GETTING A GRIP ON MICROHABITAT USE AND ECOLOGICAL PERFORMANCE IN THE CHAMELEON *FURCIFER OUSTALETI*

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Thesis submitted to the

University of Nottingham (School of Geography)

for the degree of MSc (by research)

180 Credit Dissertation Module

January 2018

Word count (not including Abstract,

References, & supporting information): 10, 944

ABSTRACT

Aim: Identifying associations between phenotype and habitat use can elucidate how species have adapted to different local environments. Organism performance capacities are key functional links between morphology and habitat use. Yet, the idea that performance is optimised in specific environmental conditions remains an untested assumption for most habitats. This paucity of data connecting environment to individuals and their functional capacities hinders attempts to build fuller understanding of adaptive systems. With this in mind, I examined chameleon optimal grip performance and tested for relationships with microhabitat use and availability.

Location: Mahamavo forest region, northwest Madagascar.

Methods: *Furcifer oustaleti* were captured in the wild during diurnal surveys in June and July of 2017 and the diameter of their perch was measured. Random surveys were also used to determine the empirical distribution of available perch diameters in my research area. Individual grip strength was measured on wooden dowels of varying diameter. Grip strength was modelled as a hump-shaped function of dowel diameter to determine the optimum grip diameter for each chameleon. I used the empirical distribution of available perches to test whether chameleons perched closer to their optimum than expected if perch selection was random. I also tested whether individual grip optima were closer to the mode of the available perch diameter distribution than expected due to chance.

Results: Seven individuals showed grip optima within the range of dowel diameters tested, while five had the tightest grip on the smallest diameter tested. Larger, heavier chameleons with longer limbs had greater average grip strength, but did not select wider perches or have higher optimal grip diameters. Chameleons selected perches significantly wider than available perches—suggesting non-random selection of microhabitat. However, selected perches were not closer to grip optima than expected if perching was random with respect to grip optima. Optimal diameters were closer to the mode of available perch diameters than expected by chance.

Main conclusions: My findings provide the first tentative evidence that chameleon optimal grip diameters are commensurate with modal available perches in their habitat. Which factors determine chameleon perch selection remains an open scientific question. Further research on these topics should seek to test these findings with a larger sample size and on a wider dowel diameter range. Explaining functional links between chameleon grip–performance and perch characteristics in other species and habitats on Madagascar may help build a fuller understanding of the effects of forest restructuring on their ecology, and inform practical conservation of Malagasy herpetofauna in general.

ACKNOWLEDGEMENTS

To my supervisors, Adam Algar and Richard Field, go my deepest thanks for their continued guidance, support and advice throughout my Master's.

I would also like to thank Operation Wallacea for their help in facilitating my research period in Mahamaovo, northwest Madagascar. Further, I thank all their project partners for allowing my research to be conducted without impediment.

TABLE OF CONTENTS

FIGURES

TABLES

1 INTRODUCTION

Organism performance—the capacity to perform specific ecological functions, e.g. sprint speed—has far-reaching consequences for individual fitness (Arnold 1983; Emerson & Arnold 1989; Irschich 2000; 2002; Irschick & Garland 1989). Understanding how these capacities affect species functionality within their local environments can help identify causal links between morphology and habitat use, and if these traits are ecologically pertinent, i.e. trait utility (Schluter 2000). Indeed, demonstrating habitat – performance – morphology correlations provides indirect evidence of natural selection (Baum & Larson 1991; Larson & Losos 1996).

Although many studies have examined habitat-induced morphology, or 'ecomorphology' (e.g. Des Roches et al. 2015; Herrel et al. 1998; Irschick et al. 1997; McGuire 2003; Schaad & Poe 2010; reviewed in Wainwright & Reilly 1994), relatively few have explored functional capacities as intermediate factors in these relationships (Goodman et al. 2008; Kingsolver et al. 2001; Melville & Swain 2000). Yet, these data can elucidate the underlying drivers of species' adaptive responses to different habitats (Elstrott & Irschick 2004; Herrel et al. 2005; Huey 1983; Irschick 2000; 2003; Lailvaux & Irschick 2006; Vanhooydonck & Van Damme 2003). Overlooking functional performance traits may yield incomplete interpretations of actual evolutionary dynamics (Hagey et al. 2017). Moreover, understanding if/how phenotypes predict habitat requirements or preferred habitat characteristics, can inform practical conservation efforts (Lindenmayer & Burgman 2005).

Locomotion and navigational performance capacities are very influential to total individual fitness and are thought to be among the most ecologically pertinent aspects of organism function (Aerts et al. 2000; Arnold 1983; Full et al. 2002; Huey & Stevenson 1979; Kohlsdorf & Necas 2012; da Silva et al. 2014). Animals' capacity to hold on to substrates with hands/feet (grip–performance) is a large determining factor in how they move through their habitat (Cartmill 1985; Full et al. 2002), and is particularly relevant to the ecology of arboreal species (Hagey et al. 2017; Losos 2009; Zani 2000).

The variety of morphological 'equipment' that animals possess to facilitate gripping is extensive. This holds true even when narrowing focus to just lizards. Geckos adhere to their substrates by taking advantage of intermolecular bonding and shear surface area of millions of microscopic hairs, setae, located on adhesive toe-pads (Autumn et al. 2002). Iguanas, and many other lizards (Irschick et al. 1996; Zani 2000), interlock to substrates using sharp claws that penetrate surfaces to varying degrees (Tulli et al. 2009). Anoles are thought to use a combination of these two methods (Crandell et al. 2014).

Chameleons have a unique strategy among lizards: zygodactylous hands and feet, and a prehensile tail allow individuals to envelope elongate perches (typically wooded branches (Tolley & Herrel 2014)) and comfortably grip substrates narrower than their body (Peterson 1984; Higham & Jayne 2004), in a similar way to many primates and birds (Biewener 2003).

Chameleons are cruise foragers that move through their habitat slowly (Butler 2005), using their ballistic tongue to predate invertebrates at distance (Wainwright & Bennett 1992) and relying heavily on crypsis to avoid predation themselves (Burrage 1973; Tolley & Burger 2007; Tolley & Herrel 2014). Their specialised digit morphology, while allowing navigation of relatively narrow substrates, may mean that chameleons do not conform to typical locomotor performance predictions that hold true for other lizards (Tolley & Herrel 2014), e.g. sprint speed trade-offs between perch diameter and leg lengths (Losos & Sinervo 1989). However, chameleon grip–performance is known to correlate with ecomorphology in particular habitats (Herrel et al. 2011; 2013; Losos et al. 1993; da Silva et al. 2014).

Madagascar's primeval forests host more than 50% of the world's chameleon species (Glaw 2015). These biologically unique habitats are declining in total area and becoming fragmented owing to a gamut of anthropogenic threats (Clark 2012; Harper et al. 2007). The ecological consequences of this structural change to Madagascar's woodland species are still poorly understood, especially at population and microhabitat levels (Langrand & Wilme 1997; Vallan 2000; Watson et al. 2004). Intense selective logging on Madagascar may mean that microhabitats in these shrinking forests are undergoing particularly unique structural reorganisation (Clark 2012; Ganzhorn et al. 1990).

Little is known about chameleon's habitat requirements and preferences on Madagascar, especially their diurnal habitat use. This lack of knowledge is thought to impede assessments of their tolerance to habitat restructuring (Herrel et al. 2011; Randrianantoandro et al. 2010). Here, I examine relationships between microhabitat (perch use and availability) and ecological performance (grip strength) of *Furcifer oustaleti*, the largest chameleon on Madagascar. First, I examine whether morphology influences grip strength and optimal perch diameter.

Next, I test two hypotheses:

H1: Chameleons select perches that maximize grip performance.

- Prediction: Perches selected by chameleons will be more similar to their optimal grip diameter than expected based on random perch selection.

H2: Chameleons' optimal grip diameters have evolved to maximize grip strength on the most abundant perch diameter.

- Prediction: Optimal grip diameters will be closer to the mode of the distribution of available perch diameters than expected if optimal grip diameter is random with respect to the modal diameter.

2 LITERATURE REVIEW

Diversity of form and function is one of the most conspicuous features of life. The idea that this variety across taxa is a product of asymmetrical fitness—capacity to leave viable offspring—amid heterogeneous and changeable environmental conditions, is central to neo-Darwinian theory (Aerts et al. 2002; Darwin 1859; 1871; Endler 1980; 1986; Grant 2003; Herrel et al. 2006; Jemvall et al. 1996; Losos 2009; Rieseberg et al. 2002; Schluter 2000). Explaining the adaptive origins of phenotypic variation can develop understanding of the processes that generate and maintain biological diversity, and is thus among the most captivating and enduring themes of evolutionary biology (Gavrilets 2004; Gould 1983; 2002; Losos et al. 2013; Raeymaekers et al. 2017).

2.1 Phenotype

An organism's phenotype is its suite of observable characteristics, or traits (Johannsen 1911). These include organism's ontology, physiology, behaviour, and products of behaviour such as burrows or nests (Dawkins 1978; Ehrlich & Raven 1969; Wainwright & Reilly 1994). Phenotypes are targets of selection, indeed natural selection could not occur without phenotypic variation (Lewontin 1970; Rieseberg et al. 2002).

Phenotypes come about as a result of complex interactions between genotype (genetic constitution) and environment (Levins 1968; Schluter 2000). This is well demonstrated by the phenomenon of phenotypic plasticity, wherein heterogeneous phenotypes emerge from analogous genotypes in different environmental conditions (Dewitt & Scheiner 2004; Ghalambor et al. 2007; Moczek et al. 2011; Noble et al. 2017; Woltereck 1909). It is therefore useful to consider phenotypes as genomic avatars, real-world expressions of genotype that provide surfaces through which organisms interface with their surroundings, physically interact with their environment, and exchange organic molecules and information. Phenotypic variation is an evolutionary forerunner to adaptive divergence and speciation (Losos et al. 2013). Although non-adaptive processes such as genetic drift (Masel 2011) and allele impoverishment post-bottleneck events can generate phenotypic variety (Schluter 2000, Whitlock 2013), most often, novel properties of phenotype come about owing to divergent selection in different local environments (Futuyma 2013; Yoder et al. 2010).

Organisms are exposed to myriad biotic and abiotic factors that vary over space and time. These factors can be heterogeneous even within local ecological areas (Aerts et al. 2002). Consider a tropical forest, environmental conditions beneath a leaf on the forest floor are

likely to be different than those in the exposed high canopy of emergent evergreens. These are examples of microhabitats—organism's immediate surroundings, ecologically distinct in some way from the surrounding matrix (Aerts et al. 2002; Ausden 2007). Microhabitats can impose selection pressures that influence fitness, such as environmental factors like light availability and ion concentrations. Intensities of these factors are points along ecological gradients that confer advantages and disadvantages to organisms (Schluter 2000; Losos et al. 2013). Phenotypic responses to these environmental conditions determine how individuals function within their environment and in turn lead to evolution. That is, differential selective pressures can generate asymmetric reproductive success, certain phenotypic traits become more advantageous for individuals in specific habitats, and over generations, allele frequencies can shift towards specific phenotypes (Falconer & Mackay 1996; Losos et al. 2013; Schluter 2000).

Adaptation to specific microhabitats is thought to be a major factor determining phenotypic variation among animals (Clabaut et al. 2007; Gavrilets & Losos 2009; Grant 1999; Nosil 2012; Rieseberg et al. 2002; Wainwright & Reilly 1994). Examples of convergent evolution, independent evolution of similar organisms inhabiting similar environments, provide the best evidence for this (Mcghee 2011). Yet, different habitat use is not always associated with divergent phenotypes (Schulte et al. 2004; Vanhooydonck & Van Damme 1999).

2.2 Adaptation and divergence

When examining evolutionary processes with broad frames, looking at divisions and changes at high taxonomic levels and macroevolutionary systems, environmental stochasticity, complexity of nonlinear biological networks, and long time periods, frequently leave these dynamics more driven by 'chance' (Heard & Hauser 1995; Parent & Crespi 2009; Yodel et al. 2010) and difficult to marry with finer-grained evolutionary interactions (Arnold et al. 2001; Bennett 2010; Nee 2006; Reznick & Ricklefs 2009). Adaptation involves changes on smaller scales (Kutschera & Niklas 2004; Whitlock 2013), where allele frequencies in populations shift to produce phenotypes better suited to their environment. Divergence, the disassociation of phenotypic means (Wainwright & Reilly 1994), is central to this process (Futuyma 2013).

In exploring adaptation and divergence it is useful to introduce the adaptive landscape metaphor. Wright's (1931; 1932) fitness landscape analogised topographical contours to a surface representing fitness (Svensson & Calsbeek 2012), creating a powerful tool for visualising evolution (McGhee 2007). While Wright's original model plotted gene

frequencies against a z-axis of fitness, Simpson (1944; 1953) repurposed its x- and y-axes to illustrate phenotypic traits, while elevation represented degree of adaption (McGhee 2007). It is important here to stress the similarities between Simpson's (1944; 1953) model and Janet's (1895) evolutionary landscape, a two-dimensional 'heat-map' of phenotypic characters; Wright's (1931; 1932) and Simpson's (1944; 1953) landscapes may have lent from this original concept (McCoy 1979). Simpson's model is what modern evolutionary biologists term an 'adaptive landscape' (Schulter 2000). This model has been extremely influential in guiding thinking on adaptive processes (Arnold et al. 2001; Dennett 1996; Kauffman 1993, 1995; Mahler et al. 2013; McGhee 2007; Schulter 2000; Svensson & Calsbeek 2012).

