factor must have differed between males and females, to cause females to more frequently deviate from feeding on preferred resources, producing higher within individual isotopic variance in females.

While male mandrills are often solitary during the non-breeding season, females live in hordes of several hundred animals throughout the year (Abernethy *et al.,* 2002). Feeding competition is expected to be higher for individual primates that live in larger groups (Sterck *et al.,* 1997). Food selection by female mandrills should therefore be impacted to a far greater extent by within-group feeding competition than solitary male food selection. Differences in the levels of resource competition experienced by each sex would explain why males exhibited lower within individual isotopic variance than females. Thus, abandoning social groups outside of the breeding season may be a male strategy to avoid feeding competition and gain more consistent access to preferred food sources (Chapter 5).

However, stable isotope analysis alone cannot determine whether the males we sampled were feeding outside the horde, especially given that each male was within the horde when it was sampled. Dominant individuals may exclude subordinate individuals from feeding patches during within-group contest competition (Houle and Wrangham, 2021). It is therefore possible that the dietary consistency of individual males arose through large males dominating feeding patches whilst within the horde. Knowledge of each sex's spatial ecology was therefore needed to explore alternative explanations for the isotopic differences between male and female mandrills (Chapter 5).

Data from GPS collars revealed that male and female mandrills exhibited differing seasonal patterns in spatial behavior (Chapter 6). Females were mostly present in gallery forests throughout the year, as were males during the breeding season. However, during the non-breeding season, male use of continuous forest increased, with a concomitant decrease in gallery forest use (Figure 6.3). The fact that males used continuous forest frequently during the non-breeding season, but females remained almost exclusively within gallery forests strongly suggests that males at least sometimes left the horde during the non-breeding season.

Furthermore, male home-range size (Figure 6.2) and Brownian motions variance (Figure 6.4) were also similar to females during the breeding season, but fell during the non-breeding season. Groups containing more individuals should occupy larger home-ranges (White *et al.* 2010) and should also more regularly switch between feeding in patches and travelling between patches (Stevenson and Castellanos, 2001), which would result in high Brownian motion variance. Therefore, the lower home-range size and motion variance of males during the non-breeding season is consistent with observations that male mandrills leave hordes outside of the breeding season and forage alone or in groups of less than five individuals (Abernethy *et al.,* 2002; Hongo *et al.,* 2016). Thus, the spatial behavior of collared males, the same individuals as stable isotope data were obtained from, suggests that the male dietary consistency revealed by the stable isotope analysis results from males leaving the horde, as opposed to dominating feeding patches within the horde (Chapter 5; Chapter 6).

The GPS collar data also showed that males travelled shorter distances, and moved at slower speeds, during the non-breeding season, compared to both males in the non-breeding season and females in both seasons (Figure 6.5; Figure 6.6). Lower travel distances and speeds suggest that males expended less energy on travel during the non-breeding season (Taylor, 1982; Marcus Rowcliffe *et al.,* 2012). Thus, lower energetic expenditure on travel may be another benefit to males of leaving mandrill hordes, in addition to having more consistent access to preferred resources (Chapter 6).

Prior studies of wild mandrills suggest that males experience nutritional and oxidative stress during the breeding season (Beaulieu *et al.,* 2014; Oelze *et al.,* 2020), and evidence from semi-free ranging groups indicates that males also suffer higher physiological stress and parasite loads during this period (Setchell *et al.,* 2010). These results also suggest that males are in relatively poor body condition by the end of the breeding season. As mandrill hordes occupy exceptionally large home-ranges (White *et al.,* 2010), the large size of males may leave them unable to travel alongside the horde whilst in poor condition (Hongo *et al.,* 2016). Leaving hordes outside of the breeding season, when the availability of fertile females is low, may therefore allow males to recoup body condition, by expending less energy on travel and increasing their intake of preferred resources (Chapter 5; Chapter 6).

