Behavioural Partitioning of Mainland and Island Lava Lizard Assemblages in Ecuador

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Statement of Authorship

This thesis includes work by author that has accepted or submitted for publication as described in the text. Except where reference is made, this thesis contains no other material published elsewhere or extracted in whole or in part form a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgement in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Ethical note and research permits

The work was conducted under La Trobe University Animal Ethics Committee Protocol No. AEC17-62, and Universidad San Francisco de Quito collection permits authorized by Parque Nacional Galápagos, Galápagos, Ecuador: PC 98-19 (2018-2020).

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Acknowledgements

General Abstract

Species respond in different ways to extrinsic constraints, to avoid competition or adapt to new and changing environments. A common response is to modify their behaviour to meet their needs and to suit the ecological context. Taxonomic groups that are found on islands and mainland habitats have become model organisms to understand the process of evolution of closely related species, which have evolved in different biogeographical conditions. The lava lizards (genus *Microlophus*) are an ideal system in this regard as their distribution spans mainland South America and the Galápagos Islands, and they possess diverse patterns of behaviour. In this thesis, I examine the influence of extrinsic ecological and environmental constraints on species phenotypes, with a particular focus on the role that behavioural and ecological specialisations play in niche delimitation of *Microlophus* species from Ecuador.

In Chapter 1, I investigated the effect of interspecific competition on the behavioural patterns of two mainland species, *Microlophus occipitalis* and *M. peruvianus* in the environmental and ecological context. I found that both species exhibited behavioural, and microhabitat shifts in sympatry, consistent with an increase in interspecific competition and difference in habitat composition. In addition, microhabitat shifts lead to morphological (smaller limbs and slender bodies) and territorial display structure variations (lower amplitudes) for *M. occipitalis.* I broadened my investigation in Chapter 3 to consider behavioural diversification in the context of phylogenetic relatedness for the mainland species and six species on the Galápagos Islands. I employed a phylogenetic comparative approach to show that lava lizard behaviour varies to varying degrees as a function of the ecological context, the environmental conditions as well as social factors. I inferred that lava lizards' behavioural divergence does not strongly reflect their evolutionary history. Instead, I proposed that extrinsic ecological, environmental, and social factors played a more important role in their behavioural adaptation. In the final data chapter of my thesis (Chapter 4), I focus on the extent to which anthropogenic factors influence Galápagos lava lizards' behaviour in the context of varying levels of human population and tourism activities.

I also considered habitat modification, by including vegetation assessments and published habitat composition data. I concluded that the accelerated human growth and tourism on the Galápagos islands have negatively impacted the lava lizards' behaviour leading to possible boldness-awareness behavioural syndromes on species inhabiting urban areas with high visitor rates.

Overall, my study demonstrates the important role of ecological and environmental contexts on species phenotypic adaptations. In addition, it is the first research project to take a multifaceted approach to documenting the behavioural ecology of Ecuadorian lizards, laying the groundwork for future research and conservation projects targeting non-emblematic species that are an important component of the natural ecosystem.

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CHAPTER ONE

General Introduction

Determinants of Animal Behaviour

Animal behaviour has attracted scientific interest due to its striking complexity and diversity. Behaviour results in response to an external stimulus following a range of internal processes and with varying degrees of genetic influence (Richards et al., 2010). Thus, animals act as an integrated and coordinated unit to show a repertoire of behaviour patterns, which is often species specific (Arora & Kanta, 2009). Behaviour is also a bridge that enables animals to exploit the environment to suit their requirements and has become a crucial component to understanding adaptive and evolutionary process. However, given the diversity of behaviour, research continues to develop explanations for why animals behave the way they do. Guiding research activities in the field are Tinbergen's four questions that can be applied to all behaviour (Davies et al., 2012): 1) what are the immediate causes of the behaviour?, 2) how did it develop?, 3) what are the adaptive advantages or functions of the behaviour?, and 4) what is the evolutionary history of the behaviour?. Pioneering ethological studies focused on the first two questions before interest extended to questions of function (Krebs & Davies, 1997). More recently, it has become increasingly common for the consideration of behaviour in enabling species adaptations to the surrounding environment to be placed in an evolutionary context (Campbell et al., 2009; Niemelä & Dingemanse, 2018; Owens, 2006).

Behavioural ecologists group Tinbergen's questions into the proximate and ultimate causes of behaviour (Arora & Kanta, 2009; Davies et al., 2012). Proximate causes are related to the causal and ontogenetic factors that motivate a given individual to behave in a particular way (Campbell et al., 2009; Davis et al., 2012). In contrast, the ultimate causes are related to factors influencing adaptive advantages (function) and evolution, thus explaining why particular phenotypes might have been favoured by natural selection (Davies et al., 2012). These causes are often unpredictable and lead to significant extrinsic changes where animals must adapt to exploit potential opportunities (Dall et al., 2005). A common way to cope with these changes is through behavioural adaptation, where the accurate assessment of ecological parameters will allow

animals to adjust their behaviours to meet their demands (Dall & Johnstone, 2002; Davies et al., 2012; Sih et al., 2012).

Ecology and Environment

Major selection pressures arise when species coexist, promoting competition for available natural resources such as food and microhabitats (Jones & Barmuta, 1998; Nash et al., 2012; Svanbäck & Bolnick, 2007). Research suggests that resource competition is a prevalent driver of ecological and phenotypic variation among and within species (Dieckmann & Doebeli, 1999; Mitchell et al., 1990; Svanbäck & Bolnick, 2007). Indeed, Atwood and Gese (2010) believe that after wolves (*Canis lupus*) recolonised Greater Yellowstone, the coyotes (*Canis latrans*) started to exploit carrion killed by wolves in bigger groups initially to minimize the risk of encounters with wolves and increase resource holding potential. In the same way, blue (*Balaenoptera musculus*) and humpback (*Megaptera novaengliae*) whales appear to shift their foraging behaviours spatially and temporally depending on the congener's activity, reducing use of the same resource at the same time (Fossette et al., 2017). Such resource partitioning has been observed in many other organisms (Bergeron & Blouin-Demers, 2020; Cloyed & Eason, 2017; Dieckmann & Doebeli, 1999; Gordon et al., 2010; Nguyen et al., 2020; Nicastro et al., 2010; Oviedo et al., 2018), particularly by closely related species where the ecological preferences tend to be equivalent and significant competition could have higher impact (Conners et al., 2015; Hu et al., 2019; Sbragaglia et al., 2019; Villanueva-Bonilla et al., 2019).

Habitat structure also has been shown to play a determinant role in influencing animal behaviour (Angilletta et al., 2009; Cartar & Real, 1997). Environmental heterogeneity usually modifies the availability of resources that species use in their habitat, thus influencing the selection of appropriate habitats in which to engage important behaviours (Tyne et al., 2017). The selection of optimal locations for a particular behaviour is thought to be adaptive and favoured by selection (Kamath et al., 2013), and include choosing sleeping sites with relatively low predation

(Acerbi & Nunn, 2011; Clark & Gillingham, 1990) or foraging sites with lower energetic costs

(Cartar & Real, 1997; Mitchell et al., 1990; Nash et al., 2012). For example, female eastern fence

lizards (*Sceloporus undulatus*) tend to select warmer nesting sites outside their home range to

ensure the development and survival of their embryos (Angilletta et al., 2009). However, changes

to species' microhabitat preferences can also arise as a consequence of interspecific interactions

(Kamath et al., 2013). For instance, once again in order to avoid competition, species might exploit

new microhabitats to engage a specific behaviour, such as the intertidal mussel *Mytilus*

galloprovincialis, which exploits upper mussel zones in the presence of the indigenous species

Perna perna by keeping the shell valves closed for longer periods (Nicastro et al., 2010).

Nevertheless, habitat structure can also represent an obstacle for behaviour. For many

communication systems, habitats can be a source of background noise (Goutte et al., 2018; Peters

et al., 2008), such that the physical properties of the environment impose diverse environmental

constraints on signal transmission and reception (Fleishman & Pallus, 2010; Forrest, 1994; Goutte

et al., 2018; Hopkins, 1973; Morton, 1975; Ord et al., 2002). Consequently, signallers alter

behaviour to overcome constraints imposed by habitat structure and background noise. One

strategy is to adjust the signals to alter the signal-to-noise ratio, which is reported for birds

(Brumm & Todt, 2002; Cynx et al., 1998; Dooling & Popper; Luther & Baptista, 2010), mammals

(Brumm et al., 2004; Holt et al., 2011; Holt et al., 2009), amphibians (Goutte et al., 2018; Grafe et

al., 2012; Halfwerk et al., 2016), and reptiles (Ord et al., 2007; Peters, 2008).

Environmental fluctuations are a prevalent feature of natural habitats and impose

constraints on organisms (Briffa et al., 2013; Gordon et al., 2010; Stapley, 2006; Taylor, 1963).

Temperature is a key abiotic factor that has the capacity to influence the behaviour of animals

across several taxa (Abram et al., 2017; Biro et al., 2010; Briffa et al., 2013; Sbragaglia et al., 2019;

Shrestha et al., 2018). This is the case particularly for ectotherms because of the proposed

connection between their metabolism and activity (Angilletta, 2006; Angilletta et al., 2002). Often

an increase in temperature is associated with higher metabolic rates and energetic demands, yet individuals might differ in their responsiveness to temperature (Angilletta et al., 2002). Thus, it is expected that animals will adjust the behaviours affecting their metabolism to increase their food intake and energy levels to avoid threating situations. Foà and Bertolucci (2001) claim that ectotherm Ruin lizards (*Podarcis sicula campestris*) can develop bimodality patterns associated with seasonality, where individuals might reduce their usual activity as a strategy to avoid overheating during the summer.

The rate and/or structure of communicative signals also vary as a function of ambient temperature for a wide range of taxa (Connaughton et al., 2000; Greenfield & Medlock, 2007; Hedrick et al., 2002; Llusia et al., 2013; Navia et al., 2015; Ord & Stamps, 2017; Papes & Ladich, 2011; Ritchie et al., 2007), affecting acoustic (Gayou, 1984), visual (Michelangeli et al., 2016; Ord & Stamps, 2017), olfactory (Webster & Yin, 1997) and electric (Dunlap et al., 2000) signals in different ways. The *performance model* predicts that physiology constrains maximal performance thereby limiting the production rate of behaviours that involve locomotor processes (Gunderson & Leal, 2016). For instance, territorial display rate of eleven species of Puerto Rican anoles (genus: *Anolis*) increases with temperature initially before peaking at moderately high temperatures and declining thereafter, matching metabolic processes (Ord & Stamps, 2017). Environmental conditions also influence signalling behaviour. For movement-based signals, wind represents a major source of environmental noise limiting the detection of important visual events (Naguib, 2013; Peters, 2008; Velilla et al., 2020). As noise can affect the reliability with which information travels from sender to receiver, animals must alter their signals to cope with noise (Brumm & Slabbekoorn, 2005; Naguib, 2013; Peters et al., 2007). The Australian lizard *Amphibolurus muricatus,* which modified its display structure and increased the duration of introductory tail flicking to overcome sustained wind conditions, provide an excellent example of behavioural adaptation to noise (Peters et al., 2007). The unpredictability of abiotic factors

ensures that we have much to discover about the relationships between extrinsic conditions and animal behaviour.

Population structure and sexual selection

Sociality is another relevant ecological factor that drives the evolution of behavioural complexity (Daniel & Kenneth, 1997; Ord & Garcia-Porta, 2012). Complex communication is usually linked with complex animal societies as elaborate communication systems allow animals to mediate the frequency and context of social interactions (Ord & Garcia-Porta, 2012). These interactions have been linked with social organisation, sexual selection, predation risk, and other abiotic factors (Butler, 1980; Littlewood et al., 2021; Ord et al., 2001; Rowe et al., 1964). Populations with high densities usually featured higher rates of interactions due to closer spatial proximities (Freeberg et al., 2012). In addition, the increased use of available resources at higher densities, can lead to strong competition thereby promoting antagonistic interactions (Bennett & Gorman, 1979; Freeberg et al., 2012; Peters et al., 2016). Peters et al. (2016) suggest that under limited resources and intense competition, resource holders must exhibit territoriality. This was the case of the house mouse (*Mus musculus*) where male territoriality occurred significantly more often in populations of greater size (Butler, 1980). In contrast, when populations are dense, communicating with conspecifics might become challenging. For example, male fiddler crabs (*Uca vomeris*) have developed bigger and stronger claw size in highly abundant populations producing more reliable signals to avoid the potential cost of injuries and advertise their underlying strength (Bywater & Wilson, 2012). Lastly, when encounters with heterospecific are greater, species require an accurate recognition system to assess species identity (Ord et al., 2011). Therefore, the design of complex social signals that are species-specific are supposed to facilitate species recognition among sympatric congeners (Dietrich & Wehner, 2003; Hess & Losos, 1991).

When animal populations are skewed towards either sex, there is often an increase in sexual competition with concomitant behavioural adjustments. Mate choice decisions can impact

species behaviour through elaborate ornaments (Chen et al., 2012; Klomp et al., 2016; Watkins, 1998) and complex behavioural traits (Blanckenhorn, 2005; Borgia, 1980; Debuse et al., 1999). In many taxa, intrasexual competition over resources often promotes an asymmetry in body size between sexes (sexual size dimorphism), where bigger individuals often accrue fitness advantages (Blanckenhorn, 2005; Clutton-Brock, 2009; Cox et al., 2003). In the blue crab (*Callinectes sapidus*), males become more aggressive in male-biased populations forcing females to mate, and large males are more successful at take-overs (Jivoff & Hines, 1998). In addition, when male-male agonistic interactions are frequent, it has been suggested that long display duration and complex signals generated by bigger males might reduce dreadful interactions (Davies et al., 2012; Jenssen, 1978; Krebs et al., 1978). Consequently, sexual selection plays an important role in the evolution of social behaviour, allowing them to develop several strategies to gain fitness benefits, avoid costly or deadly interactions, and the misrecognition of heterospecific.

Anthropogenic effects on animals' behaviour

Although relatively recent, anthropogenic factors have also been associated with species behavioural adjustments (Bhattacharjee et al., 2015; Dylewski et al., 2020; Kaiser et al., 2018; Thompson & McLachlan, 2007). Human development is among the major causes of alterations to natural ecosystems, which introduces new challenges for resident species. It has been demonstrated that anthropogenic structures (e.g. buildings, parks) can impact species in a variety of ways including changes to prey availability (Chapman et al., 2012; Merrall & Evans, 2020), habitat features (Lee & Thornton, 2021; Luther & Baptista, 2010), and potential predators (Gotanda, 2020; Pellitteri-Rosa et al., 2017). In addition, urban areas can expose species to novel disturbances such as interactions with invasive species and humans, thereby influencing population density and competition dynamics (Audsley et al., 2006; Ditchkoff et al., 2006; Meffert & Dziock, 2013). Often these significant biotic and abiotic changes are perceived by species as additional stressors forcing them to either adjust to them or be excluded (Amdekar et al., 2018; Bhattacharjee et al., 2015; Killen et al., 2013). Consequently, numerous negative impacts on

wildlife, such as the loss of species richness and diversity, have been associated with urbanisation (Blair, 1996; Blair & Launer, 1997; Piano et al., 2020). However, human influence on wildlife extends beyond urbanisation and includes an increasing demand on wildlife tourism (Roe et al., 1997). Wildlife watching and photography tourism are characterised by direct and constant contact with animals in their natural environments (Burger & Gochfeld, 1998; Granquist & Sigurjonsdottir, 2014; Li et al., 2017; Roe et al., 1997). This raises concerns about the negative impacts of wildlife tourism, as animals may perceive this direct contact with humans as a form of predatory threat and subsequently alter their physiology (Ditchkoff et al., 2006; Semeniuk et al., 2009; Tablado & D'Amico, 2017) and behaviour (Dammhahn et al., 2020; Hume et al., 2019; Moorhouse et al., 2015; Szott et al., 2019), which may have detrimental consequences (Trave et al., 2017). This wildlife tourism impact is particularly conspicuous in worldwide recognize nature wonders such as the Galapagos islands, where tourism is the main economic activity. Therefore, understanding and constraining the negative impacts of human development is key for the conservation of wildlife.

Biogeographical conditions influence behaviour

Species from mainland and island populations often experience significant ecological differences that permits consideration of the impact of biogeographic factors and processes leading to phenotypic differentiation (Innes & Kavaliers, 1987; Irschick et al., 1997; Peer et al., 2007; Stuart et al., 2012; Travis & Ricklefs, 1983). Geographic isolation promotes distinctive selective pressures on island species such as climatic differences, fewer predators and competitors, and the effect of colonisation events structuring population genetics (Irschick et al., 1997; Schlotfeldt & Kleindorfer, 2006; Shine, 1987; Spears, 1987). As a consequence, insular species develop unique phenotypical traits over a short time, usually referred to as the 'Island syndrome', which is considered to be adaptive and key for species to exploit novel resources (Brodin et al., 2013; Castilla et al., 2008; Raia et al., 2010). The fact that island species featured smaller population size, lower predation risk and greater survival rates has promoted reduced aggressiveness and the gradual loss of

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antipredator behaviours (Blumstein & Daniel, 2005; Brock et al., 2015; Butler, 1980; Stuart et al., 2012). Indeed, Cooper et al. (2014) claim that tameness of lizards is a real phenomenon in island populations, where individuals tend to decrease the flight initiation distance in the presence of possible threats. This 'island tameness' phenomenon has been observed in several insular taxa (Baier & Hoekstra, 2019; Blumstein & Daniel, 2005; Cabrera et al., 2017; Huxley et al., 2008; Rödl et al., 2007; Wright et al., 2016) and is thought to reduce the costly escape responses when strong natural predators are absent, and also serves to reduce conspecific aggression. Likewise, if resources are difficult to acquire and predation risks are low, the foraging risk is highly skewed promoting exploration and boldness on islands (He et al., 2017; Stratton et al., 2021). When contrasting island and mainland populations of the common frog (*Rana temporaria*), Brodin et al. (2013) observed that both tadpoles and froglets from isolated populations were bolder and more exploratory than conspecifics from the mainland. Therefore, organisms that colonise islands face unique environmental changes that demand a range of novel adaptations to survive.

Phylogenetic history relatedness and species behaviour

Since the lates-1970s, ethologists have been employing comparative approaches to test for links between behavioural traits that vary in a complex manner among closely related species (Dingemanse & Araya-Ajoy, 2015; McKinney, 1978; Owens, 2006). This is because phylogenetic history can limit evolutionary outcomes and trait diversity with respect to behaviour (Borzée et al., 2019; Davies et al., 2012; Garcia et al., 2020). It can be expected that phylogenetically related organisms might resemble each other for most aspects of their phenotype; the extent of similarity is known as phylogenetic signal (Blomberg et al., 2003). Such is the case of the giant mice (*Mus musculus domesticus*) from Gough island, where island populations were bolder and more exploratory than their mainland congeners, yet they avoid predator odours in the same way as mainland mice despite the absence of natural predators (Stratton et al., 2021). Thus, despite different extrinsic factors, relaxed selection has not been sufficient for them to diverge. Bailey et al. (2018) claims that behavioural plasticity and environmental sensibility is supporting its

influence on species evolution, which is expected to be stronger in circumstances where behaviour is sensitive to variation in the social environment. Therefore, closely related species have proven to be useful organisms to fully understand the inherited features of behaviour related to their evolutionary history.

Lizards as a model system for behavioural ecology

Lizards have become a relevant model system for the study of behaviour and communication signals, due to their wide distribution, ecological plasticity, and complex social systems (Anderson & Poe, 2018; Baird et al., 2013; Camargo et al., 2010; Eloy De Amorim et al., 2017; Patton et al., 2021). A large body of work worldwide has focused on visually conspicuous displays and aggressive behaviours (Baird et al., 2013), which involve a variety of stereotypical movements including lateral compressions (Baird & Hews, 2007), dewlap extension (Bloch & Irschick, 2006), head bobs and push ups (Carpenter, 1983), tail flicking (Peters et al., 2016), circular movements of front limbs (Carpenter & Ferguson, 1977) and gaping displays (Lappin et al., 2006). Furthermore, some lizards complement their aggressive repertoires with the development of colourful patterns (Klomp et al., 2016; Stapley, 2006), chemical (Martín & López, 2006; Martín et al., 2015) and even acoustic signals (Hibbitts et al., 2007; Marcellini, 1977). Lizards use these displays during courtship interactions (Carpenter, 1983), as well as during territorial contests (Ord et al., 2001). However, territorial contests have been considered antagonistic interactions as they can be energetically costly and lead to death. Therefore, lizards have evolved these complex signalling displays to asses rivals and avoid unnecessary confrontations (Baird et al., 2013). Many of these aggression displays have been thoroughly studied in diurnally active and visually oriented lizards such as the Iguanidae group, which inhabit relatively open habitats that are conducive to observation (Baird et al., 2013). A well study sub-group are the Caribbean lizards from the genus *Anolis*. These lizards are characterised by their striking diversity, colourful dewlaps and complex display movements, and have helped researchers to understand the role of behavioural traits in sexual selection and

species evolution (Losos, 1994; Pallus et al., 2010). This is because many of these traits reflect

environmental constraints (Fleishman, 1992; Leal & Fleishman, 2002; Steinberg & Leal, 2013).

On the other hand, as ectotherms, lizards have proven to be extremely useful to

understand the effects of temperature on animal physiology and ecology (Abram et al., 2017;

Angilletta et al., 2002; Buckley & Jetz, 2010; Garrick, 2008; Gunderson & Leal, 2016). A well-

documented thermal process on lizards is their diverse thermoregulatory behaviours employed to

achieve and maintain optimum body temperatures (Garrick, 2008). It has been stated that

temperature has a determinant role in lizards as it can modify the performance of a behaviour

and determine whether or not a given behaviour is expressed (Abram et al., 2017; Angilletta et al.,

2009; Buckley & Jetz, 2010; Dias & Rocha, 2004). In addition, as mentioned above, display rates

and signal structure can vary as a function of the ambient temperature, especially when reaching

maximal performance temperatures (Ord & Stamps, 2017). Therefore, temperature has a direct

impact on lizard performance through the thermal dependence of physiology (Diaz, 1991; Gordon

et al., 2010; Sagonas et al., 2017; Stapley, 2006), which has become more relevant with the

current and predicted changes in climate (Gunderson & Leal, 2016).

Another important feature of lizards are their social interactions that has been linked with

the expression of complex social behaviours. Variation in signal design or display repertoire arises

as a consequence of the frequency and context of interactions (Ord & Garcia-Porta, 2012). For

many species of lizard, social interactions can be biased by sexual selection due to strong sexual

dimorphism or sexually skewed populations (Cox et al., 2003; Muralidhar & Johnson, 2017). In

fact, Ord et al. (2001) suggest that signal complexity in lizards has evolved in conjunction with

sexual size dimorphism to improve opponent assessment under high male-male competition, and

reduce the risk of injuries. However, an increase in male-male competition has also proven to be

harmful for female lizards, as males tend to become more aggressive when competing for access

to mating partners leading to harmful encounters for adult females and threatening population

viability (Le Galliard et al., 2005). In the same way, female lizards also exhibit increased aggressiveness in female biased populations as they compete for access to food resources to ensure their reproductive capacity and offspring (Tokarz, 1995). Ultimately, faster and elaborated movements, and longer displays, are thought to evolve with sexual size dimorphism on male lizards to ensure the detection of display advertisements by distant recipients, especially on noisy environments (Fleishman, 1986; Ord & Garcia-Porta, 2012; Ord et al., 2010; Peters, 2008).

A focus on South America

Despite substantial research on lizard behaviour, few studies target South American species (Jaffe et al., 2020; Spinelli Oliveira et al., 2014). Historical data suggest that the study of animal behaviour in South America started with the visit of famous naturalists such as Alexander von Humboldt (1799-1804) and Charles Darwin (1831-1836) (Jaffe et al., 2020). Yet, it was not until the 1970s when biology departments of Venezuela, Chile, Brazil and Argentina started to offer courses on 'Ethology' (Jaffe et al., 2020). Although behavioural ecology research has progressed in Latin America, it is still a developing field, with Brazil, Argentina and Chile considered the leading countries in terms of research and publications (Jaffe et al., 2020; Spinelli Oliveira et al., 2014). Nevertheless, model organisms for a vast majority of these studies comprise mammals, birds and insects, neglecting other organisms such as lizards (Jaffe et al., 2020). This does not at all reflect the suitability of South American lizards, as they exhibit complex social systems and striking phenotypical features. A few, mostly descriptive, behavioural studies of South American lizards have demonstrated diverse patterns of thermoregulatory (Corbalán & Debandi, 2013; Dias & Rocha, 2004; Maia-Carneiro & Rocha, 2013; Medina et al., 2009), antipredator (escape) (Constanzo-Chávez et al., 2018; Jaksić & Núñez, 1979; Santoyo-Brito et al., 2020; Schulte et al., 2004; Vaz E Nunes et al., 2012) and social (Costa Caldeira et al., 2010; Lisboa et al., 2017; Robles & Halloy, 2008; Trigosso-Venario et al., 2002) behaviours, along with the employment of interesting chemical and display signals (Labra et al., 2001; Martins et al., 2004). However, behavioural studies in Latin America are skewed towards highly diverse species form the Iguanidae family such

as the *Liollaemus* group (approx. 280 species), leaving important knowledge gaps for less diversified species.

Lava lizards on the field of behavioural ecology and Ecuador.

Among these less studied South American groups are the lava lizards (Genus: *Microlophus*). There are currently 22 recognised species, with 12 distributed along the western coast of Ecuador to the central north of Chile, and ten species endemics to the Galápagos Islands (Benavides et al., 2007; Benavides et al., 2009; Frost, 1992). Interestingly, species on the islands have evolved under allopatric conditions from two different colonisation events (West and East clades) and are isolated from congeners (Benavides et al., 2007; Benavides et al., 2009), unlike mainland populations were species can occur in sympatry (Benavides et al., 2007). Behavioural studies of *Microlophus* species started with the detailed descriptions of the territorial display patterns of males by the naturalist Charles Carpenter (Carpenter, 1966), who reports that movement-based territorial displays comprise head-bobs and push-ups patterns that are thought to be species–specific due to genetic drift. Since then, others have suggested intrasexual behavioural variation in lava lizards species where females exhibit polygynous mating systems, and males exhibit high territoriality and sexual dimorphism in conjunction with complex social displays used by both sexes to mate or avoid intra-sexual agonistic interactions (Carpenter, 1970; Clark et al., 2019; Clark et al., 2017; Watkins, 1996, 1997). In addition, a strong sexual dimorphism in both colour and size observed in lava lizards' group has also been associated with intrasexual behavioural variations (Watkins, 1997). As adult females' colourful patches can elucidate their reproductive state varying from white and light read (non-reproductive or early in the cycle) to deep orange-red (carrying oviductal eggs), stimulating males' courtship by signalling females receptivity but also increasing females intrasexual competition for oviposition sites and mating partners (Clark et al., 2017, Watkins, 1996).

On the other hand, despite prior research has proposed that lava lizards possess a unimodal activity and a generalist diet consuming mostly insects and plants, but also small

vertebrates (Chávez-Villavicencio et al., 2018; Hervias-Parejo et al., 2019; Jordan & Perez, 2012; Moore et al., 2017; Quispitúpac & Pérez, 2008; Sepulveda et al., 2014). It has also been observed a strong variation on their thermal behaviours and foraging strategies as a result of habitat differences (Burger, 1993; Farina et al., 2008; Jordan & Perez, 2012; Jordan et al., 2008; Jordan et al., 2005; Rowe et al., 2020; Rowe et al., 2019; Sepúlveda et al., 2008), resource availability (East, 1995; Hervias-Parejo et al., 2019; Hervías-Parejo et al., 2020; Sepulveda et al., 2014; Snell et al., 1988) and sexual competition (Clark et al., 2019; Clark et al., 2017; Koening, 2017; Vidal et al., 2002; Watkins, 1997). Nevertheless, skewed attention towards the behaviour of Galápagos lava lizard species has provided only a partial understanding of the *Microlophus* group's behavioural evolution, and thus speciation.

As a matter of fact, apart from Watkins (1996, 1997, 1998), Toyama et al. (2019) and Rowe et al. (2019), who observed complex territorial and social behaviours in *Microlophus occipitalis*, no further behavioural research has been undertaken on mainland lava lizards in Ecuador. Therefore, among the 12 species found on Ecuadorian territory mostly the ten species distributed on the Galápagos Archipelago have been widely studied, neglecting the two occurring along the Ecuadorian west coast (*Microlophus occipitalis and M. peruvianus*) (Benavides et al., 2009). Thus, Galápagos lava lizards' research has contributed to most of the behavioural knowledge of the group as mentioned previously (Carpenter, 1966, 1970, 1977; Chamorro et al., 2012; Clark et al., 2016; Clark et al., 2019; Clark et al., 2017; Clark et al., 2015; Macedonia et al., 2019; Rowe et al., 2020; Rowe et al., 2019). Yet, as behavioural ecology is a growing field in Ecuador, it is not surprising that behavioural knowledge is relatively scarce. However, there is an urgent need for behavioural studies to elucidate the role of external factors in driving behavioural divergence among species as an approach to build accurate background knowledge for future conservation.

Thesis outline

Reviewing the available literature on behavioural ecology of lava lizards in Ecuador elucidated significant gaps in knowledge, such as the lack of information on several species, as well as detailed and updated descriptions of behavioural patterns and communication displays in an ecological and evolutionary context. My research aimed to fill some of these gaps by focusing on the role that behaviour plays in ecological specialisations and niche delimitation of the *Microlophus* species from Ecuador. During my fieldwork, I surveyed two mainland and six island species of lava lizards in Ecuador (Figure 1.1-1.2), and I employed a consistent data collection strategy at 15 sites (Figure 1.3-1.4). Each site was sub-divided into three non-overlapping linear transects at the edges of each site to enhance the lizards' visibility. Then, using the established sampling area, I recorded encounter rates and completed vegetation assessments. In addition, behavioural observations of focal males and females were undertaken across intervening days, along with the filming of male territorial displays. This standardised methodology supports the collection of a comprehensive set of data related to the behaviour and ecology of *Microlophus* species. Updating the territorial display action patterns (DAP) of male lava lizards was a strong aim of my research too, so I applied an improved filming approach that enables three-dimensional (3D) reconstruction of motion displays and thus a detailed and more accurate description of the display action pattern. At the outset, my target was to study all 12 Ecuadorian lava lizard species. However, because of logistical issues concerning access to remote islands, and limited funding, I was unable to access four Galápagos species (*M. habelii* – Marchena Island, *M. delanonis* – Espanola Island, *M. barringtonensis* – Santa Fe Island, and *M. pacificus* – Pinta Island, see Figure 1.3).

M. occipitalis

M. peruvianus

M. albemarlensis

M. indefatigabilis

M. grayii

M. bivittatus

M. jacobi

M. duncanensis

Figure 1.1 – Males of Ecuadorian *Microlophus* species sampled during fieldwork. Two photos on top represent mainland congeners. Photography by Estefania Boada and Estefany Guerra and used with permission.

Figure 1.2 – Females of Ecuadorian *Microlophus* species sampled during fieldwork. Two photos on top represent mainland congeners. Photography by Estefania Boada and Estefany Guerra and used with permission.

Figure 1.3 – Mainland and island Ecuadorian lava lizards' (*Microlophus* species) distribution with sampled points for the sites surveyed during the three fieldwork seasons.

Figure 1.4 – Habitat features of sampled sites surveyed in season one (a), two (b) and three (c) along the west Ecuadorian coast and the Galápagos Islands, respectively. Photography by Estefania Boada and Estefanya Guerra and used with permission.

Figure 1.4 - continuation.

Figure 1.4 - continuation.