Within adaptive landscapes, elevated regions are termed adaptive peaks, and low regions adaptive valleys; these features represent areas where selection moves phenotypes towards or away from respectively. Hence, populations occupying these theoretical spaces always tend to move up adaptive slopes over generations. Any individual phenotypes that stochastically emerge at lower elevations (e.g. due to random mutation) would be penalised by their lower fitness, and 'fade-out' over multiple generations due to sub-optimal reproductive success. This introduces the concept of optima—phenotypic zones that maximise the ability of an organism to function within its environment. Optima are the apex of adaptive peaks. Under this model we can see that movement off of an adaptive peak, away from an optimum, would be selected against during so-called stabilising selection (McGhee 2007). Groups of organisms 'chasing' alternative optima will become phenotypically distinct in some way(s), and are less likely to come in contact or mate with each other (Schluter 2000); in this way, reproductive isolation can accumulate and populations diverge (Hendry 2001).

Real-world adaptive landscapes are complex and dynamic; populations have multiple adaptive peaks in 'rugged' landscapes that rise and fall frequently amid environmental change (Svensson & Calsbeek 2012). Simpson (1953, p.81) described his landscapes as "in almost constant motion" and "like a choppy sea". This has contributed to significant criticism of the adaptive landscape model (Gavrllets 1997; Kaplan 2008: Pigliucci 2012; Skipper & Dietrich 2012). Specifically the model's capacity to be applied to actual populations has been questioned, i.e. including higher dimensionalities needed to plot all actual phenotypic trait values of a population is not possible in a three-dimensional model (Gavrllets 1997; Tews et al. 2004). Kaplan (2008) questioned the mathematical relevance of adaptive landscapes and suggested discarding the model. Other authors have suggested alternate visual tools, such as adaptive 'ridges' (Gravner et al. 2007) or Gavrilets's (1997) 'holey' landscape that only visualises adaptive peaks. Much of this

criticism is focused on the implied impermeability of adaptive valleys, with many authors suggesting that organisms are able to move between adaptive peaks more readily (Gavrilets 2004; Gravner et al. 2007; McGhee 2007); this touches upon Gould & Eldridge's (1977) theory of punctuated equilibria. These criticisms leave the adaptive landscape model less able to describe specific cases of adaptive divergence, speciation, and cladogenesis, but for the models original purpose: a metaphor meant to convey a complex idea, it is still useful. Indeed, many authors have suggested that the model's value as a heuristic tool is greater than its capacity for practical application (Gravner et al. 2007; McGhee 2007; Pigliucci 2012; Schulter 2000; Tews et al. 2004).

The adaptive landscape model helps contextualise and visualise the texture of phenotypic variation. From this, three main points can be garnered: (*a*) trait values are often heterogeneously distributed in populations, (*b*) certain phenotypes can confer selective advantages to organisms under similar environmental regimes and optimise functionality, and (*c*) these optimal phenotypes tend to become more numerous in populations over time.

2.3 Form, function and environment

Arnold (1983) built upon previous models (Lande 1976; 1977; 1979; Lande & Arnold 1983) to outline an approach to quantify the intensity and direction of selection pressures and concluded that habitat, morphology, and performance are linked in a causal nexus.

Morphology—gross organismal form, including shape, appearance, and internal structure (anatomy)—is archetypal of phenotype (Wainwright & Reilly 1994). Common examples include: dermis colouration, bone lengths, and head-body ratio. Generally, taxa differ morphologically from other taxa; before the advent of genetics, comparative morphology was the primary method used to taxonomically categorise species (Kardong 2015; Löw et al. 2016). Morphological correlations with microhabitat structure are well established (Langerhans et al. 2003) and have received significant empirical attention (e.g. Bennett 1991; Garland & Losos 1994; Macrini & Irschick 1998; Miles 1995; Robson & Miles 2000; Vanhooydonck et al. 2002; reviewed for lizards in Kohlsdorf et al. 2001; Schulte et al. 2004).

Many studies have suggested strong relationships between morphological traits and performance capacities (e.g. Grizante et al. 2010; Huey et al. 2003; Irschick et al. 1996; Losos 1990a; Losos 2009; Peterson 1984; Zani 2000), thus highlighting intrinsic links between form and function. Yet performance is rarely examined in the context of

ecomorphology (Goodman et al. 2008; Irschick 2000). Relative difficulty in obtaining most performance data, often requiring laboratory work or *in situ* experiments, is generally implicated as the reason for this gap in research (Elstrott & Irschick 2004; Irschick 2000; Vanhooydonck & Van Damme 2003). Nevertheless, performance traits are known to correlate with certain aspects of microhabitat. For instance, Losos (1990b) demonstrated that anoles capable of jumping further in the wild generally selected wider perches. Identifying relationships between morphological and performance traits and habitat use can build fuller understanding of specific adaptive situations (Lossos 1990a; 1994; Lossos & Irschick 1996).

2.4 Grip–performance

Many animals have evolved means to grip substrates and move vertically through their environment, allowing expansion of available niches beyond terrestrial habitats (Cartmill 1985; Fontanarrosa & Abdala 2015; Full et al. 2002). Animals' capacity to hold on to substrates is termed grip–performance (Herrel et al. 2011; 2013; da Silva et al. 2014), or cling capacity in some literature (Losos 1990a; Losos et al. 1993; Zani 2000; 2001). How species grip, in what contexts, and whether this capacity varies (or not), has myriad ecological consequences for animals that employ this strategy (e.g. Brandt et al. 2015; Crandell et al. 2014; Van Damme et al. 1997; Wikelski & Trillmich 1994; Zani 2000; 2001). In addition to the axiomatic involvement in locomotion and navigating habitats, grip–performance could be important for other ecological activities such as gripping mates during reproduction, intraspecific combat (territorial behaviour), and anti-predation behaviour (Zani 2000). Ecological consequences of grip–performance are thought to be particularly pertinent for arboreal species (Hagey et al. 2017; Mattingly & Jayne 2004; 2005; Zani 2000). Woodland habitats are three-dimensionally complex; substrates used by animals (perches)—branches, twigs, and trunks of trees and woody shrubs—often vary in diameter, length, orientation, and flexibility (King 1998; McCoy & Bell 1991). Generally, narrower perches are more common in forests and usually surround wider perches (McCoy & Bell 1991; Percy et al. 2005). Narrower perches are, on average, more likely to rupture under analogous force (Morgan & Cannell 1987). Thus, arboreal animals must choose to navigate these 'risky' perches or travel greater distances (and possibly take longer) to move through their habitat (Gilman & Irschick 2013).

Arboreal animals have a diverse repertoire of physiological features that facilitate grip and climbing. For example, many lizards have developed elongated claws that penetrate substrates, creating a novel perpendicular surface which digits can exploit (Biewener

2003; Irschick et al. 1996); limb bone lengths (Zani 2000) and claw shape (Tulli et al. 2009) are particularly important morphological traits for these modes of grip. Adhesive toe-pads are another common grip method. Elstrott & Irschick (2004) studied Caribbean *Anolis* and found that individuals living in the higher canopy had larger toe-pad area and number of lamella than those living closer to the ground. Geckos exploit van der Waals force, a weak bonding between uncharged molecules, to adhere to substrates by using millions of microscopic hairs called setae that provide huge surface areas on their toe-pads (Autumn et al. 2002). The variety of strategies employed by lizards to overcome similar ecological hurdles underscores the breadth of scansorial/arboreal niches and highlights the importance of exploring specific grip–performance relationships in adaptive contexts.

2.5 Chameleons

The Chamaeleonidae family are a charismatic, diverse, and evolutionary intriguing clade of lizards (Tolley & Herrel 2014). They are thought to be one of the only taxa to have dispursed intercontinentally from a Madagascan epicentre (Tolley et al. 2013; Townsend & Larson 2001) in a post-Gondwanian era (Raxworthy 2002). There are ~200 extant chameleon species, over 50% of which are found only on Madagascar (Glaw 2015; Klaver & Böhme 1997). Chameleon range extends throughout Madagascar and continental Africa, into parts of southern Europe and Asia, as well as being introduced to several island groups as far away as the Pacific and mainland North America (Klaver & Böhme 1997; Tolley & Herrel 2014).

Although a few species exhibit partially terrestrial lifestyles (Branch 1988), the vast majority of chameleons are exclusively arboreal (Raxworthy et al. 2002), and are typically found in tropical forests but occasionally occupy savannahs, deserts, and steppes and montane regions (Tolley & Herrel 2014). Chameleons are thought to be ‘cruise foragers’ (Butler 2005), that move through their habitat relatively slowly (Abu-Ghalyun et al. 1988; Mutungi 1992) and are able to predate invertebrates from distances beyond their own body lengths with ballistic tongues (Burrage 1973). This slow mode of life conserves energy and allows chameleons to easily disguise their silhouette with the aid of pseudo-cryptic colouration (Tolley & Burger 2007).

Chameleons have evolved a suite of highly specialised traits, including: independently moving eyes, compressed lateral bodies, ballistic tongues, zygodactylous feet/hands, and prehensile tails (Edmonds 2015). Chameleons’ sensory systems are heavily geared towards visual stimuli, with other senses known to be significantly less developed, this is

thought to assist visual acuity during predation of flying insects (Tolley & Burger 2007; Tolley & Herrel 2014). Their snout-vent lengths (SVL) range from 2.9 cm in *Brookesia micra* (Glaw et al. 2012) to 68 cm in *Calumma parsoni* (Cuvier 1825). Chameleons host the world's shortest lived tetrapod species, as well as species living over 20 years (Raxworthy et al. 2002). Many species possess impressive ornamentations such as spiny crests, facial horns (in numerous quantities and arrangements), and tail sails (Edmonds 2015). Aspects of chameleon phenotype have evolved in tandem with their choice of microhabitat.

Chameleon hands and feet rearrange during development to form grasping appendages (Fischer et al. 2010). These are accompanied by their uniquely muscular prehensile tail (Peterson 1984). Together they allow chameleons to grip and navigate substrates narrower than their body (Higham & Jayne 2004). This ability may allow chameleons to access to habitat unavailable to similar-sized lizards and could open up novel niche opportunities. During locomotion, fused-digits on their zygodactylous hands and feet envelop perches in a grip approaching 360°. Usually chameleons are anchored by all four appendages (and tail), but when bridging gaps between perches, individuals often rise up on their hindlimbs leaving forelimbs free to grasp other substrates (see Fig. 4.2). As a result, hindlimbs generally have more contact with chameleon's substrates than forelimbs (Ischick & Jayne 1999). As chameleons have such a unique interaction with their microhabitat perch network, they may not conform to typical performance predictions that hold true for other arboreal lizards, particularly those suggesting decreased locomotor performance on narrow substrates (Cartmill 1974; Losos & Irschick 1996; Losos & Sinervo 1989; Macrini & Irschick 1998; Spezzano & Jayne 2004).

2.5.1 Chameleon grip and microhabitat use

Although several studies have examined the underlying physiological factors that determine aspects of chameleon grip performance (e.g. Abu-Ghalyun et al. 1988; Mutungi 1992), studies linking these capacities to habitat use are uncommon.

Losos et al. (1993) measured sprint and grip–performance of *Chamaeleo jacksonii* (arboreal) and *Chamaeleo dilepis* (semi-terrestrial), attempting to identify if/how performance capacities varied as a function of perch diameter. Their data did not support the hypothesis that each species would perform relatively better on perch diameters that they used most often in the wild. Rather, results suggested that performance trade-offs exist between sprint and grip performance in these species, where *C. dilepis* had greater sprint speeds on all dowels, and *C. Jacksonii* had greater gripping ability on all dowels.

These results imply performance specialisation to different microhabitats. Further findings indicated that foot/hand length varied independently from maximal gripping diameters. However, optimal grip in this investigation was assumed to be the dowel diameter on which chameleons exerted the most grip force. This approach assumes that one of the dowel diameters chosen in testing is likely to be 'maximal'. While this may indicate which dowel diameter chameleons optimal grip is closest to, it does not identify individual's true optimal grip diameter.

da Silva et al. (2014) studied chameleons of the *Bradypodion melanocephalum* – *Bradypodion thamnobates* species complex, exploring locomotor morphology and grip–performance as they relate to microhabitat use. Chameleons occupying open-canopy habitats were found, on average, to be smaller and have lower overall grip strength than individuals found in closed-canopy habitats. These results highlighted a grip performance asymmetry between *B. melanocephalum* and *B. thamnobates* stark enough to diagnose two distinct ecomorphs in these populations.

Herrel et al. (2011) examined grip strength and suspected associations with morphological traits (fore- and hindlimb bone lengths, and hand and feet pad sizes) and microhabitat use of *Bradypodion pumilum*. Similar to da Silva et al. (2014), this study targeted populations of *B. pumilum* that occupied open- and closed-canopy microhabitats. They sought to determine if performance varied as a function of microhabitat use. Results indicated that larger *B. pumilum* with longer limb morphology were generally stronger and selected wider perches. These results indicate firstly, that *B. pumilum* selected their microhabitat non-randomly based on perch diameter, and secondly, that there is a positive correlation between perch diameter, morphological traits, and average grip performance in this species. Herrel et al. (2013) built upon this work; terrestrial chameleons of the genera *Bradypodion* and *Chamaeleo* were found to have smaller hands and feet and have poorer grasping ability than arboreal counterparts. However, aspects of these apparent relationships may have been clade specific (Herrel et al. 2013).