The temporary nature of male group presence has two impacts on the mandrill mating system. Firstly, the dominance hierarchies among males are unstable (Smit *et al.,* 2022), meaning males must compete for dominance upon entering the horde. Secondly, males are unable to form long-term relationships with females (Abernethy *et al.,* 2002) and must therefore communicate their quality to females through other means, such as ornaments. Intra- and inter-sexual breeding competition, the two components of pre-copulatory sexual selection, are thus likely to be exaggerated by males entering and leaving the horde, compared to primate species that form more stable societies. Chapter 5 and Chapter 6 suggest resource competition and energetic trade-offs compel males to leave mandrill hordes. These results imply that ecological factors, unrelated to reproduction, may have altered the mandrill mating system to raise the intensity of sexual selection on male morphology. Thus, this thesis provides novel evidence that is consistent with an interaction between selection mediated by ecology and reproduction explaining why mandrill dimorphism is so extreme, compared to other primates.

One shortcoming of this conclusion, that mandrill dimorphism is enhanced by males re-entering the horde on a seasonal basis, is that is does not directly match the ecological character displacement theory outlined in the General Introduction (Chapter 1). In the

General Introduction, scenarios were introduced in which ecologically mediated disruptive selection acts directly on morphological traits, such as body size, to produce sexual dimorphism in response to resource competition. Instead, the above conclusion states that resource competition and energetic constraints compel male mandrills to move and forage alone, in order to expend less energy on movement and feed under lower feeding competition. In this case, ecologically mediated disruptive selection acts on mandrill spatial and social behavior, rather than morphology, resulting in two alternative behavioral phenotypes: permanently social females and seasonally solitary males. These sex differences in behavioral phenotype then create the conditions necessary for amplified sexual selection, once males re-enter the horde to breed, that might explain the extremity of mandrill dimorphism. Thus, disruptive selection arising from resource competition and energetic constraints may be considered to indirectly impact the evolution of sexual dimorphism, via an effect on the social behavior of each sex, as opposed to directly acting on the morphology of males and females.

A potential issue with concluding that the ecological sex differences found in this thesis are evidence of a role for ecologically driven dimorphism is the magnitude of the ecological sex differences found. The average isotopic and spatial sex differences in Chapters 5 and 6 are small compared to both the variation exhibited within each sex and to ecological sex differences found in other species (e.g. Jones et al. 2020). Small ecological sex differences in mandrills could be viewed as supporting assertions made for other species that the role of ecologically mediated selection in the evolution of sexual dimorphism is relatively minor (De Lisle and Rowe 2015; Bauld et al. 2022). Given the weight of evidence for sexual selection as a driver of mandrill sexual dimorphism (Setchell et al. 2016), a minor role for ecologically mediated selection would seem reasonable.

Alternatively, it has been argued that documenting ecological sex differences (of any magnitude) may not provide evidence of the origins of dimorphism, as ecological differences between males and females could result from dimorphism arising from sexual or fecundity selection (Shine 1989). The existence of ecological sex differences in the present day might instead be taken as evidence of ecologically mediated selection acting to maintain, instead of produce, sexually dimorphic traits (Slatkin 1984). It could therefore be the case that strong sexual selection has driven the evolution of extreme sexual dimorphism in mandrills, with the relatively minor ecological sex differences documented in this thesis acting to maintain, as opposed to exaggerate, dimorphism. It is challenging to disentangle the effects of trait maintenance and evolution via observational field investigations of the sort conducted in this thesis. For example, predation pressure is often cited as a driver of larger primate groups, but present day mortality rates may be an inappropriate measure of predation pressure, as mortality may demonstrate the rate of predation after primates have executed the formation of large groups as an evolved anti-predation strategy (Hill and Lee, 1998). Further work is therefore needed to develop appropriate field based methods to differentiate the evolution and maintenance of ecological dimorphisms (and other traits) in primates.

Whether viewed as a cause or consequence of mandrill sexual dimorphism, the ecological sex differences found in this thesis open a number of interesting avenues for future mandrill research. Firstly, the GPS data strongly implies that males expend less energy during the non-breeding season, but energetic expenditure could be more closely approximated by monitoring the activity levels of individuals. Past studies have shown that accelerometers can be fitted to primates with collars, to record the activity patterns of individuals (Kappeler and Erkert, 2003; Fernandez-Duque and Erkert, 2006). Like GPS collars, fitting accelerometers to primates allow behavioral data to be gathered remotely, meaning that activity pattern data could be gathered on males, even when they are solitary and difficult to track and observe. In baboons (*Papio ursinus*), accelerometers have successfully recorded the duration and timing of behaviors including locomotion, foraging, resting, and grooming (Fehlmann *et al.,* 2017). Accelerometers could therefore be used to determine whether males devote more time to locomotion during the breeding season and more time to resting and foraging during the non-breeding season. Seasonal differences in activity patterns could further support our conclusion that male energetic expenditure varies between the breeding and non-breeding seasons.