Studying the Ecuadorian lava lizards was particularly remarkable as they appear to be adapted to a wide range of habitats and exhibited strikingly diverse behavioural patterns. In addition, diversification on the Galápagos Islands allowed me to explore further the interesting evolutionary processes occurring on these islands, which possess a unique biodiversity and are considered a natural laboratory. Because the Galápagos Islands have experienced significant human development over the past 30 years, I was also able to make use of a marked gradient of

urbanisation among islands (Figure 1.5) from heavily urbanised islands with introduced predators to totally isolated islands with natural predators. In fact, during my fieldwork I observed the presence of the Galápagos hawk (*Buteo galapagoensis*), the Galápagos short-eared owl (*Asio flammeus galapagoensis),* and the Santiago racer *(Pseudalsophis hephaestus)* only on the isolated islands Pinzon and Santiago (Figure 1.6a-c). In contrast, the presence of rats and ants was very common on all the islands, while dead lizards on roads was registered only on the urbanised islands (Figure 1.6d). This is definitely indicative of new threats for Galápagos lava lizards and is one of the reasons I pivoted my research to focus on this current and exponential threat, which has placed the Galápagos Islands on the list of World Heritage in Danger, affecting the species inhabiting the archipelago.

Santa Cruz Island - main street

San Cristobal Island - main street

Isabela Island - main street

Floreana Island - main street

Pinzon Island - Playa Escondida

Santiago Island - Flamingo pond

Figure 1.5 – Urbanisation gradient on the Galápagos islands from highly urbanised (top left) to human isolated islands (two bottom). Photography by Richard Peters and Estefania Boada and used with permission.
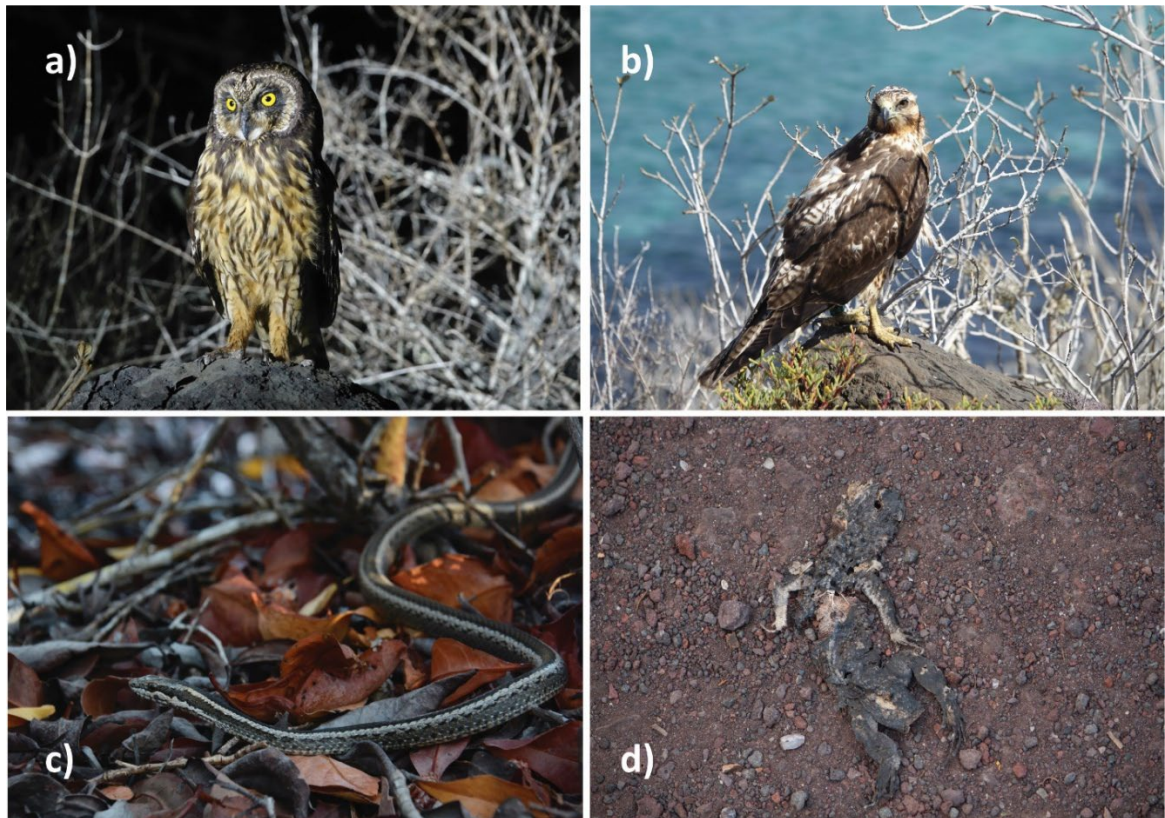
Figure 1.6 – Native predators observed on Pinzon and Santiago island - a) Galápagos short-eared owl (*Asio flammeus galapagoensis*), b) Galápagos hawk *(Buteo galapagoensis),* c) Santiago racer *(Pseudalsophis hephaestus), and d)* Santa Cruz lava lizard *(Microlophus indefatigabilis)* dead on the road. Photography by Estefany Guerra and Estefania Boada and used with permission.

All three field seasons were successful, and I report in this thesis substantial new information on the ecology and behaviour of the *Microlophus* group in Ecuador. In addition, I have initiated separate projects on their diet and colour patterns (see **Chapter 5**), as well as future phylogenetic studies in collaboration with local institutions. My three empirical data chapters, outlined below, consider the effect of competition on the behaviour of sympatric species (**Chapter 2**), ecological and environmental influences of behaviour in a phylogenetic context (**Chapter 3**) and the effect of urbanisation on the behaviour of island species (**Chapter 4**).

Chapter Two – inter-specific competition on lava lizard (Microlophus occipitalis & M. peruvianus) populations from the Ecuadorian west coast.

Species coexistence has been widely recognised as one of the factors leading to niche partitioning. However, understanding the processes underlying niche partitioning can become challenging as

numerous factors must be considered. *Microlophus* lizards are thought to feature high plasticity that allows them to exploit different habitats and overlapping populations of different species on the mainland provides an excellent opportunity to explore the role of inter and intraspecific interactions. My objective was to assess the effect of different levels of inter-specific competition on *Microlophus occipitalis* and *M. peruvianus* populations along the Ecuadorian west coast. While several comprehensive ecological studies have been performed on island *Microlophus* congeners, our understanding of the potential influencing factors on the dynamics of sympatry in mainland species is limited. Thus, further research is needed to comprehend the behavioural partitioning mechanisms in mainland communities.

Chapter Three - Ecological influences on the behaviour of Ecuadorian lava lizards in the context of phylogenetic relatedness.

When studying closely related species it is often expected that there is some degree of similarity between species due to their phylogenetic history. However, behaviour has also been demonstrated to develop in response to external conditions, so it is likely that animals adapt their behaviour to survive in novel environments or changing situations and be less constrained by shared ancestry. More advanced comparative approaches have allowed ethologists to explore behaviour in terms of phylogenetic history and natural selection. I studied Ecuadorian lava lizards, which are closely related species distributed on the mainland and Galápagos islands, to examine the extent to which external factors have influenced behaviour. Using established phylogenetic comparative methods, I aimed to test alternative evolutionary models to assess the evolution of behaviour and signals under ecological and environmental conditions, biogeographical setting, and phylogenetic history. In addition, I update the territorial display action patterns (DAP) of males, not revised in detail since Carpenter (1966,1977), using a more accurate approach. Lastly, I discuss my results as a snapshot of the full picture of behavioural and signal differentiation and

propose the *Microlophus* group as a useful model to further explore behavioural adaptations among related species.

Chapter Four - The effect of urbanisation on the behaviour of Galápagos lava lizards (genus Microlophus) with insights for forthcoming conservation research.

Understanding the impacts of human influence on wildlife has become imperative for future conservation. It is not new to scientists that there is a relationship between habitat and species diversity loss with the increment of anthropogenic factors. Insular ecosystems are among the most vulnerable due to species-specific adaptations to unique environments. Often urbanisation represents a series of threats to native species by introducing new ecological stressors. I focused on the island species of the *Microlophus* groups, which are endemic to the Galápagos Archipelago. In the last 30 years, the Galápagos Islands have faced exponential human growth along with high touristic demand. I aimed to estimate for the first time the impact of urbanisation and wildlife tourism on the Galápagos lava lizards' behaviour where the islands featured a gradient of urbanisation going from highly urbanised to isolated.

Summary

In this dissertation, I have used a comprehensive approach to examine the influence of extrinsic ecological and environmental constraints on species phenotypes, with a particular focus on the role that behavioural and ecological specialisations play in niche delimitation. Although my outcomes are only a snapshot of the full picture when it comes to understanding the complex relationships between species behaviour and their environment, my research highlights specific areas for future research, including the effect of species interactions (Chapter 2) and phylogenetic history (Chapter 3) in species evolution and diversification. In addition, I explore for the first time the impacts of urbanisation on the Galápagos lava lizards, contributing benchmark knowledge relevant for conservation projects (Chapter 4).

Overall, my research has exposed the important role of ecological and environmental contexts on species phenotypic adaptations. Also, it is the first project to take a multifaceted approach to documenting the behavioural ecology of Ecuadorian lizards. In so doing, my dissertation represents an important contribution to the field of behavioural ecology in Ecuador, and Latin America more generally, highlighting wonderful opportunities for further research and conservation projects.

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CHAPTER TWO

Living together: inter-specific competition in lava lizard (*Microlophus occipitalis* & *M. peruvianus*) populations from the Ecuadorian west coast.

Abstract

Species coexistence can be accomplished by resource partitioning through interspecific competition. Even so understanding the processes underlaying niche partitioning is a complex task as several interacting factors must be considered. Previous research on the *Microlophus* group suggest a high plasticity that allows them to use of different habitats. Yet, the role of inter and intraspecific interactions has been relatively neglected, especially on mainland congeners. I assessed the effect of different levels of inter-specific competition on *Microlophus occipitalis* and *M. peruvianus* populations along the Ecuadorian west coast. I found that both species exhibited behavioural shifts such as reducing the time spent on foraging to avoide time overlapping with the other species. Likewise, microhabitat use preferences for *M. occipitalis* switch to vegetation and higher perches, while *M. peruvianus* preferred ground and lower perches. In addition, *M. occipitalis* showed morphological and territorial display structure variations that were consistent with the microhabitat shift and habitat differences. As individuals in sympatry exhibited smaller limbs, slender and lighter bodies with longer tails, whereas for the territorial display males showed a lower amplitude. It is likely that habitat variations such as higher vegetation composition on sympatric sites played an important role on both species' differentiation. However, I cannot rule out the influence of interspecific competition as an important factor during this process. Therefore, further research is needed to disentangle the potential influencing factors on the dynamics of sympatry in these species. Lastly, I propose this group as a model to comprehend the behavioural partitioning mechanisms in mainland communities.

Introduction

Exploring the circumstances in which niche partitioning takes place helps us to understand species

coexistence and diversity, without leading to extinction (Cloyed & Eason, 2017). Interspecies

interactions have been widely recognised as one of the factors leading to niche partitioning

between closely related species (Schoener, 1974a; Zani & Esposito, 1999). Coexistence for

ecologically similar species might lead to agonistic interactions, intraguild predation, and

reproductive interference which could negatively impact one or both species (Kamath et al., 2013;

Schoener, 1974b). However, species can coexist by exploiting similar resources in different ways

leading to major shifts in foraging (Correa & Winemiller, 2014), space use (Zhong et al., 2016), and

activity time (Ord & Klomp, 2014). This ecological differentiation is often followed by changes in

morphology and physiology allowing species to exploit specific parts of the resources available

more effectively (Greiner et al., 2007; Verwaijen et al., 2002).

Resource partitioning has been well documented in many organisms including mammals

(Oviedo et al., 2018), spiders (Villanueva-Bonilla et al., 2019), frogs (Cloyed & Eason, 2017), fishes

(Sbragaglia et al., 2019) and lizards (Sagonas et al., 2017). These data suggest that species may

utilise their limited resources as a consequence of pre-existent ecological preferences and their

interactions with the environment (Winck et al., 2016). Many species take advantage of

environmental heterogeneity (Cloyed & Eason, 2017). For instance, similar species often shift their

foraging preferences, feeding at different habitats or microhabitats (Langeland et al., 1991), or

choosing different types of prey (Beaulieu & Sockman, 2012). Also, some species could divide

their niche temporally by having either different daily or seasonal activity periods (Knickle & Rose,

2014). Finally, species can partition their niche by making adjustments across multiple axes

simultaneously (space use, food and time) to decrease competition (Laughlin & Werner, 1980).

Past interspecific interactions also play an important role in niche separation between coexistent

species (Vitt et al., 2005). Prior competition scenarios may indirectly influence the present-day

structure of communities impacting on the functional components of a species community organisation (Vitt et al., 1999). Vitt et al. (2005) suggest that differences in ecological features among species occurring early in their evolution can influence the structure of present-day assemblages. For example, species assemblages of Amazonian lizards from Brazil reveal that community structure with respect to microhabitat and diet is also associated with phylogenetic similarity (Vitt et al., 1999). This is important because it suggests niche partitioning in the present day is not just the result of current coexistence.

Much of the research focus on niche partitioning concerns habitat use and diet, while the time axis of a species niche has been relatively neglected. Time relates to activity patterns, particularly how animals distribute their activity over the day (Frey et al., 2017). Understanding how species use time as a resource is an important dimension of animal behaviour, since it can provide relevant information about their ecological niche and natural history (Schoener, 1974b). For many species, some behaviours can be tied to different parts of their habitat, time of the day or prey availability. Thus, engaging in a given behaviour likely depends on the structure of the environment that can differ among populations and be affected by interspecific interactions (Kronfeld-Schor & Dayan, 2003). For instance, using low predation sites for sleeping or high energetic return sites for foraging shows a partition of their behavioural repertoire that might be favoured by selection (Kamath et al., 2013). This variation in species' behavioural repertories may arise as a strategy to mediate ecological interactions modifying the structure of ecological communities.

Studies of behavioural partitioning in lizards are scarce, or are restricted to a few behaviours and particular ecological circumstances, such as island communities (Edwards & Lailvaux, 2012). In these studies, the genus *Anolis* have become a model for lizards due to their behavioural plasticity and distribution (Hess & Losos, 1991; Johnson et al., 2010; Losos, 1992). Studies of this kind do suggest that the presence of coexistent species, whether they are closely

related or not, can alter the behavioural repertoire of one or both species. Major differences are related to the microhabitat preferences when engaging in a given behaviour (Johnson et al., 2010), and variation in the frequency of some behaviours (Edwards & Lailvaux, 2012). Although not as widely studied, similar patterns can be observed in mainland desert communities of lizards (Huey et al., 1974; Pianka, 1969; Winck et al., 2016). Here temporal changes are evident in their diel activity patterns (Nguyen et al., 2020), sometimes linked to prey (Gordon et al., 2010) or habitat (Asbury & Adolph, 2007) available to the coexistent species. In some circumstances, shifts related to habitat use led to phenotypic divergence among taxa in ecologically relevant traits as they adapt to the requirements of the given habitat, referred to as character displacement (Ord & Klomp, 2014). In most study groups, this divergence in size (snout-vent and limb length), activity, microhabitat use and prey preferences, reduces interspecific competition within assemblages (Echternacht, 1967; Goodman, 2007; Vitt & Zani, 1998).

The lava lizards group (genus *Microlophus*, Tropiduridae) is becoming a popular group for ecological, biogeographical, evolutionary and behavioural studies (Benavides et al., 2007; Benavides et al., 2009; Carpenter, 1970; Clark et al., 2016; Clark et al., 2019; Clark et al., 2017; Clark et al., 2015; Kizirian et al., 2004). They also have a distinct geographic distribution, which is unusual in terrestrial vertebrates (Benavides et al., 2009). Twenty-two species are recognised with 12 distributed along the western coast of Ecuador to the central north of Chile, while ten species are endemic to the Galápagos Islands (Benavides et al., 2007; Benavides et al., 2009; Frost, 1992). Like many iguanids, *Microlophus* sp. use movement-based territorial displays comprising head-bobs and push-ups, which are species–specific, female-display polygyny, male-male territoriality, and sexual size dimorphism (Carpenter, 1970; Clark et al., 2019; Watkins, 1996, 1997). Species on the Galápagos Islands have attracted more attention, while mainland species have been largely overlooked, apart from basic ecological studies related to sexual dimorphism (Watkins, 1996), intersexual signalling and female coloration (Watkins, 1997, 1998), microhabitat use (Chávez-Villavicencio et al., 2018; Rowe et al., 2019), diet (Farina et al., 2008), morphology (Toyama

Campos, 2016), and thermal ecology (Catenazzi et al., 2005; Huey, 1974; Jordan & Perez, 2012).

However, behavioural traits are poorly studied and are restricted to activity patterns (Sepulveda et al., 2014; Sepúlveda et al., 2008) or single behaviours (Toyama et al., 2019; Watkins, 1998) mostly related to the species thermal ecology without taking account of species interactions. *Microlophus occipitalis* and *M. peruvianus* are distributed along the west coast of Ecuador and Peru (Benavides et al., 2007), and some comunities overlap and presumably share ecological resources. As both species have similar activity patterns, exploit similar ecological resources (Toyama Campos, 2016) and are closely related (Benavides et al., 2007), understanding the influence of inter-species interaction in their ecology is imperative.

The purpose of this study was to examine the effect of species interactions on mainland *Microlophus* lizards by comparing populations of *M. occipitalis* and *M. peruvianus* that co-occur with populations of each species that exist alone. I investigated the effect of different levels of inter-specific competition on *M. occipitalis* and *M. peruvianus* under four specific aims, which were to quantify:

1. relative abundances of both species across the different populations

2. environmental variation at these sites by examining vegetation and substrate structure

3. morphological differences between populations

4. variation in the behavioural repertoire

I expected to quantify for the first time the relative abundance and habitat structure for both species across several populations (Maura et al., 2011; Ruiz de Infante Anton et al., 2013). I predicted that the coexistence of these closely related *Microlophus* species will affect competition for available resources in sympatry, leading to niche partitioning and concomitant effects on morphological adaptations (Herrel & Holanova, 2008; Herrel et al., 2002b), behavioural repertoires, including communicative displays (Kamath et al., 2013; Peters et al., 2016; Watkins, 1997; Yin et al., 2011) , and shifts in habitat use to avoid interspecies competition (Pianka, 1973; Vitt & Zani, 1998).

Methods

Focal species and study sites

I studied *Microlophus occipitalis* and *M. peruvianus* in western mainland Ecuador during December 2017 and January 2018. These species differ in size (snout-vent lengths of 50-80 mm and 68-98 mm respectively) and colouration and are easily distinguished in the field (Figure 2.1). Both species are characterised by strong sexual dimorphism, whereby males are larger than females and exhibit a well-developed dorsal crest (Watkins, 1998). Additionally, female *M. occipitalis* are cryptically coloured, except for the presence of red pigmentation on neck, throat, and chin, while males exhibit black patches on their dorsal section (Watkins, 1997). In contrast, female *M. peruvianus* display a brownish pattern with yellow pigmented marks on the hind limbs, while male *M. peruvianus* exhibit a black striped pattern with yellow and black patches on the chest (Figure 2.1). Both species exhibit male and female territorial behaviour, with the breeding season occurring from January to May, although it does vary with rainfall intensity (Dixon & Wright, 1975; Watkins, 1996, 1997).

Data were collected from six localities on the western coast of mainland Ecuador (Table 2.1; Figure 2.2). The sites were chosen in advance to sample allopatric populations (only one species occurring) of each species, as well as sites where the species occur in sympatry (two species occurring in the same area). One site, Chanduy, was subsequently deemed to contain parapatric populations (two species occurring in the same area but with a small encounter zone) of each species. The vegetation of each study site was diverse with deciduous shrubs and herbs near the coast (Los Frailes, El Pelado and Chanduy: (Aguirre et al., 2006; Ministerio del Ambiente del Ecuador, 2013), and a desert scrub habitat in more inland localities (Ancón, "Península de Santa Elena" National Park, and Cerro Alto (Ministerio del Ambiente del Ecuador, 2013; Watkins, 1996). The timing of the present study was chosen specifically to coincide with the lead-in to (December), and start of (January), the breeding season. This represents the summer season in

Ecuador and is characterised by mean temperatures exceeding 30°C and 400mm of rain through the last days of December until March (Ministerio del Ambiente del Ecuador, 2013).

Figure 2.1 Male (left) and female (right) lizards of (A) *Microlophus peruvianus* and (B) *Microlophus occipitalis* sampled on the Ecuadorian west coast.

Table 2.1 Localities and habitat types sampled from the Ecuadorian west coast. Ref number indicates the location in Figure 2.2.

Map Ref	Province	Locality	Coordinates	Altitude (m)	Distribution (Species)	Habitat
1	Manabi	Los Frailes	1° 27' 56.0519" S, 78° 23' 49.9530" W	0 - 50	Allopatry (M. occipitalis)	Dry coastal shrub
2	Santa Elena	Cerro Alto	2°10'51.7802" S, 80°45'48.0652" W	0 - 400	Allopatry (M. occipitalis)	Deciduous coastal forest
3	Santa Elena	"Península de Santa Elena" National Park	2°11'18.2" S, 81°00'35.0" W	0 - 50	Sympatry (Both sp.)	Dry coastal shrub
4	Santa Elena	Ancón	2°19'3.1437" S, 80°51'21.7200" W	0 - 50	Allopatry (M. peruvianus)	Dry coastal shrub
5	Santa Elena	Chanduy	2°24'10.8" S, 80°40'56.2" W	0 - 50	Parapatry (Both sp.)	Dry coastal shrub
6	Guayas	El Pelado	2°37'31.1" S, 80°27'10.1" W	0 - 50	Sympatry (Both sp.)	Dry coastal shrub
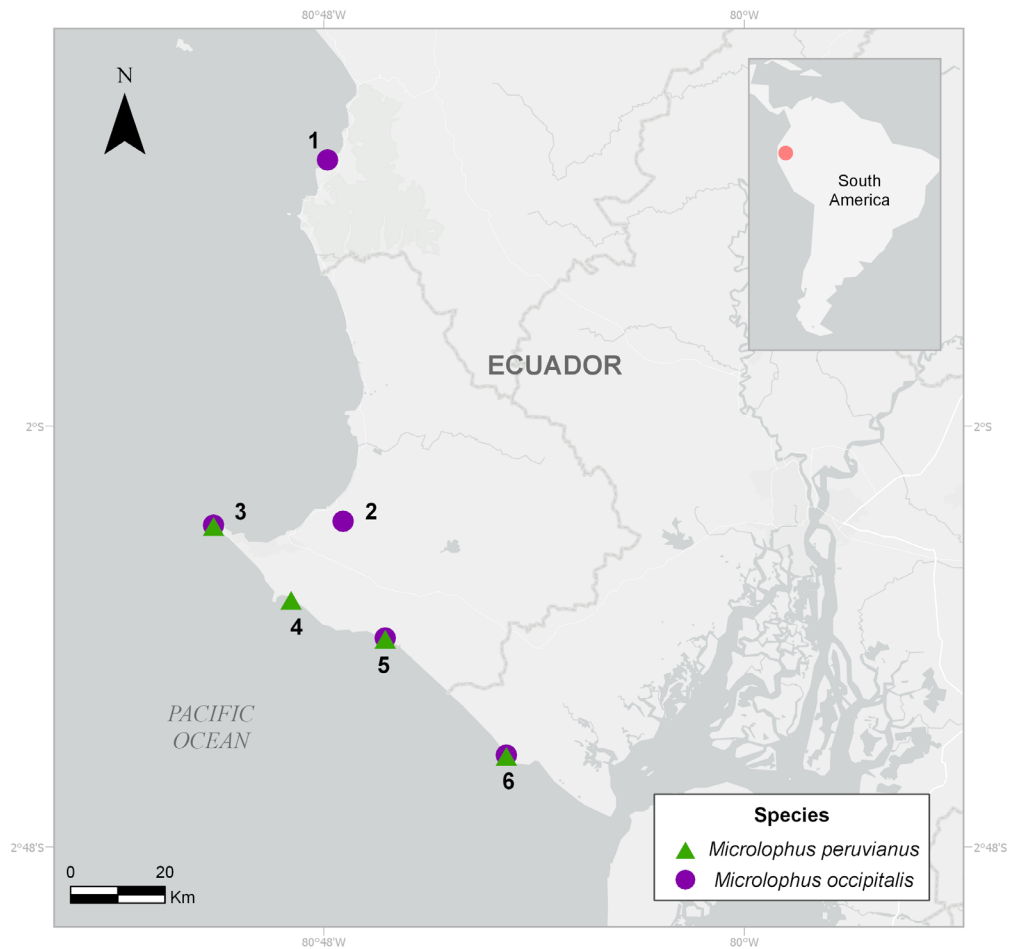
Figure 2.2 Map of sampled locations of *Microlophus occipitalis* and *M. peruvianus* populations along the Ecuadorian west coast. Numbers correspond to the localities listed on table 2.1

Data collection

My data collection strategy at each site was consistent. Sites were sub-divided into three non-overlapping linear transects of 120 m. Due to dense vegetation, transects were located at the edges of my study sites (e.g. paths, forest limits) to enhance the probability of locating lizards (Maura et al., 2011). I recorded encounter rates along each transect at the beginning of our activities at each site and completed vegetation assessments after all other activities were completed. Behavioural observations were undertaken across intervening days, including filming of intra-specific visual (territorial) displays by males. Morphological data was obtained for focal animals, as well as other individuals from each of the transects after completing activities along the transect.

Biotic and abiotic factors

<u>Encounter rates</u>

I estimated the number of lizards at each study site using three line-transects of the same area (120m x 4m). Following Ruiz de Infante Anton et al. (2013), each transect was walked slowly by an observer from 0800-0900 for three consecutive days registering all the individuals on the left hand side of the path as well as the transect path itself. Although transects and observation areas were spatially separated, I considered the transects to be non-independent as the separation was approximately 20 m. The age class and sex of the counted individuals were also registered during population surveys, as well as humidity, air temperature and wind conditions at the start of each survey.

<u>Vegetation assessments</u>

For each study site, the three previously established line-transects were used to assess the vegetation composition. Forty points were distributed in a zig-zag pattern across each transect at 3m intervals, with odd-numbered points located near to the transect edge and even-numbered points position 5m away from the transect path (Figure S2.1). A touch pole was used at each point and the substrate type were classified as ground, sand, leaf litter, rock, or cliff. Vegetation height was scored at 0.1 m increments to 2m height, with vegetation greater than 2m categorized as woody plant. Plant types were grouped into 7 categories based on the life form: ground cover, grass, herb and forbs, shrubs, woody plants, cactus, and non-vegetation.

Morphology

At least 10 individuals per species at each study site were caught and measured in the field. As per previous studies (Herrel & Holanova, 2008; Herrel et al., 2001) the following morphological variables were taken from adult male and female lizards using a digital calliper (Tresna EC05, resolution 0.01 mm): snout-vent length (SVL), tail length (TL), femur length (FL), tibia length (TL),

metatarsus length (MTL), IV hind toe length (HTL), humerus length (HL), radius length (RL), metacarpus length (MCL), IV fore toe length (FTL), body width (BW), body height (BH), interlimb length (IL), total forelimbs (FL), total hindlimbs length (HL), head length (HL, from the snout to the fore Edge of the parietal bone), head width (HW, measure at the jugal bone or the widest part of the head), head height (HH, measure behind the orbits), and lower-jaw length (LJL, from the retroarticular process to the tip of the lower jaw). All measurements were taken on the left side of the animal. Additionally, we registered the body mass of each measured individual using Pesola spring scales (to the nearest 0.5 g).

Behaviour

I developed a partial ethogram of the behavioural repertoire of *Microlophus* species based on previous studies (Carpenter, 1966; 1977; Watkins, 1997; Clark et al 2015; Yin et al, 2011) and personal observations (see Table S2.1). On site, I undertook focal sampling of male and female lizards. For three consecutive days, and focussing on one transect per day, I conducted three-hour observations during the morning (0900-1200) and afternoon (1400-1700). Focal sampling registered the activity of a selected individual at two-minute intervals, for both male and female focal lizards observed separately by two trained observers per session. The microhabitat type and height from the substrate was also recorded every two-minutes. Different focal animals were selected for the morning and afternoon sessions, with a total of 90 behavioural observations obtained for each of 12 adult individuals sampled at each locality (two males and females at three transects). In addition to focal observations, environmental conditions including air temperature were measured using a Kestrel-4000 anemometer every 10 minutes and at the start of each session. For the sympatric localities, one species was observed in the morning and the other species in the afternoon, which was reversed on subsequent days. Four days of observations were completed at these locations.

<u>Filming territorial displays</u>

I recorded five to eight interactions of adult males at each sample site following the approach of Peters et al (2016). While effort was made to record displays for both species, I was only able to film two interactions of *M. peruvianus,* so I limit analyses to *M. occipitalis*. Briefly, a tethered male from a different location was introduced to an unconstrained resident male. To record displays, I used two video cameras (Sony-CX625) positioned with greater than 20° angular separation and filmed at 100 frames per second. Once filming started, the camera settings and positions were not adjusted. Before recording ceased, a calibration object featuring 20 non-coplanar points, distributed evenly across the volume of space occupied by the resident lizard was placed in view of both cameras. To allow for an accurate three-dimensional reconstruction of the displays, as per Hedrick (2008), the calibration object was placed in a way that most of the points were visible in the cameras (see Peters et al. 2016 for further details).

Statistical Analysis

Biotic and abiotic factors

<u>Encounter rate</u>

To infer whether the number of individuals per species varied between sites, I summed across transects within a given session and compared the maximum value from the three days using a generalized linear mixed model with species and population as fixed effects using the *glmer* function from the LME4 package (Bates et al., 2015) in the R statistical environment (RCoreTeam, 2018) and fitting Poisson error distribution. I then used the *anova* function with the Chi-square statistic to test the significance of the model factors, and when relevant, examined the significance of pairwise differences using z scores.

Vegetation assessments

I used non-metric multidimensional scaling (NMDS) using Bray-Curtis similarities to visualise differences in habitat structure between sample sites. I then used analysis of similarity (ANOSIM) to test whether the sample sites varied statistically. All statistical analyses were performed using the VEGAN package (Oksanen et al., 2010) in the R statistical environment (RCoreTeam, 2018).

Morphology

Morphological analysis was limited to *M. occipitalis* as the sample size for *M. peruvianus* was small; I excluded the parapatric population for the same reason. Population means (±SD) are presented in Table 2.3 and were logarithmically transformed (log10) before analysis to meet the assumption of normality. Species differences in body size (SVL) were tested using a two-way ANOVA (population and sex as fixed effects). All the other measurements were regressed against the SVL to eliminate the size effect, and residuals calculated to analyse differences between competition levels (sympatric and allopatric). I then used principal component analysis (PCA) on the residuals and compared the resulting factor scores among competition levels using a two-way analysis of variance (competition and sex as fixed effects). I then used the Broken Stick Method (Herrel et al., 2001) to determine which principal components were significant. All morphological data analysis was performed in the R statistical environment (RCoreTeam, 2018).

Table 2.3 Morphological variables summary with population averages and standard deviations (SD) for *M. occipitalis* adult males and females.