Some common threads run through these studies. Hand/foot size appears to be positively correlated with average grip strength in multiple chameleon species (Herrel et al. 2011; 2013; da Silva 2014). Chameleons select their microhabitat non-randomly with reference to perch diameter (Herrel et al. 2011; 2013; Losos et al. 1993; da Silva 2014). And, perch diameter, limb morphology and size, and grip performance, are causally linked in chameleon ecology. However, there are limitations to these studies in the context of my research. Firstly, none of the articles discussed above focused on Malagasy chameleons. Species on Madagascar have been isolated from most others for millions of years (see

2.6) and have likely evolved unique ecological relationships with their local environment. Herrel et al. (2011; 2013) and da Silva et al. (2014) focused on a particular radiation of South African chameleons occupying fynbos habitat; some ecological conditions, especially at the microhabitat level, are likely to be different to that of Madagascan habitats. Thus, chameleons on Madagascar may not conform to the ecological predictions of studies on African species. Secondly, in da Silva et al. (2014) and Herrel et al. (2011; 2013), only two dowel diameters were tested (4 and 9.25mm, and 5 and 10mm respectively). These widths were meant to represent narrow and wide perches, and were chosen based on available habitat data (da Silva & Tolley 2013). However, these diameters could not have represented the range of available perches in chameleon's habitat; in similar fynbos habitat to the study site of Herrel et al. (2011; 2013), chameleons have frequently been observed using perches much narrower and wider than this (Hopkins & Tolley 2011a; 2011b). Hence, a sample size of two dowel diameters is not sufficient to speculate on maximal grip performance capacities. Further, these studies focused on hand–, not foot–, griping. Hindlimb performance in chameleons may provide a different function and be more ecological pertinent (Ischick & Jayne 1999). Finally, previous literature has tended to make interspecific comparisons of grip–performance and perch use; my research seeks to explore these relationships intraspecifically in *F. oustaleti*.

2.6 Madagascar

"Continental Island of the First Rank"—Wallace (1892, p.563).

Madagascar is a biodiversity 'hotspot' (Myers et al. 2000) and safeguarding its biological communities is considered a global conservation priority (Ganzhorn et al. 2008; 2014; Goodman and Benstead 2005; Hannah et al. 1998). Primarily, this is because most animals and plants on Madagascar are found nowhere else on earth (Ganzhorn et al. 2014). Recent estimates hold that more than 90% of Madagascar's 13,000 plant species , 99% of its amphibians, 92% of its reptiles, 52% of its birds, and 100% of its terrestrial mammals, are endemic (Goodman & Benstead 2005; Phillipson et al. 2006; Samonds et al. 2013; Wilme et al. 2006). Moreover, Madagascar's endemic radiations are ancient and represent taxonomic distinctness up to the family level, leading some to claim that higher taxa endemism leaves Madagascar peerless in biological uniqueness (Ganzhorn et al. 2014).

Much of Madagascar's extraordinary biological distinctness is thought to have arisen because of its isolation from other landmasses that has lasted at least 90 million years

(Rabinowitz et al. 1983; Storey et al. 1995). Compounded by the Cretaceous–Tertiary extinction event (K–T) (Alvarez et al. 1980), geographic isolation has allowed Malagasy taxa to radiate into previously impoverished niche space (Ali & Krause 2011; Fortey 1999; Renne et al. 2013; de Wit 2003). Throughout the latter half of the 20th century the role of dispersal in the post-Mesozoic faunal colonisation of Madagascar was largely ignored in favour of a vicariance dominated narrative (Yoder & Nowak 2006); the first years of the 21st century have seen this status quo reversed (Salmonds et al. 2012). Current thinking is that the majority of Madagascar's basal fauna stocks originated from Cenozoic colonisation events from 65 million years ago onwards (Samonds et al. 2013). Fossil records buttress this model by revealing that most extant Madagascan vertebrate taxa were not present during the Cretaceous (Krause et al. 1997; 1998; 1999), hence their arrival must have been later. Though some clades have survived from Madagascar's shared plate tectonic history with Gondwanaland (Gaffney & Forster 2003; Noonan & Chippindale 2006). This stochastic dispersal post-K–T has given rise to peculiar taxonomic assemblages (Goodman & Benstead 2005; Poux et al. 2005; Reinthal & Stiassny 1991), where a handful of speciose radiations make up the majority of Madagascar's extant fauna (Bossuyt & Milinkovitch 2001; Nagy et al. 2003; Vences 2004) and entire animal groups, such as large mammals, are absent. However, human driven extinctions of certain taxa during the Holocene may compound our ability to assess 'natural' patterns of Madagascan biodiversity (Crowley 2010). Nevertheless, current biological communities on Madagascar are widely thought to be unique in structure and composition (Ganzhorn et al. 2014; Horvath et al. 2008; Kohler et al. 2010; Reddy et al. 2012; Salmonds et al. 2012).

2.6.1 Modern biogeography and forest cover

Often cited as a pseudo-continent (de Wit 2003), Madagascar is the world's fourth largest island (587,000 km^2), lying ~400km east of Mozambique in the Indian Ocean. Madagascar's topography is dominated by an eastern massif running north-south which divides the island into two slopes: a steep eastern escarpment, and a gentler western slope (27% and 73% of land cover respectively (Ganzhorn et al. 2014)). This rugged topography influences moisture deposition from humid prevailing winds rolling in off the Indian Ocean (Jury 2003), resulting in a fine-grain diversity of microclimes—discrete abiotic pockets of different weather conditions (Dewar & Richard 2007; Rakoto-Joseph et al. 2009). These heterogeneous moisture patterns shape Madagascar's local landscape diversity, and although ~65% of the island's land cover is savannah, excluding agricultural

land (Moat & Smith 2007), habitat mosaics of scrub, wetland, and forests typify most regions (Mayaux 2000; 2004). The centrepieces of these landscapes are scattered woodland blocks, forest archipelagos that host more than 90% of endemic species on Madagascar.

Our understanding of the historic relationship of Madagascar's human population with its forests is mired in conflicting interpretations and innuendo (Kline 2002). The interplay between humans and forests has shaped significant aspects of Madagascar's modern ecology (Randrianja & Ellis 2009). Forest clearance for agriculture using methods such as 'tavy' (slash and burn), and oxen grazing are central to Malagasy culture, widely practiced, and considered to be highly detrimental to biodiversity (Clark 2012; Gade 1996; Marcus 2001; Peet & Watts 2007). These factors are exacerbated by rapidly rising and increasingly poor human populations, to the extent that deforestation is considered an ecological crisis on Madagascar (Harper et al. 2007).

2.6.2 Forests in flux

Tropical forests are the world's largest reservoir of biodiversity (Gibson et al. 2011; Mittelbach et al. 2007; Weir & Schluter 2007; Wiens & Donoghue 2004). They girdle the planet and form a disjunct haven for unique species (Myers et al. 2000; Sheil & Ghazoul 2010). Under intense and increasing anthropogenic threats (Geist & Lambin 2002; Newbold et al. 2015), these forest are in rapid decline (Dirzo & Raven 2003; Laurence 1999; Tittensor et al. 2014). Inflicted with widespread deforestation, tropical biodiversity has never been in worse shape (Bradshaw et al. 2009) and extinction rates have soared (Huxel & Hastings 1999; MEA 2005; Pimm & Raven 2000).

Although habitat change occurs 'naturally' over time (Weigand et al. 2005), human activity is known to dramatically increase rates of habitat conversion (Lorenzen et al. 2011; Tittensor et al. 2014) and reorganise biological communities (Pereira et al. 2010). Generally, biodiverse habitats are replaced by species depauperate ones (Hansen et al. 2013).

Heterogeneous deforestation can modify woodland structure and often divide habitats (Ewers & Didham 2006; Noss & Csuti 1997), leaving islands of fragmented forest (Fischer & Lindenmayer 2007). This can reduce access to resources and potential mates, and expose species to novel ecological boundaries (Lindenmayer & Fischer 2006), such as higher rates of predation on habitat edges (Bereczki et al. 2015). Evidence that forest loss and fragmentation reduce biodiversity is overwhelming (Andrén 1994; Baillie et al. 2004;

Bender et al. 1998; Collen et al. 2009; Cushman 2006; Foley et al. 2005; Fraser et al. 2015; Haddad et al. 2015; Haila 2002; Laidre et al. 2015; Newbold et al. 2015; Noss & Csuti 1997; Pereira et al. 2010; Ponce-Reyes et al. 2013; Pratchett et al. 2012; Purvis et al. 2000; Tittensor et al. 2014; Weigand et al. 2005; With & Crist 1995). However, several recent articles by Fahrig (2003; 2013; 2016; 2017) have suggested that positive effects of habitat fragmentation outweigh the negative, and that fragmentation is often conflated with habitat loss in the literature. These processes represent significant ecological shifts at landscape level and likely have diverse and specific implications for forest species (Debinski & Holt 2000; Ewers & Didham 2006).

Fifty two percent of Madagascar's forest cover has been lost since the 1950s (Harper et al. 2007; Schwitzer et al. 2014); ~17% of its terrestrial surface remains forested (Mayaux et al. 2000; Moat & Smith 2004) and ~200,000 hectares are lost annually (WWF 2007). This rapid forest loss is implicated as the prime impetus for species decline in Madagascar (Green & Sussman 1990; Harper et al. 2007; Raxworthy 1988). Allnutt et al. (2008) estimated that 9.1% of Malagasy species went extinct from 1950 to 2000. Impacts of deforestation and fragmentation on Malagasy biodiversity have been observed in every forest region (Langrand & Wilme 1997; Vallan 2000; Watson et al. 2004).

2.7 Summary statement

Identifying microhabitat – performance – morphology links can allow glimpses into adaptation and elucidate evolutionary trajectories. Contextualising these relationships within the adaptive landscape framework, as phenotypic frequencies 'chasing' optimal ecological functionality within particular local environments, can develop fuller understanding of how traits confer advantages (or not) for organisms in specific microhabitats, and how these dynamics change over space and time.

Locomotor performance is among the most ecologically relevant aspects of morphological functionality as it is required to find mates, escape predation, and find food resources. Exploring how arboreal lizards grip substrates in their microhabitat is thus a fruitful avenue to explore functional capabilities. While previous studies have identified correlations between chameleon morphology, grip performance, and microhabitat use, identifying phenotypic optima in these contexts has, to the best of my knowledge, not been attempted for this taxon. Exploring this theme in Madagascar's biologically exceptional forests may provide a unique lens through which to view microhabitat use and functional capability, and broaden ecology understanding of some of the world's most threatened and charismatic ecosystems.

3 MATERIALS AND METHODS

3.1 Study area

This study was conducted in northwest Madagascar, in the Mahamavo forest (5°29′23″S, 46°38′25″E), an area 50 km northeast of the city of Mahajanga (Majunga) (Fig. 3.1). Northwest Madagascar lies between the central highlands and the Indian Ocean. The steppes and massifs of the highlands impede eastern trade winds rolling inland off the Indian Ocean, and consequently western Madagascar is left in a seasonal rain-shadow and experiences pseudo-monsoon conditions (Jury 2003). This pattern of water flow into the west defines large elements of the region's ecology (Gautier & Goodman 2003; White 1983). There is a distinct asymmetry in species assemblages during the wet and dry season, with many species common in the wet season not appearing during dry season surveying (Long et al. 2013).

Palm-savannah is the dominant land-cover around my research area (Moat & Smith 2007); deciduous forests, wetlands, and human-altered landscapes scatter this grassland matrix in a habitat mosaic (Fig. 3.1) that typifies the region's ecology (Guillaumet & Koechlin 1971; Mayaux et al. 2004; Washington et al. 2009). Forest blocks host the majority of the region's biodiversity and endemism (Ganzhorn et al. 1999; Landgrand 1990; Raselimanana et al. 2000). White (1983) estimated regional plant endemism in these habitats at 70 percent. Forest blocks are characterised by more open, evergreen, canopies and thicker shrub layers than other Madagascan woodlands (Koechlin et al. 1974). As with other Madagascan habitats, Mahamavo's western dry forest archipelago faces anthropogenic threats that deforest and fragment remaining patches (Clark 2012; Jenkins 1987). Around 3% of forest cover is lost annually in the region (Ackermann 2003). As these habitats are increasingly isolated and fragmented (Mayaux et al. 2004; Smith 1997), they are thought to be among the most degraded woodland on the island (Burns et al. 2016; Crowley & Samonds 2013) and are a high conservation priority (Crowley 2002; Jenkins 1987). Mahamavo is dominated by two blocks of deciduous woodland that are bordered by several satellite fragments (Fig. 3.1). Hereafter all woodland blocks are referred to collectively as Mahamavo or Mahamavo forest. Mahamavo occupies a unique transitional zone between the relatively distinct species pools of Madagascar's north and west, and is thought to host assemblages unique on Madagascar (Long et al. 2013). These forests have particularly high lemuriform diversity and abundance (Olivieri et al. 2006). Globally threatened/flagship species hosted in Mahamavo include: the Madagascar Fish Eagle, *Haliaeetus vociferoides* (Razafimanjato et al. 2014), Western Falanouc, *Eupleres major* (Evans et al. 2013), and Fossa, *Cryptoprocta ferox* (Kerry et al. 2015).