Another open question concerns the traits under sexual selection in the context of males entering and remaining in mandrill hordes to compete for females. Results from semi-free ranging individuals indicate that higher body mass and brighter coloration are positively associated with rank attainment and reproductive success in male mandrills (Setchell, 2005; Setchell *et al.,* 2008). Though measuring animal color with camera traps presents a number of issues, including the need to control for variation in lighting conditions (Stevens *et al.,* 2007), technological innovations are improving the application of digital photography to the measurement of animal color (Stevens *et al.,* 2009; Troscianko and Stevens, 2015). For example, the inclusion of color cards within photographs, alongside software for color standardization, can enhance the precision of color measurement under varying light conditions (Bergman and Beehner, 2008). Camera traps can also be used to estimate the body mass of wild animals (Tarugara *et al.,* 2019).

Hongo *et al.* (2016) demonstrated that male presence in mandrill hordes, as well as mate-guarding behavior, can be recorded using camera traps. As technology develops, it would be interesting to investigate whether the brightness of red sexual skin or the body size of males are associated with joining the horde or mate-guarding behavior. As mate-guarding is associated with reproductive skew in semi free-ranging mandrills (Wickings *et al.,* 1993), an association between coloration or body size and mate-guarding behavior could provide indirect evidence of sexual selection on these traits in wild mandrills. Furthermore, if the average brightness of males declines over the course of the breeding season, it might indicate that the average body condition of males also declines during the breeding season. Such a result would be consistent with the conclusions drawn in this thesis that poor body condition, resulting from mating competition, is part of the explanation for male mandrills leaving hordes outside of the breeding season.

Why mandrill females form such large groups is also an important knowledge gap, given that large group size likely leads to high resource competition and extensive travel (Emlen and Oring, 1977; Sterck *et al.,* 1997; White *et al.,* 2010; Cassini, 2020b). Groups of mandrills rarely encounter each other (White *et al.,* 2010), so between-group contest competition is perhaps unlikely to explain why mandrills form such large groups. Two other factors that may drive large group formation are inter-specific feeding competition and predation (Isbell, 1994; Sterck *et al.,* 1997). Mandrills co-occur with a number of other frugivorous species (Tutin *et al.,* 1997) and are preyed upon by leopards (*Panthera pardus*), African golden cats (*Profelis aurata*), birds of prey and African rock pythons (*Python sebae*) (Abernethy and White, 2013), though predation pressure in African tropical forests is presumed to be lower than for primates in open savanna habitats (Hongo, 2016). The influence of inter-specific competition and predation on mandrill behavior could be investigated using camera trap data to examine temporal and spatial patterns of co-occurrence of mandrills with competitor species and predators (Murphy *et al.,* 2019; Andrade-Ponce *et al.,* 2022). Comparative analysis which other semi-arboreal primate species would likely be needed to truly answer why mandrill groups are so large. But directly comparing the influence of competitor species and predators on mandrill space use could reveal which of these factors is more influential on mandrill behavior.

7.4 Ensuring robust application of stable isotope analysis to wild mandrills.

Stable isotope analysis is best applied to wild animals, with knowledge of the feeding ecology of the focal species, the stable isotope routing within the species' tissues (Martinez del Rio *et al.,* 2009), and of the sources of isotopic variation to which the focal animals may be exposed (Roberts *et al.,* 2017). The fecal analysis we conducted produced reliable information on the feeding ecology of the focal horde, thanks to which we could draw stronger dietary inferences from the stable isotope ratios of mandrill tissues (Chapter 3). The diet-switch experiment provided data on the growth rates of mandrill hairs and isotopic turnover and fractionation within mandrill hairs (Chapter 4). Finally, stable isotope analysis of mandrill food items revealed the sources of isotopic variation within the focal horde's home-range (Chapter 5).