Variable	Sympatric populations		Parapatric populations		Allopatric populations	
	Female	*Male*	*Female*	*Male*	*Female*	*Male*
N	13	13	NA	3	9	17
SVL	57.07 ± 3.52	69.63 ± 7.47	NA	67.82 ± 2.00	55.88 ± 4.54	69.67 ± 5.04
Mass	6.93 ± 0.93	12.34 ± 3.57	NA	13.33 ± 1.23	5.88 ± 1.16	12.31 ± 2.80
Tail length	75.24 ± 16.85	107.91± 18.23	NA	117.37 ± 3.94	74.25 ± 17.91	106.84 ± 24.37
Head length	13.28 ± 0.61	12.17 ± 1.49	NA	16.17 ± 0.94	13.34 ± 0.81	16.27 ± 0.87
Head width	9.44 ± 0.68	11.78 ± 1.07	NA	11.84 ± 0.68	10.01 ± 0.99	12.35 ± 0.87
Head height	7.99 ± 0.89	9.77 ± 1.23	NA	9.93 ± 0.39	8.04 ± 0.83	10.29 ± 1.03
Lower jaw length	14.28 ± 1.28	17.43 ± 1.78	NA	16.92 ± 1.17	13.99 ± 1.28	17.15 ± 1.05
Interlimb	26.44 ± 2.12	30.80 ± 3.78	NA	32.2 ± 1.78	26.36 ± 3.07	30.97 ± 3.37
Body width	16.03 ± 1.63	17.48 ± 1.78	NA	17.76 ± 0.54	14.53 ± 1.90	17.96 ± 1.84
Body height	10.80 ± 0.76	12.92 ± 1.93	NA	12.93 ± 1.01	10.45 ± 2.01	14.52 ± 2.08
Femur length	13.40 ± 1.28	16.29 ± 1.86	NA	14.82 ± 0.59	12.78 ± 0.86	16.49 ± 1.65
Tibia length	11.51 ± 0.75	14.67 ± 1.44	NA	13.73 ± 0.65	11.43 ± 0.89	14.66 ± 1.15
Metatarsus length	5.21 ± 0.24	6.49 ± 0.99	NA	6.73 ± 0.98	6.11 ± 0.52	7.86 ± 0.70
Longest toe length (hindlimb)	8.90 ± 0.59	11.02 ± 1.01	NA	9.72 ± 1.85	9.30 ± 0.84	11.38 ± 1.14
Humerus length	9.92 ± 0.77	11.98 ± 1.46	NA	11.91 ± 0.40	10.33 ± 0.65	12.94 ± 0.99
Radius length	8.14 ± 0.51	9.53 ± 1.19	NA	9.93 ± 0.44	7.85 ± 0.55	9.56 ± 0.97
Metacarpus length	2.53 ± 0.12	3.06 ± 0.43	NA	3.81 ± 0.29	2.68 ± 0.22	3.54 ± 0.48
Longest toe length (forelimb)	4.91 ± 0.41	5.56 ± 5.56	NA	5.94 ± 0.45	4.83 ± 0.34	5.89 ± 0.42

Behaviour

As lizard behaviour can be influenced by prevailing environmental conditions, I first considered the weather conditions in which observations were made at each location. I then explored behaviour as a function of inter-species competition (allopatry, parapatry, sympatry) to address three overarching questions related to the time spent engaged in different behaviour categories and utilising different microhabitats, as well as the height at which lizards were observed.

Weather conditions

I examined variation in air temperature across levels of inter-species competition of each study population. Morning and afternoon sessions were considered separately. The eighteen values per

lizard within a session were ordered according to sampling time and a linear regression line was fit

to the data. I extracted the intercept and slope from the resultant regression and plotted them in

two-dimensional space. I used Hotelling's two-sample $T2$ tests to determine whether the

distributions between different levels of inter-species competition were significantly different.

Focal sampling behavioural observations

I tested whether the time engaged in different behaviours, microhabitat use, and substrate height

preferences for specific behaviours varied across levels of inter-species competition. Nine

behaviours were selected for the focal sampling analysis as they were the most frequent (see

Table S2.2). I converted to proportions the data for time spent in each behaviour and microhabitat

use and used beta regression models using the *betareg* function from the BETAREG package

(Cribari-Neto & Zaileis, 2010) in the R Statistical Environment. Each behaviour was analysed

separately and individuals that did not exhibit a given behaviour were assigned a score of zero.

Values exactly equal to 0 or 1 were adjusted as per Smithson and Verkuilen (2006) using the

formula:

$$p \ transformed = \frac{p(n-1) + 0.5}{n}$$

Where *p* was the proportion value, and *n* was the sample size. I fitted the regression model with

competition, species, and sex as factors. The microhabitat models were assembled to examine the

time spent utilising different microhabitats across competition levels. I classified the microhabitats

into ground, rock, vegetation, and other, and separate models were fitted for each microhabitat

category with competition and species as factors. The significance of factors in models for

behaviour and microhabitat use were examined using the *joint-tests* function from the EMMEANS

package v1.6.1 (Lenth et al., 2021), yet only significant outcomes were further explored

graphically.

The height above the ground was determined for each focal animal observation and compared using linear mixed effects models. I examined behaviours separately such that the dependent variable was the height at which the given behaviour was performed, and males and females were considered separately. The *lme* function from the NLME package v3.1-153 (Pinheiro et al., 2013) in the R Statistical Environment was used to construct models with Competition and Species as fixed factors and lizard identity as a random effect. Individual lizards that did not perform a given behaviour were excluded from the analysis. The significance of factors was considered using the *anova* function, and as prior only significant outcomes were further explored graphically.

Analysis of territorial displays

To investigate whether the territorial displays varied in the presence of congeners, I focus on *M. occipitalis* displays at allopatric and sympatric sites as the sample size for *M. peruvianus* and *M. occipitalis* at parapatric sites were inadequate. The territorial displays of *M. occipitalis* consisted of a sequence of rapid push-ups, dewlap extension, lateral compression of the trunk and lateral presentation to an opponent (Carpenter, 1966). I digitised two sequential bouts of push-up displays by tracking the position of one eye over time in recordings from both cameras and applied direct linear transformation (DLT) in Matlab (MathWorks Inc.) following Hedrick (2008) to reconstruct movements in 3-dimensional space. This process ensures that digitised movement is not constrained by the position of the cameras during filming; see Hedrick (2008) and Peters et al (2016) for a more complete description of the technical aspects of this approach and its application to lizard displays, respectively. I computed the change in position of the eye in 3D space to produce display action pattern graphs and used this to identify the largest amplitude movement of the display (Figure 2.3a). In addition, I computed the speed of movement as the change in position between successive frames (Fig 2.3b) and calculated the average for the bout. This process was repeated for the first two bouts of each display. The maximum amplitude, speed and display duration were then compared statistically using linear mixed effects models in R. I

used the *lme* function from the NLME package v3.1-153 (Pinheiro et al., 2013) with fixed factors of

competition (allopatric or sympatric) and order (first or second bout) and setting individual

identity as a random effect. The significance of factors was provided by an F-test.
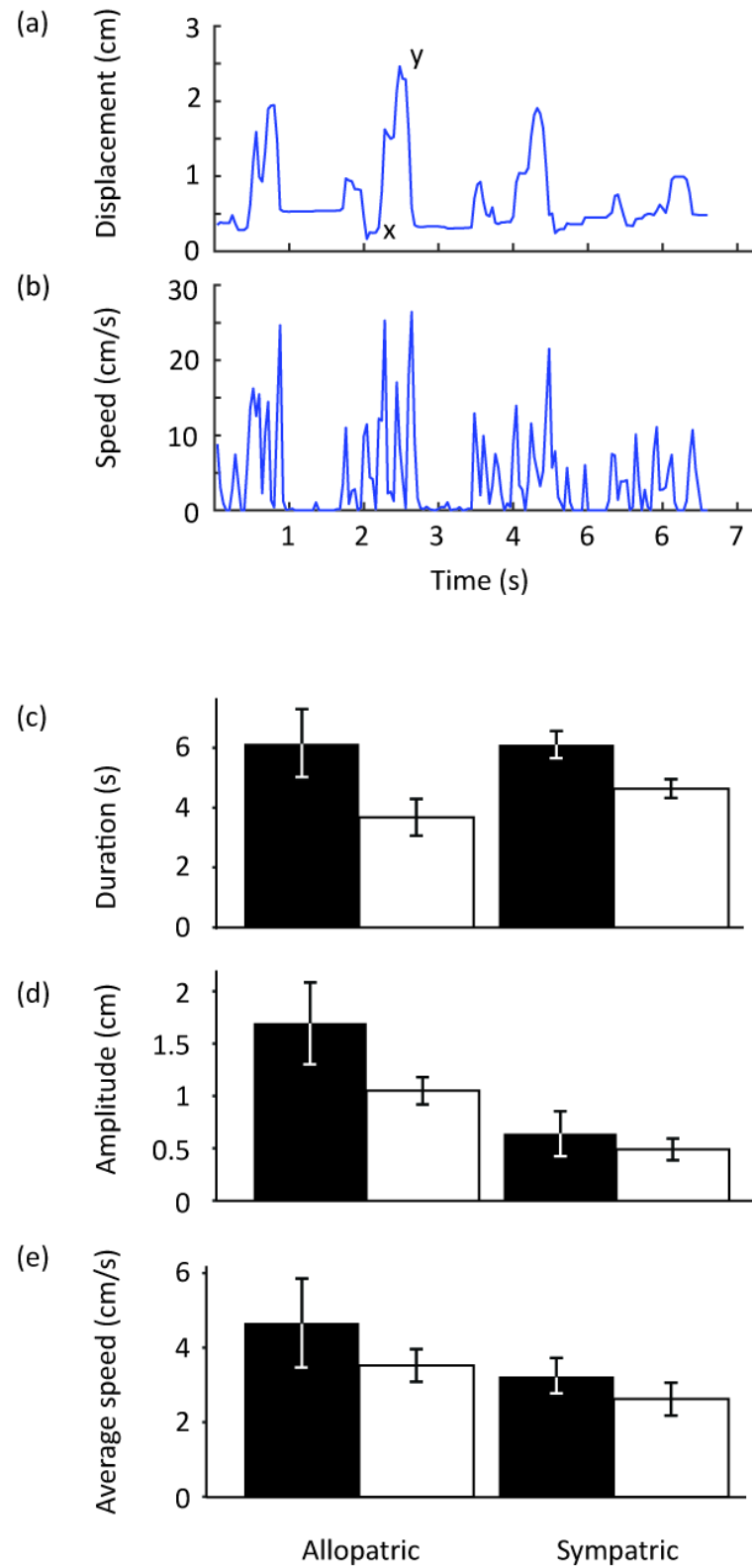
Figure 2.3 Structure of territorial display for adult males of *Microlophus occipitalis* on sympatric and allopatric populations.

Results

Biotic and abiotic factors

Encounter rate

I registered 308 lizards across our study sites, although the number of individuals observed varied between species and populations (Table 2.2). Overall, *Microlophus occipitalis* (n=246) was more abundant than *M. peruvianus* (n=62) across all populations (χ^2=35.8, df = 1, p<0.001). However, a higher number of individuals for *M. occipitalis* were registered in allopatry compared with parapatry (z=3.654, p=0.0003) and sympatry (z=2.090, p=0.0366). Additionally, females of *M. occipitalis* in allopatry were relatively more abundant than in parapatry (z=4.058, p<0.001) and sympatry (z=-3.070, p=0.0021). The number of *M. peruvianus* did not differ significantly across populations.

Table 2.2 Encounter rates of adult and juvenile mainland Ecuadorian lava lizards' populations across sampled sites.

Locality	Distribution	M. occipitalis			M. peruvianus		
		Male	Female	Juvenile	Male	Female	Juvenile
Los Frailes	Allopatric	16	27	51	N/A	N/A	N/A
Cerro Alto	Allopatric	13	15	9	N/A	N/A	N/A
Ancón	Allopatric	N/A	N/A	N/A	4	11	0
Chanduy	Parapatric	19	10	11	3	7	7
El Pelado	Sympatric	11	13	8	2	8	1
"Península de Santa Elena"	Sympatric	16	20	7	4	14	1
	Total	75	85	86	13	40	9

Habitat structure

Variation among sites in substrate and vegetation composition were considered using NMDS, whereby two-dimensional ordinations were enough to achieve low levels of stress for both measures of habitat structure (stress values of 0.00009 and 0.07098 for substrate and vegetation respectively). The NMDS plot for substrate composition showed that cliff and sand was negatively correlated with NMDS1, while ground and leaf litter was positively correlated. In the case of NMDS2, only rock showed a positive correlation. The ordination partitioned the study sites in five groups with a high degree of dissimilarity between them (ANOSIM: r=0.2912, p value= 0.03). The allopatric sites for *M. occipitalis* were represented by the presence of ground and sand, while cliff was characteristic for *M. peruvianus* (Figure 2.4a). The parapatric sites were outlined by the presence of rock, whereas sympatric sites had mostly leaf litter (Figure 2.4a).

The NMDS plot for vegetation composition showed a positive correlation for shrub, woody plant, and cactus for NMDS1 (Figure 2.4b). While for NMDS2, ground cover and grass were positively correlated, and herbs and forbs negatively correlated. The ordination plot outlined significant vegetation composition dissimilarities along the different competition levels (ANOSIM: r=0.5802, p value=0.002). Where allopatric sites for *M. occipitalis* were characteristic for the presence of shrubs, herbs and forbs, woody plants, and cactus (Figure 2.4b). Whereas allopatric sites for *M. peruvianus* were characterized for the absence of vegetation. In the case of sympatric and parapatric sites, the presence of grass and ground cover was outlined (Figure 2.4b).

(a)

(b)
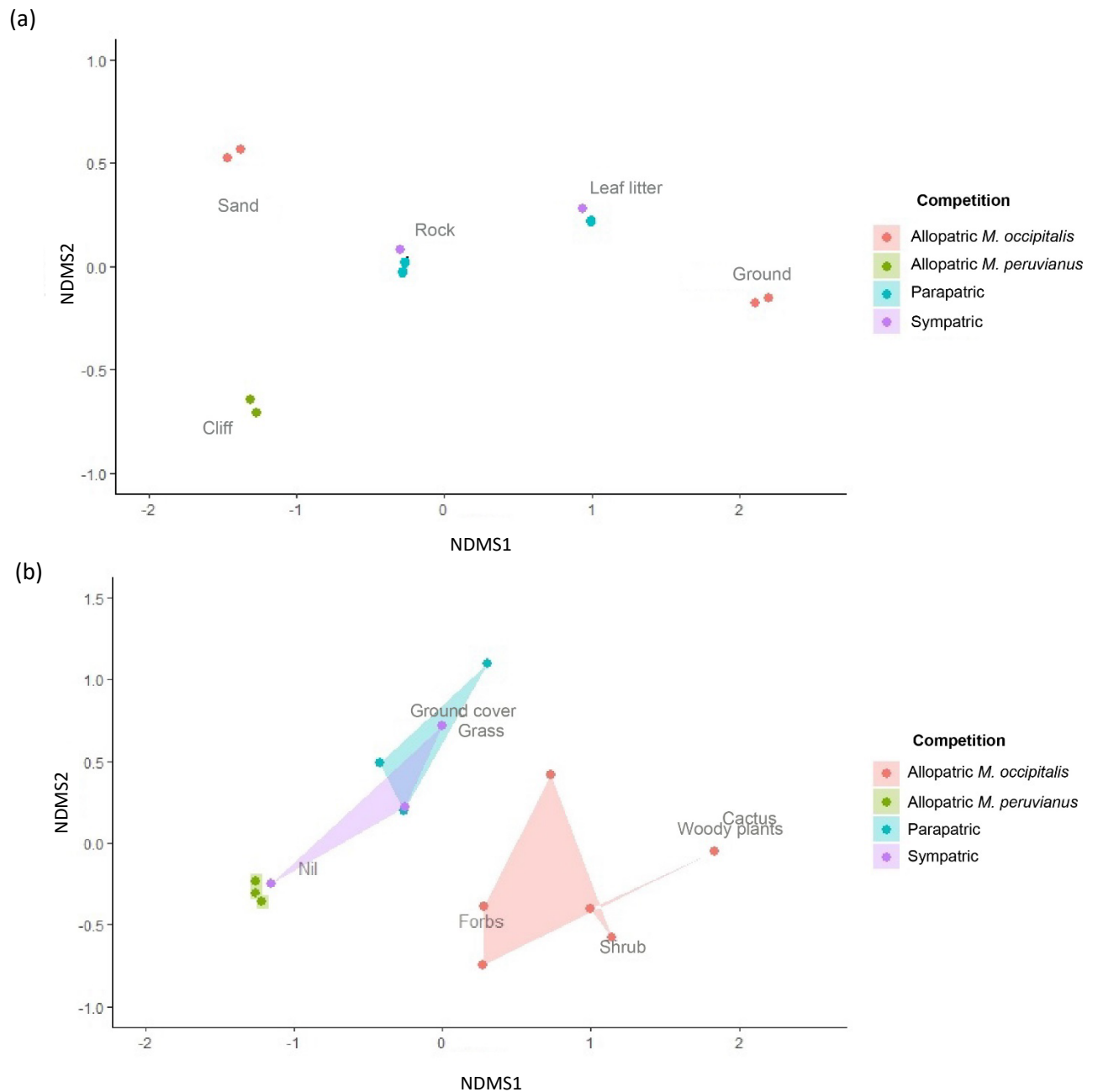
Figure 2.4 Non- metric multidimensional scaling (NMDS) analysis for (a) substrate and vegetation (b) composition on each sampled site.

Morphology

The snout-vent length of *M. occipitalis* lizards across sympatric and allopatric populations is presented in Table 2.3. Male lizards were significantly larger than females ($F_{1,48}$=77.56, p<0.001), but individuals from sympatric and allopatric populations did not differ significantly in snout-vent length ($F_{1,48}$=0.28, p=0.601). Principal component analysis for the full set of morphological measurements, utilising residuals obtained from linear regression with snout-vent length, resulted

in two components that explained ~36% of the total morphological variation between sympatric

and allopatric populations, while the third component explained 10% of the variation.

The first component correlated negatively with residuals of limbs and head (Table 2.4). A

two-way ANOVA showed significant differences between populations ($F_{1,48}$=14.20, p=0.001) and

sex ($F_{1,48}$=9.73, p = 0.003), but not for their interaction ($F_{1,48}$=0.25, p = 0.623). This suggest that

individuals in sympatry are characterized by shorter limbs and smaller heads than individuals in

allopatry (Figure 2.5a). The second component correlated negatively with residuals of body

height, body width and mass (Table 2.4), and a two-way ANOVA indicated that sympatric and

allopatric populations significantly differ ($F_{1,48}$=10.69, p<0.001; Figure 2.5b). This may imply that

individuals in sympatry have flat and narrow bodies generally smaller than those in allopatry. The

third component showed high positive loadings for residual total tail length and low jaw length,

and negative for residual interlimb (Table 2.4). The analysis of variance revealed significant

differences between populations ($F_{1,48}$=4.10, p=0.0489), indicating that sympatric individuals

present longer tails and long jaws, but shorter inter-limb measurements (Figure 2.5c).

Table 2.4 PCA results for *Microlophus occipitalis* morphological variables. Eigen values > 1 indicate the variance explained by its associated eigenvector. % Variance indicates the variance accounted for by each component to the total variance in all the variables.

	Factor 1	Factor 2	Factor 3
Eigenvalue	*5.41*	*2.13*	*1.95*
% Variance	*24.29*	*11.61*	*10.27*
Residual mass	-0.20833	**-0.44805**	0.13372
Residual tail length	-0.16902	-0.20841	**0.34129**
Residual head length	**-0.33717**	0.02293	0.1524
Residual head width	-0.26975	0.06364	**-0.28667**
Residual head height	-0.21982	0.07266	**-0.27912**
Residual lower jaw length	-0.08828	-0.28417	**0.33112**
Residual interlimb	0.02106	-0.29006	**-0.53299**
Residual body width	0.02271	**-0.50343**	-0.00023

Table 2.4 (continuation)

	Factor 1	Factor 2	Factor 3
Residual body height	-0.24548	**-0.33825**	-0.18319
Residual femur length	-0.12950	-0.08714	**0.18037**
Residual tibia length	**-0.28786**	-0.08629	0.16951
Residual metatarsus length	**-0.32683**	0.25537	-0.09406
Residual longest toe length (hind foot)	**-0.32061**	0.03139	0.27224
Residual humerus length	**-0.31554**	0.26255	-0.12402
Residual radius length	-0.12043	-0.07035	**-0.29448**
Residual metacarpus length	**-0.27387**	0.23559	-0.06333
Residual longest toe length (fore foot)	**-0.35484**	-0.05078	0.07314
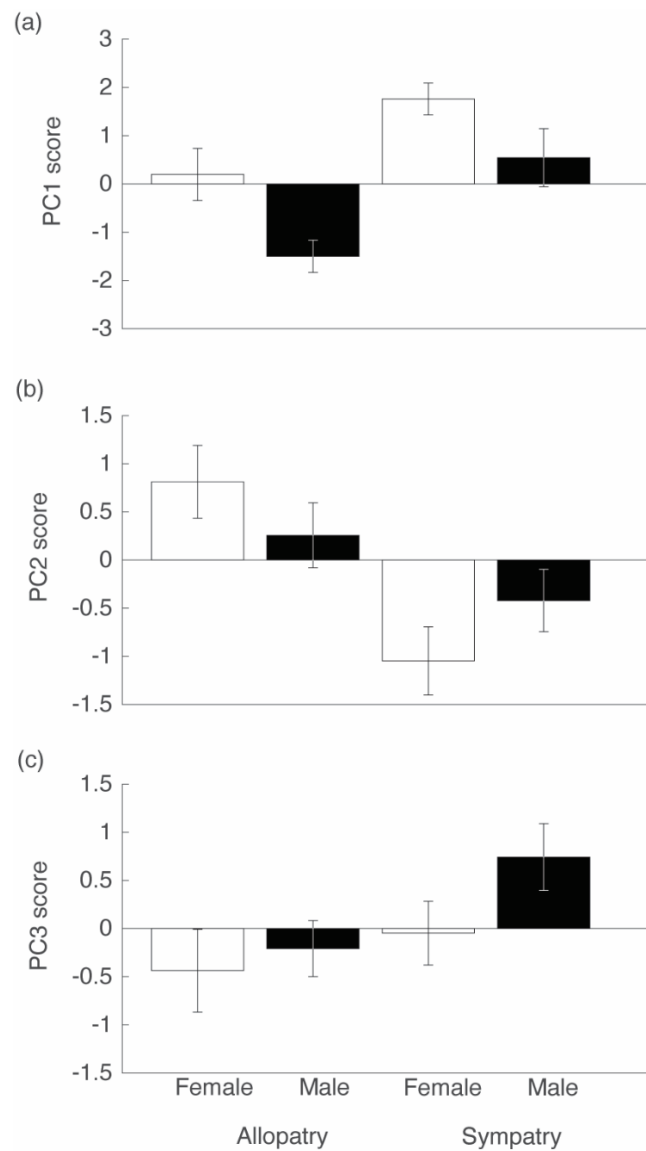
Figure 2.5 Principal component analysis scores for males and females in sympatric and allopatric populations for *Microlophus occipitalis*. PC1 outlined small heads and limbs, PC2 outlined low mass and small bodies, and PC3 outlined long tails and jaws, but short inter-limbs.

Behavioural observations

Weather conditions

There was variation in air temperature within and between sessions across the six study sites. To summarise this variability, I computed the starting point (intercept) and change over time (slope) for each lizard and present these as scatter plots in Figure 2.6. I used Hotelling's two-sample $T2$ tests to determine whether these distributions differ across levels of inter-species competition (Table 2.5). Pairwise contrasts suggest that air temperature was mostly similar across sites, with the exception of allopatric and parapatric sites in the morning (Figure 2.6, Table 2.5.
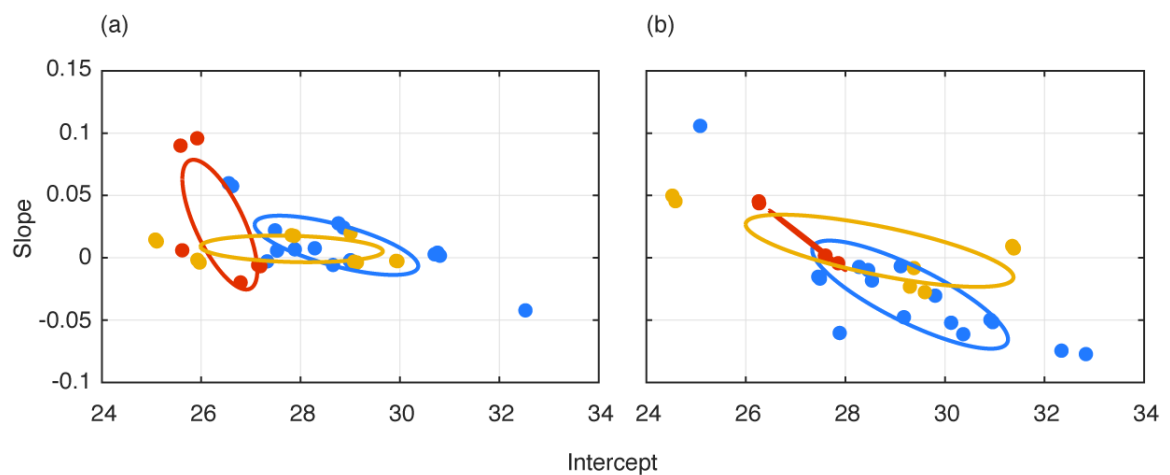
Figure 2.6 Weather variation for air temperature across sampled sites in the (a) morning and (b) afternoon. Data points represent the intercept (starting temperature) and slope (change over time) from linear regressions (see text for details), with distributions summarised using standard ellipses, for allopatric (blue), sympatric (yellow) and parapatric (orange) populations.

Table 2.5 Results of Hotelling's $T2$ analysis of air temperature between different levels of interspecific competition in the morning (AM) and afternoon (PM).

	AM		PM	
Contrast	*Hotelling's T*	*p-value*	*Hotelling's T*	*p-value*
Allopatric v Parapatric	**11.2795**	**0.0136**	5.8615	0.0870
Allopatric v Sympatric	3.3519	0.2184	5.7737	0.0866
Sympatric v Parapatric	3.6732	0.2122	1.6144	0.4995

Behavioural observations

A summary of results from focal sampling covering all behaviours is provided in Table S2.2. From these, I selected a subset for further analysis that represent four broad behavioural categories: thermal (basking, shade sites), active (foraging, walking), vigilance (scan high, scan low) and social (territorial, push-up/head-bob displays and inter-specific interactions) behaviours. Beta regression models were used to compare the proportion of time engaged in each behaviour as a function of competition, species, and sex. These were undertaken separately for morning and afternoon sessions and the outcomes are summarised in Tables 2.6 and 2.7, respectively.

Variation in thermal behaviours were limited to sex differences in basking during the morning (Table 2.6), with females spending more time basking (Figure 2.7a), and species differences in time spent in the shade in the afternoon (Table 2.7), with *M. peruvianus* spending more time in the shade (Figure 2.8a). Active behaviours varied along the day for both species. In the morning, time spent walking did not vary, but foraging varied as a function of species, competition, and sex (Table 2.6). Focusing on contrasts between levels of competition within species and sex (Figure 2.7b), I found that *M. peruvianus* males in allopatry forage longer than those in sympatry (z=2.168, p=0.030) and parapatry (z=2.016, p=0.044). In addition, sympatric *M. occipitalis* females spent more time foraging than allopatric and parapatric ones (z= -2.875, p=0.004; z=4.097, p<0.001, respectively). Also, allopatric females foraged more than those in parapatry too (z=2.308, p=0.021). Lastly, females of *M. peruvianus* in parapatry foraged more than in sympatry (z=-2.902, p= 0.004).

Table 2.6 ANOVA results for the focal sampling behaviours during morning sessions of observation for adult *Microlophus occipitalis* and *M. peruvianus*.