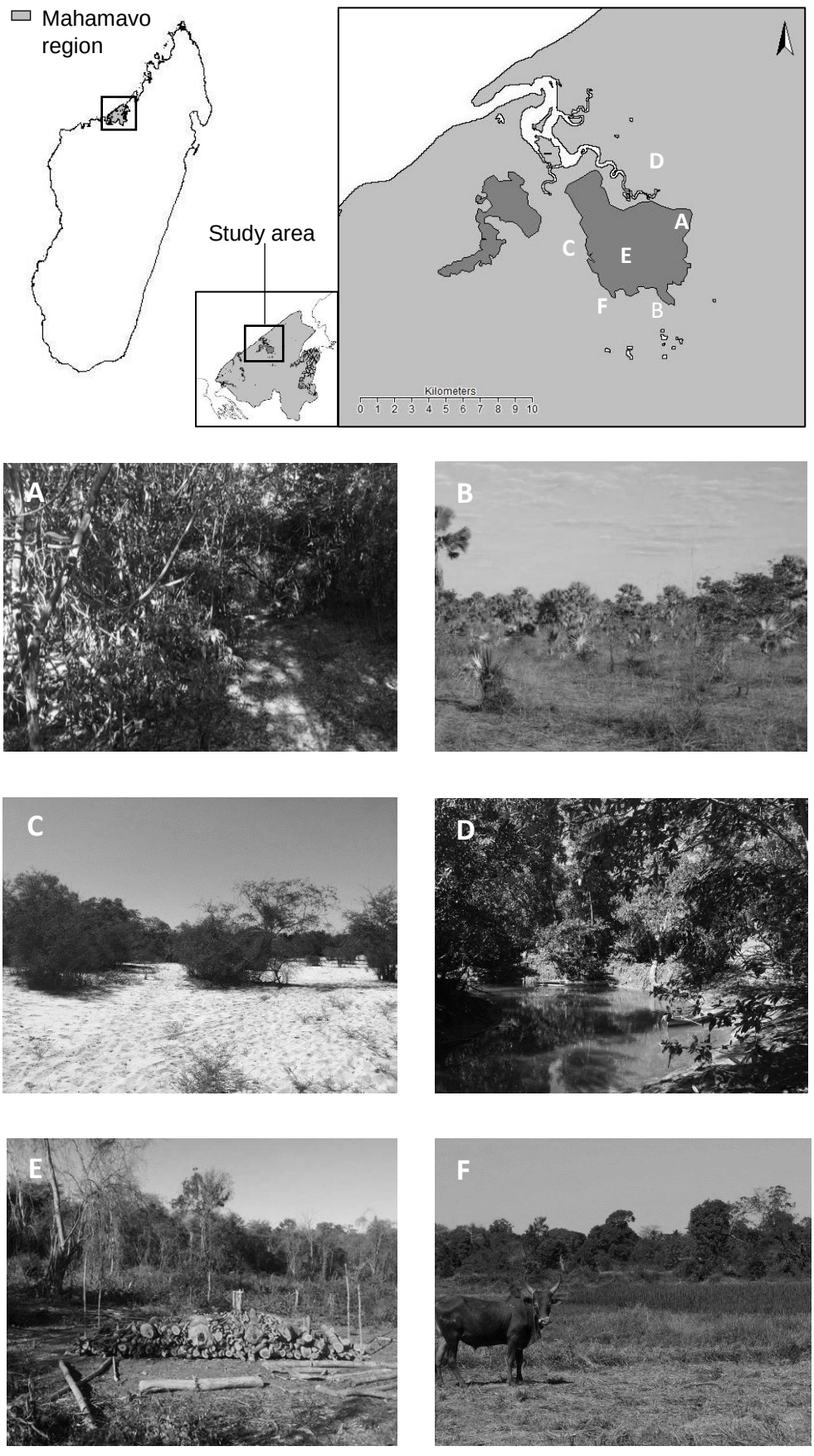

Figure 3.1: Map of Mahamavo forest region and examples of land uses in study area. Note variety of habitats: (A) dry forest, (B) palm savannah, (C) xeric scrub, (D) mangrove, (E) cleared forest, used for charcoal production, and (F) agricultural land.

3.2 Study species

The Malagasy giant chameleon or Oustalet's chameleon (*Furcifer oustaleti*) is endemic to Madagascar (though feral populations are found elsewhere (Spawls et al. 2002, 2014; Tilbury 2010)). Distributed throughout the island, this species is tolerant of a range of habitats and can thrive in forests, savannah, scrub, and human-altered landscapes (D'Cruze & Kumar 2011). Adults reach up to 284 mm SVL, making them the joint largest extant chameleon with *Calumma parsonii* (Glaw & Vences 1996; 2007; Nečas 2004). *F.oustaleti* is an arboreal predator, usually feeding on arthropods (Hofer et al. 2003) but known to opportunistically consume small vertebrates including birds (Garcia & Vences 2002). Although listed as 'Least Concern' on IUCN's Red List (Jenkins et al. 2011), *F.oustaleti* is considered a flagship species and is frequently mentioned in conservation management plans in Madagascar (Glaw & Vences 2007).

Within my study area, *F.oustaleti* is abundant and is often found close to human settlements. Across their Mahamavo range *F.oustaleti* are sympatric with two other chameleon species: *Brookesia brygoo* (Raxworthy & Nussbaum, 1995) and *Furcifer angeli* (Brygoo & Domergue 1968). *B.brygoo* are found commonly throughout Mahamavo forest during the wet season (Rakotoarison et al. 2015). However, they were not encountered during my study period, likely because they were in burrows waiting out the more hostile dry season. *F.angeli* were found in sympatry with *F.ousteleti* across my research area (Long et al. 2012; pers. obvs.). No area hosted just one or the other, but generally *F.angeli* were seen more often on surveys. These species are thought to partition resources and niches (Carpenter 2003).

3.3 Data collection

Fieldwork was carried out in June and July of 2017. Eight pre-existing survey routes were repurposed to survey for chameleons; these paths were created through a 'no chop' policy to avoid unnecessary disturbance and destruction of forest by utilising forest paths and roads. Survey routes ranged in length from 1.6–3.6 km. Visual-encounter surveys were used to locate *F.oustaleti*. Surveys were conducted during daylight hours, as roost perch (used at night to sleep on) ecology is thought to be underpinned by different environmental factors (Randrianantoandro et al. 2007; 2010). Individuals were spotted and identified using field guides and dichotomous keys. Due to the aforementioned reliance on crypsis, when approached chameleons tended to remain still or make a 'branch in the wind' motion (Raxworthy 1988; Tolley & Herrel 2014), making it straightforward to identify their perch use prior to being disturbed.

3.3.1 Body and habitat measurements

F. oustaleti were captured by hand. After capture, individuals were held at the rear of the neck and provided a perch to grip to reduce stress. Digital callipers (LUPO) were used to measure several morphological traits: tail length was recorded as the distance from the vent to the tail tip, hind and forelimb lengths were measured from the point of insertion into the abdomen to the femoral-tibial and humero-radio-ulnar joints (on animal's right side). Mass was recorded using Pesola ™ scales and a pre-weighed fabric bag. Body temperature was measured immediately after capture by inserting a type T thermocouple <8mm into the cloaca.

Microhabitat was measured at initial sighting locations of *F. oustaleti*. Perch height was measured using a measuring tape and perch diameter with digital callipers. A handheld weather station (LM-8000) recorded wind speed and humidity. Surface and air temperature were measured using a type T thermocouple. Chameleons were transported to camp after these measurements were taken for grip experiments.

3.3.2 Measuring grip–performance

Experimental and care protocols are based on the work of Herrel et al. (2013). Foot, rather than hand, grip was tested because of chameleon's habit of rearing up on their hindlimbs (Fig. 3.2) and thus generally having more contact with their perches than forelimbs (Ischick & Jayne 1999).

Figure 3.2: *F. oustaleti,* perched, seeking out substrate to grip (photo credit: R.M. Clark). Note that feet are gripping the individual's current perch while the right forelimb is reaching elsewhere, a common behaviour among chameleons.

A specially designed rig was built to hold hardwood dowels of six diameters (3, 6, 10, 20, 30, and 45 mm) horizontally above a level surface. Chameleons were fitted with a 'lizard leash' harness; a spring-balance was attached to the rear-mid-body section. Individuals were prompted to grip each dowel with their right back foot. The right foot was chosen at random but kept consistent across experiments. After individuals grasped the dowel they were steadily pulled from the dowel horizontally via the spring-balance until their grip broke and they fell to a cushioned area. The fall was ~15cm; *F. oustaleti* fall substantially further onto the ground during regular activity in the wild (pers. obvs.). Experiments were recorded dorsally using a HD camera and peak-force taken to break chameleons grip was extracted by later analysing footage.

Chameleons were tested once at each dowel width, with a rest period of 30 minutes between each test. Experiments commenced >1 hour after individuals were captured.

3.4 Care of individuals

Chameleons were transported from their point of capture to the research station in a breathable fabric bag filled with appropriate foliage to mimic chameleon microhabitats and to provide substrates for chameleons' zygodactylous feet which are tensed when not gripping (Edmonds 2015). Bags were kept in the shade at all times and within a cool box if temperature exceeded 30 degrees. Chameleons were housed individually in large mesh enclosures ~0.5x0.5x1m filled with vegetation to reduce stress and limit visual contact with humans or other chameleons. Animals were kept in the shade with access to natural light, supplied with drinking water ad libitum, and sprayed with a misting bottle once a day. A Garmin GPSMAP 64S handheld geographic positioning system device was used to record the exact points of capture, where individuals were released less than 48 hours later.

Only adults were used for this study. Any individual with obvious injury, maiming, or displaying signs of stress, e.g. excessive small movements or 'quivering' (Langkilde & shine 2006), were immediately released. Gravid females (determined by body size and coloration at the time of collection (see Cuadrado 2000)) were also immediately released. All procedures and care protocols were approved by the University of Nottingham's Animal Welfare and Ethical Review Body and the School of Geography's Ethics Committee.

3.5 Analysis

3.5.1 Morphology

Measured morphological traits were compared to each other, average grip strength, and optimal grip diameters using Pearson correlation coefficient.

3.5.2 Fitting grip–performance curves

To determine the diameter of maximum grip strength (d_{opt}), I, with assistance of A. Algar, fit a grip–performance curve for each lizard using a Gompertz*Gaussian function. This function, used for thermal performance curves (e.g. Frazier et al. 2006, Frishkoff et al. 2015), allows performance—in this case, grip strength—to rise and fall asymmetrically around an optimum. While many functions of a similar shape could be used (Angilletta 2006), the Gompertz*Gaussian also has the advantage of directly fitting the diameter at which curve's maximum occurs (d_{opt}). The Gompertz*Gaussian function is:

$$G=G_{max}\exp(-\exp(\rho(d-d_{opt})-6)-\sigma(d-d_{opt})^2)$$

Where G is grip strength, G_{max} is the maximum grip strength inferred from the curve, d is dowel diameter, d_{opt} is the dowel diameter at G_{max} and ρ and σ are parameters that determine how quickly the curve rises and falls. Models could not be fit for those individuals where the curve's maximum did not fall within the range of dowel diameters tested. Curves were fit using the nlsLM function in the minpack.lm package (Elzhov et al. 2016) in R v3.4.2 (R Core Team).

3.5.3 Testing for non-random perch selection and optimal grip diameters

I tested whether *F. oustaleti* were found on perches closer to their optimal grip diameter (d_{opt}) than expected if they were selecting perches randomly. For each animal, I used the empirical distribution of available perches (culled to the range of perch diameters that *F. oustaleti* was observed using during my study period) to calculate the probability of *F. oustaleti* being found on a perch as close in size to d_{opt} as it was observed. To achieve this, I calculated the proportion of available perches that were closer in absolute size to d_{opt} than the perch on which it was observed (this is equivalent to calculating the area under the curve of a continuous probability distribution function that is between the

optimum and used perch. Thus this value is called area under the curve (AUC). I also calculated the mean AUC across all species and compared this to the distribution of mean values obtained by randomly assigning perches to animals, calculating individual AUCs and finding their mean. This procedure was repeated 1000 times to obtain a null distribution of mean AUC values from which to calculate a P-value. I used the mean AUC across all animals as an overall measure of how optimal grip performance influences perch selection.

I tested whether d_{opt} values were more similar to the most common available perch diameter, i.e. the mode of the empirical distribution of available perches (3.2mm) than expected if d_{opt} was random. The mode was calculated by taking the midpoint of the modal bin of the histogram, with bin resolution of 1mm. I used the same procedure as above to calculate AUC of the area between d_{opt} and the mode for each individual and a mean overall value.

The above analyses were carried out twice. Once with only the individuals who had d_{opt} values that fell within the range of tested dowel diameters (seven individuals) and once including all individuals, with d_{opt} values equal to the narrowest dowel tested (3mm) assigned to individuals who did not have optima within the tested range of dowels (n = 6). For all of these individuals, the highest grip strength was on the 3mm dowel.

4 RESULTS

Fourteen *F. oustaleti* were caught over ~120 person hours spent searching for chameleons; two individuals were excluded due to suspected ill health. Henceforth these twelve animals (eight male, four female) are referred to as individuals *a–l*, based on the chronological order in which they were tested.