7.4.1 Summary of results impacting the application of stable isotope analysis

We found that the Lopé mandrill horde are highly generalist feeders that consume a diverse range of food types when fruit production falls (Chapter 3). From the diet-switch experiment, we found that mandrill hair growth rates were variable between body parts and individuals. We also found that mandrill hair stable isotope ratios reach equilibrium with a new diet after 23 days for $\delta^{15}N$ and 38 days for $\delta^{13}C$. The isotopic discrimination factors of mandrill hairs were 3.1‰ and 2.8‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Chapter 4). Analyzing the stable isotope ratios of mandrill food items, we found high diversity within major food types and very little clustering between food types. Isotopic variation between mandrill food items did not appear to be strongly influenced by systematic spatial or temporal isotopic baseline variation (Chapter 5).

7.4.2 Implications for stable isotope analysis of mandrills and future research directions

Analysis of mandrill fecal samples revealed that the horde are highly generalist feeders that consume a wide range of fallback foods when fruit availability declines (Tutin *et al.,* 1997; Hongo *et al.,* 2018). Because of the social structure of the horde, that often contains very few males (Abernethy *et al.,* 2002), the information from the fecal data largely applies to females and juveniles. However, the long-term, eight year duration of the study means that our inferences about the hordes' feeding niche can probably account for inter-annual changes in fruit supply. We can therefore be confident that females are generalist feeders when interpreting female stable isotope data. This knowledge of females then provides a robust context within which to interpret the stable isotope data of male mandrills, whose ecology is less well known.

To further improve our application of stable isotope analysis to mandrills, we conducted a diet-switch experiment to quantify hair growth rates, isotopic tissue turnover times and hair-diet isotopic discrimination factors. Measuring hair growth rates showed substantial amounts of variation between the growth rates of different hair types and between the same hair type from different individuals. Inter-individual differences in hair growth rates are clearly difficult to account for in wild individuals. However, our results indicate that error can be minimized by analyzing samples of the same hair type from different individuals. We therefore analyzed only mustache hairs from wild individuals. Mustache hairs were also advantageous because they are relatively thick, meaning they contain more mass per unit of length. We found the minimum length we could use to achieve analytical precision was 2 mm, equivalent to an ecological window of approximately 5.5 days (Chapter 4).

Tissue-diet isotopic discrimination factors describe the typical enrichment between the stable isotope ratios of animal tissues and animal diets. Discrimination factors must be accounted for to accurately reconstruct animal diets from stable isotope data. The need to account for discrimination factors can be seen in Figure 5.1 (Chapter 5) which displays the adjusted isotope ratios of male and female mustache hairs, relative to mandrill food items. Both the male and female adjusted $\delta^{15}N$ values are approximately 3‰, in the lower range of the forest plant $\delta^{15}N$ distribution. Without adjustment, the $\delta^{15}N$ position of both sexes would be above

6 ‰, perhaps incorrectly suggesting a greater contribution of animal prey to the diet of both sexes, compared to the adjusted values.

The importance of quantifying discrimination factors is greatest when applying stable isotope mixing models to animal stable isotope data (Kadye *et al.,* 2020). These models allow the relative contribution of different food types to an animals' diet to be estimated using stable isotope data (Parnell *et al.,* 2013). However, the extensive overlap we found between the isotope ratios of mandrill food items (Figure 5.1; Figure A5.1) made the application of stable isotope mixing models inappropriate in our case, as these models rely on isotopic distinction between food sources (Phillips *et al.,* 2005). Recent advances also allow tissue turnover times to be included into stable isotope mixing models (Ballutaud *et al.,* 2022). Despite the noise within the dataset (Figure 4.3; Figure 4.4), the estimates of mandrill isotopic discrimination factors and tissue turnover times were consistent with prior studies in primates and other mammals (Schwertl *et al.,* 2003; Caut *et al.,* 2008; Huelsemann *et al.,* 2009; Tsutaya *et al.,* 2017; 2021). Our diet-switch experiment thus provides novel data that may be used in future applications of stable isotope analysis to mandrills or other African Papionines, where advanced stable isotope mixing models may be more appropriately utilized.

Stable isotope analysis is also improved by an understanding of the isotopic variation within the environment of the animals under study. Stable isotope analysis of mandrill food items revealed that substantial isotopic variation was present within the habitat of the focal horde (Figure 5.1). However, this variation was continuous between different food types, with no obvious clustering of the isotopic signal of different foods. Grouping the food items into 11 categories, including different C3 plant tissue types, did not appear to be a suitable framework within which to interpret the isotope ratios of mandrill hair samples (Figure A5.1). Numerous overlapping pairwise combinations of categories were present in the data; for example, the range of C3 plant seed isotope ratios was almost entirely overlapped by the ranges of C3 fruits and C3 leaves. Thus, we could not reliably draw inferences on the different plant tissue types that mandrills could have consumed, based on stable isotope data (Chapter 5).