	ANOVA	One Factor			Two factors			Three factors
		Species	*Competition*	*Sex*	*Species * Competition*	*Species * Sex*	*Competition * Sex*	*Species * Competition *Sex*
Thermal Behaviour								
Basking	F	2.923	1.402	**11.642**	1.636	0.616	2.165	1.638
	p	0.087	0.246	**0.001**	0.195	0.433	0.115	0.194
Shade sites	F	0.116	2.176	0.864	0.175	0.956	0.859	0.039
	p	0.733	0.114	0.353	0.839	0.328	0.424	0.962
Active Behaviour								
Forage	F	1.820	0.233	0.157	**11.404**	0.042	1.908	**6.288**
	p	0.177	0.792	0.692	**<.0001**	0.838	0.148	**0.002**
Walk	F	1.666	1.636	0.209	1.795	0.013	0.748	0.054
	p	0.197	0.195	0.648	0.166	0.910	0.473	0.947
Vigilance Behaviour								
Scan High	F	0.271	1.320	0.876	0.709	1.684	0.612	2.666
	p	0.603	0.267	0.349	0.492	0.194	0.542	0.070
Scan Low	F	0.152	0.685	2.619	0.132	0.801	0.243	0.184
	p	0.697	0.504	0.106	0.876	0.371	0.785	0.832
Social Behaviour								
Territorial	F	**4.632**	**3.195**	**6.267**	0.845	1.085	**4.086**	0.081
	p	**0.031**	**0.041**	**0.012**	0.430	0.430	**0.017**	0.446
Display (Push ups and Head bobs)	F	**7.007**	0.112	**4.696**	0.054	0.086	1.149	0.774
	p	**0.008**	0.894	**0.030**	0.948	0.769	0.317	0.461
Social interactions	F	2.642	0.019	3.186	1.477	2.010	0.612	0.965
	p	0.104	0.981	0.074	0.228	0.156	0.543	0.381

Table 2.7 ANOVA results for the focal sampling behaviours during afternoon sessions of observation for adult *Microlophus occipitalis* and *M. peruvianus.*

.	ANOVA	One factor			Two factors			Three factors
		Species	*Competition*	*Sex*	*Species * Competition*	*Species * Sex*	*Competition * Sex*	*Species * Competition* Sex*
Thermal Behaviour								
Basking	F	0.094	0.678	2.267	1.798	0.005	0.734	0.889
	p	0.759	0.508	0.132	0.166	0.942	0.480	0.411
Shade sites	F	**6.110**	0.454	0.243	0.647	0.278	0.116	0.072
	p	**0.013**	0.635	0.622	0.524	0.598	0.891	0.930
Active Behaviour								
Forage	F	3.464	2.332	1.013	**5.427**	0.759	**3.320**	**5.030**
	p	0.063	0.097	0.314	**0.004**	0.384	**0.036**	**0.007**
Walk	F	**4.65**	**3.823**	3.114	0.079	**9.066**	0.542	**6.300**
	p	**0.031**	**0.022**	0.078	0.924	**0.003**	0.581	**0.002**
Vigilance Behaviour								
Scan High	F	**4.893**	0.667	1.799	0.078	1.348	**3.849**	**5.458**
	p	**0.027**	0.513	0.180	0.925	0.246	**0.021**	**0.004**
Scan Low	F	0.254	1.175	1.170	1.976	0.003	0.508	0.195
	p	0.615	0.309	0.279	0.139	0.957	0.601	0.823
Social Behaviour								
Territorial	F	0.694	0.991	1.059	2.021	0.941	0.009	0.023
	p	0.405	0.371	0.304	0.133	0.332	0.991	0.978
Display (Push ups and Head bobs)	F	0.537	0.430	3.634	0.061	0.035	0.653	0.502
	p	0.464	0.651	0.057	0.941	0.851	0.520	0.606
Social interactions	F	0.425	2.396	**7.480**	0.774	0.018	1.781	0.150
	p	0.515	0.091	**0.006**	0.461	0.892	0.169	0.861
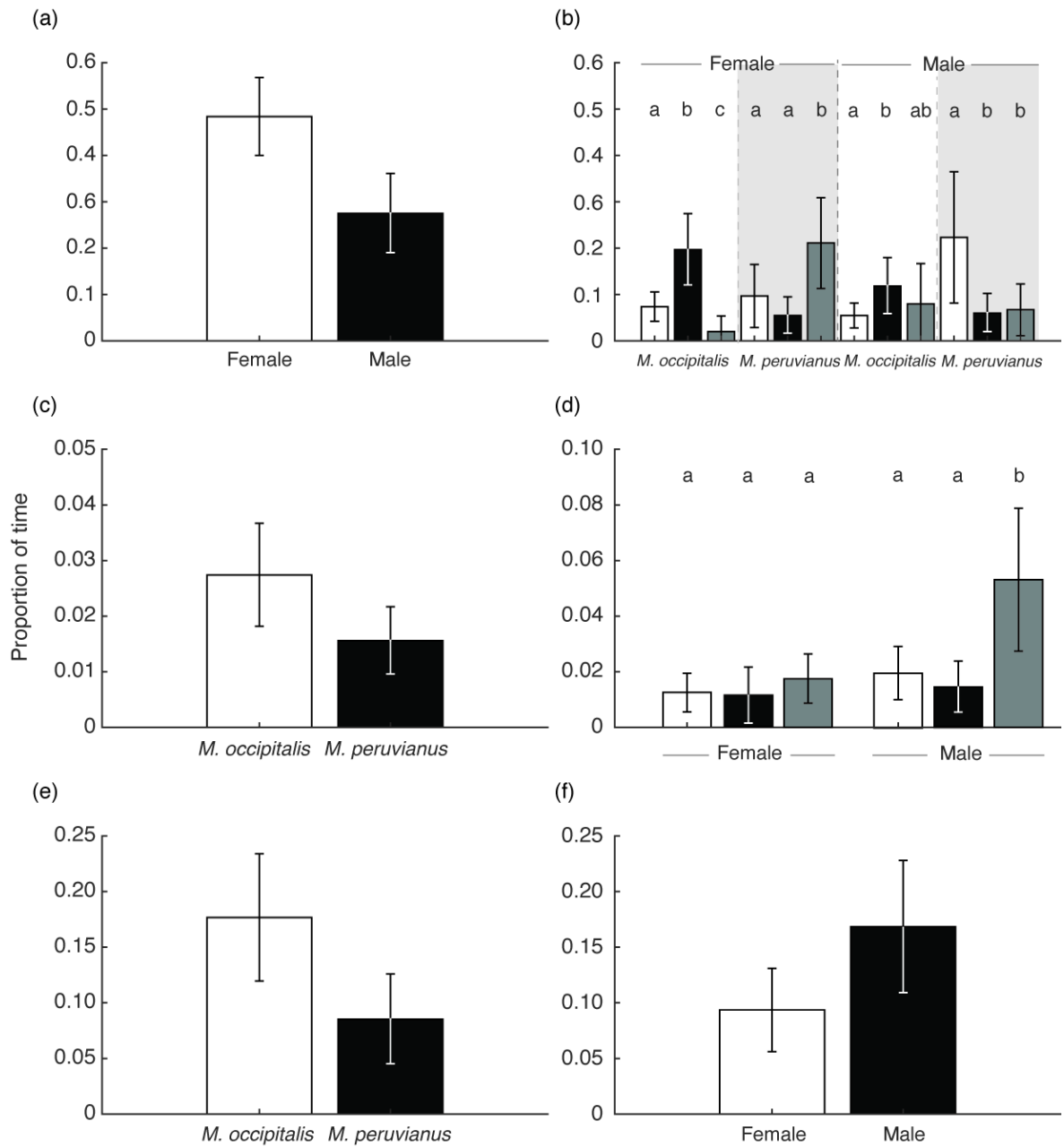
Figure 2.7 Predicted values from beta-regressions of morning sessions for (a) basking, (b) foraging, (c) territorial by species, (d) territorial by competition and sex, (e) display by species, and (f) display by sex. Levels of competition in (b) and (d) are represented by allopatry (white), sympatry (black) and parapatry (grey). Letters above bars indicate pairwise differences between levels of competition within species and sex (b) and within sex (d).
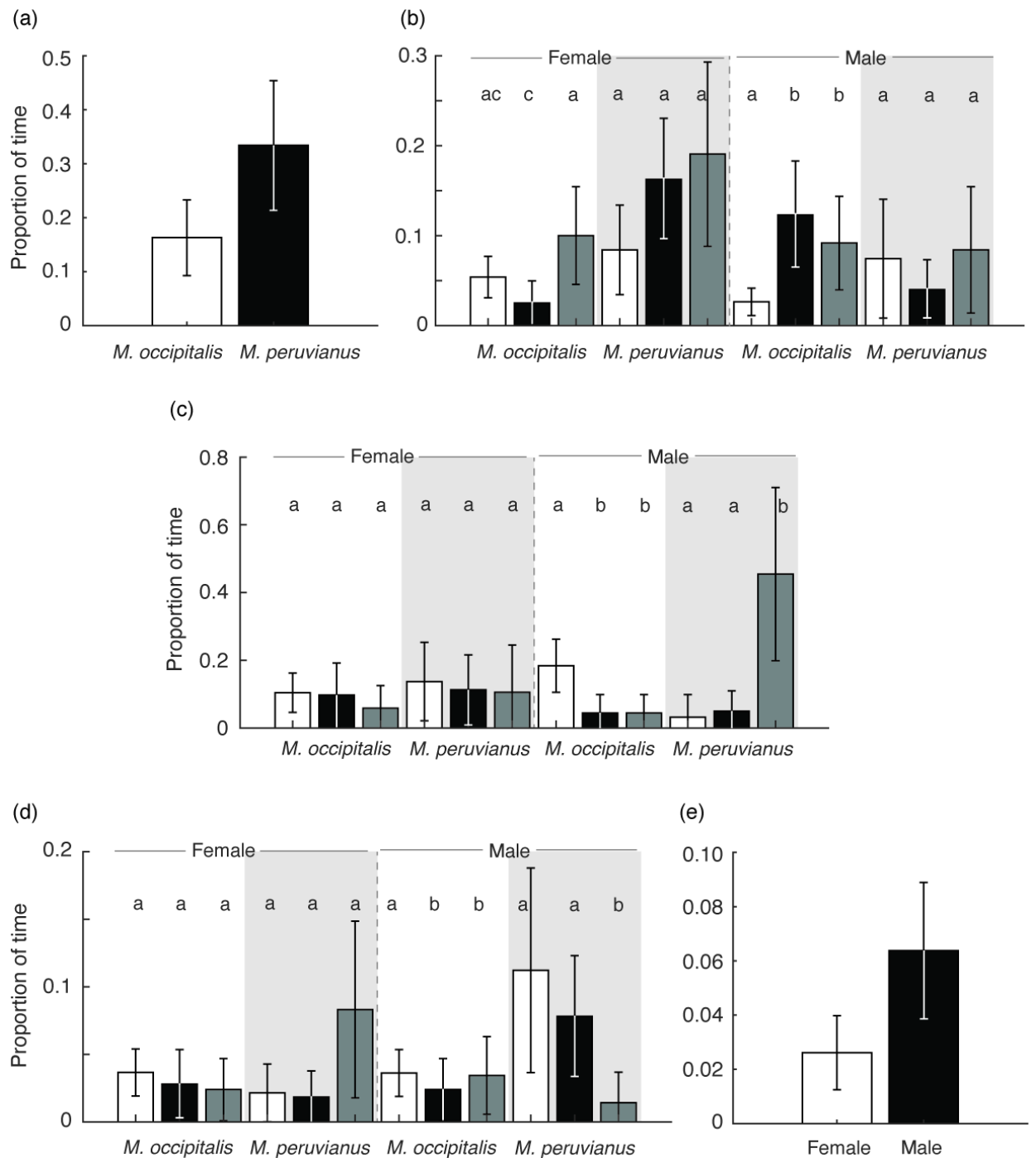
Figure 2.8 Predicted values from beta-regressions of afternoon sessions for (a) shade, (b) walk, (c) forage, (d) scan high, and (e) social interactions. Levels of competition in (b)-(d) are represented by allopatry (white), sympatry (black) and parapatry (grey). Letters above bars indicate pairwise differences between levels of competition within species and sex (b)-(d).

During the afternoon, both active behaviours (walk and forage) varied as a function of

species, competition, and sex (Table 2.7). Focusing again on contrasts between levels of

competition within species and sex (Figure 2.8b, c), *M. occipitalis* males in sympatry and parapatry walked more than in allopatry (z=-3.079, p=0.0021; z=-2.377, p=0.0174, respectively), whereas females walked less in sympatry compared to parapatry (z=-2.095, p=0.0362). For *M. peruvianus*, females walk more than males in sympatry (z=3.190, p=0.0014), yet the comparisons between populations were not statistically significant. On the other hand, foraging for females of both species was equivalent in the afternoon, while *M. occipitalis* males in allopatry foraged for longer than those in sympatry and parapatry (both contrasts: z=2.918, p=0.004). Finally, males of *M. peruvianus* in parapatry foraged more than those in allopatry and sympatry (z=3.155, p=0.002; z=3.016, p=0.003, respectively).

Scanning at low levels did not vary during the morning or afternoon, while scanning high varied as a function of species, competition, and sex during the afternoon only. Once again considering only contrasts between levels of competition within species and sex (Figure 2.8d), females of *M. peruvianus* allocated more time to high-level scanning in parapatry than females in each of the other two groups, although these differences did not reach significance. For males of *M. peruvianus,* both allopatric and sympatric lizards spent more time scanning high than parapatric lizards (z=2.435, p=0.015; z=2.500, p=0.012, respectively), but also more than its congers' males (z=-2.116, p=0,034).

Variation also occurred for social behaviours. Both territorial behaviour and displays varied due to species in the morning, with *M. occipitalis* showing higher proportions in each case (Figure 2.7c, d, e, f). Also, males display more than females (Figure 2.7f), while sex also interacted with competition for territorial behaviour (Figure 2.7d). Here, females were found to be equivalent, while the contrasts comparing competition collapsed across species for males revealed parapatric lizards spend more time than the other two (allopatry, z=-2.771, p=0.006; sympatry, z=-2.577, p=0.010; respectively). Finally, no difference on the time spent on intraspecific interactions were found in the morning, while in the afternoon males spent more

time interacting than the females regardless of species (z=-2.735, p=0.006) (Table 2.7; Figure 2.8e).

Microhabitat use and substrate height varied between species across levels of interspecific competition. Results from beta regression analyses showed a competition and species effect for ground, rock, and vegetation use (Table 2.8). Figure 2.9 shows a shift for *M. occipitalis* from the ground in allopatry to using vegetation in sympatry, while *M. peruvianus* showed greater use of rocks in allopatry but ground in sympatry (see also Table S2.4). The height above the substrate for the different behaviours is shown in Table S2.3. A significant species and competition effect was found for displays (push ups and head bobs), basking, foraging and walk behaviours (Table 2.9, Table S2.5). For display behaviour in *M. occipitalis*, males tend to use lower substrates in allopatry than sympatry and parapatry (Figure 2.10d). Meanwhile *M. peruvianus* males recorded an opposite trend from high substrates in allopatry to lower substrates in sympatry (Figure 2.10d). In the case of basking, walk and foraging behaviours, *M. occipitalis* uses higher perches in sympatry than allopatry, whereas *M. peruvianus* exhibit an inverse trend (Figure 2.10a, b, c, respectively).

Table 2.8 Microhabitat selection intraspecific variation between single and mixed populations of mainland lava Ecuadorian lava lizards.

| | One factor | | | | | | Two factors | | | | | | Three factors | |
| | *Species* | | *Competition* | | *Sex* | | *Species* *Competition* | | *Species*Sex* | | *Competition* *Sex* | | *Species* *Competition* *Sex* | |
	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Ground	7.70	0.006	6.57	0.001	0.33	0.563	22.79	<.001	4.01	0.045	0.40	0.671	2.26	0.104
Rock	8.23	0.004	5.38	0.005	0.00	0.983	3.92	0.011	0.08	0.778	0.89	0.410	0.47	0.628
Veg	34.54	< 0.001	8.86	<0.001	0.46	0.497	6.19	0.002	1.72	0.189	0.79	0.455	0.47	0.624
Other	6.35	0.012	1.76	0.172	0.00	0.974	1.76	0.172	0.00	0.974	0.33	0.721	0.33	0.721

Table 2.9 Microhabitat height preferences when engaging a behaviour across Ecuadorian mainland lava lizard levels of competition.

		One Factor			Two factors
	ANOVA	*Intercept*	Species	*Competition*	*Species * Competition*
Display (Push ups and Head bobs) +	F	**16.985**	**7.119**	0.530	**5.698**
	p-value	**<0.0001**	**0.019**	0.601	**0.017**
Basking	F	**50.757**	**7.763**	1.604	**7.416**
	p-value	**<0.0001**	**0.011**	0.223	**0.003**
Forage (males)+	F	2.114	0.109	0.965	**3.994**
	p-value	0.151	0.747	0.411	**0.050**
Forage (females)	F	2.682	4.706	0.289	**17.395**
	p-value	0.105	0.053	0.602	**0.002**
Walk	F	**47.017**	**6.171**	0.576	**3.570**
	p-value	**<0.0001**	**0.020**	0.570	**0.043**

+Behaviours mainly observed in males.
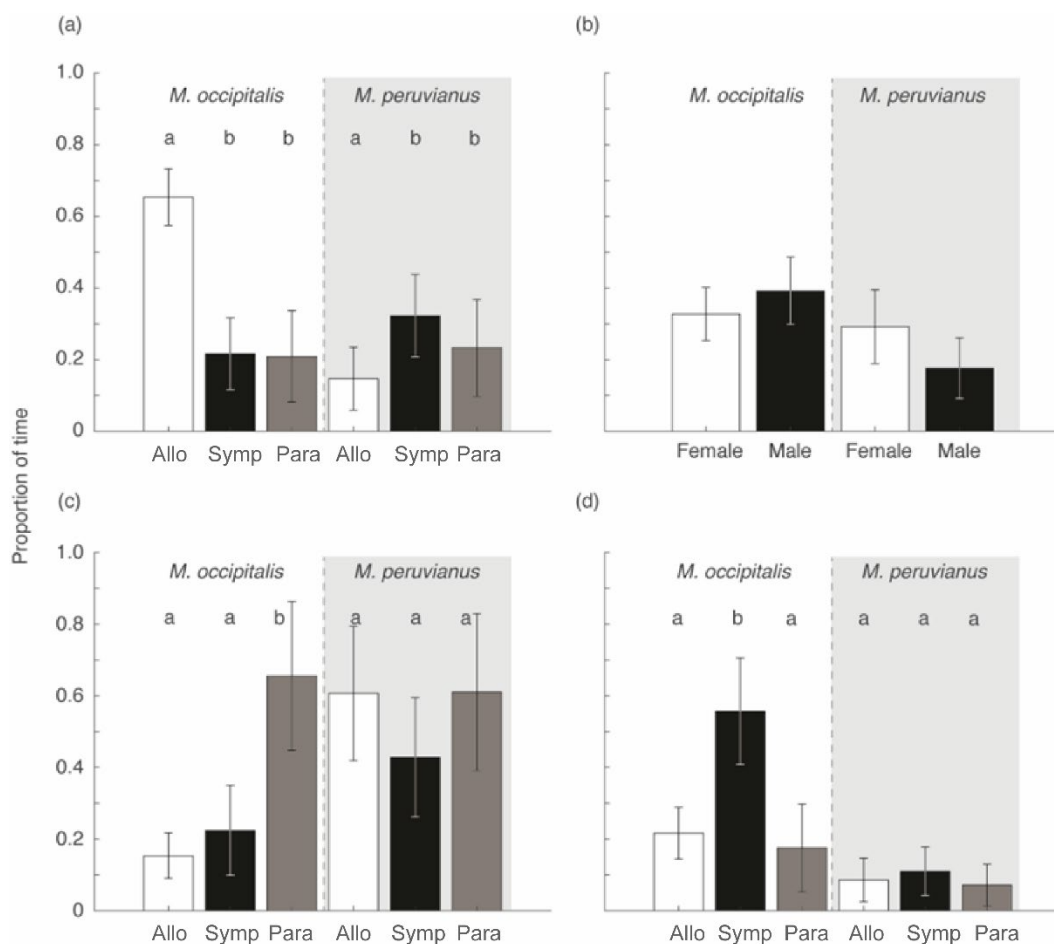
Figure 2.9 Predicted values from beta-regressions of time spent on (a) ground by competition and species effect, (b) ground by sex and species effect, (c) rock and (d) vegetation by competition and species effect. Levels of competition are represented by allopatry (white), sympatry (black) and parapatry (grey). Letters above bars indicate pairwise differences between levels of competition within species (a)-(c-d).
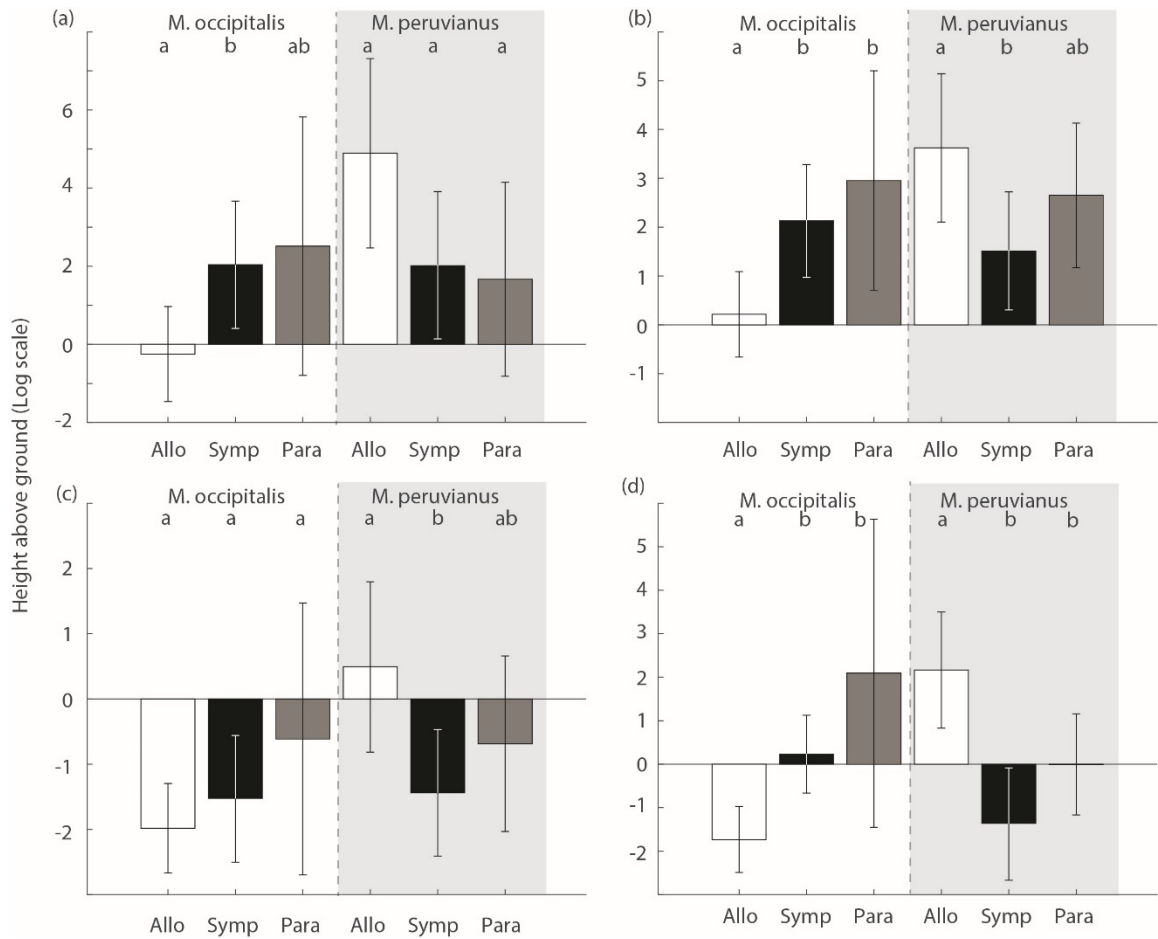
Figure 2.10 Behavioural height preferences for (a) display (males only), (b) basking, (c) walk, and (d) foraging. Levels of competition are represented by allopatry (white), sympatry (black) and parapatry (grey). Letters above bars indicate pairwise differences between levels of competition within species (b)-(e).

Structure of territorial displays

The displays of *M. occipitalis* filmed at sympatric and allopatric populations matched the broad

descriptions of Carpenter (1966). LME models were used to compare the duration, maximum

amplitude, and average speed for two display bouts between the sympatric and allopatric

populations of *M. occipitalis*. The duration of display bouts is shown in Figure 2.3c and were found

to be equivalent across sites ($F_{1,8}$=4.408, p=0.069) and bouts ($F_{1,9}$=2.961, p=0.119). The maximum

amplitudes achieved are shown in Figure 2.3d and were significantly higher for allopatric males

($F_{1,8}$=8.708, p=0.018) but did not differ between bouts ($F_{1,9}$=2.079, p=0.183). Finally, display

average speeds are shown in Figure 2.3e. Although allopatric male displays were generally faster,

the difference was not significant ($F_{1,8}$=1.8156, p=0.2158). However, the first bout was significantly faster than the second one regardless of location ($F_{1,9}$=7.624, p=0.022).

Discussion

Interspecific competition is a major determinant of resource partitioning along multiple ecological niche dimensions (Bergeron & Blouin-Demers, 2020; Goodman, 2007). I studied the effect of interspecific competition along the time and spatial dimensions of two lizard species distributed along the Ecuadorian west coast. My objective was to identify evidence suggesting one or both species shift their ecological niche to minimise competitive pressures. *Microlophus occipitalis* and *M. peruvianus* are closely related and ecologically similar (Benavides et al., 2007; Rowe et al., 2019), so it is not surprising that my results are consistent with the notion of variation due to interspecies competition. Specifically, I identified differences between levels of competition in terms of abundance, behaviour, including display structure, microhabitat use and morphology. I designed my project to sample two levels of competition (allopatry and sympatry), so it was surprising to discover that one of the planned allopatric sites was actually supporting parapatric populations of both species. This was quite unexpected and worthy of further consideration, but it complicated the analysis and interpretation of results. Consequently, in considering the role of interspecific competition below I focus on differences between allopatric and sympatric populations that more clearly delineates my points of interest.

Relative abundance and habitat

Encounter rate differed across competition levels for both species and are consistent with higher relative abundance in allopatric populations. Yet relative abundances of *M. peruvianus* observed in my study was low compared with previous studies (Perez & Balta, 2007), regardless of the competition level. Thus, only *M. occipitalis* registered a significant decrease in their relative abundance in sympatry. Various studies have shown that when closely related species live in sympatry, competition for similar resources is common and will negatively impact fitness

(Bergeron & Blouin-Demers, 2020; Dietrich & Wehner, 2003). As *M. occipitalis* and *M. peruvianus* are closely related (Benavides et al., 2007) it was expected that competition pressure has played an important role in the formation of community structures and therefore would support fewer individuals.

Lower encounter rates of *M. occipitalis* in sympatry may also reflect habitat preferences of the species. Habitat structure differed between population-type exposing both species to different ecological scenarios. Species-specific responses to local environmental conditions by three lacertid sympatric species are argued to have resulted in variation in population density, such that species occur in higher densities in certain habitats that fulfill their ecological preferences (Maura et al., 2011). Although both species in my study overlap in coastal localities, *M. occipitalis* occurs in mostly vegetated areas with a high percentage of shrubs and trees, dried forests, sandy beaches, and disturbed habitats (Chávez-Villavicencio et al., 2018; Rowe et al., 2019). Conversely, *M. peruvianus* seems to prefer deserted areas, sandy beaches, cliffs, pebbles, and other near shore structures (Catenazzi et al., 2005). Consequently, the change in abundance from allopatric to sympatric sites for *M. occipitalis* could be a response to a more suitable environment in allopatry, where there is a high availability of vegetation (forbs, shrubs, woody plants, and cactus). Formal investigations into population density, factoring in habitat characteristics are required to distinguish between these competing explanations.

Effects of competition on behaviour

Competitive pressures often have harmful impact on individual's fitness. To minimise this, potentially competing species tend to partition their resource use on at least one ecological niche dimension: temporal, spatial, and diet (Bergeron & Blouin-Demers, 2020; Pianka, 1973; Schoener, 1974a). Combining beta regressions across all populations, I found that both species may partition their behavioural repertoire when sharing resources in two ways: by allocating different

proportions of time to specific behaviours (temporal partitioning), by differential use of microhabitats (spatial variation).

Temporal partitioning

Microlophus occipitalis and *M. peruvianus* differ along the temporal niche dimension when comparing single with mixed populations. Major differences were observed on the proportions of time for foraging, walk, and scan high behaviours when both species co-occur. Overall, foraging activity patterns exhibit greater variation across competition levels; individuals of both species reduced their foraging activity when the other species was foraging, which might reflect efforts to avoid intrasexual interspecific interactions. During the morning, *M. peruvianus* sympatric individuals spent less time foraging when individuals of the same sex of *M. occipitalis* increased its foraging activity. Along with these changes an increase in walking behaviour during the afternoon was observed mostly by *M. peruvianu*s females in sympatry, possibly as a consequence of the reduction in foraging time. Taken together, the presence of both species might be having an impact on the available resources. Often when ecologically similar species come into contact, drastic reductions in resource densities can occur leading to variations in foraging strategies and diet (Eifler & Eifler, 1999; Mitchell et al., 1990). Therefore, as both species are sit-and-wait foragers with a generalist diet (Chávez-Villavicencio et al., 2018; Quispitúpac & Pérez, 2008), it is likely that there is a significant overlap along the food axis resulting in increased interspecific competition. Optimal foraging theory states that species foraging decisions can be partially based on the resource availability, thus limiting the species foraging effort (Mitchell et al., 1990). Consequently, because both species avoid foraging in the presence of the other during the day, they exhibit an increase in foraging effort by walking more to find additional prey to fulfill their daily requirements and avoid competition (Eifler et al., 2007). Nevertheless, prey availability and diet composition analysis were not carried out during my study, and I consider they are necessary to understand the possible temporal variations occurring between the study species. As possible diet specializations could also be leading to foraging strategy differences in species.

Intraspecific variations in sympatry were also observed for scan high behaviour, as *M. peruvianus* males scanned more than females during the afternoon. Although, it is possible that this shift was influenced by the activity of *M. occipitalis* males, as they walked more during the same time in sympatry. Therefore, because of their ecological similarity, it is possible that an increase in the activity of a congener influenced the behaviour of the other species by either increasing or decreasing its frequency (Gordon et al., 2010). Consequently, *M. peruvianus* males may scan more to avoid accidental interspecific interactions that can be harmful and energetically costly (Kamath et al., 2013). On the other hand, relative abundance could also trigger this kind of increase on both behaviours combined with the breeding season. Overall, because *M. occipitalis* has a higher relative abundance biased towards females, moving around is a behaviour that is usually used as a strategy to increase the mating chances and defend their territory (Watkins, 1998). In contrast, *M. peruvianus* populations were significantly smaller but with males almost twice the size of *M. occipitalis* males. This might cause males to increase their scanning effort not only to find a mate but also to avoid predation, as they may be easily detected by predators. In addition, their relatively small populations may limit the use of a collective detection system often observed in social species. Thus, increasing their vigilance enhances the safety of passive behaviours in order to assure their survival (Lanham & Bull, 2004). Nevertheless, my study did not analyse the effect of possible predators, other non- related species, and even human presence on both species' populations, which are relevant factors on species vigilant behaviours. Although there is still much to learn, my study introduces a system that could help us to understand social behaviour in closely related species.

Spatial variation

Both species showed differences in the use of microhabitats between allopatric and sympatric populations. *Microlophus occipitalis* shifted from the use of ground in allopatry to rocks and vegetation in sympatry, while *M. peruvianus* used mostly rocks in allopatry but ground in sympatry. It is tempting to consider this a result of interspecies competition, and I encourage

future research to explore this possibility. However, my results might simply reflect the microhabitat preferences of each species whereby *M. peruvianus* is associated with sparsely vegetated areas while *M. occipitalis* prefers highly vegetated habitats (Catenazzi et al., 2005; Huey, 1974; Jordan & Perez, 2012; Péfaur & López-Tejeda, 1983; Rowe et al., 2019). Previous studies have shown that abiotic and biotic factors may affect species spatial distribution leading to differences in their preferences (Asbury & Adolph, 2007; Kamath et al., 2013; Ortega & Pérez-Mellado, 2016). Thus, suggesting that when individuals inhabit a modified environment, they appear to seek alternative microhabitats with similar physical and structural characteristics (Terán-Juárez et al., 2020). This capacity of shifting to new microhabitats is known as habitat plasticity and can have evolutionary consequences on species behaviour driving to physiological and morphological adaptations (Huey et al., 2003).

An apparent greater use of vegetation by *M. occipitalis* is consistent with observed differences in morphology. Smaller limbs and body size were characteristics of individuals in sympatric populations that make greater use of vegetation. Past studies claim that having short hind limbs and slender bodies may enhanced climbing performance on smooth surfaces by increasing the stability when placing the centre of gravity closer to the substrate (Herrel et al., 2001; Vanhooydonck et al., 2000). The biomechanical theory also predicts clear associations between habitat use and morphology as the physical demands influencing the locomotor system are distinct in different habitats (Herrel & Holanova, 2008; Herrel et al., 2001, 2002a; Huyghe et al., 2007). Fine-scale microhabitat structure analysis (e.g., perch diameter) is needed as such characteristics have an important role on the species morphology and the way they exploit a specific habitat (Catenazzi et al., 2005; Penalver-Alcazar et al., 2016; Toyama et al., 2019). Also, my data does not explore other biotic factors (e.g., predation, seasonal variation, parasites) that might be relevant in determining microhabitat use. Notwithstanding these suggestions for future work, my results still propose for the first time a possible morphological local adaptation to different habitat characteristics for mainland Ecuadorian populations of *M. occipitalis*, as they

corroborate previous biomechanical models for lizards found on vegetated habitats (Herrel, 2001;

Vanhooydonck et al., 2007).

In addition, the observed shift in microhabitat use between allopatric and sympatric

populations was likely the main reason I identified reliable height differences when engaging in

multiple behaviours. As *M. occipitalis* was observed basking, displaying (push up and head bob)

and foraging on higher perches, while *M. peruvianus* was closer to the ground in sympatry

compared with allopatry. However, previous studies of behavioural partitioning propose that

microhabitat selection to engage in a specific behaviour could be related to the use of optimal

sites that offer several benefits (e.g. avoid competition, improve their fitness, increase signal

propagation and raise survival rates) (Angilletta et al., 2009; Kamath et al., 2013). Therefore, it is

possible that both *Microlophus* species shift to use higher or lower perches as a strategy to avoid

competition (Edwards & Lailvaux, 2012; Thornton & Hodge, 2009), resulting from similar

ecological preferences and leading to a significant overlap on their spatial niche axis (Benavides et

al., 2007; Dias & Rocha, 2004; Edwards & Lailvaux, 2012). Consequently, segregation on their

spatial resource use may facilitate coexistence by exploiting different resources.

Variations in display structure: response to competition or environmental context?

Comprehensive analyses of the displays of *M. occipitalis* have not been undertaken since

Carpenter (1977). Here I show structural variations of the territorial display of *M. occipitalis* were

observed between allopatric and sympatric males, with lizards exhibiting significantly lower

display amplitude within sympatric populations. Prior research in *Anolis carolinensis* displays has

found temporal differences as a results of population density and habitat use variations (Bloch &

Irschick, 2006). My data suggested that the population density of *M. occipitalis* is greater in

allopatry, so differences in display structure might be attributable to intraspecific pressures more

than to interspecific competition. In addition, allopatric sites were more vegetated and thus

create a higher motion noise context for *M. occipitalis* males, necessitating an increase in display

amplitude to enhance signal transmission (Bian et al., 2021). My data in this context are informative, but I am unable to differentiate between the effect of inter-species competition and environmental context. Further work is needed including analyses of *M. peruvianus* displays, but this study system could prove to be quite useful in disentangling these effects.