4.1 Microhabitat

All individuals were found in dry forest patches perched on wooded plants. Chameleons selected semi-shaded areas (83.3% of individuals were found in dappled sunlight; average canopy density was 51%). Surface temperatures of selected perches (average: 29.8°C (*se* = ±0.93)) were not significantly warmer than ambient temperatures (average: 29.6 °C (*se* = ±0.76)) (Wilcoxon signed-rank test: $W = 45.5$, $P = 0.286$). Microhabitat humidity (average 53.8 % (*se* = ±2.65)) was positively correlated with surface and air temperature (Pearson correlation coefficient (respectively): $r = -0.66$, $df = 10$, $P = 0.0194$; $r = -0.677$, $df = 10$, $P = 0.0157$). Average perch height above ground was 57.7 cm (*se* = ±10.534); no chameleons were observed above 1.32 m. Higher perches were not significantly warmer ($r = 0.335$, $df = 10$, $P = 0.287$) or more humid ($r = -0.0153$, $df = 10$, $P = 0.962$). Further, there was no observed relationship between perch height and diameter ($r = -0.452$, $df = 10$, $P = 0.141$). Average selected perch diameter was 11.9 mm (*se* = ±1.33); the thinnest perch a chameleon was observed on was 2.7 mm, the largest was 18.8 mm.

Available perches in my research area had an average diameter of 5.6 mm (*se* = ±0.07). After excluding measurements outside the perch diameter range that chameleons were observed on (2.7–18.8mm), the average available perch diameter was 6.5 mm (*se* = ±0.09). More than 50% of all perch measurements were <3 mm diameter; 2.57% were >26 mm. Thus, available perch diameter data were non-normally distributed (Fig. 4.1); narrower perches were far more common than wider perches in my research area.

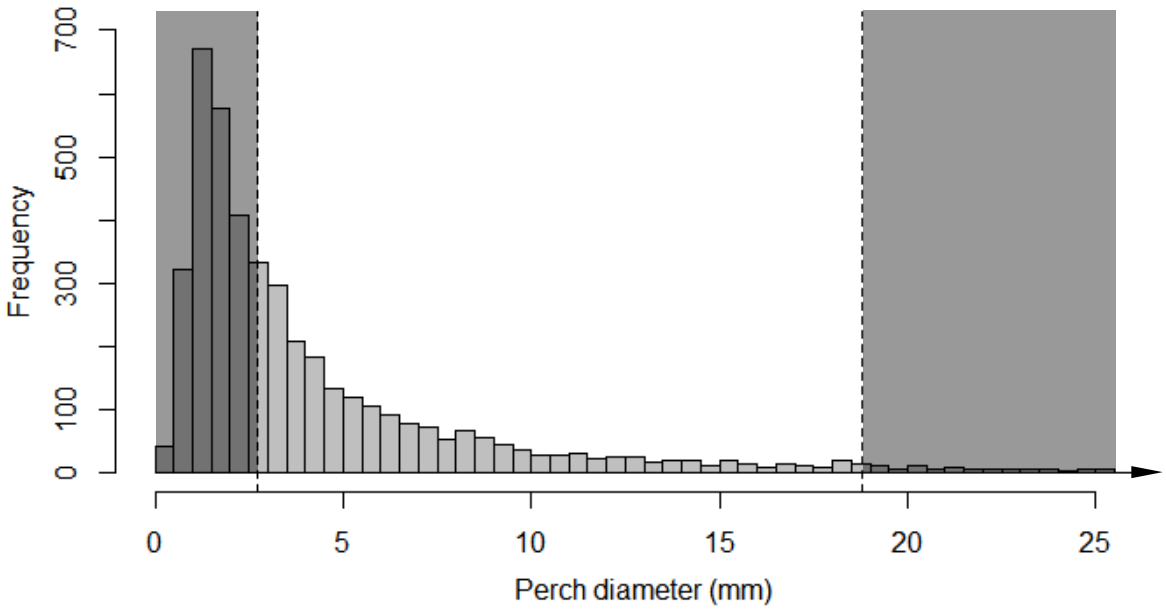

Figure 4.1: Histogram showing empirical distribution of available perch diameters in my study area. Shaded areas indicate perch diameters <2.7 mm and >18.8 mm: minimum and maximum perch diameters that chameleons were observed using during my investigation. X-axis arrow indicates that data extend to perch diameters of 180mm; perch diameters >100 mm were extremely rare.

4.2 Grip performance curves and optima

Chameleon grip-strength data were fit to a Gompertz*Gaussian function to determine grip–performance curves performance curves (Fig. 3.2). Seven of the twelve individual's showed relationships between voluntary grip strength and dowel diameter that had a maximum within the range of the perch diameters tested. Relationships for individuals *c*, *d*, *f*, *h*, and *l* did not peak within the range of the data and thus had grip optima that were ≤ 3 mm. As this is below the thinnest artificial perch diameter used in experiments, these individuals were included in analyses as having d_{opt} of 3mm. D_{opt} ranged from 3–9.8 mm and had a mean of 5.2 mm (*se* = ±0.67). The difference between optima and selected perch diameters ranged from 0.3-15.8 mm with a mean of 6.7 mm (*se* = ±1.39). After excluding individuals with optima ≤ 3 mm, the mean d_{opt} was 6.87 mm (*se* = ±0.87), and on average these optima were 4.3 mm (*se* = ±0.47) away from selected perch diameters.

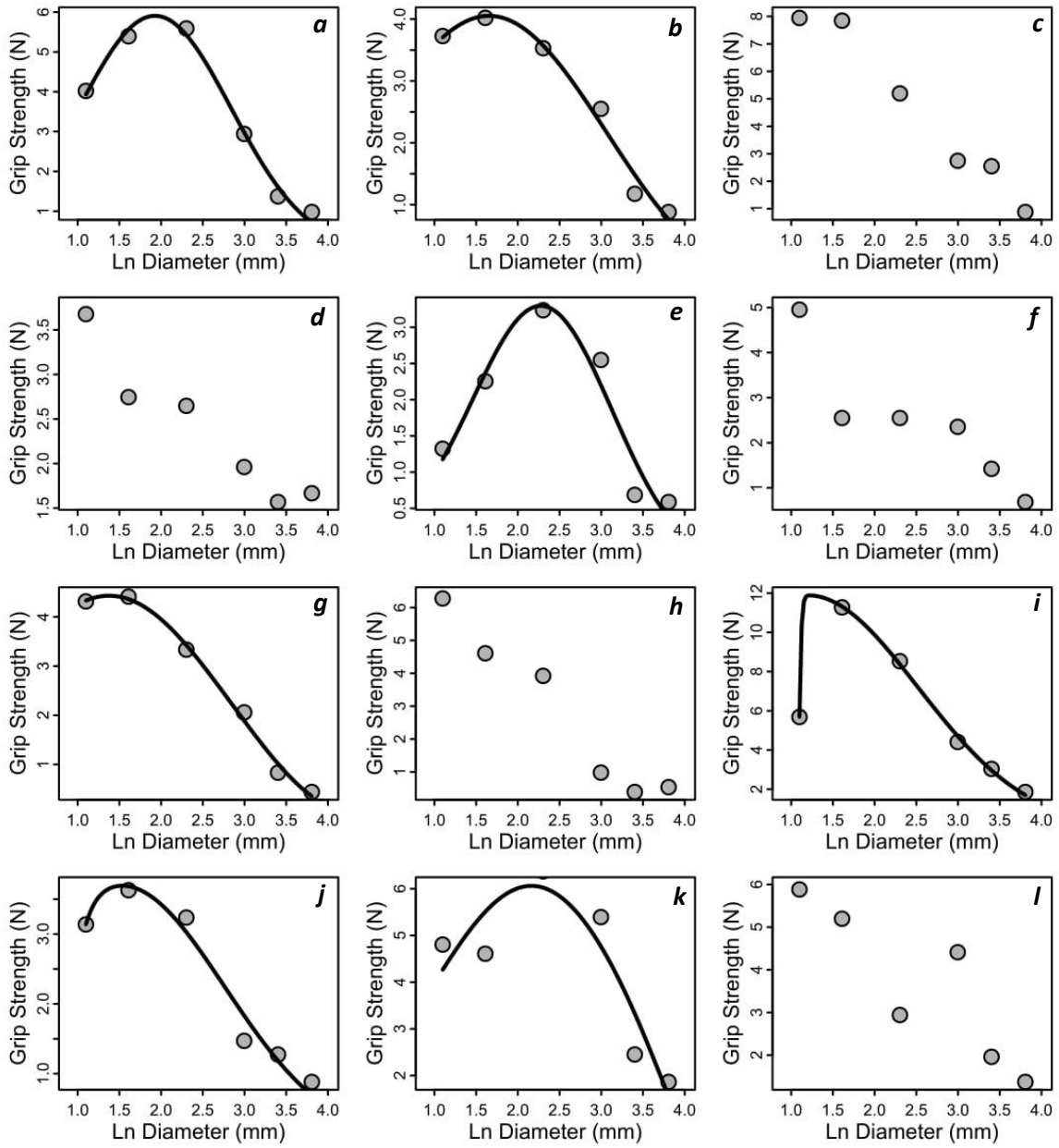

Figure 4.2: Gompertz*Gaussian grip performance curves. The diameter at the maximum of each curve was taken as chameleon's optimal grip diameter. Note that individuals *c*, *d*, *f*, *h*, and *i* were found to have optima outside of the tested range of dowels, optima for these animals was taken as 3 mm as true optimal diameters will not exceed this value.

4.3 Morphology

All morphological traits measured were positively correlated with each other (Table. 4.1) and with average grip strength (Fig. 4.3). Larger and heavier *F. oustaleti* with longer limbs were able to exert greater average grip force. Measured morphological traits were not correlated with selected perch diameter (Fig. 4.4), other microhabitat variables (Table. 4.2), or d_{opt} (Fig. 4.5), indicating that these variables vary independently from *F. oustaleti*'s size.

Table 4.1: Results of Pearson correlation coefficient tests on morphological traits. All significant at $P < 0.001$.

Morphological trait comparison	*r* =	*P* =
weight-SVL	0.951	0.000002
weight-tail length	0.945	0.000002
weight-tibia length	0.896	0.000063
weight-femur length	0.92	0.000028
weight-foot length	0.937	0.000007
SVL-tail length	0.971	<.000001
SVL-tibia length	0.918	0.000016
SVL-femur length	0.95	0.000003
SVL-foot length	0.896	0.000081
tail-tibia length	0.863	0.00015
tail-femur length	0.934	0.0000045
tail-foot length,	0.901	0.000032
tibia-femur length	0.935	0.000004
tibia-foot length	0.895	0.000042
femur-foot length	0.904	0.000028

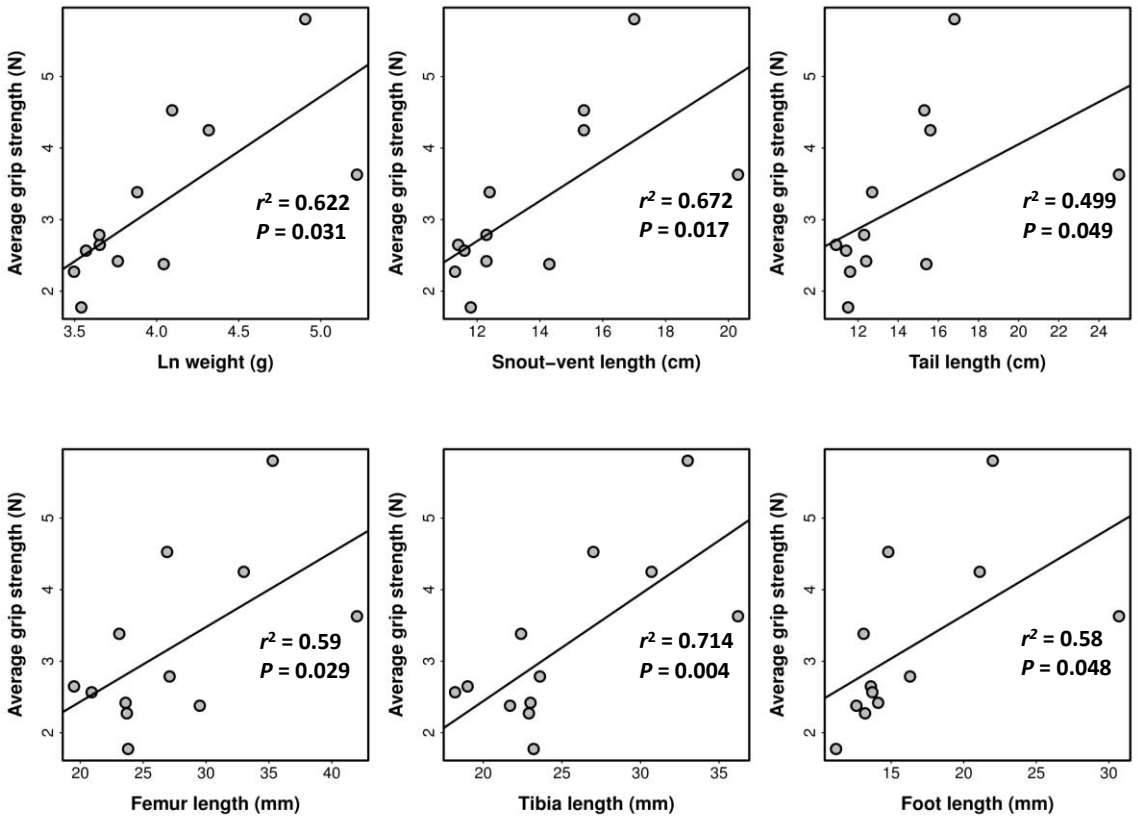

Figure 4.3: Average voluntary grip strength and morphological trait scatterplots. All significantly correlated at $P < 0.05$.