Grouping food types into five categories appeared to be a more suitable solution. C3 forest plants were relatively easily distinguished from C4 savannah plants along the $\delta^{13}C$ axis and animals were, on average, ^{15}N-enriched relative to plants (Figure 5.1). We were therefore more confident that we could draw inferences on mandrill diets using more general principles of stable isotope ecology, concluding that: greater diversity in plant consumption through time would lead to greater $\delta^{13}C$ variation along the length of mandrill hairs, and greater trophic level variation through time would increase $\delta^{15}N$ variation along hairs.

We did not find systematic spatial or temporal variation in the stable isotope ratios of mandrill food items (Chapter 5). Thus, we did not find any reason, nor have any means, to adjust the stable isotope values of mandrill tissue samples to account for sampling season or location, before interpreting the data from wild mandrill hairs. One factor we did not consider is the 'canopy effect', which describes vertical stratification of the isotope ratios of plant tissues, due to differences in transpiration rate between the canopy and forest floor (Lowry *et al.* 2021). The canopy effect is not universal across forests, however, and depends on local conditions (Blumenthal *et al.,* 2015). As the home-range of the focal horde largely consisted of gallery forests, that are less dense relative to continuous forest, we assumed that differences between the canopy and forest floor in relative humidity, temperature, and light availability that impact transpiration rates would be low, compared to closed canopy continuous forest. We therefore did not account for vertical stratification of the isotope ratios of mandrill food items. However, Oelze *et al.* (2020) concluded that age related inter-individual differences in mandrill blood isotope ratios could have resulted from younger individuals feeding higher in the canopy. Given that other mandrill hordes also forage in the continuous forest in Lopé (Lahm, 1986), investigation of the canopy effect in this study site may be useful. If the canopy effect is found, it may be possible to use stable isotopes to reveal sex differences in foraging height, which could add a three dimensional component to analyses of sex differences in mandrill isotopic niche.

7.5 Mandrill Conservation

Mandrill socioecology remains understudied, with potential adverse impacts for mandrill conservation. Mandrills are classified as Vulnerable to extinction on the IUCN Redlist, with habitat loss, climate change and subsistence hunting by humans constituting the principal threats to mandrill populations. Though this thesis does not directly address questions related to mandrill conservation, the results from Chapters 3, 4 and 5 contain dietary and spatial information that could inform the direction of future work to improve the management of these threats to mandrills.

7.5.1 Summary of results relevant to mandrill conservation

We found fruit to be the most frequently consumed resource by mandrills, with consumption covarying positively with availability. Fruit consumption exhibited clear peaks during the two wet seasons, when fruit abundance was high. During periods of low fruit availability, mandrills consumed a range of fallback foods, including animal prey, leaves, crushed seeds, and other, lower quality plant fibers (Chapter 3). Using GPS collars, we found that the focal hordes' home-range was almost entirely limited to the village enclave in the buffer zone of Lopé National Park, and that the horde sometimes crossed the boundary of the park into unprotected areas (Chapter 5).

7.5.2 Implications for mandrill conservation and future research directions

Our results suggest that mandrills are omnivores, with a preference for fruit, which is consistent with previous studies (Hoshino, 1985; Lahm, 1986; Rogers *et al.,* 1996; Nsi Akoué *et al.,* 2017). Also following previous studies, we found that fruit consumption was seasonal, and followed patterns of fruiting tree phenology (Hongo *et al.,* 2018). Fruit production has dropped by around 30% in Lopé National Park over the previous three decades, as a result of ongoing climate change (Bush *et al.,* 2020a; 2020b), meaning availability of the mandrills' preferred resource has fallen. The available information on mandrill diets indicates dietary plasticity that could confer resilience under environmental change scenarios, as species which demonstrate flexibility in already varying environments may be adapted to cope with future change (Jones, 2005). However, the sensitivity of mandrills to tree phenology may, like other fruit dependent vertebrates, leave them vulnerable to climate change induced reductions in fruit supply (Butt *et al.,* 2015). Whether dietary flexibility will facilitate adaptation by mandrills to novel environmental conditions is unclear, however, there are several promising avenues for answering this question, as noted below.