Conclusion

Competition effects have been a major field of research in ecological studies of closely related species and has been tagged as a key factor for species niche partitioning (Genov et al., 2019; Gordon et al., 2010; Sagonas et al., 2017). Yet, understanding the forces underlying niche partitioning is a complex task as many interacting factors must be taken into account. In the case of the *Microlophus* group, previous studies have proposed high plasticity that allows them to exploit different microhabitats (Chávez-Villavicencio et al., 2018; Farina et al., 2008; Sepúlveda et al., 2008). However, the role of inter and intraspecific interactions has been relatively neglected thereby limiting our understanding of their ecological adaptations. My results propose that the coexistence of both species could influence their temporal and spatial niche axis in multiple ways. I have laid groundwork for further research on the myriad factors influencing the dynamics of sympatry in these species and propose this study system as a possible model to understand the mechanisms leading to behavioural partitioning in mainland lizard communities.

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Appendix

Table S2.1 Ethogram summary of lava lizards from the west Ecuadorian coast.

Behaviour	Definition
Walk	Forward movement of fore and hindlimbs on different substrates.
Basking	Individual positioned in the sun on different substrates, not displaying other behaviour.
Foraging	Looking for prey items or capturing them.
Shade sites	Individual position away from the sun, not displaying other behaviour.
Climb	Moving upwards in a vertical substrate.
Display	For the statistical analysis the head bobs and push ups behaviours were combined to avoid observer error.
Head bobs	Vertical up and down movement of an individual's head independent from the body. Motion repeated several times without a visual individual near.
Push ups	Vertical up and down movement of an individual's head accompanied with the flexion of hind limbs. Motion repeated several times without a visual individual near.
Tail movement	Ventral part of the body Up and down or looped movement of the tail.
Scan high level	Side to side head movement on a high substrate.
Scan low level	Side to side head movement on a low substrate.
Social interactions	Any interaction with an individual of the same species that could not be defined as feeding or predation.
Territorial	Display including a sequence of head bobs, push ups, persecution, intimidation, biting and aggressive attack from and individual to another regardless the sex.
Mating	Male and female engaging mating display.
Interaction with other species	Any interaction with an individual of the different species that could not be defined as feeding or predation.
Predation	An individual is captured and eaten.
Dig	Forward and back movements of forelimbs on the ground removing substrate.
Drinking	Using tong or snout to drink water from a small pond or water body.
Buried	Hide the whole body under soft soil or sand using the limbs and remains in the same place.
Out of sight (OoS)	Lost sight of observed individual

Table S2.2 – Observed behaviours for Ecuadorian lava lizards during focal sampling sessions. Values represent the mean time proportion per species and standard deviation (SD).

Behaviour	*M. occipitalis*		*M. peruvianus*	
	N	Proportion	N	Proportion
Basking	82	0.142 ± 0.152	44	0.204 ± 0.176
Shade sites	53	0.141 ± 0.153	33	0.157 ± 0.155
Foraging	59	0.071 ± 0.072	37	0.055 ± 0.076
Walk	60	0.057 ±0.047	41	0.076 ± 0.068
Scan high	32	0.045 ±0.052	15	0.055 ± 0.049
Scan low	27	0.039 ± 0.033	9	0.039 ± 0.033
Territorial	19	0.025 ± 0.024	8	0.057 ± 0.047
Display	94	0.075 ± 0.074	42	0.034 ± 0.031
Social interactions	42	0.043 ± 0.057	27	0.041 ± 0.042
Out of sight	20	0.155 ± 0.174	15	0.324 ± 0.325
Tail	17	0.028 ± 0.020	3	0.010 ± 0.000
Mating	3	0.017 ± 0.006	1	0.003 ± NA
Buried	8	0.279 ± 0.330	1	0.080 ± NA
Drinking	1	0.040 ± NA	NaN	NaN
Dig	2	0.025 ± 0.021	NaN	NaN
Climb	NaN	NaN	1	0.05 ± NA

Table S2.3 – Substrate height preferences for all the observed behaviours during focal sampling sessions. Values represent the time proportion per species and standard deviation (SD).

Behaviour	*M. occipitalis*	*M. peruvianus*
Basking	11.45 ± 18.75	64.38 ± 124.73
Shade sites	6.37 ± 13.81	4.81 ± 23.12
Foraging	4.93 ± 8.90	20.94 ± 38.77
Walk	3.83 ± 23.73	19.27 ± 74.10
Scan high	14.54 ± 11.87	117.24 ± 115.15
Scan low	0 ± 0	0 ± 0
Territorial	6.76 ± 7.53	242.08 ± 266.21
Head bobs	8.76 ± 13.62	34.06 ± 39.65
Push ups	11.70 ± 9.21	99.65 ± 149.18
Social interactions	4.74 ± 10.10	41.72 ± 79.36
Tail	0 ± 0	7.5 ± 10.61
Mating	0 ± 0	20 ± 0.00
Buried	0 ± 0	0 ± 0
Dig	0 ± 0	NaN
Out of sight	NaN	NaN

Table S2.4– Pairwise comparisons for substrate use (see Figure 2.9)

	GROUND		ROCK		VEGETATION	
	z score	p-value	z score	p-value	z score	p-value
M. occipitalis						
Allopatric v Sympatric	6.6	<.0001	-1.041	0.298	-4.001	0.0001
Allopatric v Parapatric	5.751	<.0001	-4.461	<.0001	0.588	0.5567
Sympatric v Parapatric	0.086	0.9317	-3.434	0.0006	3.854	0.0001
M. peruvianus						
Allopatric v Sympatric	-2.398	0.0165	1.387	0.1654	-0.551	0.5815
Allopatric v Parapatric	-1.053	0.2924	-0.02	0.9839	0.354	0.7231
Sympatric v Parapatric	0.997	0.3186	-1.287	0.1982	0.895	0.3709

Table S2.5 – Pairwise comparisons for height above the substrate (see Figure 2.10)

Contrast	z score	p-value
WALKING		
M. occipitalis		
Allopatric v Sympatric	-0.777	0.4432
Allopatric v Parapatric	-1.271	0.2133
Sympatric v Parapatric	-0.808	0.4255
M. peruvianus		
Allopatric v Sympatric	**2.419**	**0.0216**
Allopatric v Parapatric	1.281	0.2098
Sympatric v Parapatric	-0.925	0.3624
BASKING		
M. occipitalis		
Allopatric v Sympatric	**-2.712**	**0.0111**
Allopatric v Parapatric	**-2.321**	**0.0275**
Sympatric v Parapatric	-0.665	0.5112
M. peruvianus		
Allopatric v Sympatric	**2.224**	**0.0341**
Allopatric v Parapatric	0.937	0.3563
Sympatric v Parapatric	-1.219	0.2327
FORAGE		
M. occipitalis		
Allopatric v Sympatric	**-3.415**	**0.002**
Allopatric v Parapatric	**-2.161**	**0.0394**
Sympatric v Parapatric	-1.043	0.3058
M. peruvianus		
Allopatric v Sympatric	**3.869**	**0.0006**
Allopatric v Parapatric	**2.511**	**0.0181**
Sympatric v Parapatric	-1.59	0.1231
DISPLAY (MALES)		
M. occipitalis		
Allopatric v Sympatric	**-2.406**	**0.0317**
Allopatric v Parapatric	-1.687	0.1154
Sympatric v Parapatric	-0.278	0.7853
M. peruvianus		
Allopatric v Sympatric	2.02	0.0645
Allopatric v Parapatric	2.008	0.0659
Sympatric v Parapatric	0.239	0.815

Figure S2.1 Graphic schema of the zig-zag pattern vegetation sampling employed on each study site.
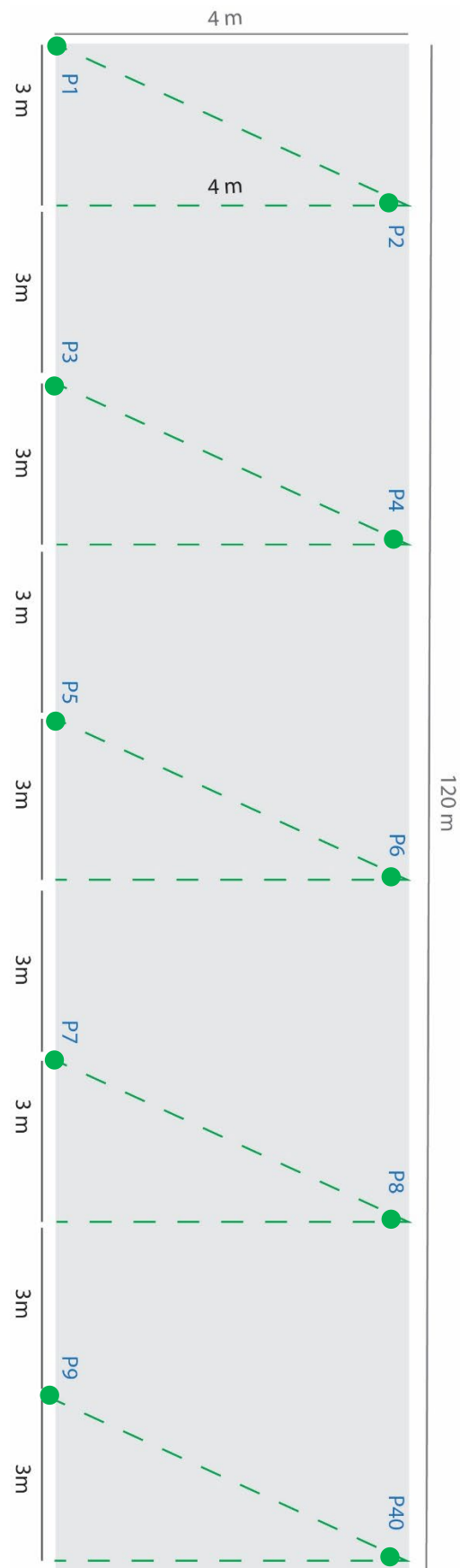
CHAPTER THREE

Ecological influences on the behaviour of
Ecuadorian lava lizards in the context of
phylogenetic relatedness.

Abstract

Establishing the causes that drive behavioural and signal divergence among closely related species is key to comprehend speciation and evolutionary processes. Such diversification is often adaptive, where variable selection pressures might favour certain behavioural traits under different ecological and environmental conditions. Biogeographical factors can also lead to behavioural variations, where closely related species from mainland and island populations have been key to document phenotypic differentiation processes. The Ecuadorian lava lizards (*Microlophus* genus) distributed from the western coast of Ecuador to the Galápagos Islands offer an opportunity to study the factors leading to behavioural divergence of closely related species with similar evolutionary history. To test alternative evolutionary models, I consider several phylogenetic comparative methods to assess behaviour under the ecological context and environmental conditions, biogeographical setting, and phylogenetic history. I predicted that the behaviour of lava lizards will be influenced by ecological and environmental factors shifting their behavioural patterns to exploit the available resources; also, that island and mainland populations' behaviour will differ due to their markedly different ecological circumstances such as geographical isolation, limited resources, and lower predation on islands. Results showed that evolutionary history has not constrained behaviour elucidating an important role of extrinsic ecological, environmental, and social factors in their behavioural evolution. Male territorial display action patterns (DAP) were updated using a more accurate approach and reveal a strong association with habitat structure. I discuss my results as representing a valuable piece of a larger puzzle concerning the behavioural and signal differentiation of lava lizards and propose future research on *Microlophus* group as model to explore behavioural adaptations among related species.

Introduction

The behaviour of closely related species can vary dramatically since behaviour is considered to be a rapidly evolving phenotype (Carter et al., 2013; Hernández et al., 2021). These behavioural variations tend to be interpreted as adaptive, with predominant explanations alluding to the outcome from variable selection pressures. Yet, understanding how behavioural components are affected by different selection pressures can become challenging for researchers. Previous studies have suggested some possible causes for behavioural adaptation, which include interspecific competition (Cabrol et al., 2015; Daniel & Kenneth, 1997; Dietrich & Wehner, 2003; Mc Vittie, 1979; Tyne et al., 2017), features of the environment (Angilletta et al., 2009; Asbury & Adolph, 2007; Dylewski et al., 2020; Edwards & Lailvaux, 2012; Ord et al., 2007; Peters, 2008; Shrestha et al., 2018; Stuart et al., 2012; Tyne et al., 2017), and the degree of competition for mates in sexually dimorphic species (Blanckenhorn, 2005; Johnson & Wade, 2010; Meyers et al., 2006; Ord et al., 2001; Snell et al., 1988; Watkins, 1997). Other non-adaptive processes such as genetic drift (Luther & Baptista, 2010; Ord & Martins, 2006; Ringo et al., 1986) and stochastic factors can also explain behavioural adaptations (Bailey et al., 2018; Brock et al., 2015; Ord & Garcia-Porta, 2012). Taken together, behavioural divergence likely results from animals seeking to overcome diverse constraints imposed by the context in which they live (Briffa et al., 2013).

Behavioural traits are thought to be linked with ecology where evolutionary radiation can lead to convergent patterns of behavioural evolution correlated with convergence in ecology (Johnson et al., 2010). Therefore, behaviour provides an ideal framework within which to understand the way animals respond to diverse intrinsic and extrinsic ecological constraints (Cartar & Real, 1997; Carter et al., 2013; Johnson & Wade, 2010). Among the numerous ecological factors that can influence behaviour, habitat structure has been widely recognised as a key factor (Asbury & Adolph, 2007; Brockmark et al., 2010; Höjesjö et al., 2004). Habitat selection is extremely important in animals as the selective forces associated with choosing an appropriate

habitat might shape the evolution of behavioural strategies (Cartar & Real, 1997; Sbragaglia et al.,

2019; Tyne et al., 2017). Behavioural flexibility therefore allows animals to respond rapidly to

external changes that might confer fitness advantages when shifting to new habitats (Brockmark

et al., 2010). For example, territoriality in Caribbean *Anolis* lizards has been influenced by habitat

structure and light features leading to variations among species (Edwards & Lailvaux, 2012;

Fleishman & Pallus, 2010; Johnson & Wade, 2010) and within populations (Bloch & Irschick, 2006;

Kamath et al., 2013). Moreover, species' behavioural development might also be highly influenced

by population density, which is related to the increase of resource and sexual competition among

and within congeners (Brockmark et al., 2010; De Boer, 1981; Hess & Losos, 1991; Jirotkul, 1999).

Therefore, animals might become more aggressive or otherwise modify their behaviour due to

higher encounter rates with potential competitors and mates, or variation in relative access to

available resources (Eckert et al., 1994; Jirotkul, 1999; Maura et al., 2011; Pajunen, 1966).

Understanding the effect of ecological constraints on behaviour is important as it facilitates

adaptation to new or varying habitats and speciation (Hernández et al., 2021; Ord et al., 2016).

Variation in environmental conditions is also relevant to explaining behavioural diversity

(Goutte et al., 2018; Killen et al., 2013). Fundamental behaviours such as foraging, reproduction,

migration and social interactions are mediated by the physiological capacities of species to deal

with the environmental conditions (Killen et al., 2013; Seebacher & Krause, 2017). Environmental

factors such as ambient temperature can strongly influence animal performance. In ectotherms,

in particular, ambient temperature can speed up metabolic reactions that directly affects

physiology and behaviour (Abram et al., 2017; Angilletta et al., 2009). Several studies on

ectotherms from a wide range of taxa (Biro et al., 2010; Briffa et al., 2013; Magnuson et al., 1979;

Pérez-Granados et al., 2020; Shrestha et al., 2018; Taylor, 1963) have demonstrated that the

production rate and structure of communication signals can differ as a function of ambient

temperature (Ord & Stamps, 2017). In the case of lizards, studies have shown that temperature

can strongly constrain locomotor performance (Angilletta, 2006; Angilletta et al., 2002) and

signalling behaviour (Ord & Stamps, 2017). This thermal dependency had led to shifts in

microhabitat preferences to avoid overheating (Angilletta et al., 2009; Farina et al., 2008; Ortega

& Pérez-Mellado, 2016; Sepulveda et al., 2014), constraining of activity periods (Foà & Bertolucci,

2001; Gordon et al., 2010; Rowe et al., 2020; Sepúlveda et al., 2008), and alter the rate of

signalling (Hertz et al., 1982; Kondo & Downes, 2007; Ord & Stamps, 2017).

Another environmental condition that is of growing importance to behaviour is wind.

Signalling animals must ensure reliable detection by receivers, with wind resulting in background

noise for acoustic (Peters et al., 2007; Velilla et al., 2020) and for visual signals (Fleishman, 1992;

Goutte et al., 2018; Grafe et al., 2012). For lizards that communicate via dynamic visual signals,

the movement of windblown vegetation is considered the major source of background noise

limiting signal detectability (Leal & Fleishman, 2002; Peters, 2014). Nevertheless, individuals have

optimised their visual signals by either modifying their display form (i.e., amplitude, acceleration,

speed) (Fleishman, 1992; Luther & Baptista, 2010; Ord et al., 2007; Peters, 2008; Peters et al.,

2007) or adjusting behaviour (Ord et al., 2016) to compensate for the prevailing noise

environment. This increase in signal efficiency is thought to be adaptive, and might also influence

species recognition mechanisms, mate selection and territorial defence (Luther & Gentry, 2013).

Behavioural diversity should also be considered in the context of sexual selection

mechanisms. An increase in male-male competition can affect mate-choice decisions resulting in

differences within populations (Chen et al., 2012; Cox et al., 2003; Muralidhar & Johnson, 2017).

On the other hand, intersexual conflict can lead to differences in the ecological needs of each sex,

resulting in diversity of behaviour between males and females (Jivoff & Hines, 1998).

Furthermore, when males consign less time and energy to offspring, there is the potential for

increased rates of reproduction, potentially influencing the ratio of reproductive males and

intensifying the competition for mates (Debuse et al., 1999). Therefore, males enhance their

reproductive success by using different morphological and behavioural strategies based on their

size and the array of their competitors (Borgia, 1980; López Juri et al., 2018; Scott et al., 2004). In many species, bigger males are more successful at resource defence leading to advantages in aggressive interactions and reproduction (Baird et al., 2012; Blanckenhorn, 2005). In the same way, populations skewed towards either sex tend to increase conspecific aggression (Grafen & Ridley, 1983). Many lizard species exhibit marked sexual size dimorphism that favours adult males, and sex ratios biased toward one sex (Angel et al., 2015; Cox et al., 2003; Herrel et al., 2007; Johnson & Wade, 2010; Muralidhar & Johnson, 2017; Stamps et al., 1997), which has been widely related to behavioural variations between species. For instance, males of two populations of green anoles (*Anolis carolinensis*) in southern Louisiana significantly increased the time spent displaying and employed different display types when male density was higher (Bloch & Irschick, 2006). Similarly, male aggression and territoriality have been positively correlated with sexual size dimorphism thus conferring an advantage in intrasexual mate competition (Cox et al., 2003).

Biogeographical factors also affect behaviour, and closely related species from mainland and island populations have proven useful for documenting several of the processes leading to phenotypic differentiation, not only in behaviour but also on morphology, colour patterns, and many other features (Innes & Kavaliers, 1987; Irschick et al., 1997; Peer et al., 2007; Stuart et al., 2012; Travis & Ricklefs, 1983). Mainland and island species face different selective pressures influenced by geographical isolation, lower predation and competitors, climatic differences, and the effect of colonisation events structuring population genetics (Irschick et al., 1997; Schlotfeldt & Kleindorfer, 2006; Shine, 1987; Spears, 1987). This allows researchers to study the rapid divergence of phenotypical traits, which is considered to be adaptive and key for species to exploit novel resources (Brodin et al., 2013; Castilla et al., 2008). Lizards have been widely used as a model system for these studies as few taxa have radiated extensively in both environments showing striking ecological plasticity (Anderson & Poe, 2018; Eloy De Amorim et al., 2017; Patton et al., 2021; Pinto et al., 2008; Siliceo-Cantero et al., 2016). Indeed Ord and Martins (2006) have suggested that the different selective forces are linked to variation in display components,

whereas display complexity is associated with the need to facilitate species recognition influenced by habitat type. In the same way, fluctuations in resource availability on islands can lead to shifts in prey preferences and foraging strategies, allowing the exploitation of available resources that might not be the first option for mainland populations (Castilla et al., 2008). While lizards have been useful models in studies of this nature, few have focused on behavioural adaptations.

Lava lizards (*Microlophus* sp.) are distributed from the western coastal region of mainland Ecuador to north-central Chile and the Galápagos Islands (Benavides et al., 2007; Sepúlveda et al., 2008). Unlike mainland populations where species can occur in sympatry (Chapter 2), island species are isolated from congeners and have evolved under allopatric conditions from two different colonisation events (Benavides et al., 2007). Studies of mainland populations suggest intrasexual behavioural variation where females also display to attract males or avoid intra-sexual agonistic interactions (Watkins, 1997, 1998). In addition, variation in thermal behaviours and foraging strategies have also been observed as a result of habitat differences (Burger, 1993; Farina et al., 2008; Jordan & Perez, 2012; Jordan et al., 2008; Jordan et al., 2005; Rowe et al., 2020; Rowe et al., 2019; Sepúlveda et al., 2008), resource availability (East, 1995; Hervias-Parejo et al., 2019; Hervías-Parejo et al., 2020; Sepulveda et al., 2014; Snell et al., 1988) and sexual competition (Clark et al., 2019; Clark et al., 2017; Koening, 2017; Vidal et al., 2002; Watkins, 1997). Behavioural studies have focused mostly on aggressive behaviour that is thought to be species-specific due to genetic drift (Carpenter, 1966, 1977; Clark et al., 2015; Jordan & Snell, 2002, 2008; Koening, 2017). However, skewed attention towards the territorial behaviour of Galápagos lava lizard species has provided only a partial understanding of the *Microlophus* group's behavioural evolution, and thus speciation. Consequently, more effort is required to elucidate the role of external factors in driving behavioural divergence among closely related species (Mendelson & Shaw, 2012).

In the present chapter, I studied lava lizards from the west coast of mainland Ecuador and the Galápagos Islands to explore behavioural and signal diversification among closely related taxa with similar evolutionary histories. Specifically, I considered whether behaviour varies in response to ecological context and environmental conditions, biogeographical setting, and phylogenetic history. I obtained population level averages for multiple behavioural traits, including signalling behaviour, and sought to explain variation using phylogenetic comparative methods. I predicted that behaviour will be influenced by external factors of ecology and environmental conditions altering species behavioural patterns to exploit the available resources, also that island and mainland populations will differ due to markedly different ecological circumstances such as geographical isolation, limited resources, and lower predation on islands. Nevertheless, as closely related species are genetically correlated, I did not rule out the possibility that lava lizards' behaviour reflects the influence of their phylogenetic history and relatively recent diversification events (Jordan & Snell, 2008; Jordan et al., 2005). Data were collected at multiple sites on the mainland and on multiple islands of the Galápagos and phylogenetic comparative methods were then used to assess diversity in *Microlophus* behaviour.

Methods

Subjects and study sites

The *Microlophus* genus possess a distribution that spans endemic species on the Galápagos Islands and the western coastal region of mainland Ecuador to north-central Chile (Benavides et al., 2007; Sepúlveda et al., 2008). Two well supported groups with 21 species divide the genus into the *Occipitalis* and *Peruvianus* clades, where ten of the 12 species of the *Occipitalis* group comprise the Galápagos species from two separate radiation events (Benavides et al., 2009). As iguanids, this group is characterised by male territorial behaviour, female-defence polygyny, and strong sexual dimorphism, whereby males are larger than females and exhibit a well-developed dorsal crest (Carpenter, 1977; Clark et al., 2019; Clark et al., 2017; Rowe et al., 2019; Watkins, 1997). My target species for comparative analysis were selected based on their behavioural

features and evolutionary history (Benavides et al., 2007; Benavides et al., 2009; Carpenter, 1966, 1977; Clark et al., 2016; Clark et al., 2015). Eight species from the *Microlophus* group were chosen, with five belonging to the West clade (*M. grayii, M. albemarlensis, M. indefatigabilis, M. jacobi, M. duncanensis,* see Fig 3.1a), one to the East clade (*M. bivittatus,* see Fig 3.1a) and two to the mainland clade (*M. occipitalis* and *M. peruvianus*, see Fig 3.1b). Fieldwork was carried out on the Ecuadorian west coast (Nov 2017 – Jan 2018) and the Galápagos Islands (Nov 2018 – Jan 2019 & Nov 2019 – Jan 2020). Overall, 15 localities were surveyed, six for the mainland species and nine for the island species (Table 3.1, Figure 3.2). The vegetation of each study site was diverse from deciduous shrubs and forests to urban settings (Ministerio del Ambiente del Ecuador, 2013; Rivas-Torres et al., 2018).

Microlophus albemarlensis

Microlophus indefatigabilis

Microlophus jacobi

Microlophus grayii

Microlophus duncanensis

Microlophus bivittatus
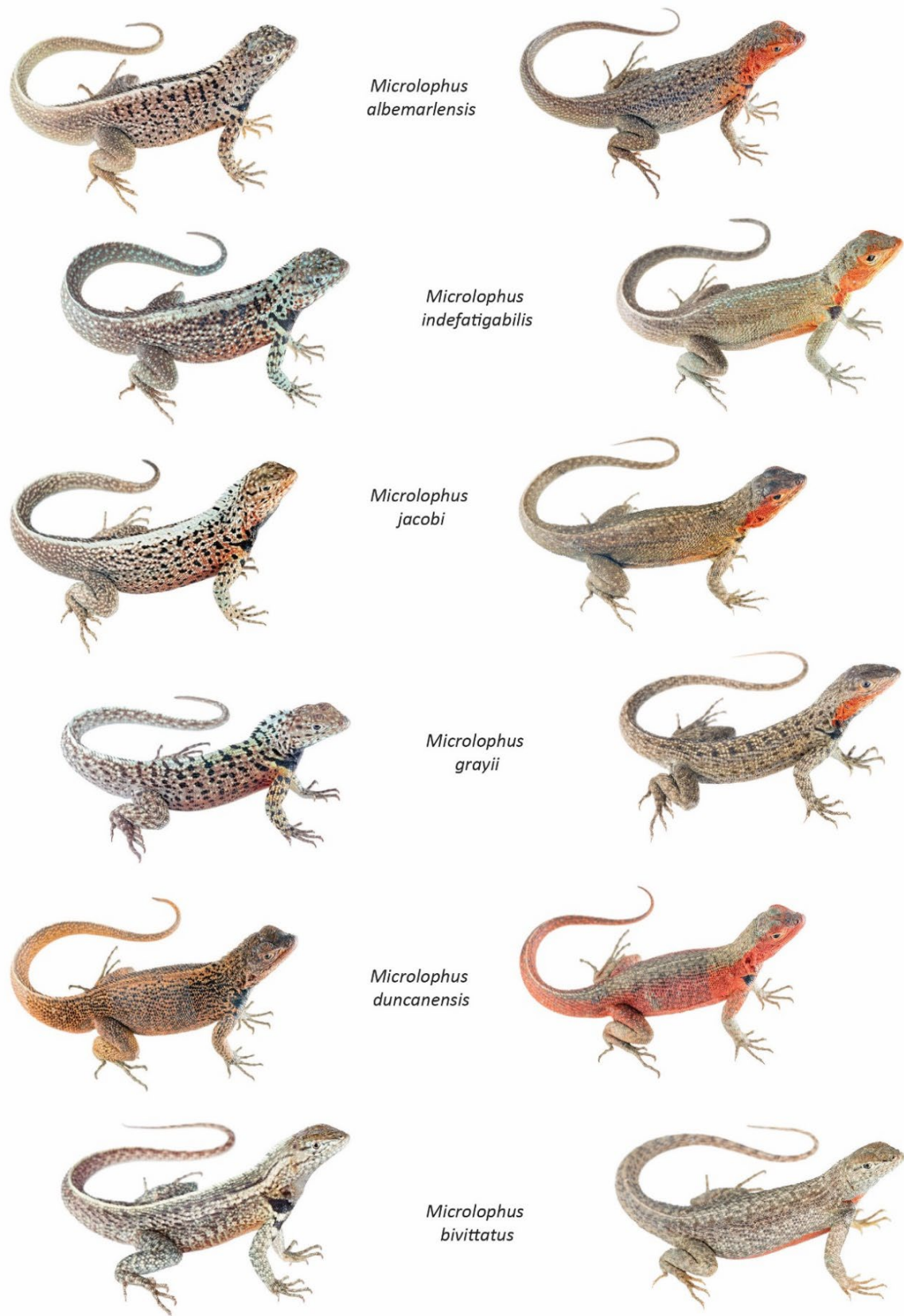
Figure 3.1a Male (left) and female (right) of *Microlophus* species sampled on the Galápagos Islands. Photography by Jose Vieira and Alejandro Artega-Tropical Herping (see https://www.tropicalherping.com) and used with permission**.**
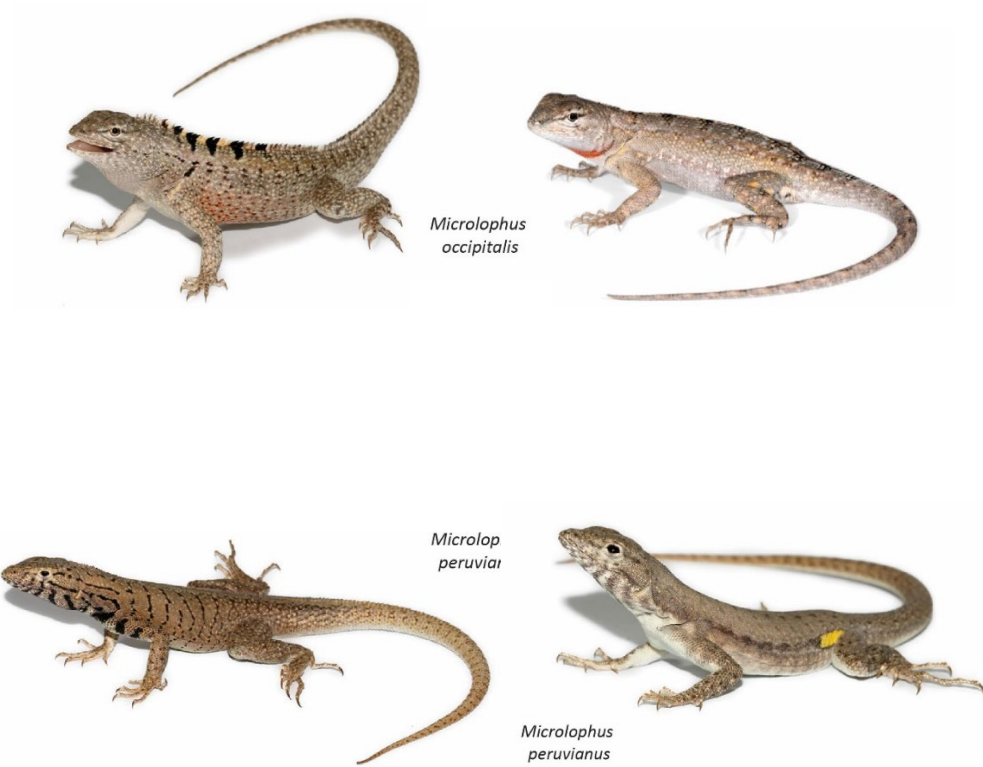
Figure 3.1b Male (left) and female (right) of *Microlophus* species sampled on the west coast of Ecuador. Photography by Omar Tores-Carvajal-BIOWEB (see https://bioweb.bio) and used with permission.

Table 3.1a Sampling locations of *Microlophus* species on the Galápagos islands.