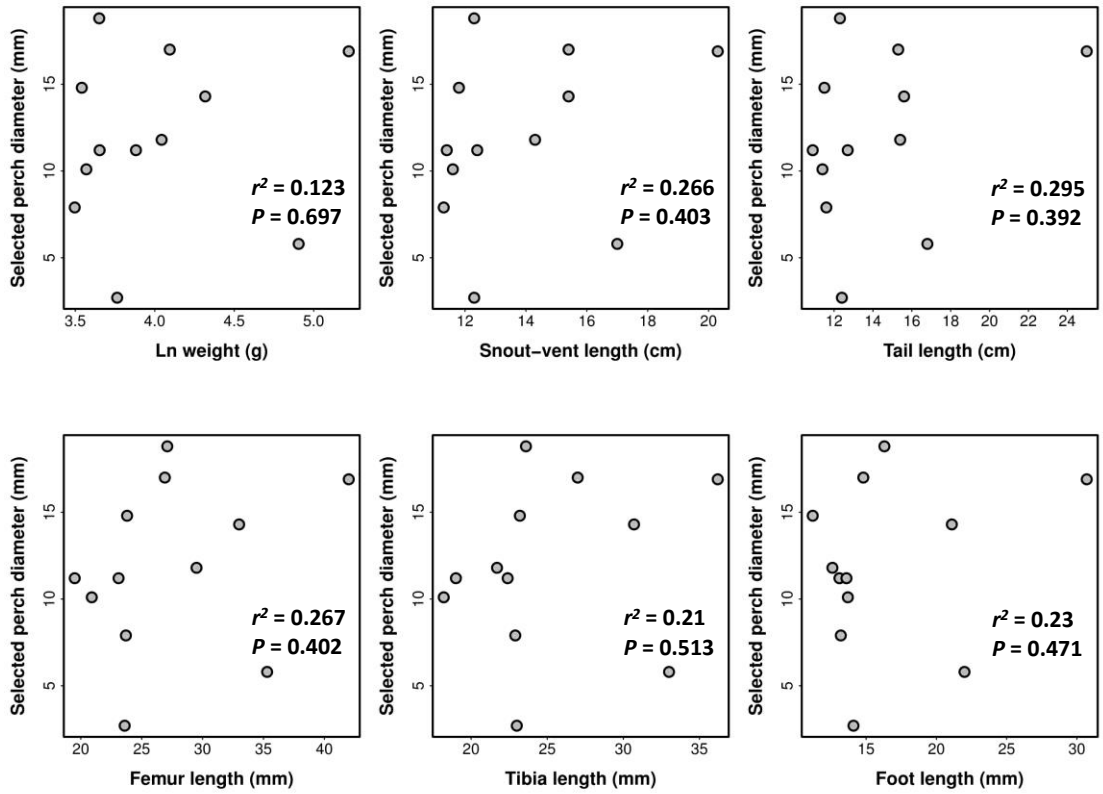

Figure 4.4: Scatterplots of morphological traits and perch diameters selected by *F. oustaleti* in the wild. No significant correlations were detected.

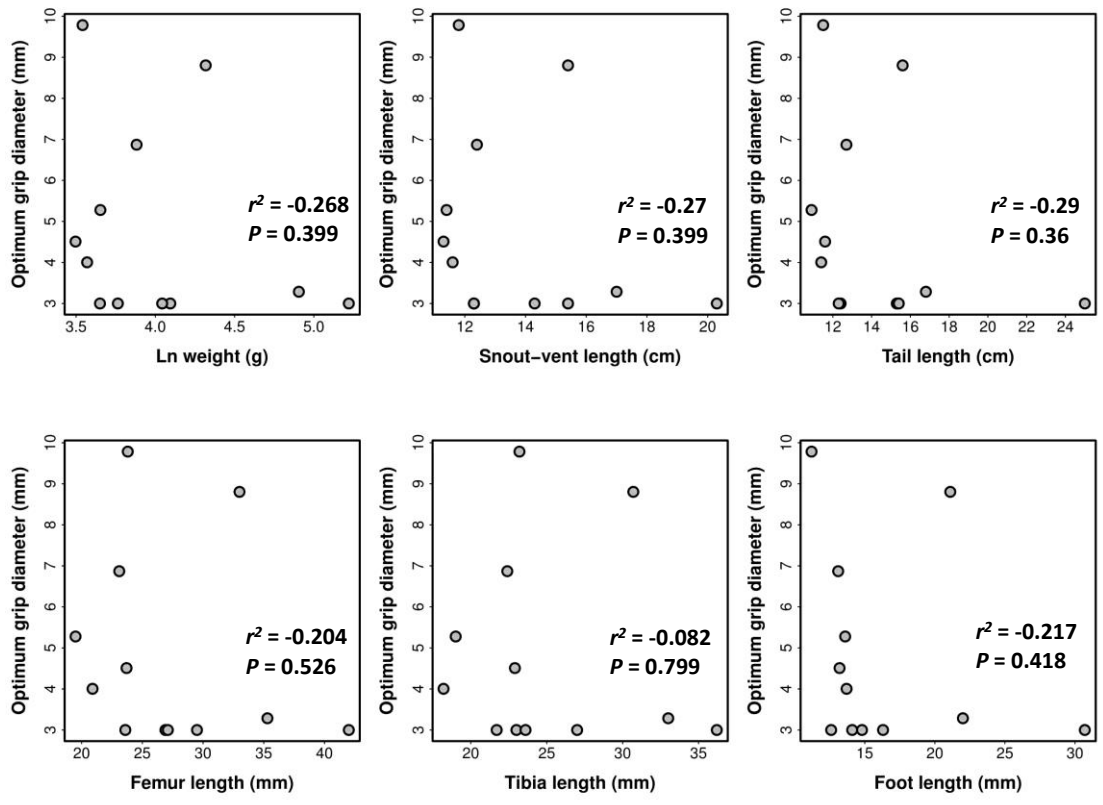

Figure 4.5: Scatterplots of morphological traits and calculated optimal grip diameters of *F. oustaleti*. No significant correlations were detected.

Table 4.2: Results of Pearson correlation coefficient testing on morphological traits and microhabitat variables. No significant correlations were detected, however weight, and foot and tibia length's relationship with humidity is unlikely to be due to chance.

	Microhabitat variables							
	Air temperature		**Substrate temperature**		**Humidity**		**Perch height**	
	***P* =**	***r* =**	***P* =**	***r* =**	***P* =**	***r* =**	***P* =**	***r* =**
Weight	0.197	0.401	0.243	0.366	0.0568	-0.563	0.65	0.146
Snout-vent length	0.261	0.353	0.384	0.277	0.209	0.391	0.815	0.076
Tail length	0.194	0.403	0.279	0.34	0.184	0.411	0.97	-0.012
Femur length	0.153	0.439	0.211	0.389	0.103	-0.493	0.874	0.051
Tibia length	0.251	0.359	0.359	0.291	0.083	-0.52	0.883	0.048
Foot length	0.124	0.469	0.145	0.447	0.051	-0.572	0.971	0.012

4.4 Testing for non-random perch selection

A Mann-Whitney U test determined that selected perch diameters were significantly higher than available perch diameters (W = 18031, P = 0.0003), suggesting that *F. oustaleti* selected significantly wider perches than expected due to chance (Fig. 4.6). This implies non-random perch selection. Area under the curve (AUC) analysis found that selected perch diameters were not more similar to d_{opt} than expected by chance (P = 0.902; Figs. 4.7 and 4.8). When individuals with optima outside of the tested range of dowels were excluded a similar non-significant result was found (P=0.866). Individual results are shown in Table 4.3 and Fig. 4.8.

Table 4.3: individual results of area under the curve analysis.

Individual	**Selected perch diameter (mm)**	**Calculated optima (mm)**	**Distance**	**Area under the curve values**
a	11.2	6.87	4.33	0.864
b	11.2	5.278	5.922	0.864
c	17	3	14	0.977
d	11.8	3	8.8	0.885
e	14.8	9.784	5.016	0.484
f	2.7	3	-0.3	0.198
g	10.1	4.004	6.096	0.835
h	18.8	3	15.8	1
i	5.8	3.286	2.514	0.579
j	7.9	4.509	3.391	0.731
k	14.3	8.803	5.497	0.741
l	16.9	3	13.9	0.976

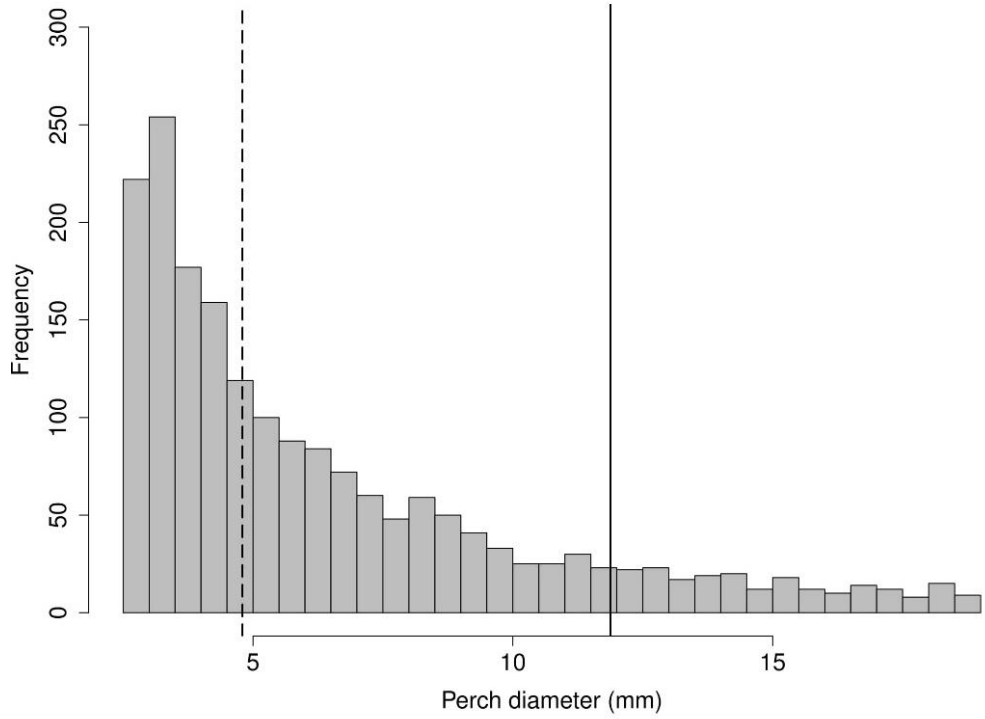

Figure 4.6: Histogram showing empirical distribution of available perch diameters with mean optimum grip diameter (dashed line) and mean selected perch diameter (solid line). Selected perches are wider than most available perches and calculated optima.

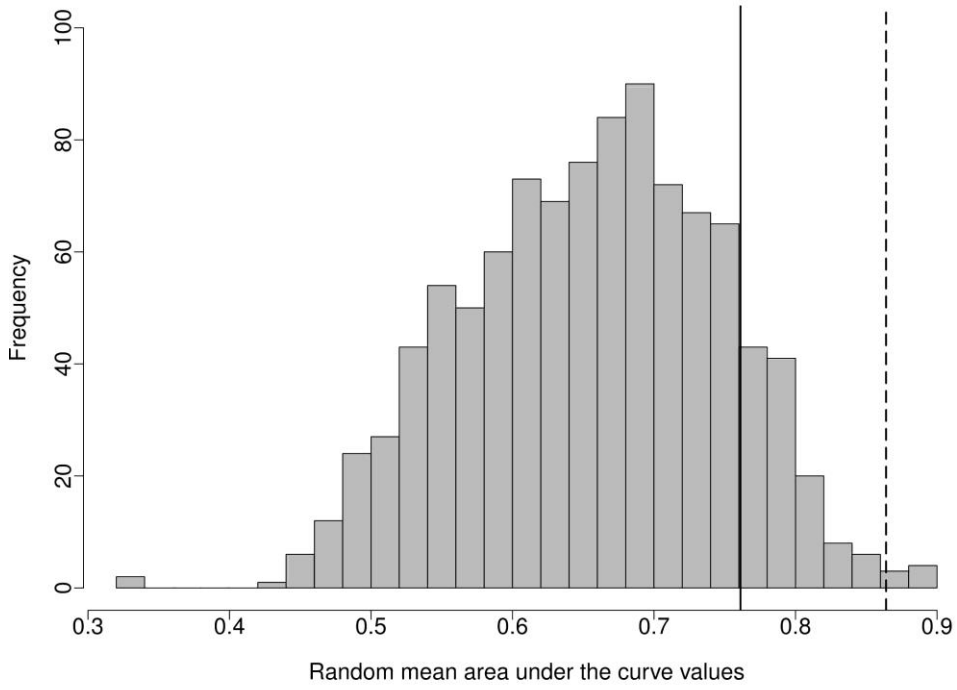

Figure 4.7: Histogram showing distribution of mean AUC values from random draws; mean AUC values for all individuals (solid line) and those that had optima within the tested range (dashed line) are shown. If *F. oustaleti* are choosing, on average, perches closer to their optima, then the observed AUC mean(s) should be in the lower tail of the random AUC mean distribution.