As outlined in Chapter 3, data from Lopé indicate that forest elephants are consuming lower quality diets in 2020 than in 1990 (Tejler *et al., unpublished data*) and exhibit more frequent and severe emaciation (Bush *et al.,* 2020). Therefore, a useful next step regarding mandrills would be to investigate whether present day mandrill diets contain greater amounts of fallback foods or lower quality fruit, compared to the 1998 - 2004 period examined in Chapter 3. A present day analysis of the focal hordes' diet may be especially useful if coupled with nutritional analysis to elucidate, for example, whether disrupted phenological patterns and warmer temperatures are adversely impacting mandrill macronutrient intake (Rothman *et al.,* 2015), or associated with increasing levels of plant secondary metabolite consumption (Windley *et al.,* 2022).

The change in the hordes' spatial behavior over the past twenty years may also be concerning. In Chapter 6 we found that the hordes home-range has shifted northwards and eastwards, since the horde was first tracked between 1998 and 2004 (White *et al.,* 2010). This new area of occupation contains greater amounts of oil palm (*Elaeis guinensis*) fruits (David Lehmann *personal communication*), which are a keystone resource to the horde (Chapter 3). However, this area partially falls outside the strictly protected area of Lopé National Park, and overlaps with village enclaves in the buffer zone. We even observed the horde crossing the Offoué river, moving outside of the park boundaries.

If the home-range of the horde has shifted closer to human habitation due to falling fruit availability, other hordes throughout the mandrill range could be exhibiting similar behavioral changes. Thus, mandrills may be exposed to increasing levels of human contact, which could increase the hunting pressure on mandrill populations. Of greater concern is that mandrills are known to crop-raid in human plantations (Djoko et al., 2022). Therefore, changing mandrill spatial behavior could potentially lead to increased human-wildlife conflict, through crop-raiding behavior that disrupts the livelihoods and food supplies of local people (Redpath *et al.,* 2013). Research to determine whether the rate of crop-raiding behavior by mandrills (and other species) is increasing in areas impacted by forest loss or climate change would therefore be useful. Investigations into the environmental factors and management interventions that could mitigate the costs of mandrill crop-raiding will also be of benefit, both to mandrill conservation and local stakeholders affected by human-wildlife interactions (Ngama *et al.,* 2019).

7.6 Conclusion

This thesis contains new knowledge of mandrill ecology and makes novel contributions to the debate about how diversity in sexual dimorphism arises. We have found that mandrills are extreme generalists and this flexibility may confer some ability to adapt to ongoing environmental changes. However, the sensitivity of mandrills to fruiting tree phenology, high feeding competition among females and recent changes to the focal hordes' spatial behavior that we have documented could all suggest that mandrills are vulnerable to declining habitat quality. These results can therefore guide further research to enhance the knowledge base underpinning mandrill conservation policy.

Though sexual selection is likely to be the primary cause, why mandrill dimorphism is so extreme is still an unanswered question. Our analysis of mandrill feeding and spatial ecology strongly suggest a role for ecologically mediated selection. Our results indicate that a combination of resource competition and energetic trade-offs compel males to leave mandrill hordes outside of the breeding season. This response by males to ecological pressures then leads to an influx of males to mandrill hordes during the breeding season, with these males unfamiliar to each other and to the females resident within hordes. The resulting need of males to establish dominance and attract females likely produces strong intra- and inter-sexual mating competition, triggering strong sexual selection for traits such as large size, long canines, and bright ornamentation. It therefore seems likely that a combination of selective pressures, mediated by both ecology and reproduction, are responsible for the evolution of extreme sexual dimorphism in mandrills.

Our findings contribute to the growing body of evidence that sexual dimorphism can be driven by ecologically mediated selection. In addition to evidence of ecological drivers of dimorphism in mandrills, we also found cross-species associations between sexual size dimorphism and ecological sex differences. These associations suggest that an interplay between sexual dimorphism and ecology may be widespread. However, our meta-analysis also highlighted that ecological sex differences are pervasive and potentially explained by factors other than sex differences in size. We therefore hope that our results will stimulate new investigations into the drivers of ecological sex differences, that will generate a complete answer to the question of how sexual dimorphism evolved.

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