Map Ref	Island	Species	Locality	Coordinates	Habitat
Galápagos Islands					
PNG	Santa Cruz	*M. indefatigabilis*	Parque Nacional Galápagos (PNG)	0° 44' 19.3056'' S, 90° 18' 9.0108'' W	Deciduous forest and urban settings
Gar	Santa Cruz	*M. indefatigabilis*	El Garrapatero beach	0° 41' 37.374'' S, 90° 13' 9.7572'' W	Coastal humid forest and shrubland
TB	Santa Cruz	*M. indefatigabilis*	Tortuga Bay	0° 45' 29.5128'' S, 90° 19' 48.9468'' W	Coastal humid forest, evergreen seasonal forest and shrubland
ML	Isabela	*M. albemarlensis*	Muro de Lágrimas	0° 57' 53.7696'' S, 91° 0' 44.3952'' W	Deciduous forest
CC	Isabela	*M. albemarlensis*	Centro de Crianza "Arnaldo Tupiza Chamaidan"	0° 56' 50.8956'' S, 90° 58' 26.6592'' W	Deciduous forest and urban settings
Lob	Floreana	*M. grayii*	La Lobería	1° 16' 49.3356'' S, 90° 29' 20.9364'' W	Deciduous forest
CI	San Cristobal	*M. bivittatus*	Centro de Interpretación Ambiental Gianni Arismendy	0° 53' 24.3168'' S, 89° 36' 33.6564'' W	Deciduous forest
PEsp	Santiago	*M. jacobi*	Playa Espumilla	0° 12' 12.3516'' S, 90° 49' 43.464'' W	Deciduous forest, mangrove, and deciduous tallgrass
PEsc	Pinzon	*M. duncanensis*	Playa Escondida	0° 35' 57.8112'' S, 90° 39' 17.8056'' W	Old lava, deciduous tallgrass, and deciduous forest

Table 3.1b Sampling locations of *Microlophus* species on mainland Ecuador.

Map Ref	Province	Species	Locality	Coordinates	Habitat
Mainland					
Fra	Manabi	*M. occipitalis*	Los Frailes	1° 27' 56.0519" S, 78° 23' 49.9530" W	Dry coastal shrub
CA	Santa Elena	*M. occipitalis*	Cerro Alto	2°10'51.7802" S, 80°45'48.0652" W	Deciduous coastal forest
Choc	Santa Elena	*M. occipitalis/ M. peruvianus*	"Península de Santa Elena" National Park	2°11'18.2" S 81°00'35.0" W	Dry coastal shrub
Cha	Santa Elena	*M. occipitalis/ M. peruvianus*	Chanduy	2°24'10.8" S 80°40'56.2" W	Dry coastal shrub
EP	Guayas	*M. occipitalis/ M. peruvianus*	El Pelado	2°37'31.1" S 80°27'10.1" W	Dry coastal shrub
Anc	Santa Elena	*M. peruvianus*	Ancón	2°19'3.1437" S, 80°51'21.7200" W	Dry coastal shrub
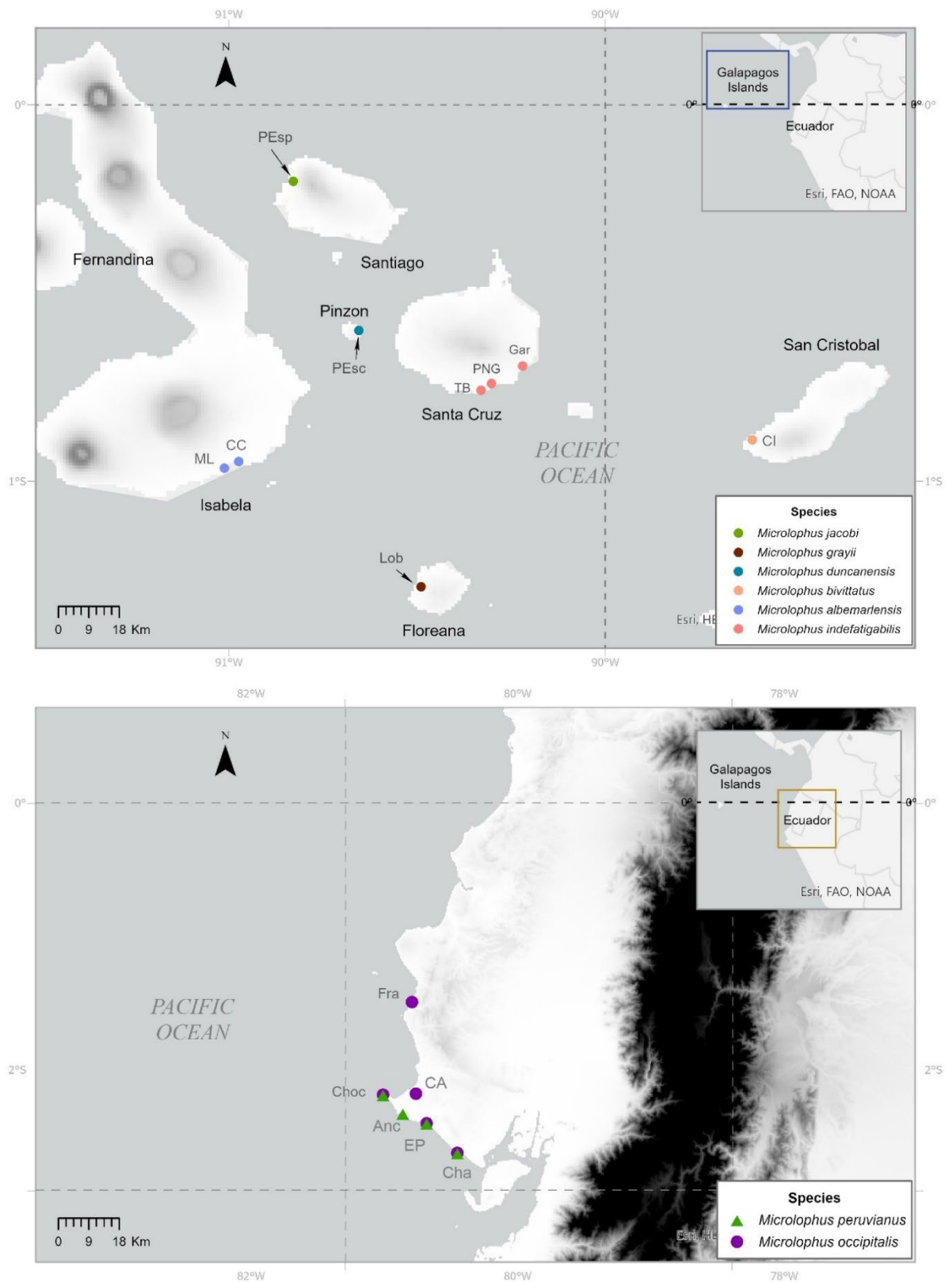
Figure 3.2 Sampled localities for the *Microlophus* species on the Galápagos Archipelago (top) and the Ecuadorian west coast (bottom). Refer to table 3.1 for localities details.

Data Collection

The data collection strategy was consistent at each site. Three non-overlapping transects (120m x 4m) were used to subdivide the sites, and were allocated at the edges to enhance the probability of locating lizards (Maura et al., 2011) and minimise disturbance of the natural environment.

Dependent variables: behavioural and signal traits

I developed a partial ethogram of the behavioural repertoire of *Microlophus* species based on previous studies (Carpenter, 1966; 1977; Watkins, 1997; Clark et al 2015; Yin et al, 2011) and personal observations (see Table S1.1). For three to four consecutive days, I undertook focal sampling of male and female lizards. Focussing on one transect per day, I conducted three-hour observations during the morning (0900-1200) and afternoon (1400-1700). Focal sampling registered the activity of a selected individual at two-minute intervals, with both male and female focal lizards observed separately by two trained observers per session. Different focal animals were selected for the morning and afternoon sessions, with a total of 90 behavioural observations obtained per adult individual sampled at each locality.

To quantify territorial displays, I recorded interactions of adult males at each sampling site following the approach of Peters et al. (2016). Briefly, a tethered male from a different location was introduced to an unconstrained resident male, and interactions were filmed using two video cameras (Sony) positioned with greater than 20° angular separation and filmed at 100 frames per second. Camera settings and positions were not adjusted after filming started, and before recording ceased, a calibration object featuring 20 non-coplanar points, distributed evenly across the volume of space occupied by the resident lizard was placed in view of both cameras. The calibration object facilitated three-dimensional reconstruction of displays following Hedrick (2008).

Predictor variables: ecological, environmental, and social parameters

Behavioural variation exhibited by Ecuadorian lava lizards was considered in relation to ecological (population size, habitat structure, island effect), environmental (temperature and wind conditions) and social (sex ratio, sexual-size dimorphism) parameters. I estimated population size by assessing encounter rate at each study site using the previously established line transects. All individuals to the left of the path, as well as on the transect path itself, were registered by one observer at each transect for three consecutive days during the early morning (0800-0900) (Ruiz de Infante Anton et al., 2013). Age class (adult or juvenile) and sex were also registered during the surveys. These data were used to determine the number of individuals and adult sex-ratio of each locality.

I surveyed vegetation composition along each transect to characterise each habitat. Forty points were distributed across each transect at 3 m intervals, with odd-numbered points located near to the transect edge and even-numbered points position 5 m away from the transect path (Appendix 3.1). A touch pole was used at each point and the plant types were grouped into 7 categories based on the life form: ground cover, grass, herbs and forbs, shrubs, woody plants, cactus, and non-vegetation. Vegetation height was scored at 0.1 m increments to 2 m height, with vegetation greater than 2m categorized as woody plant. During focal sampling of lizard behaviour, I also obtained information about microhabitat use and weather conditions (Table S3.3 and 3.4). The microhabitat utilised by the lizard and height above the substrate was recorded every two minutes, while air temperature and prevailing wind was registered every 10 minutes using a Kestrel 4000 anemometer.

To estimate the possible strength of sexual selection, I computed the sex ratio and sexual size dimorphism per species for each population. For the sex ratio (SR), I used the proportion of adult males in the population

$$SR = \frac{\text{N } males}{(\text{N } males + \text{ N fe} males)}$$

where values >0.5 indicate a male biased population (Ancona et al., 2017). Sexual size

dimorphism (SSD) was calculated using snout-vent length data measured in the field from at least

10 individuals per species and sex (Clark et al., 2015; López Juri et al., 2018):

$$SSD = \frac{\text{SVL } males}{\text{SVL } females}$$

Phylogeny

I compile a composite tree from available published calibrated trees as no complete phylogeny of

all my populations of interest was available.The first phylogeny used was based on the time

calibrated tree of the Galápagos Island species (Benavides et al., 2009), that included populations

near to, or the same as, my study sites. This phylogeny also included populations of *M. occipitalis*

from the mainland. However, to include *M. peruvianus* and additional populations *for M.*

occipitalis, I used the phylogeny of the *Microlophus* genus developed by Benavides et al. (2007) to

place these species without altering the divergence times (Figure 3.3). Then, to infer the branch

lengths and internal nodes of my topology, I measured the branches and internal nodes of prior

calibrated phylogenies published by Benavides et al. (2007, 2009) using the millions of years axis

scale bar as reference on the ImageJ software. Lastly, all the branch lengths of my topology were

reset to resemble the branch lengths previously obtained and an ultrametric tree was generated

in Mesquite v. 3.61.

Data Processing

All statistical analysis were conducted using R v.4.0.4 (RCoreTeam, 2018). The 31 behaviours in my

ethogram were observed to varying levels across my study sites (see Table S3.1). I chose a subset

of these for analysis and grouped them into four categories: explore, social interactions, signalling

and territorial displays (see Table S3.1). The frequency of occurrence of these behaviours in a

given session was converted to the proportion of time spent in each category, and I computed the

mean per population and sex (Figure 3.3). Each category was analysed separately and populations

that did not exhibit a given behaviour were assigned a score of zero. Values exactly equal to 0 or 1

are not appropriate for the subsequent analysis. Consequently, I adjusted as per Smithson and

Verkuilen (2006) using the formula:

$$p\ transformed = \frac{p(n-1) + 0.5}{n}$$

Where *p* was the proportion value, and *n* was the sample size. As intrasexual differences in

behaviour within species has been previously reported (Carpenter, 1977; Clark et al., 2017;

Koening, 2017; Watkins, 1996, 1997), females and males were analysed separately. In addition,

population means were computed for height above the substrate, air temperature and wind

speed during focal sampling.

(a) Males

Signalling Explore Interactions Territorial
Proportion of time
0.1 0.2

M. theresiae
M. peruvianus (EP)
M. peruvianus (Choc)
M. peruvianus (Anc)
M. peruvianus (Cha)
M. occipitalis (Choc)
M. occipitalis (Cha)
M. occipitalis (EP)
M. occipitalis (Fra)
M. occipitalis (CA)
M. bivittatus (CI)
M. indefatigablis (TB)
M. indefatigablis (Gar)
M. indefatigablis (PNG)
M. jacobi (PEsp)
M. duncanensis (PEsc)
M. grayii (Lob)
M. albemarlensis (CC)
M. albemarlensis (ML)

Phylogenetic signal		Signalling	Explore	Interactions	Territorial
	Blomberg's K	0.08	0.11	0.04	0.01
	Lambda	0.21	0.54	0.11	0.00

(a) Females

Proportion of time
0.1 0.2

M. theresiae
M. peruvianus (EP)
M. peruvianus (Choc)
M. peruvianus (Anc)
M. peruvianus (Cha)
M. occipitalis (Choc)
M. occipitalis (Cha)
M. occipitalis (EP)
M. occipitalis (Fra)
M. occipitalis (CA)
M. bivittatus (CI)
M. indefatigablis (TB)
M. indefatigablis (Gar)
M. indefatigablis (PNG)
M. jacobi (PEsp)
M. duncanensis (PEsc)
M. grayii (Lob)
M. albemarlensis (CC)
M. albemarlensis (ML)

Signalling Explore Interactions Territorial

Phylogenetic signal		Signalling	Explore	Interactions
	Blomberg's K	0.08	0.07	0.07
	Lambda	0.31	0.29	0.00

Territorial displays were obtained for a subset of the study sites on the mainland and

Galápagos Island. I digitised the first push up display for each species by tracking the position of

one eye over time in recordings from both cameras and applied direct linear transformation (DLT)

in Matlab (MathWorks Inc.) following Hedrick (2008) to reconstruct movements in 3-dimensional

space. This process ensures that digitised movement is not constrained by the position of the

cameras during filming (Hedrick, 2008; Peters et al., 2016). Then, I computed the change in

position of the eye in 3D space to produce display action pattern (DAP) graphs and used the DAP

profile (Figure 3.4a) to identify 12 display characteristics for each lizard relating to temporal and

spatial properties of the movements. First, I identified the start and end point of each display to

determine the *sequence duration*. Each display can be broken up into multiple bursts of push-up

movements, so I also computed the *number of bursts*, the *mean duration of bursts* and the burst

interval duration mean (Figure 3.4a, d). From the DAP I determined the amplitude of movement

within each burst (Figure 3.4a) and subsequently calculated the *burst amplitude mean* (Figure

3.4c). The change in position of the eye over time represents the speed of movement (Figure

3.4d), and I computed the *mean* and *maximum sequence speed.* I also considered speeds within

each burst separately before obtaining the *mean burst speed* (Figure 3.4e). Many of the display

characteristics obtained above vary within a given display. Consequently, for burst durations,

within burst speeds and amplitudes and inter-burst intervals, I obtained the slope of a linear

regression line fit to the data (Figure 3.4b-f) thereby defining *burst duration slope, burst speed

slope, burst amplitude slope* and *interval duration slope*. In each case, a positive value indicates an

increase over time, while a negative value represents a decrease in the display characteristic over

time.
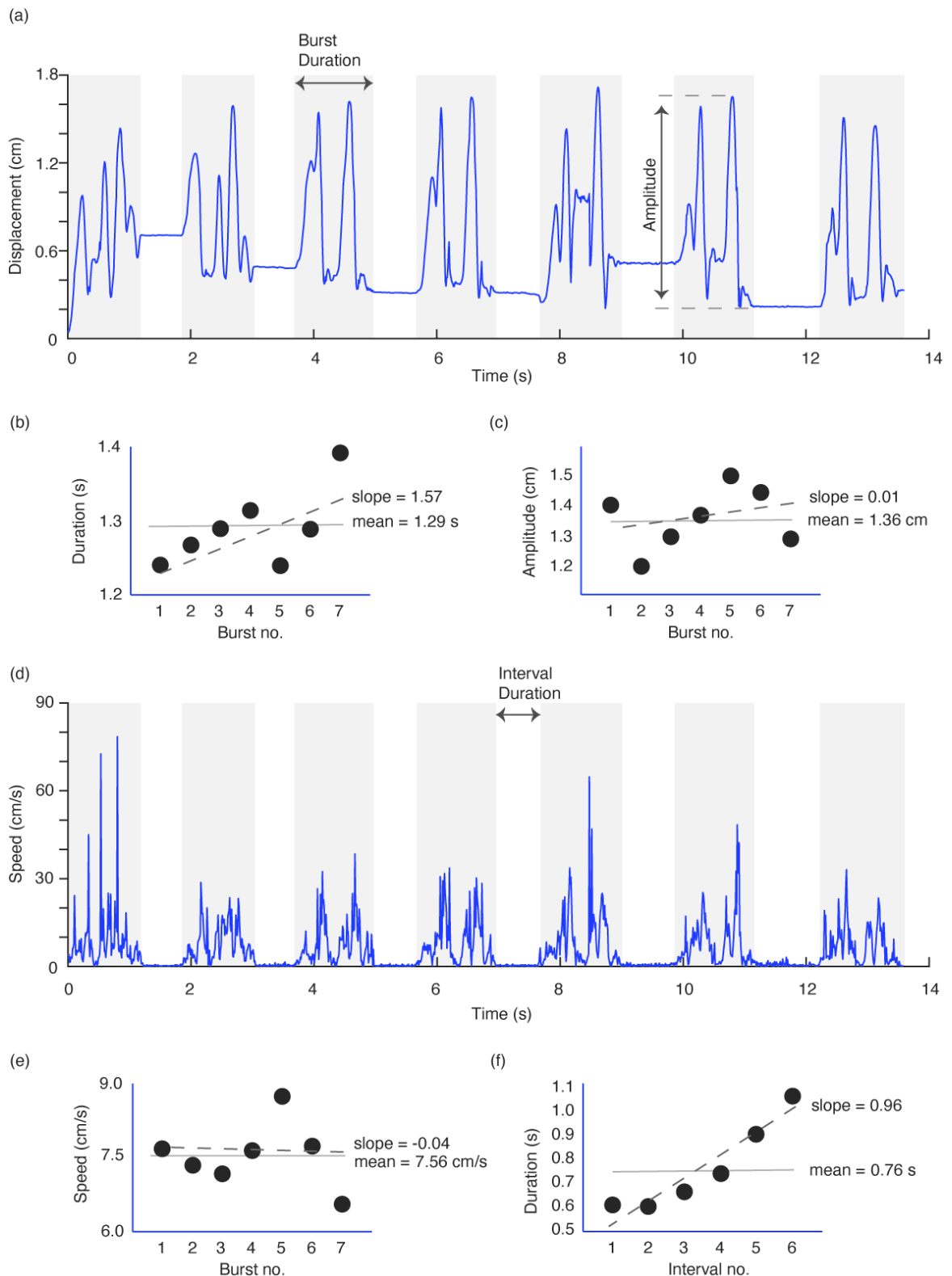
Figure 3.4 Characterising the territorial display of *Microlophus* sp. starts by defining a display action pattern (DAP) of the movement of the eye over time (a), from which we can determine the amplitude of movements. The change in position between successive time-points represents the speed of movement (b). Displays comprise one or more bursts of head movements, and the duration (d), amplitude (c) and speed (e) of these movements computed for each burst, along with the interval between bursts (f). We can quantify how these parameters (c-f) change over the course of the display by fitting a regression line to the data and recording the slope depicting the relationship between time (burst/interval number) and the given parameter.

Population means for each of these display characteristics were computed and subjected to principal component analysis (PCA) in the R Statistical Environment to reduce the number of variables for subsequent analysis. The first two components explained 65% of the variation, while the third component explained an additional 14% (Table 3.2). PC1 correlated positively with the number of bursts, and negatively with burst duration, mean amplitude, and interval duration slope (Table 3.2). This suggest that high scores on PC1 indicate displays with a high number of bursts, but at low amplitude and short duration. PC2 correlated positively with overall speed and mean burst speed and with burst duration slope (Table 3.2), suggesting high scores are indicative of faster burst speeds with increasing burst duration. PC3 exhibited positive loading on both burst speed and burst amplitude slope parameters and interval duration (Table 3.2), indicating that high PC3 scores reflect sequences in which burst speed and amplitude increases over time. PC scores for each population are presented in Figure 3.5.

Table 3.2 Principal component analysis loadings for 12 characteristics of male territorial displays.

Display Characteristic	PC1	PC2	PC3
Sequence duration	0.28	-0.25	-0.15
Mean sequence speed	-0.09	**0.51**	-0.05
Maximum sequence speed	0.22	**0.34**	-0.16
Number of bursts	**0.44**	0.00	-0.16
Mean duration of bursts	**-0.41**	-0.16	-0.22
Burst duration slope	-0.08	**0.39**	-0.04
Mean burst speed (mean)	0.11	**0.49**	-0.11
Mean burst speed slope	0.28	0.06	**0.48**
Burst amplitude mean	**-0.36**	**0.31**	-0.01
Burst amplitude slope	0.19	0.18	**0.56**
Interval duration mean	-0.22	-0.09	**0.54**
Interval duration slope	**-0.43**	0.00	0.17
Variance explained	**0.38**	**0.27**	**0.14**
Cumulative variance	**0.38**	**0.65**	**0.79**
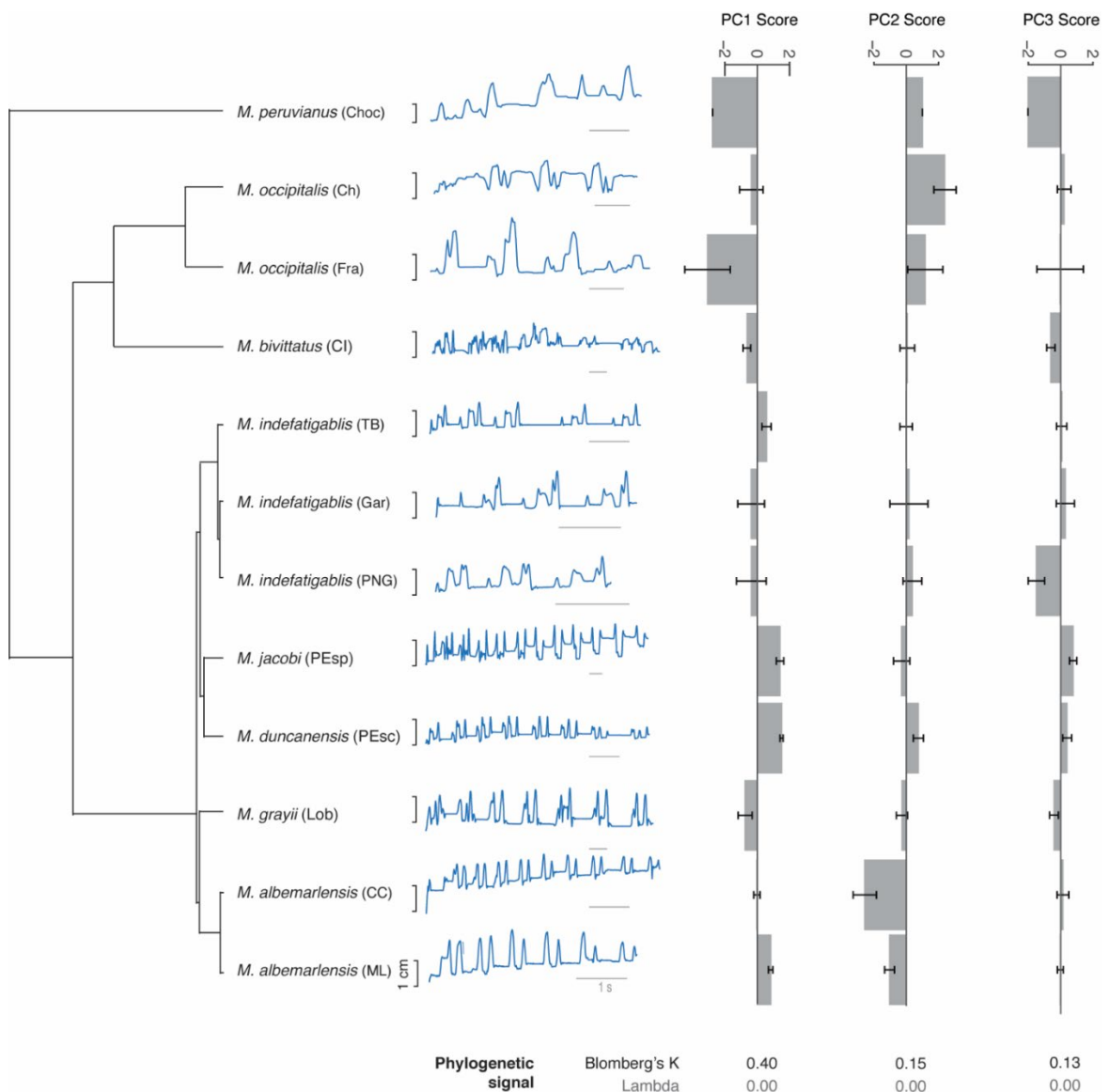
Figure 3.5 Phylogeny of *Microlophus* species based on Benavides et al. 2007 and 2009. Diagrams at the tips of the phylogeny depict the display action pattern (DAP) of adult male territorial displays. Bar charts include the principal components of DAP characteristics (mean ± SE) per population sampled. Bottom values indicate the phylogenetic signal parameters outcomes. Refer to table 3.2 for principal components details.

To prepare weather and habitat data for subsequent analysis, I log10 transformed wind data and ran non-metric multidimensional scaling (NMDS) with Bray-Curtis similarities on habitat characteristics using the VEGAN package (Eichel et al., 2016; Oksanen et al., 2010). The ordination helped to visualise differences in habitat structure between populations, which I subsequently compared using analysis of similarity (ANOSIM). The NMDS analysis showed two-levels of ordination (stress value: 0.184) to explain variation among sites in vegetation. Cactus and shrub

were negatively correlated with NMDS1, while 'nil' was positively correlated. For NMDS2, herbs and forbs and woody plant correlated positively, and ground cover negatively. The ordination classified the study sites in three groups with a high degree of dissimilitude between then (ANOSIM: r=0.6584, p=0.001). The absent vegetation sites were represented by ground cover and nil vegetation (Figure 3.6). The medium vegetated sites were outlined by herbs and forbs and woody plants, while the highly vegetated sites were represented by shrubs and cactus (Figure 3.6). I extracted dimension scores for the first two dimensions for each population to be used in subsequent phylogenetic comparative analyses.

Figure 3.6 Non-metric multidimensional scaling (NMDS) analysis for vegetation composition on island and mainland sampled sites. Site acronyms correspond to localities listed on Table 3.1.

Phylogenetic comparative analyses

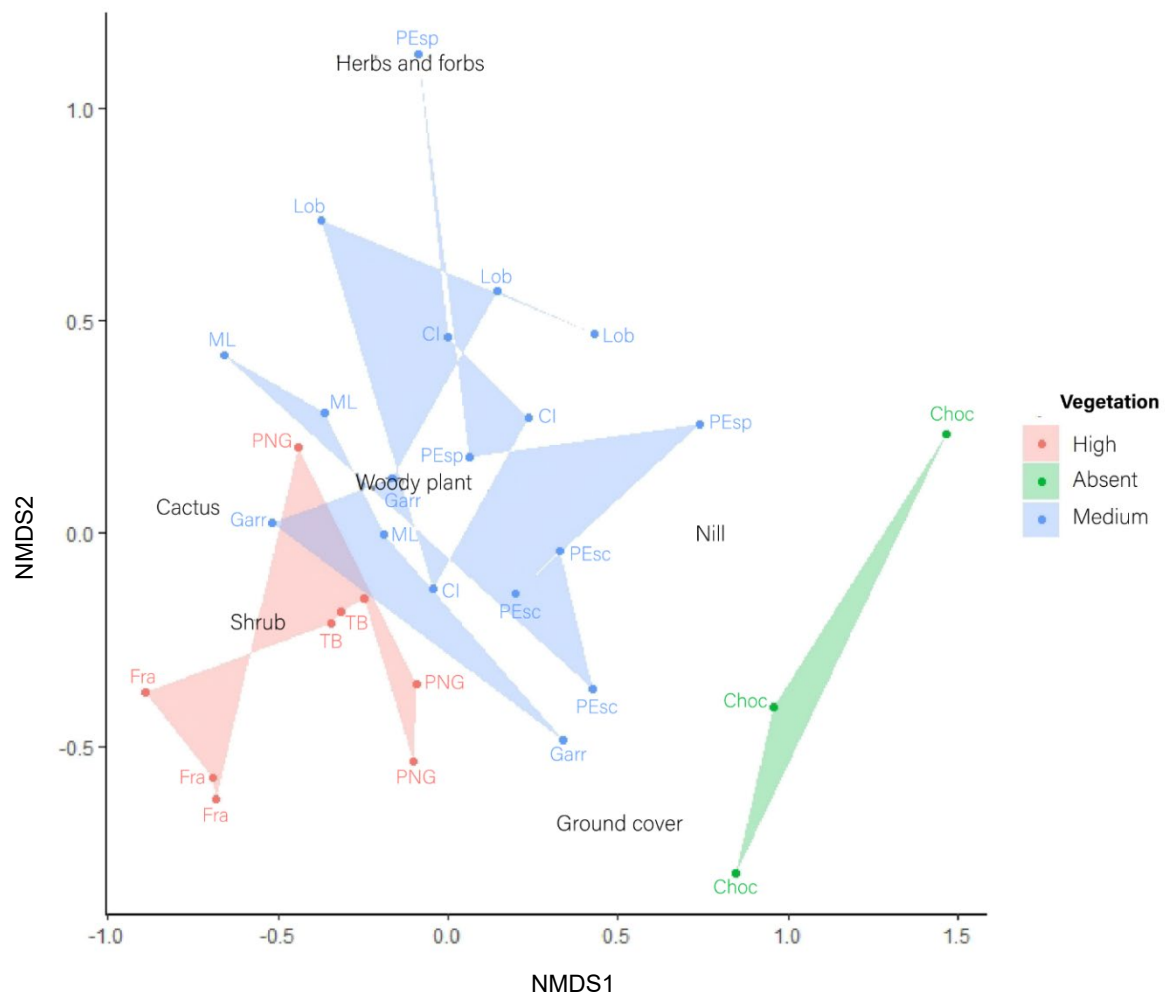I constructed evolutionary models to investigate variation in explore, social interaction and signalling behaviour categories, examining males and females separately. Additional models were also constructed to examine territorial behaviour and display structure of males. My approach for each behaviour category was to build multiple models that might account for variation in the response variable and to use second order Akaike's Information Criterion (AIC_c) to determine the level of support for each model. The set of models used differed for each behaviour category. Common to most models were a *relative abundance* model that assumed behavioural variation is in response to population density (number of lizards), two *intrasexual competition* models that assumed variation in behaviour and display structure reflects differences in male-male competition (SSD) and sex-ratio, an *island effect* model that assumed evolutionary processes differed between the mainland and Galápagos populations and a *null* model that assumed variation among taxa reflects Brownian motion and genetic drift (stochastic processes) or untested predictor variables. Additional models related to environment and habitat structure were also included in various places. Consideration of *environmental* influences assumed variation in behaviour was a function of the external conditions (Ord & Stamps, 2017; Peters et al., 2007). I used air temperature, both as a linear term and as a quadratic function, when examining variation in behaviour categories, while wind speed was used for examining display structure. To explore the influence of *habitat* on social interactions I included height above the substrate (Johnson et al., 2010), while NMDS1 and NMDS2 scores (always used together), which capture habitat structure more generally, were used when examining variation in display structure as this is likely to mediate signal transmission (Bian et al., 2021).