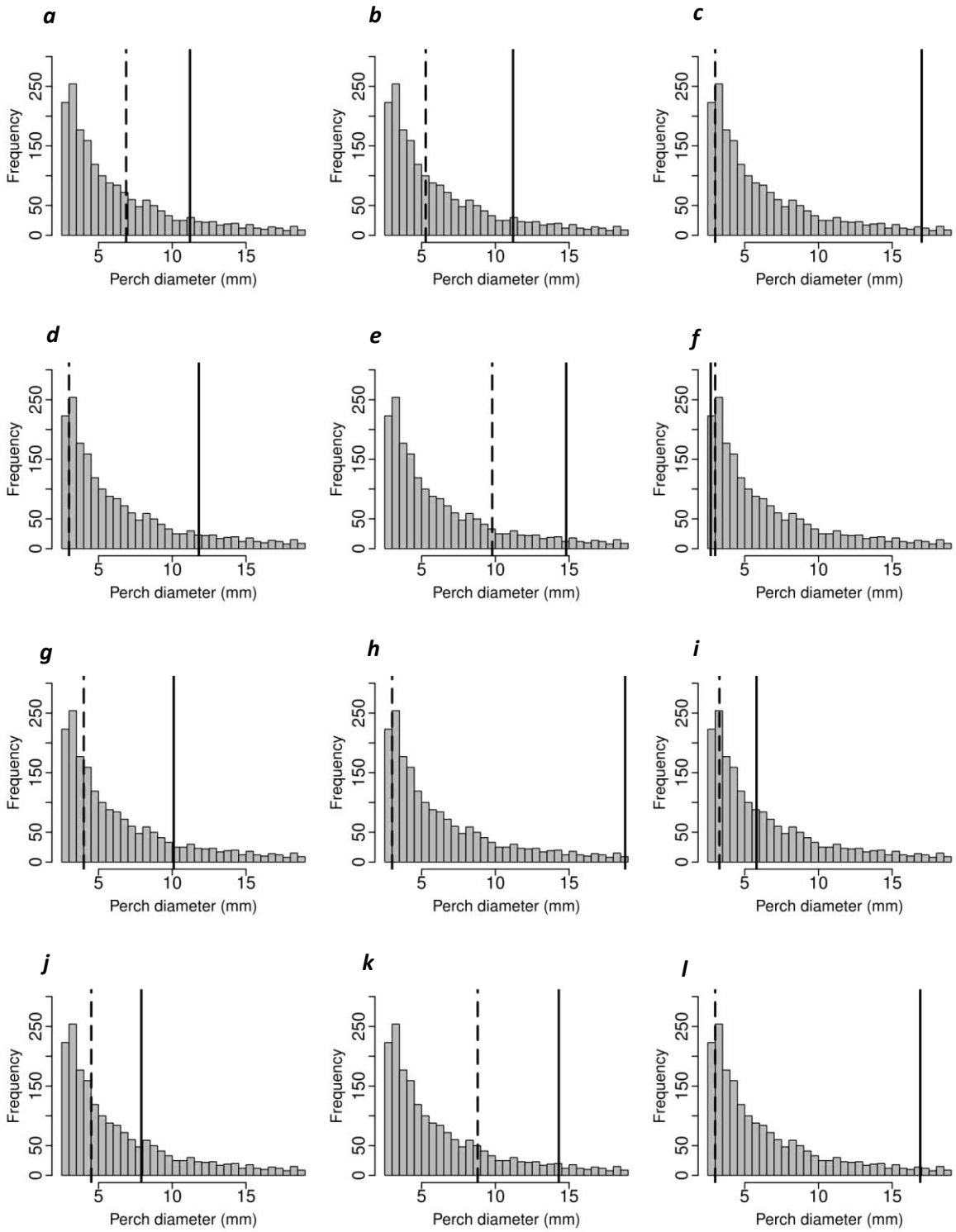

Figure 4.8: Histograms of the empirical distribution of available perches with selected perch diameters (solid lines) and d_{opt} (dashed lines) for each individual.

4.6 Optimal perch diameters and the mode of available perches

I defined the mode of available perches (MAvP) as the middle value of the modal perch diameter bin (2.7–3.7 mm) in my perch diameter histogram. MAvP was 3.2 mm. As this value was extremely close to the assumed optima of individuals that were strongest on the narrowest dowel tested (3 mm), these individuals were removed from this analysis to avoid biasing results. All optima were wider than MAvP but none exceeded 10 mm (Fig. 4.9). Analysis of AUC values found that optimal perch diameters were closer to the MAvP than expected by chance (P = 0.014; Fig. 4.10).

Calculated optima were generally much closer to the MAvP than were perch diameters selected by *F. oustaleti* (Fig. 4.11).

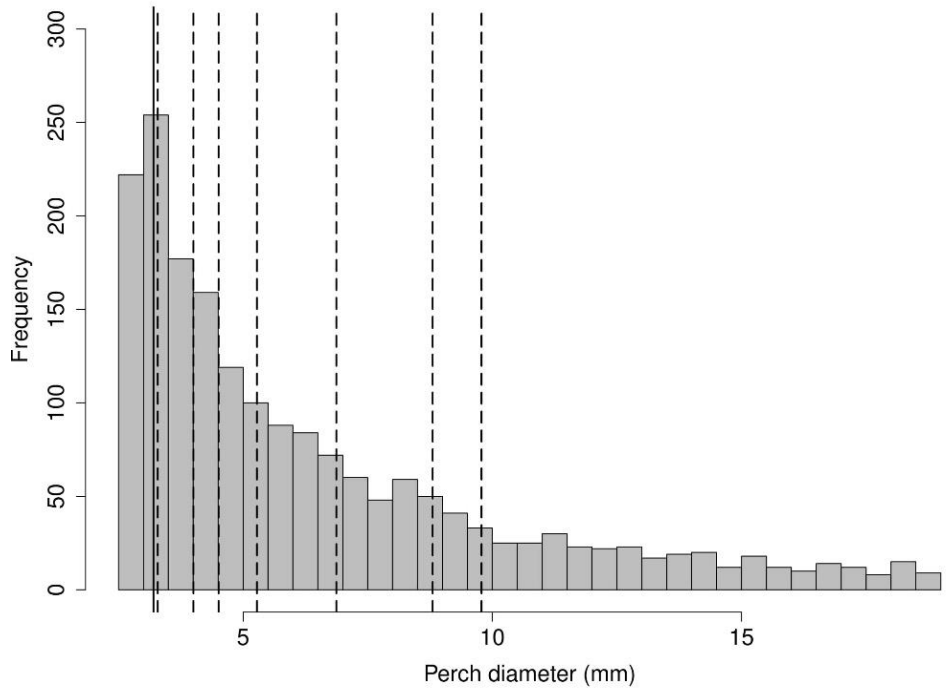

Figure 4.9: Histogram of underlying empirical distribution of available perches with mode (solid line) and d_{opt} (dashed lines) for each individual, excluding those with optima ≤ 3mm.

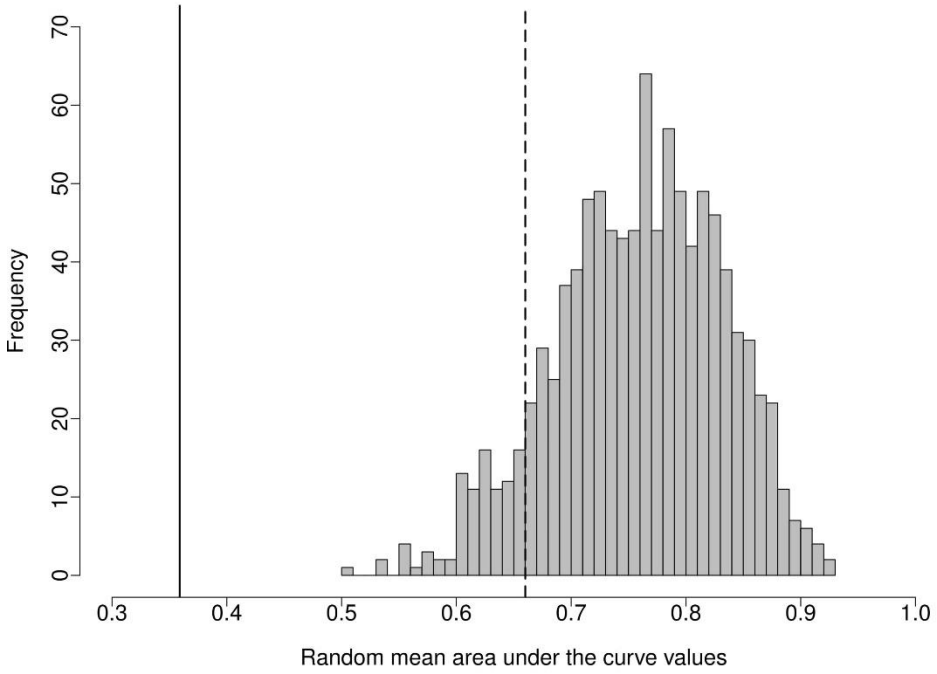

Figure 4.10: Histogram showing mean AUC values from random draws against MAP with mean AUC value of all individuals (solid line), and for individuals that were strongest on the narrowest perch tested for (dashed line). As the mean UC values are in the lower tail of the random AUC mean distribution, it is unlikely that optima are this close to the MAP if grip performance optima were random.

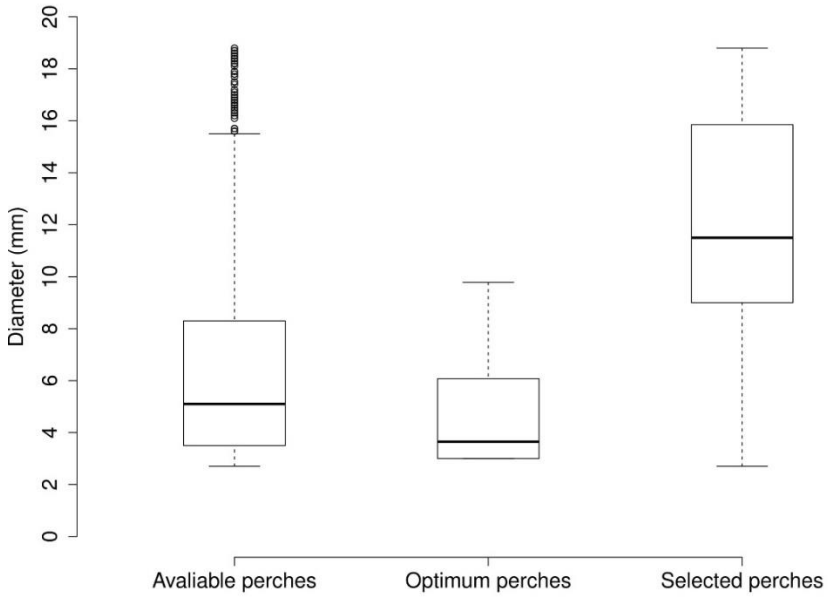

Figure 4.11: Plot of the distribution of available perch, optimal grip, and selected perch diameter data. Selected perches were, on average, wider than available and optimal perches, and likely selected non-randomly. Optimal and available perch diameters were closer to each other than expected by chance.

5 DISCUSSION

5.1 Main findings

Individuals that perform better in their microhabitat are often fitter (Emerson & Arnold 1989; Futuyma 2013; Irschick 2002; Yoder et al. 2010). This is thought to be especially pertinent for locomotor functional capacities (Arnold 1983; Irschick & Jayne 1999; Kohlsdorf & Necas 2012) and in arboreal species (Mattingly & Jayne 2004; 2005; Irschick 2000; Vanhooydonck & Van Damme 2001). Chameleon's unique method of grasping to their perches (Tolley & Herrel 2014; Edmonds 2015) and their ability to navigate relatively narrow substrates (Higham & Jayne 2004) mean that examining their grip–performance in the context of microhabitat structure may provide novel insights into how these species have adapted to their environment, and elucidate possible impacts of structural change in their habitat.

I tested whether *Furcifer oustaleti* select perch diameters that maximise their grip strength. My null modelling approach found no evidence that these chameleons selected perches more similar to their optimal grip diameter than expected by random perch selection. However, I did find that the mean perch size on which chameleons were found was greater than the mean available perch size. These contrasting results indicate that *F. oustaleti* do not preferentially select perches that have diameters that are closest to diameters where they have maximal grip strength, suggesting that natural selection for optimal grip on preferred perches is not the only factor influencing grip strength in this species; other factors (but not just random perch use) are influencing perch selection. My results did suggest that *F. oustaleti's* optimal grip diameters (d_{opt}) are closer to the mode of available perch diameters (MAvP) than expected by chance, though there was still considerable variability among individuals. My research provides tentative evidence that chameleon optimal grip performance diameter has evolved to maximise grip strength on the most abundant perch diameters in their habitat. These findings leave the actual impetuses of chameleon's choice of perch diameter in the wild an open scientific question and call for further research on observed correlations between optimal grip and perch availability.