Various combinations of the above-mentioned models were fit to the data using phylogenetic regression with the *phylolm* function specifying an OU fixed evolutionary model and 1000 boots from the phyloLM package v 2.6.2 (Tung Ho et al., 2020) in the R Statistical Environment (RCoreTeam, 2018). All models in the set for any given response variable were

limited to one or two predictor variables given my relatively small sample size (n=18 populations). I used AIC_c values to evaluate support for each model (Richards et al., 2010; Shipley, 2013). The model with the best fit to the data possessed the lowest AIC_c value, and all other models were compared against this one and the relative difference between each model and the top model was computed (ΔAIC_c), with models possessing $\Delta AIC_c \leq 2$ considered further. For the propose of this thesis, I explored graphically the relationship between the response variable and parameters in the models within 2 ΔAIC_c, where the relationships for parameters of the model that exhibited t-values ≥ 1.96 were represented with a solid line. In each case, I obtained predictions directly from the model.

In addition, I undertook further phylogenetic analysis using the 'phytools' R package v0.3-93 (Revell, 2012) to measure the extent to which behavioural and display traits are dependent on phylogenetic history. I computed Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003) indexes where values close to 1 correspond to phenotypic traits that have been influenced by phylogeny and the variation among species reflects an accumulation of incremental changes consistent with the Brownian motion process. In contrast, values close to 0 assumes that a trait has evolved independently of phylogeny. To test whether these values were significant I use the likelihood ratio test for Pagel's λ and 10 000 simulations for Blomberg's K (Clark et al., 2015).

Results

Phylogenetic comparative analysis of behaviour categories

The set of models used to examine variation in behaviour differed between behaviour categories, and between females and males within each behaviour category (Tables 3.3 and 3.4 respectively). For females, the number of individuals combined with sex ratio was the best fit for explore and social interactions (Table 3.3a, b respectively). Females reduced the time exploring as the number of individuals in the populations (Figure 3.7a) and the sex ratio increases (Figure 3.7b), although

these parameters did not reach the significance threshold (Table 3.3a). In contrast, for social

interactions the proportion of time engaged in social interactions by females significantly

increased with the number of individuals in the population (Figure 3.8a) and significantly

decreased as sex ratio increased (Figure 3.8b). For female signalling, the *island effect* model was

found to be the best supported, with females on islands spending significantly less time in

signalling behaviour than females on the mainland (Figure 3.9a).

Table 3.3 Delta Akaike's information criterion (ΔAICc) and t-score parameter of phylogenetic regressions models for female behaviour. Values in bold highlight statistically significant values (|t-score| > 1.96).

(a) Explore

Rank	Model Structure	ΔAICc	Model parameter T-score		
	Top models				
1	LizardNo + Sex Ratio	0	*LizardNo: -1.47; Sex ratio: -1.38;*		
2	LizardNo	0.14	*LizardNo: -1.56*		
3	Sex Ratio	0.43	*Sex Ratio: -1.46*		
4	Null Model	0.68	***(Intercept only): 4.84***		
5	Temperature + Sex Ratio	1.46	*Temperature: -0.91; Sex Ratio: -1.35*		
6	Temperature	1.52	*Temperature: -1.04*		
7	Temperature + LizardNo	1.83	*Temperature: -0.51; LizardNo: -1.22*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
8	Quadratic Temperature (QT)	2.97	10	QT + LizardNo	3.69
9	QT + Sex Ratio	3.39			

(b) Social Interactions

Rank	Model Structure	ΔAICc	Model parameter T-score		
	Top model				
1	LizardNo + Sex Ratio	0	***LizardNo: 2.02; Sex ratio: -2.63;***		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
2	Sex ratio	2.22	12	IslandEffect	6.31

Table 3.3 (Continued)

	Other models		*Rank*	*Model Structure*	*ΔAICc*
3	Temperature + Sex Rat	2.52	13	Temperature + IslandEffect	7.77
4	Sex Ratio + IslandEffect	3.39	14	QT	8.28
5	Temperature + LizardNo	3.48	15	QT + IslandEffect	9.74
6	QT + Sex Ratio	4.23	16	LizardNo + MicroHeight	11.61
7	QT + LizardNo	4.63	17	QT + MicroHeight	13.28
8	LizardNo	4.82	18	MicroHeight + Sex Ratio	13.89
9	Null Model	5.27	19	MicroHeight	15.15
10	LizardNo + IslandEffect	5.50	20	MicroHeight + IslandEffect	16.08
11	Temperature	6.31	21	Temperature + MicroHeight	16.36

(c) Signalling

Rank	Model Structure	ΔAICc	*Model parameter T-score*
	Top models		
1	IslandEffect	0	*IslandEffect: 2.33;*
2	Temperature + IslandEffect	1.62	*Temperature: -0.62; IslandEffect: 1.84;*
3	LizardNo + IslandEffect	1.84	*LizardNo: 0.37; IslandEffect: 2.30;*
4	Sex Ratio + IslandEffect	1.86	*Sex Ratio: 0.35; IslandEffect: 2.30;*

	Other models		*Rank*	*Model Structure*	*ΔAICc*
5	Temperature	3.02	11	Temperature + LizardNo	4.94
6	Null Model	3.02	12	LizardNo	4.99
7	QT + IslandEffect	3.26	13	QT + Sex Ratio	6.15
8	QT	4.31	14	QT + LizardNo	6.30
9	Temperature + Sex Ratio	4.87	15	LizardNo + Sex Ratio	6.51
10	Sex Ratio	4.93			
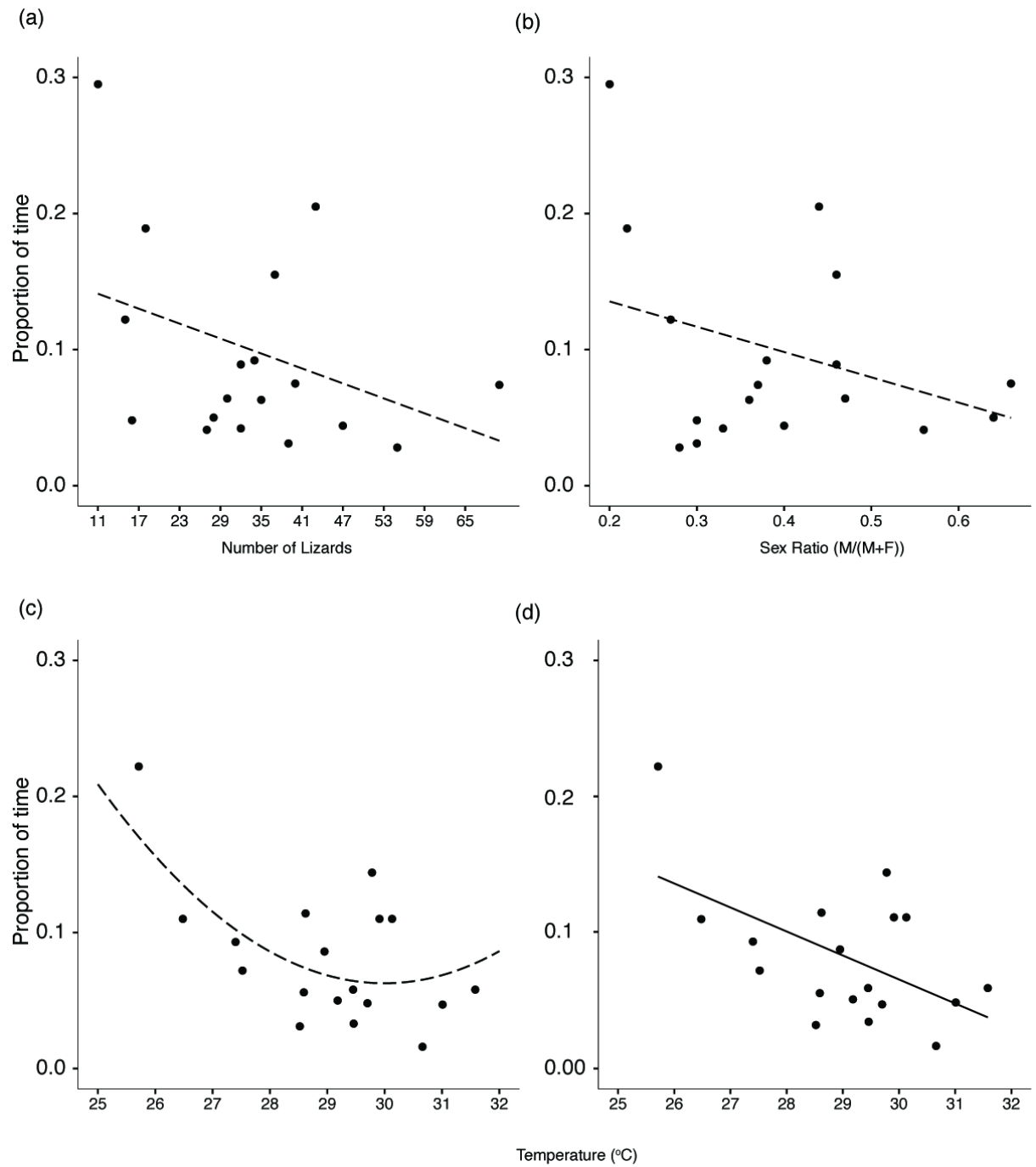
Figure 3.7 Predicted proportion of time spent exploring as a function of (a) the number of lizards and (b) sex ratio for females, and (c) quadratic temperature and (d) temperature for males. Solid line represents a significant relationship and dashed lines indicate a non-significant trend.

Figure 3.8 Predicted proportion of time females spent in social interactions as a function of (a) the number of lizards and (b) sex ratio. Solid line represents a significant relationship and dashed lines indicate a non-significant trend.

(a)

(b)

(c)

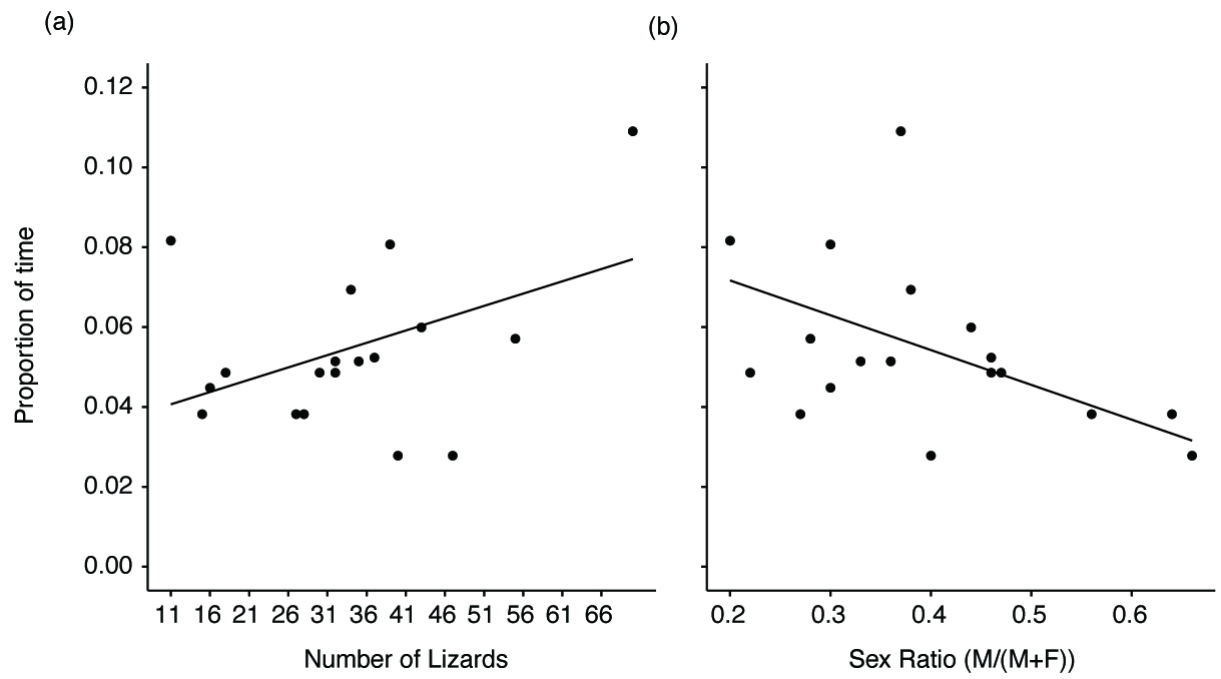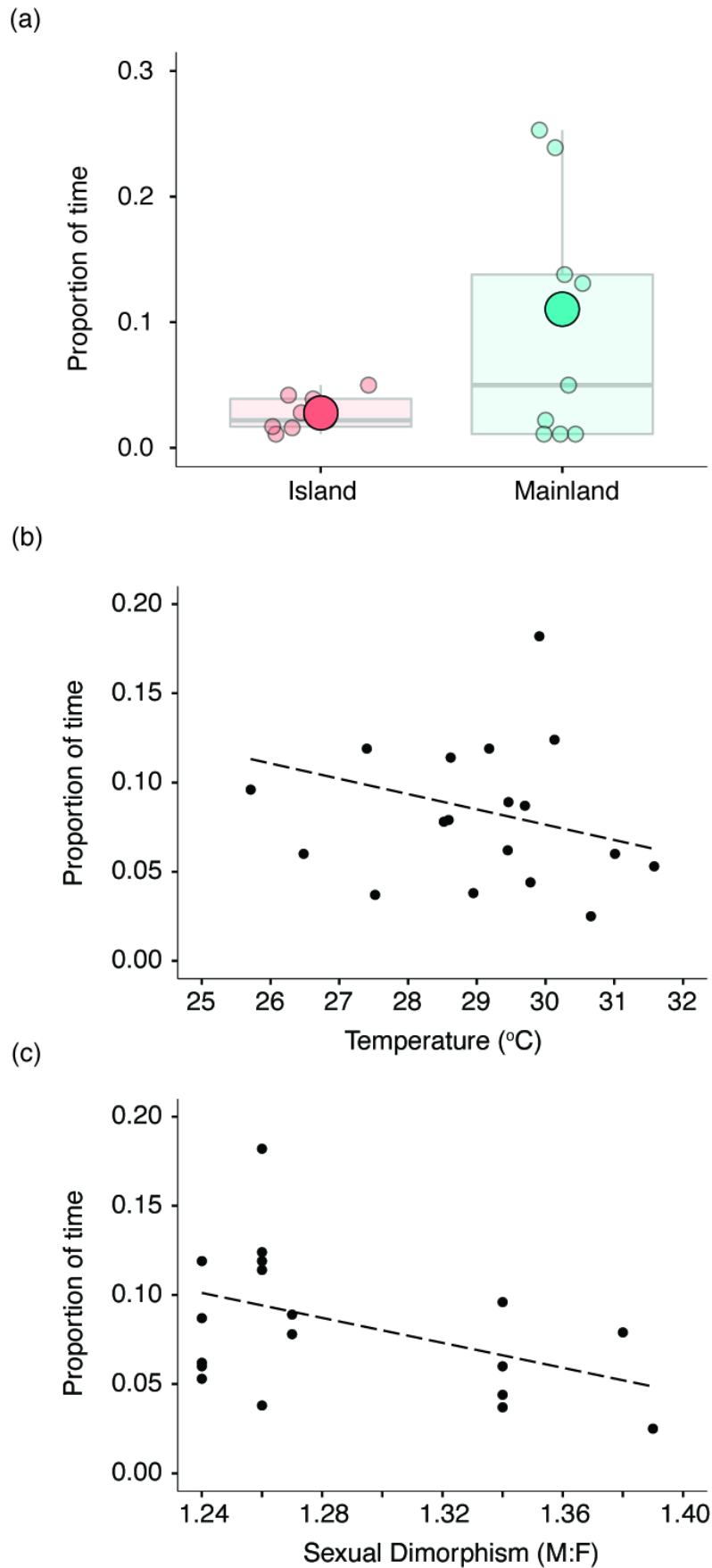**Figure 3.9** Predicted proportion of time signalling as a function of the (a) island effect for females and (b) temperature and (c) sexual dimorphism for males. Dashed lines represent a non-significant trend.

Model outcomes for examining variation in male behaviour are reported in Table 3.4. A quadratic temperature model was the best performing model for explaining exploratory behaviour (Table 3.4a; Figure 3.7c), although the parameters were not significant. However, (linear) temperature featured in other top models and was found to be significant in these (Table 3.4a), presenting a negative relationship with time spent exploring (Figure 3.7d). Variation in time spent signalling was best explained by (linear) temperature and SSD (Table 3.4c), suggesting a non-significant decrease in the proportion of time signalling as the temperature and SSD increases (Figure 3.9 b and c, respectively). The *null* model was the best performing model in explaining variation in social interactions and territorial behaviour, with none of the top models yielding significant parameters (Table 3.4 b, d respectively).

I found some evidence that phylogenetic inertia may have influenced behaviour as the *null* model was found to be either the best supported model or among the top models. However, phylogenetic signal analyses returned significant outcomes only for exploring behaviour of males (Figure 3.3a; Table S3.2); note that the null model was in fact more than 2 ΔAIC_c from the top model (Table 3.4a).

Table 3.4 Delta Akaike's information criterion (ΔAICc) and t-score parameter of phylogenetic regressions models for male behaviour. Values in bold highlight statistically significant values (|t-score|> 1.96).

(a) Explore

Rank	Model Structure	ΔAICc	*Model parameter T-score*
	Top models		
1	Quadratic Temperature (QT)	0	*QT: -1.84 and 1.76*
2	QT + Sex Ratio	0.97	*QT: -1.38 and 1.31; Sex Ratio: -0.91*
3	Temperature + Sex Ratio	1.04	***Temperature: -2.11;*** *Sex Ratio: -1.45*
4	Temperature	1.39	***Temperature: -2.21***
5	QT + SSD	1.92	*QT: -1.80 and 1.72; SSD: -0.25*
6	QT + LizardNo	1.99	*QT: -1.65 and 1.58; LizardNo: -1.04*

Table 3.4 (Continued)

Rank	Model Structure	ΔAICc		Model parameter T-score	
	Other models		*Rank*	*Model Structure*	*ΔAICc*
7	Null Model	2.44	12	LizardNo + Sex Ratio	3.72
8	Temperature + LizardNo	2.95	13	SSD + Sex Ratio	3.98
9	Sex Ratio	2.99	14	SSD	4.44
10	Temperature + SSD	3.38	15	LizardNo + SSD	5.53
11	LizardNo	3.64			

(b) Social Interactions

Rank	Model Structure	ΔAICc	*Model parameter T-score*		
	Top models				
1	Null Model	0	*(Intercept only): 8.466*		
2	Sex Ratio	1.19	*Sex Ratio: -0.86*		
3	IslandEffect	1.39	*IslandEffect: -0.74*		
4	Temperature	1.50	*Temperature: -0-.01*		
5	LizardNo	1.57	*LizardNo: -0.62*		
6	SSD	1.96	*SSD: -0.20*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
7	Null Model	2.10	18	QT + IslandEffect	3.36
8	Sex Ratio + IslandEffect	2.37	19	Temperature + SSD	3.50
9	Temperature + LizardNo	2.46	20	LizardNo + MicroHeight	3.71
10	Temperature + Sex Ratio	2.50	21	Temperature + MicroHeight	3.81
11	LizardNo + Sex Ratio	2.85	22	SSD + MicroHeight	3.95
12	LizardNo + IslandEffect	2.87	23	MicroHeight + IslandEffect	3.96
13	QT	2.97	24	MicroHeight + Sex Ratio	4.10
14	SSD + Sex Ratio	3.09	25	QT + LizardNo	4.27

Table 3.4 (Continued)

(b) Social Interactions

	Other models		Rank	Model Structure	ΔAICc
15	LizardNo + SSD	3.20	26	QT + Sex Ratio	4.34
16	Temperature + IslandEffect	3.21	27	QT + SSD	4.96
17	SSD + IslandEffect	3.36	28	QT + MicroHeight	5.68

(c) Signalling

Rank	Model Structure	ΔAICc	Model parameter T-score
	Top models		
1	Temperature + SSD	0	*Temperature: -1.46; SSD: -1.72*
2	SSD	0.37	*SSD: -0.64*
3	Null Model	0.51	*(Intercept only): 7.39*
4	IslandEffect	0.89	*IslandEffect: -0-.01*
5	Temperature	1.04	*Temperature: -1.21*
6	QT + SSD	1.80	*QT: -0.40 and 0.35; SSD: -1.64*
7	LizardNo + SSD	1.98	*LizardNo: -0.58; SSD: -1.52*

	Other models		Rank	Model Structure	ΔAICc
8	Temperature + IslandEffect	2.24	15	Sex ratio + SSD	2.31
9	Sex Ratio	2.45	16	Temperature + Sex Ratio	3.02
10	LizardNo	2.50	17	QT + IslandEffect	3.92
11	QT	2.79	18	LizardNo + Sex Ratio	4.44
12	Temperature + LizardNo	2.90	19	QT + LizardNo	4.71
13	LizardNo + IslandEffect	2.86	20	QT + Sex Ratio	4.79
14	Sex Ratio + IslandEffect	2.59			

Table 3.4 (Continued)

(d) Territorial Behaviour

Rank	Model Structure	ΔAICc	*Model parameter T-score*		
	Top models				
1	Null Model	0	**(Intercept only): 2.61**		
2	QT	1.65	*SSD: -0.64*		
3	LizardNo	1.76	*LizardNo: -0.46*		
4	IslandEffect	1.95	*IslandEffect: 0.21*		
5	Sex Ratio	1.99	*Sex Ratio: 0.80;*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
6	SSD	2.00	14	LizardNo + SSD	3.66
7	Temperature	2.00	15	LizardNo + IslandEffect	3.73
8	QT + LizardNo	2.43	16	LizardNo + Sex Ratio	3.74
9	QT + Sex Ratio	3.40	17	Sex Ratio + IslandEffect	3.94
10	QT + IslandEffect	3.60	18	SSD + IslandEffect	3.95
11	QT + SSD	3.64	19	SSD + Sex Ratio	3.99
12	Temperature + LizardNo	3.74	20	Temperature + Sex Ratio	3.99
13	Temperature + IslandEffect	3.95	21	Temperature + SSD	3.99

Phylogenetic comparative analysis of display structure

I constructed 11 models to examine each of the principal components summarising display

structure (Table 3.5). The top model for PC1 comprised NMDS1 and NMDS2 along with SSD. I

depict the predicted relationship between NMDS1, NMDS2 and PC1 scores in Figure 3.10a. A

modest positive relationship is apparent between NMDS1 and PC1 scores such that low PC1

scores, which reflect higher amplitude displays of longer duration, are exhibited in the shrubbier

environments. Low PC1 scores were also associated with higher SSD (Figure 3.11a).

Table 3.5 Delta Akaike's information criterion (ΔAICc) and t-score parameter of phylogenetic regressions models for principal components summarizing male displays. Values in bold highlight statistically significant values when > 1.96 for t-score.

(a) Display structure - PC1

Rank	Model Structure	ΔAICc	Model parameter T-score		
	Top models				
1	NMDS1 + NMDS2 + SSD	0	*NMDS1: 1.77; NMDS2: -0.57; SSD: -1.64*		
2	NMDS1 + NMDS2	1.41	*NMDS1: 1.11; NMDS2: -1.29*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
3	NMDS1 + NMDS2 + LizardNo	3.22	8	SSD + Wind	6.19
4	SSD		9	LizardNo	6.80
5	NMDS1 + NMDS2 + Wind		10	Wind	7.14
6	Null Model	4.81	11	LizardNo + Wind	8.83
7	LizardNo + SSD	5.85			

(b) Display structure – PC2

Rank	Model Structure	ΔAICc	Model parameter T-score		
	Top models				
1	LizardNo + Wind	0	*LizardNo: 1.93; Wind: -1.13;*		
2	Null model	1.41	*(Intercept only): 1.73*		
3	Wind	1.70	*Wind: 1.73*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
4	SSD + Wind	3.15	8	NMDS1 + NMDS2 + SSD	4.15
5	SSD	3.36	9	NMDS1 + NMDS2	4.42
6	LizardNo	3.45	10	LizardNo + SSD	5.19
7	NMDS1 + NMDS2 + LizardNo	3.77	11	NMDS1 + NMDS2 + Wind	6.98

Table 3.5 (continued)

(c) Display structure – PC3

Rank	Model Structure	ΔAICc	*Model parameter T-score*		
	Top models				
1	NMDS1 + NMDS2 + LizardNo	0	*NMDS1: 2.42; NMDS2: 2.54; SSD: 4.16*		
2	LizardNo + Wind	1.98	*LizardNo: 2.64; Wind: 0.56*		
	Other models		*Rank*	*Model Structure*	*ΔAICc*
3	Null Model	3.08	8	NMDS1 + NMDS2	6.12
4	LizardNo	3.64	9	SSD + Wind	7.27
5	SSD	5.07	10	NMDS1 + NMDS2 + SSD	7.70
6	LizardNo + SSD	5.22	11	NMDS1 + NMDS2 + Wind	8.16
7	Wind	5.29			

However, none of the parameters in the top model reached the significance threshold, nor did parameters in the next best model (Table 3.5a). The number of lizards and wind speeds featured in the best supported model for PC2 (Table 3.5b). Both exhibited negative relationships with PC2 scores (Figure 3.11b, c respectively), suggesting that slower speeds and lower amplitudes are utilised when there are more lizards in the population and prevailing wind is stronger. However, once again they both failed to achieve significance (Table 5.3b). There was a different outcome for PC3. NMDS1 and NMDS2 featured in the top model along with the number of individuals (Table 5.3c), although here each of the parameters were significant. A strong positive relationship was observed between NMDS1 and 2 and PC3 scores (Figure 3.10b). Low PC3 scores are indicative of displays that start fast and achieve high amplitudes before reducing in speed and amplitude over the course of the display. These are characteristic of displays of populations in shrubby environments, though not so much in habitats featuring herbs and forbs. PC3 scores exhibited a positive relationship with the number of individuals in the population (Figure 3.11d), suggesting displays that increase in speed and amplitude over the course of the display were associated with

higher population size. The encounter rate also yielded a significant parameter estimate in the second-best model (which featured by the number of lizards and wind), yielding a significant positive relationship between number of lizards and PC3 score (Figure 3.11d). In the case of the display traits evolution, it appeared that they varied independent of phylogeny as phylogenetic signal tests failed to distinguished estimates from zero (Table S3.2) and the AICc values ranked the null models higher than among the best fitted (Table 3.5).
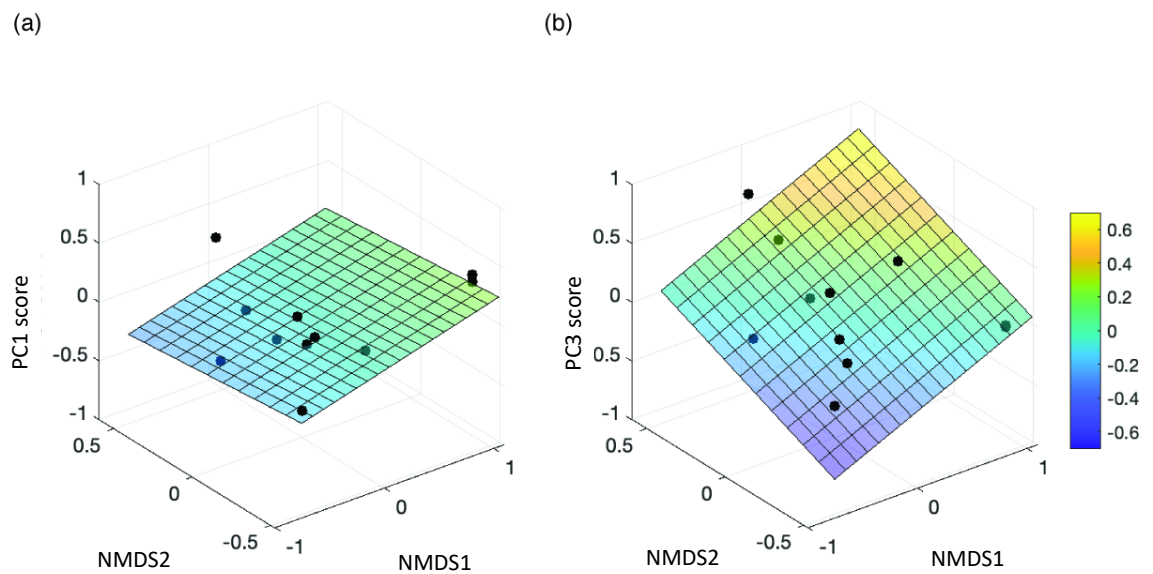
Figure 3.10 Predicted principal component scores for (a) PC1 (high burst number with low amplitude and short duration) and (b) PC3 (burst speed and amplitude increasing over time) summarising male territorial displays as a function of vegetation composition NMDS1 and NMDS2 (see text for details). Relationships in (b) are significant, while relationships in (a) are not significant.
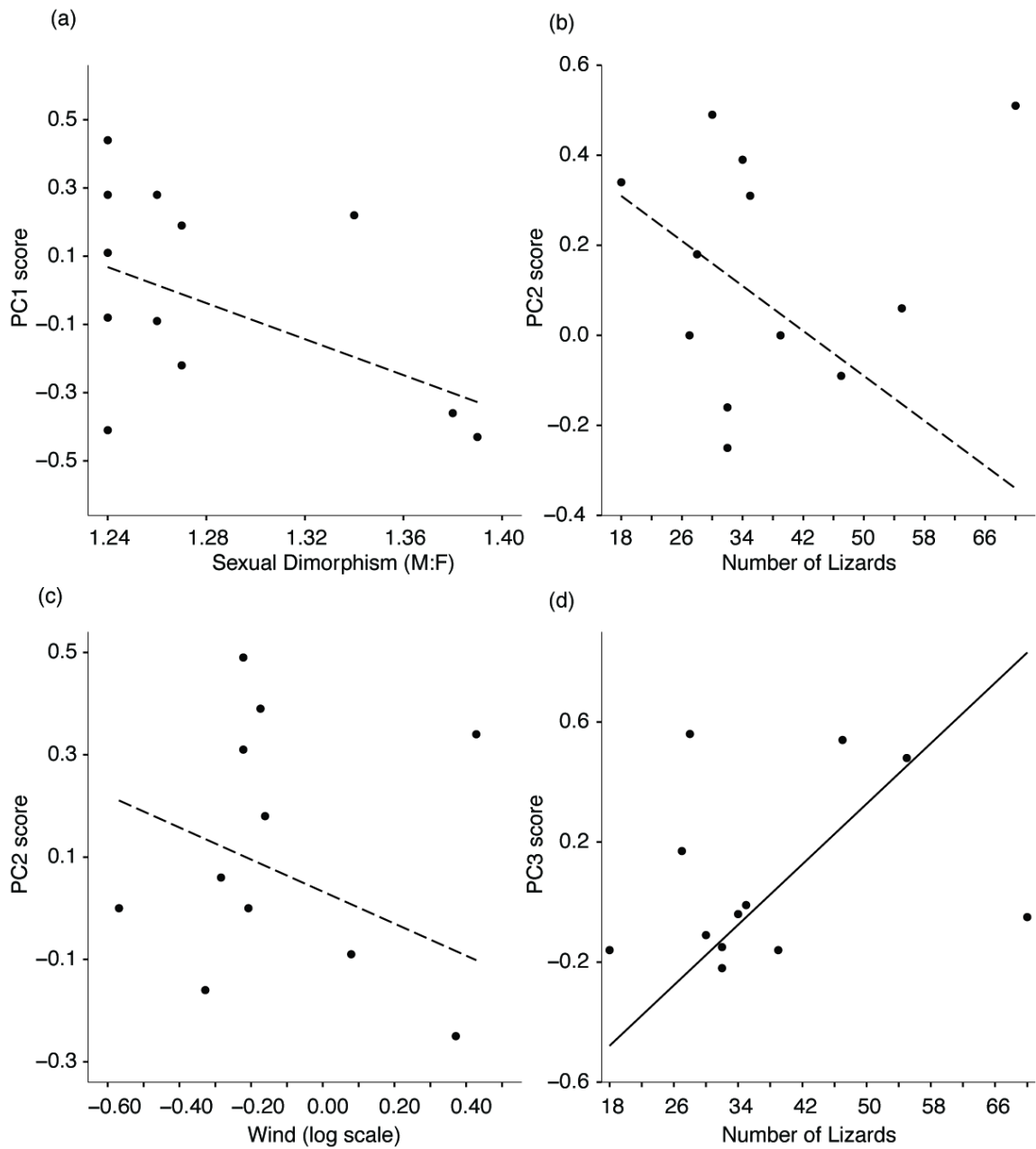
Figure 3.11 (a) Predicted PC1 (high burst number with low amplitude and short duration) score as a function of sexual size dimorphism. Predicted PC2 (faster burst speed with increasing burst duration) scores as a function of (b) the number of individuals and (c) wind. (d) Predicted PC3 (burst speed and amplitude increasing over time) score as a function of the number of lizards in the population. Solid line represents a significant relationship and dashed lines indicate a non-significant trend.