5.2 Perch selection

F. oustaleti avoided the narrowest perches in my research area (<2.7 mm), and generally selected perches significantly wider than the most abundant perch diameters. Herrel et al. (2011; 2013) made similar observations of chameleon substrate use. Owing to non-significant testing of H1, grip performance is unlikely to be the major factor determining

perch selection, and thus individuals are likely selecting wider perches for reasons other than grip strength.

Branch diameter is positively correlated with the minimum mechanic force required to rupture those branches (Morgan & Cannell 1987; Percy et al. 2005), and negatively correlated with flexibility (Gilman & Irschick 2013). Ergo, narrower branches are, on average, more likely to break or bend under force and leverage than wider branches. Considering this, observed preferences for wider perches could suggest that chameleons are less 'comfortable' on hyper-narrow branches where the likelihood of falls (and associated injury) is higher. Indeed, similar preferences for relatively wide perches have been demonstrated in other lizards (e.g. Jones & Jayne 2012; Mattingly & Jayne 2005; Thompson & Thompson 2001). However, as the downward force applied to perches by chameleons will mostly be a product of body weight and leverage, it is reasonable to expect that larger, heavier chameleons would select wider perches to minimise the risk of compromising their perch. Positive correlations between size and perch diameter has been found in other chameleon studies (Herrel et al. 2011; 2013), and frequently in anole research (e.g. Losos 1990a; Pounds 1988; Sexton et al. 1972). This correlation was not present in my data. Hence, branch viability may not be the primary driver of perch selection in this population, though my small sample size makes this a tentative conclusion.

Occupation of wider perches may confer benefits to chameleon locomotor performance. Use of narrower perches has been associated with decreased sprint speeds in chameleons (Abu-Ghalyun et al. 1988; Losos et al. 1993) and other arboreal fauna (Losos & Irschick 1996; Losos & Sinervo 1989; Macrini & Irschick 1998), and increased restrictions to limb movement and orientation (Cartmill 1974; Moermond 1986; Spezzano & Jayne 2004). Further, narrower perches generally have more connecting branches and shorter distances between nodes, which can interfere with aspects of arboreal movement (Crome and Richards 1988, Williams 1983). However, assuming that similar performance predictions apply to chameleons would be rash, considering their unique digits and ability to occupy narrower substrates than similar-sized lizards (Higham & Jayne 2004; Tolley & Herrel 2014; see 2.5). Thus, further testing is needed.

The majority of chameleon diurnal behaviour is devoted to hunting and feeding (Tolley & Burger 2007; Tolley & Herrel 2014) and thus predation success and food availability may be alternative explanations for selecting wider perches. Examinations of faecal remains have shown that individuals can consume several dozen insects per day, with arthropods making up to 100% of chameleon's diets (Hofer et al. 2003; Luiselli & Rugiero 1996; Pleguezuelos et al. 1999). Indeed, personal observations of *F. oustaleti*, perched, tongue-tip exposed, and

scanning their surroundings, were frequent during my field surveys. Moermond (1979) found that locomotor costs associated with hunting influenced anole's perch (diameter) selection. Certain snake species are known to select wider perches when hunting than during other behaviours (Byrnes & Jayne 2010; Wilson 2007). Therefore, *F. oustaleti* selecting wider perches may benefit their hunting capacity in a variety/combination of ways. For example, if wider perches have less branches and are generally longer, they may provide less interference to chameleons hunting with their ballistic tongues. More microhabitat measurements, in combination with chameleon hunting behaviour data and information on prey abundance is required to test these hypotheses.

5.3 Optimal grip

F. oustaleti d_{opt} were commensurate with the MAvP in their habitat. Returning to Simpson's (1944; 1953) adaptive landscape metaphor (see 2.2), these findings may suggest that chameleon's ability to strongly grip the most abundant perch diameter in their habitat represents an adaptive peak, where a selective impetus favours individuals with this phenotypic relationship (McGhee 2007). However, this interpretation must be met with the caveat that calculated optima varied considerably (Table 4.3) and significant results from analysis of mean area under the curve (AUC) values were likely driven by a few individuals that were very close to the MAvP. Indeed, similarities between optima of individuals that were strongest on the narrowest dowel (3 mm) and the MAvP (3.2 mm) meant that results including these individuals were poorly suited to draw conclusions about *F. oustaleti*'s optimal grip relationships (Fig. 4.10), and were excluded. Nevertheless, *F. oustaleti* may garner selective advantages from this apparent correlation between d_{opt} and the MAvP.

Many arboreal animals catch prey species by manually removing them from their perches (e.g. Craig 1990; Christensen & Kleindorfer 2009; Nekaris 2005; Yorks et al. 2003). Chameleons on Madagascar are often predated in this way by raptors and snakes (Jenkins et al. 2009). The ability to strongly grip the most abundant, and hence the most available to immediately grip, substrates in their habitat, may allow *F. oustaleti* to reduce overall risk of fatal predator encounters by resisting removal from their perch by gripping nearby substrates. Data on predator encounters (preferably multiple per individual) would be needed to test this prediction.

Similarly, *F. oustaleti* may reduce the risk of injury from falling from perches by possessing the ability to grip abundant nearby substrates. Arboreal perches are usually far enough from the ground that falling from them could cause injury, death, or inhibit mating or feeding opportunities (Clark & Higham 2011; Lammers & Zurcher 2011); this happens often *in situ*

(Full et al. 2002). Being more able to prevent falls or reduce velocities at impact with the ground or other objects by holding nearby substrates may mitigate these risks; having this capacity maximised on the most abundant substrates available to an animal would likely increase their individual chances of not suffering injury during such events. Testing this hypothesis would require observations of chameleons during falls.

5.3.1 Plasticity

The capacity of identical genotypes to develop different phenotypes in response to environmental cues, i.e. phenotypic plasticity, can be ecologically pertinent (Huey et al. 1999; Kingsolver & Huey 2003) and affect traits thought to be controlled by natural selection. For example, Losos et al. (2000) examined the role of phenotypic plasticity in leg length – perch diameter relationships that form the basis of the *Anolis* lizard adaptive radiation. Relationships between perch diameter and natural selection on leg length were inferred by Losos et al. (1997). In that study, populations of *Anolis sagrei* were introduced to Caribbean islands where either large or small diameter perches were abundant; 10–14 years later their descendants were measured and positive correlations between hindlimb length and perch diameter were observed across all populations. In a follow up investigation, Losos et al. (2000) carried out laboratory experiments on sub-adult *A.segrei* and found that hindlimb length changed depending on the perch diameter on which individuals were raised. This suggests that leg length–perch diameter relationships in these anoles may partly reflect phenotypic plasticity, though the degree of plasticity was insufficient to account for all of the leg length variation, i.e. natural selection and adaptation still play a role (Losos et al. 2000). Subsequent Studies have made analogous conclusions for different anole populations (Kolbe & Losos 2005; Langford et al. 2014). The above example indicates that plasticity can play a part in phenotype – perch diameter relationships. Currently, I cannot discount the possibility that d_{opt} reflects phenotypic plasticity. Grip optima may be closer to the most common perch diameters simply because these are the diameters that they encounter most often, strengthening the muscles required for gripping these diameters. However, if, as my results suggest, chameleons preferentially select larger perches, then they may not encounter the most common available perch more often. This suggestion weakens the plasticity explanation for the similarity of the mode of available perch diameters and optimal grip strength, but also weakens the adaptation argument as well. Observations that narrow perches are generally more abundant and often surround wider perches in forest habitats (Gilman & Irschick 2013) may explain how chameleons could encounter narrower perches more often, even when not utilising them to support their body weight. Further work, building

on my research, is needed to evaluate the role of responses to natural selection and phenotypic plasticity on the apparent link between grip optima and available perches in *F. oustaleti*, and habitat – ecomorphology relationships more broadly; data needed to predict long-term responses to selection (Isrchick et al. 2008).

However, my findings that larger, heavier *F. oustaleti* with longer limbs had stronger average grip, but did not have higher d_{opt} and did not, on average, select wider perches (discussed next), suggests that both d_{opt} and selected perch diameters may vary independently from morphology in this species. This conclusion implies that reasons other than just size, possibly different performance factors, are driving maximal grip strength and which perches *F. oustaleti* chooses to occupy in the wild.

5.4 Morphology

All morphological traits measured were positively correlated with each other and with average grip strength; larger, heavier *F. oustaleti* with longer limbs generally had stronger average grip. Similar morphology – performance correlations have been found in studies of other lizards (e.g. Losos 2009; Van Damme et al. 1997; Wikelski & Trillmich 1994; Zani 2000) and chameleons (Herrel et al. 2011; 2012; 2013; Losos et al. 1993; da Silva et al. 2014). However, Losos (1990a), studying *anolis* lizards, found that cling (grip) performance varied independently from morphology. Measured morphological traits did not correlate with d_{opt} or selected perch diameters; larger *F. oustaleti* were not, on average, stronger on wider perches, nor did they select generally wider perches. Several studies of arboreal fauna have shown positive correlations between size and perch diameter (e.g. Butler et al. 2000; Byrnes & Jayne 2010; Losos et al. 1993; Losos & Sinervo 1989). Although a wealth of literature has shown that larger lizards have stronger gross grip strength (e.g. Losos et al. 1993; Van Damme et al. 1997; Wikelski & Trillmich 1994; Zani 2000), this is not analogous to optimal grip strength. As no studies, to the best of my knowledge, have attempted to identify chameleon optimal grip diameters using performance curves, findings that optimal grip is not size dependant lack comparisons to other literature. Further research is required to confirm (or not) similar relationships in chameleons and other arboreal fauna.

5.5 Limitations

Small sample size was a severe limiting factor of my investigation. As smaller sample size increases chances of random sampling errors (Gilbert et al. 2011; Krebs 1989), my sample size of twelve individuals means that H1 and H2 were tested with relatively low statistical

power. This issue was compounded when testing whether optimal grip diameters were closer to the MAvP than expected by chance. During this analysis, the five individuals showing strongest grip on the smallest tested dowel width, individuals: *c*, *d*, *f*, *h*, and *l* (Fig. 4.2), were excluded from testing due to the assumed optimum grip diameter for these individuals (3 mm) being very close to the mode available perch diameter (3.2 mm). Hence, this testing was based on data from seven individuals. Using such a small sample size is vulnerable to stochastic outputs and may mean that my results are being driven by a few individuals. For instance, individual *i* had a calculated optima of 3.286 mm, very close the mode of available perches (3.2 mm), while others, like individual *e* had a grip optima (9.784 mm) further away from this mode. Thus, while the small sample size means that individual *i* had a large influence on the results, if I include the five individuals with grip sizes at or below 3 mm, then these would bolster my result that optimal grip diameter is close to the available perch diameter mode. Repeat experiments with larger sample sizes are recommended to buttress these findings.

The small sample size could also have affected my tests of the similarity between d_{opt} and selected perches. As described above, only seven individuals had optima within the range of tested perch diameters, which carries similar risks of sample errors. Further, I only was able to measure a single perch used by these individuals. Determining a distribution of perch diameters used by individuals, via longer observation periods or mark and recapture methods, would provide better estimates of *F. oustaleti*'s overall perch use and allow comparison of optima against an average perch diameter.

Differences in perch diameter may be associated with other aspects of microhabitat structure that were not measured during my investigation. For instance, narrower perches may be shorter in length, or have different cross-sectional shape than wider perches. Further, functional observations of how chameleons use their perch were not taken, e.g. orientation of limbs to perch. These data could explain why chameleons chose specific perches in certain environmental conditions.

During grip performance experiments aspects of claw morphology were not recorded. While the muscular ability of chameleon's zygodactylous digits will likely play a large role in their gripping of substrates, the capacity of claws to 'cling' to perches may also be very influential to grip strength, and is mentioned in other literature (Zani 2000; 2001). Further, in the wild chameleons most often grip substrates with all four limbs, and do so with their body orientated above the perch. Hence, other muscles throughout their body likely contribute to their ability to hold on to substrates. In my experiments individuals were pulled horizontally from dowels with one foot anchored. This may be an unnatural gripping stance and may

have inhibited actual maximal grip strength from being recorded. Different gripping stances should be investigated to determine their effects (if any) on average and optimal chameleon grip strengths.

5.5 Closing remarks

To the best of my knowledge, this research represents the first examination of chameleon grip–performance on Madagascar, and the first attempt to identify optimal grip diameters using performance curves for any lizard. My findings provide tentative, yet intriguing evidence that optimal grip performance of *F. oustaleti* is commensurate with the mode of available perches in their habitat. Although my results indicate that *F. oustaleti* selects its perch diameter non-randomly, the ecological factors that determine perch use remain elusive.

Further studies are needed to draw a direct functional link between chameleon optimal grip performance and available perches. Repeat experiments should be designed in such a way to identify optimal grip performance as a plastic response or a consequence of natural selection. Measuring numerous perches used by individuals with longer observation periods or mark and recapture techniques would provide a fuller understanding of chameleons' perch use. Moreover, measuring additional characteristics of microhabitat structure may yield a more detailed information of how species have adapted to their local environment.

Identifying the complex and multi-scalar effects of forest restructuring presently occurring in Madagascar's forests may help to elucidate how species are coping with biological reorganisation in their habitats, and allow for extrapolation of future ecological trajectories. Examining these factors in contexts of disturbance gradients could instruct future conservation intervention on the island, and thus provide a framework, amid changeable socio-economic climes, to improve persistence prospects for Madagascar's enigmatic forest species.

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