Discussion

The behaviour of Ecuadorian lava lizards was influenced by social, environmental, and ecological factors. As my study species have only relatively recently diverged, and I was controlling for evolutionary history, my study provides further evidence that behaviour can be plastic and related to local conditions. Social factors influenced female behaviour with the number of lizards and sex ratio as significant predictors of the proportion of time engaged in social interactions and were implicated in predicting exploratory behaviour. In addition, females of island populations spent significantly less time signalling than mainland females. Temperature, an environmental factor, was a strong predictor of male behaviour, with increasing temperatures associated with less time exploring. Interestingly, I found a trend toward reduced signalling as temperature increased, which could be a by-product of lower exploration resulting in fewer encounters with conspecifics. Also worthy of further research is the trend for males to signal less in populations with greater male-biased size dimorphism. Ecological factors appear to be important determinants of signal structure at a population level. Species that occur in shrub dominated habitats were found to commence displays at higher speeds and amplitudes, reducing as the display progresses. This measure of signal structure was also predicted by the number of lizards present, with males increasing speed and amplitude of display movements over the course of the display as the population size increased. All of the aforementioned traits represent characteristics that appear to have shifted independently of their phylogenetic history and are ideal candidates to understand behavioural divergence among species.

Sexual selection mechanisms help to explain behavioural and morphological adaptations influencing mate choice and sociality (Ancona et al., 2017; Clutton-Brock, 2009; Muralidhar & Johnson, 2017). In lizards, the effects of sexual size dimorphism (Angel et al., 2015; Blanckenhorn, 2005; Johnson & Wade, 2010; Ord et al., 2001) and population sex ratio (Ancona et al., 2017) are among the most common factors influencing variation in signal structure (Ord et al., 2001) and

the production of striking ornaments (Chen et al., 2012). I considered both sexual size dimorphism and sex ratio in the present study; however, sex ratio provided strong predictive power only for social interactions in females. Populations skewed towards females spent relatively more time engaged in social interactions, which might reflect higher intrasexual competition among females for breeding opportunities and resources (Clutton-Brock, 2009; Koening, 2017). In fact, a positive trend for encounter rate and time spent on social interactions for females may also be related to the sex ratio of lava lizard populations, because more abundant populations will have more females. A study of *M. bivittatus* on San Cristobal island (Koening, 2017), which had the second highest number of lizards among my study sites, showed that females tend to interact more with other females as they compete more intensely for resources needed for successful reproduction and offspring (Clutton-Brock, 2009; Stamps et al., 1997).

Meanwhile, the impact of ecological release, which is anticipated by the island effect, was the best predictor of signalling behaviour in females. Island species experience different selection pressures including lower predation and resource competition that can trigger significant differences with mainland species (Brock et al., 2015; Pinto et al., 2008; Stuart et al., 2012). Mainland populations were indeed different from the island with greater encounter rates, species distributed with congeners like *M. occipitalis* and *M. peruvianus*, and even different habitat composition. Therefore, consistent with previous research (Raia et al., 2010; Watkins, 1997), mainland females in my study spent more time signalling probably in response to different selection pressures that increase competition (Martins et al., 2004; Peters et al., 2016). Behavioural traits related to communication systems play an important role in species fitness and survival rates, but also in species recognition for mainland populations (Garcia et al., 2020; Ord et al., 2001, 2002). Thus, finding traits that allow us to explore further the variation among mainland and island populations is important for understand different evolutive and speciation processes among closely related species.

As ectotherms, lizard activity is highly constrained by temperature and can limit the performance of certain behaviours (Angilletta, 2006; Angilletta et al., 2002). My results show that lava lizards are no exception as temperature was among the top models for exploring and signalling behaviours. However, only explore for males showed a significant negative relationship, with high peaks of activity around 26 to 27°C consistent with previous studies in lava lizards (Farina et al., 2008; Rowe et al., 2020; Sepúlveda et al., 2008). Gunderson and Leal (2016) suggest a performance model, where the curve for the performance of a behaviour and the ambient temperature should have similar shape as the curve for maximal performance versus temperature. To test this I used the quadratic temperature model that provides a fair estimate of the performance curve relative to the function (Angilletta, 2006; Ord & Stamps, 2017). For exploring and signalling behaviours this model appeared among the top models, yet it did not reach the significance threshold. However, the model with a linear fit for temperature did reach significance depicting a negative trend probably because my sampling time limited the range of ambient temperatures. Yet, as it has been previously stated, I suspect that after midday when the temperature gets cooler the proportion of both behaviours will be lower.

Notwithstanding my sampling limitations, it is clear that at least exploring behaviour is dependent on ambient temperature in a manner that is congruent with previously reported relationships between activity and temperature in lizards (Foà & Bertolucci, 2001; Gordon et al., 2010; Hertz et al., 1982; Ord & Stamps, 2017; Stapley, 2006; Werner et al., 2006). Given that this temperature dependence dictates several physiological processes in lizards, it is not surprising that exploring behaviour for males also exhibited strong phylogenetic signal. However, given the AIC$_c$ value for the null model was above 2, it is more likely that exploring behaviour differs among taxa adaptively reflecting the influence of temperature (Ord & Garcia-Porta, 2012). The null model was also the top model for social interactions and territorial behaviours of males and exploration by females, but none of these exhibited strong phylogenetic signal. In these cases, it could be that ecological or external factors not measured in my study are contributing to behavioural diversity

(Clark et al., 2015; Ord & Garcia-Porta, 2012), or is constrained by my limited sample size. Low statistical power may indeed explain why some high-ranking models did not feature significant parameters. Of particular note here is exploring behaviour by females which suggested social factors might be affecting exploring behaviour, with the trend suggesting females reduce their activity as the number of lizards in the population increases and when populations are more male-biased. I encourage further consideration of these relationships across a larger sample size.

With this project I have been able to update and accurately represent the male territorial display, which has received little attention since Carpenter (1966, 1977). My results also contrast with Clark et al. (2015) in which display structure of Galápagos lizards was not related to colonisation, island effect and male-male competition. In accordance with Carpenter's descriptions, displays featured a series of head bobs in rapid succession, but varying in terms of duration, amplitude, and speed of movement across species. I quantified these displays in multiple ways before reducing the number of variables using PCA. Phylogenetic regression analysis suggested a significant influence of vegetation structure and the number of lizards in the population, with wind and sexual size dimorphism also influential though not quite statistically significant. Lizards occupying sites with greater amount of shrub vegetation generated displays that reduced in speed and amplitude over the course of the display. Ord et al. (2007) suggests that lizards might increase movement speed to improve communication in visually noisy environments. In that case, it is possible that males might be displaying faster at the beginning of the display to ensure reliable detection. Moreover, shrub dominated microhabitats appeared to also be slightly relevant for display amplitude and duration, where males exhibit higher amplitudes and longer duration. Fleishman (1992) stated that display amplitude tends to increase as needed for the display to be effectively visible. Fleishman and Pallus (2010) predicted that high amplitude displays may allow signals to be transmitted not only to the contender but also to other (distant) conspecifics, which is supported by Steinberg and Leal (2013) who showed that higher amplitudes were used for more distant receivers. Population density often impacts male-male

competition and female choice where males face more intense intrasexual competition at higher

densities (Jirotkul, 1999). In the present study, displays that increase in amplitude over time were

predicted in populations with more lizards, which might reflect an attempt to increase the active

space of the signal, targeting other individuals in the population. Further consideration of the

effect of population structure, including the number of individuals and the sex ratio, is warranted.

Prevailing wind conditions can reduce signal detection (Peters, 2008) and promote

structural modifications (Peters et al., 2007) by lizards. Wind did not quite achieve significance in

my study but was featured in top models in relation to PC2 (sequence and burst speeds). Here the

trend was for lower display speeds in populations experiencing higher wind conditions. My results

are somewhat puzzling given that plant movement is driven by wind and greater plant movement

is associated with faster display speeds in *Anolis* lizards (Ord et al., 2007). Importantly, previous

work relates wind conditions at the time of signalling rather than population averages, which I

have used, and so more focussed investigations are needed. Furthermore, as suggested by Peters

et al. (2008) the efficacy benefit of speed adjustments depends strongly on the proximity of

lizards to plants. Consequently, future research should note signaller-plant distances, measure

wind at the time of signalling and how the wind effects plant movements.

My findings propose that evolutionary history has not constrained behaviour, with

extrinsic ecological, environmental, and social factors playing an important role in lava lizard

behavioural evolution. The snapshot I have taken is far from the full picture, as various

behavioural traits were not predicted by the parameters I have used. However, I suspect that

there are extrinsic factors acting on these traits. Some of the factors I have considered demand

further attention, such as sexual size dimorphism, which appeared in several top models but

failed to reach the significance threshold. Also, there are other factors that I was not able to

consider that are recommended for future research, including predation and seasonality, with the

latter necessary to understand behavioural responses to changing environmental conditions.

There is also considerable support for detailed investigations within populations to examine, for example, ecological factors affecting variation in lava lizard display structure. I was fortunate to be able to work across the mainland and several islands of the Galápagos, but my sample size was relatively low and so it would be advantageous to add observations of additional populations as well as observations of the four Galápagos species I was not able to study. Clearly, *Microlophus* is a diverse and fascinating group that has much more to offer on the proximate and ultimate causes of animal behaviour.

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Appendix

Table S3.1 Summary of the proportion of time engaged in each behaviour by population and sex.

			Females		Males	
Category	**Behaviours**	**Species (Population)**	**N**	**Prop**	**N**	**Prop**
Active	Jump, Leg raised, Licking, Scratching, Spins, Tail movement	*M. albemarlensis* (CC)	1	0.011	1	0.011
		M. peruvianus (EP)	-	-	1	0.022
		M. indefatigabilis (Garr)	1	0.011	1	0.022
		M. occipitalis (Fra)	-	-	2	0.045
		M. bivittatus (CI)	2	0.011	-	-
		M. grayii (Lob)	3	0.011	-	-
		M. occipitalis (Fra)	3	0.031	-	-
		M. albemarlensis (ML)	1	0.011	1	0.022
		M. indefatigabilis (PNG)	-	-	3	0.011
		M. jacobi (PEsp)	1	0.011	-	-
		M. indefatigabilis (TB)	2	0.011	4	0.014
Explore	Climb, Digging, Walk	*M. peruvianus* (Anc)	2	0.122	2	0.072
		M. albemarlensis (CC)	4	0.031	6	0.050
		M. occipitalis (CA)	4	0.155	4	0.110
		M. occipitalis (Chan)	1	0.075	1	0.114
		M. peruvianus (Chan)	2	0.048	2	0.110
		M. occipitalis (EP)	2	0.089	2	0.092
		M. peruvianus (EP)	1	0.295	2	0.222
		M. indefatigabilis (Garr)	7	0.092	6	0.048
		M. bivittatus (CI)	6	0.063	4	0.056
		M. occipitalis (Choc)	1	0.205	2	0.110
		M. peruvianus (Choc)	2	0.189	1	0.144
		M. grayii (Lob)	4	0.050	5	0.031
		M. occipitalis (Fra)	3	0.074	3	0.086
		M. albemarlensis (ML)	4	0.042	4	0.058
		M. duncanensis (PEsc)	6	0.044	5	0.033
		M. jacobi (PEsp)	6	0.041	5	0.016
		M. indefatigabilis (PNG)	5	0.064	5	0.058
		M. indefatigabilis (TB)	9	0.028	4	0.047

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Category	Behaviours	Species (Population)	Females		Males	
			N	Prop	N	Prop
Foraging	Drinking, Foraging, Snout in dirt	*M. peruvianus* (Anc)	2	0.072	1	0.167
		M. albemarlensis (CC)	4	0.025	2	0.017
		M. occipitalis (CA)	4	0.090	3	0.059
		M. occipitalis (Chan)	-	-	1	0.057
		M. peruvianus (Chan)	2	0.195	2	0.055
		M. occipitalis (EP)	2	0.256	2	0.124
		M. peruvianus (EP)	1	0.016	2	0.044
		M. indefatigabilis (Garr)	5	0.087	5	0.029
		M. bivittatus (CI)	3	0.026	1	0.078
		M. occipitalis (Choc)	1	0.102	2	0.061
		M. peruvianus (Choc)	2	0.044	1	0.022
		M. grayii (Lob)	4	0.033	2	0.017
		M. occipitalis (Fra)	3	0.069	3	0.047
		M. albemarlensis (ML)	4	0.042	2	0.022
		M. duncanensis (PEsc)	4	0.042	3	0.019
		M. jacobi (PEsp)	4	0.042	4	0.053
		M. indefatigabilis (PNG)	5	0.089	5	0.053
		M. indefatigabilis (TB)	5	0.109	5	0.044
Hide	Buried, Hiding, Rain shelter	*M. albemarlensis* (CC)	1	0.211	-	-
		M. peruvianus (EP)	1	0.082	-	-
		M. bivittatus (CI)	1	0.015	1	0.033
		M. grayii (Lob)	-	-	1	0.056
		M. occipitalis (Fra)	-	-	1	0.096
		M. jacobi (PEsp)	-	-	1	0.078
		M. indefatigabilis (TB)	1	0.189	1	0.156
Interactions other species		*M. albemarlensis* (CC)	1	0.022	-	-
		M. occipitalis (CA)	3	0.026	2	0.083
		M. occipitalis (EP)	1	0.011	2	0.026
		M. indefatigabilis (Garr)	4	0.014	3	0.011
		M. occipitalis (Choc)	1	0.011	2	0.035
		M. duncanensis (PEsc)	-	-	1	0.011
		M. jacobi (PEsp)	1	0.022	2	0.072

Category	Behaviours	Species (Population)	Females		Males	
			N	Prop	N	Prop
		M. indefatigabilis (PNG)	1	0.011	4	0.014
		M. indefatigabilis (TB)	2	0.011	1	0.033
Out of sight		*M. peruvianus* (Anc)	1	0.289	2	0.328
		M. albemarlensis (CC)	2	0.083	2	0.017
		M. peruvianus (Chan)	1	0.033	2	0.068
		M. peruvianus (EP)	1	0.016	1	0.167
		M. indefatigabilis (Garr)	4	0.075	5	0.104
		M. bivittatus (CI)	2	0.039	3	0.033
		M. grayii (Lob)	4	0.117	3	0.133
		M. albemarlensis (ML)	3	0.037	4	0.283
		M. duncanensis (PEsc)	4	0.144	4	0.056
		M. jacobi (PEsp)	3	0.089	2	0.089
		M. indefatigabilis (PNG)	3	0.048	5	0.256
		M. indefatigabilis (TB)	4	0.039	4	0.369
Signalling	Push ups, Head bobs	*M. peruvianus* (Anc)	2	0.011	3	0.037
		M. albemarlensis (CC)	2	0.017	4	0.119
		M. occipitalis (CA)	4	0.253	6	0.124
		M. occipitalis (Chan)	1	0.050	2	0.114
		M. peruvianus (Chan)	1	0.022	2	0.060
		M. occipitalis (EP)	2	0.239	2	0.118
		M. peruvianus (EP)	1	0.131	3	0.096
		M. indefatigabilis (Garr)	4	0.039	5	0.087
		M. bivittatus (CI)	5	0.042	7	0.079
		M. occipitalis (Choc)	1	0.011	4	0.182
		M. peruvianus (Choc)	1	0.011	2	0.044
		M. grayii (Lob)	2	0.050	6	0.078
		M. occipitalis (Fra)	3	0.138	6	0.038
		M. albemarlensis (ML)	3	0.022	5	0.053
		M. duncanensis (PEsc)	3	0.011	5	0.089
		M. jacobi (PEsp)	4	0.022	8	0.025
		M. indefatigabilis (PNG)	5	0.016	7	0.062
		M. indefatigabilis (TB)	2	0.028	5	0.060

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Category	Behaviours	Species (Population)	Females		Males	
			N	Prop	N	Prop
Social interactions	Mating, Social interactions, Tail raised	*M. peruvianus* (Anc)	2	0.011	1	0.056
		M. albemarlensis (CC)	4	0.056	6	0.094
		M. occipitalis (CA)	3	0.026	3	0.095
		M. peruvianus (Chan)	2	0.018	2	0.117
		M. occipitalis (EP)	3	0.022	2	0.072
		M. peruvianus (EP)	2	0.057	1	0.067
		M. indefatigabilis (Garr)	4	0.044	7	0.156
		M. bivittatus (CI)	4	0.025	6	0.028
		M. occipitalis (Choc)	2	0.034	3	0.026
		M. peruvianus (Choc)	2	0.022	1	0.144
		M. grayii (Lob)	1	0.011	4	0.086
		M. occipitalis (Fra)	3	0.086	2	0.102
		M. albemarlensis (ML)	4	0.025	4	0.106
		M. duncanensis (PEsc)	-	-	4	0.075
		M. jacobi (PEsp)	1	0.011	1	0.111
		M. indefatigabilis (PNG)	3	0.022	6	0.102
		M. indefatigabilis (TB)	4	0.031	6	0.061
Territorial	Chase, Territorial display	*M. peruvianus* (Anc)	-	-	1	0.344
		M. albemarlensis (CC)	2	0.089	2	0.072
		M. occipitalis (CA)	-	-	2	0.014
		M. occipitalis (Chan)	-	-	1	0.057
		M. occipitalis (EP)	2	0.039	-	-
		M. bivittatus (CI)	4	0.023	3	0.011
		M. occipitalis (Choc)	-	-	2	0.078
		M. grayii (Lob)	2	0.039	1	0.078
		M. occipitalis (Fra)	1	0.033	3	0.016
		M. albemarlensis (ML)	-	-	2	0.028
		M. duncanensis (PEsc)	4	0.011	3	0.037
		M. jacobi (PEsp)	4	0.017	1	0.011
		M. indefatigabilis (PNG)	-	-	1	0.067
		M. indefatigabilis (TB)	-	-	1	0.011

Table continued over page

Category	Behaviours	Species (Population)	Females		Males	
			N	Prop	N	Prop
Thermal	Basking, Shade sites	*M. peruvianus* (Anc)	4	0.319	3	0.144
		M. albemarlensis (CC)	8	0.301	8	0.206
		M. occipitalis (CA)	7	0.239	5	0.405
		M. occipitalis (Chan)	2	0.438	2	0.229
		M. peruvianus (Chan)	4	0.304	4	0.255
		M. occipitalis (EP)	3	0.196	4	0.218
		M. peruvianus (EP)	2	0.172	2	0.408
		M. indefatigabilis (Garr)	10	0.301	9	0.157
		M. bivittatus (CI)	6	0.523	5	0.476
		M. occipitalis (Choc)	2	0.295	4	0.148
		M. peruvianus (Choc)	4	0.361	2	0.244
		M. grayii (Lob)	5	0.482	8	0.224
		M. occipitalis (Fra)	4	0.355	6	0.238
		M. albemarlensis (ML)	8	0.379	8	0.160
		M. duncanensis (PEsc)	8	0.314	8	0.257
		M. jacobi (PEsp)	4	0.619	8	0.272
		M. indefatigabilis (PNG)	9	0.419	8	0.146
		M. indefatigabilis (TB)	8	0.403	9	0.122
Wariness	Alert, Scan high, Scan Low, Predation	*M. albemarlensis* (CC)	6	0.087	2	0.044
		M. occipitalis (CA)	5	0.036	7	0.113
		M. peruvianus (Chan)	2	0.104	3	0.045
		M. occipitalis (EP)	3	0.030	1	0.086
		M. indefatigabilis (Garr)	7	0.030	2	0.046
		M. bivittatus (CI)	6	0.148	2	0.130
		M. occipitalis (Choc)	1	0.011	3	0.035
		M. peruvianus (Choc)	3	0.011	10	0.106
		M. grayii (Lob)	5	0.113	8	0.054
		M. occipitalis (Fra)	4	0.088	3	0.012
		M. albemarlensis (ML)	4	0.086	2	0.056
		M. duncanensis (PEsc)	7	0.057	7	0.097
		M. jacobi (PEsp)	8	0.081	6	0.085
		M. indefatigabilis (PNG)	4	0.042	6	0.091
		M. indefatigabilis (TB)	5	0.082	7	0.090

Table S3.2 Phylogenetic signal parameter of lava lizards' behaviours and display action patterns principal components where PC1 represents a high burst number with low amplitude and short duration, PC2 represents faster bursts speed with increasing duration, and PC3 represents burst speed and amplitude increase over time. Pagel's and Blomberg's K values close to 1 depict the influence of phylogenetic history.

Behaviour	Pagel's		Blomberg's K	
	λ	p	K	p
Explore females	0.29	0.143	0.07	0.228
Explore males	**0.54**	**0.008***	**0.11**	**0.032***
Social interactions females	0.00	1.000	0.07	0.238
Social interactions males	0.11	0.763	0.04	0.571
Signals females	0.31	0.283	0.08	0.185
Signals males	0.21	0.486	0.08	0.116
Territorial males	0.00	1.000	0.01	0.939
Display structure - PC1	0.00	1.000	0.40	0.959
Display structure - PC2	0.00	1.000	0.15	0.189
Display structure - PC3	0.00	1.000	0.13	0.267

Table S3.3 Mean microhabitat height (cm) for substrates selected when engaging a specific behaviour for lava lizards females and males.

	Explore	Social Interactions	Signalling	Territorial
Females				
M. peruvianus (PE)	0.00	10.00	-	-
M. peruvianus (Choc)	0.00	5.00	10.00	-
M. peruvianus (Anc)	112.50	5.00	25.00	-
M. peruvianus (Cha)	75.00	50.00	150.00	-
M. occipitalis (EP)	0.00	0.00	10.00	-
M. occipitalis (Cha)	0.00	-	0.00	-
M. occipitalis (Choc)	0.00	0.00	15.63	0.00
M. occipitalis (Fra)	0.00	5.00	0.00	0.00
M. occipitalis (CA)	0.00	0.00	3.75	-
M. bivittatus (CI)	22.37	10.50	31.00	35.00
M. indefatigabilis (TB)	20.56	22.50	35.00	-
M. indefatigabilis (Garr)	4.29	16.00	38.39	-
M. indefatigabilis (PNG)	9.00	3.33	36.50	-
M. jacobi (PEsp)	23.33	5.00	41.42	0.00
M. duncanensis (PEsc)	4.56	-	5.33	6.25
M. grayii (Lob)	1.38	5.00	5.63	2.00
M. albemarlensis (ML)	2.50	6.67	24.17	-
M. albemarlensis (CC)	12.50	0.00	27.50	0.00
Males				
M. peruvianus (PE)	0.00	0.00	13.33	-
M. peruvianus (Choc)	0.00	0.00	5.00	-
M. peruvianus (Anc)	362.50	3.00	152.50	476.47
M. peruvianus (Cha)	8.75	102.50	30.00	0.00
M. occipitalis (EP)	0.00	5.33	8.87	7.00
M. occipitalis (Cha)	0.00	-	16.17	20.00
M. occipitalis (Choc)	0.00	0.00	13.83	-
M. occipitalis (Fra)	0.00	0.00	0.00	0.00
M. occipitalis (CA)	0.00	16.67	12.22	0.00

	Explore	Social Interactions	Signalling	Territorial
Males				
M. bivittatus (CI)	7.50	14.79	23.29	26.67
M. indefatigabilis (TB)	0.00	20.95	21.78	0.00
M. indefatigabilis (Garr)	37.50	10.48	11.40	-
M. indefatigabilis (PNG)	0.00	8.33	46.48	0.00
M. jacobi (PEsp)	132.00	26.67	79.27	0.00
M. duncanensis (PEsc)	60.20	30.27	100.05	22.95
M. grayii (Lob)	40.00	3.13	26.45	0.00
M. albemarlensis (ML)	0.00	7.50	57.95	7.50
M. albemarlensis (CC)	83.33	66.67	105.00	71.43

Table S3.4 Mean values per population of the ecological variables used on the phylogenetic regression analysis.

	Temperature (ºC)	Wind	Number of lizards	Number of males	Number of females	Sex ratio (M/M+F)	Sexual dimorphism (males)
M. peruvianus (PE)	25.71	4.56	11	2	8	0.20	1.34
M. peruvianus (Choc)	29.78	2.68	18	4	14	0.22	1.34
M. peruvianus (Anc)	27.52	3.27	15	4	11	0.27	1.34
M. peruvianus (Cha)	26.48	4.94	16	3	7	0.30	1.34
M. occipitalis (EP)	29.91	3.56	43	16	20	0.44	1.26
M. occipitalis (Cha)	28.62	3.43	40	19	10	0.66	1.26
M. occipitalis (Choc)	27.4	2.35	32	11	13	0.46	1.26
M. occipitalis (Fra)	28.95	0.00	70	16	27	0.37	1.26
M. occipitalis (CA)	30.13	1.71	37	13	15	0.46	1.26
M. bivittatus (CI)	28.59	0.6	35	10	18	0.36	1.38
M. indefatigabilis (TB)	31.01	0.52	55	10	26	0.28	1.24
M. indefatigabilis (Garr)	29.70	0.67	34	9	15	0.38	1.24
M. indefatigabilis (PNG)	29.45	0.6	30	9	10	0.47	1.24
M. jacobi (PEsp)	30.66	0.62	27	9	7	0.56	1.39
M. duncanensis (PEsc)	29.46	1.20	47	17	25	0.40	1.27
M. grayii (Lob)	28.52	0.69	28	9	5	0.64	1.27
M. albemarlensis (ML)	31.58	0.47	32	6	14	0.33	1.24
M. albemarlensis (CC)	29.18	0.27	39	11	22	0.30	1.24

CHAPTER FOUR

The effect of urbanisation on the behaviour of Galápagos lava lizards (genus *Microlophus*) with insights for forthcoming conservation research

Abstract

The alarming growth of human population and its development worldwide represents a formidable challenge for wildlife. Urbanised areas featured a range of novel stressors such as habitat alteration, introduced predators, new food sources and human disturbance. Insular species are among the most vulnerable as their adaptations associated with the 'Island syndrome', might represent a disadvantage to face the drastic changes introduced by urbanisation. Therefore, species will need to adjust aspects of their behaviour to cope with these novel stressors and survive. Of particular interest are the Galápagos Islands, which have been facing significant anthropogenic impacts for the last 30 years due to increased tourism. My study aims to estimate the impact of urbanisation and wildlife tourism on the behaviour of Galápagos lava lizards, focussing on islands that represent a gradient of urbanisation from highly urbanised to isolated. I hypothesised that Galápagos lava lizards exposed to high urbanisations levels will show human-induced behavioural adjustments. My results suggest that species occurring on highly urbanised islands spent more time active than species on islands with lower levels of urbanisation. At the same time, lizards also showed overall lower levels of vigilance in urban areas. Interestingly, within species comparisons on Santa Cruz Island elucidated a higher vigilance in highly touristic sites; yet vigilance behaviour was generally still lower than on other islands and probably reflected a positive relationship with population abundance. Social interactions seem to be unaffected by urbanisation level. I propose that there are signs of anthropogenic disturbance of Galápagos lava lizards, and provide a basis for future, more comprehensive conservation programs.

Introduction

Urban human population development and land expansion are increasing worldwide at an alarming pace (Bhattacharjee et al., 2015; Dylewski et al., 2020; Kaiser et al., 2018; Thompson & McLachlan, 2007). Urbanisation is among the major causes for modification of natural ecosystems introducing new challenges for resident species. As a meter of fact, it has been demonstrated that urban areas can affect species in various ways where the presence of anthropogenic structures, such as buildings, causes alteration and fragmentation of natural habitats (Battles et al., 2019; Dammhahn et al., 2020). Moreover, urbanisation not only impacts the biotic components of ecosystems including changes to the available food resources (Chapman et al., 2012; Merrall & Evans, 2020), habitat suitability (Lee & Thornton, 2021; Luther & Baptista, 2010), and predation intensity (Gotanda, 2020; Pellitteri-Rosa et al., 2017). But also, can expose species to novel disturbances such as interactions with invasive species and humans that can affect local population density and competition dynamics (Audsley et al., 2006; Ditchkoff et al., 2006; Meffert & Dziock, 2013). Species usually perceive biotic and abiotic changes as additional stressors forcing them to either adjust to these human-modified environments or be excluded from them (Amdekar et al., 2018; Bhattacharjee et al., 2015; Killen et al., 2013). Consequently, it has been widely demonstrated that urbanisation has strong negative impacts on wildlife, and abundant evidence suggests that urban areas often featured a loss of species richness and diversity (Blair, 1996; Blair & Launer, 1997; Piano et al., 2020).

However, human influence on wildlife extends beyond the built environment and includes an increase in human recreational activities like wildlife tourism (Roe et al., 1997). As wildlife watching and photography tourism increases in popularity worldwide, concerns are being raised about the negative impacts of constant human presence and activity on native habitats (Burger & Gochfeld, 1998; Granquist & Sigurjonsdottir, 2014; Li et al., 2017; Roe et al., 1997). Some of these concerns are related to specific species that are sought out by tourists, the frequency of human visitors, type of activities and equipment used, and the long observation periods (Reynolds &

Braithwaite, 2001). Prior research has reported that animals may perceive this direct contact with humans as a form of predatory threat and subsequently alter their physiology (Ditchkoff et al., 2006; Semeniuk et al., 2009; Tablado & D'Amico, 2017) and behaviour (Dammhahn et al., 2020; Hume et al., 2019; Moorhouse et al., 2015; Szott et al., 2019), which may have detrimental consequences (Trave et al., 2017). For example, male African elephants (*Elephas maximus*) tend to increase aggression in the constant presence of tourists (Szott et al., 2019), while polar bears (*Ursus maritimus*) and harbour seals (*Phoca vitulina*) remain vigilant for longer periods (Dyck & Baydack, 2004; Granquist & Sigurjonsdottir, 2014). It is important to mention that these alterations are associated directly with human influence and are common along the environments where animals have direct contact with anthropogenic factors. Therefore, measuring and restraining the negative impacts of humans is key for wildlife conservation.

Island species and their environments are among the most vulnerable to human activities (Steibl & Laforsch, 2019). Insular ecosystems are often the home of unique species that evolve extensive morphological and behavioural changes over a short time, which is often referred to as the 'Island syndrome' (Raia et al., 2010). Therefore, insular species usually exhibit reduced aggressiveness, gradual loss of antipredator behaviours, gigantism, smaller population sizes and greater survival rates (Blumstein & Daniel, 2005; Brock et al., 2015; Butler, 1980; Stuart et al., 2012). It is possible that some of these features represent a disadvantage in the face of drastic changes such as the ones introduced by urbanisation (Blumstein & Daniel, 2005). A common adaptation to cope with these drastic changes is the modification of species personality, which is an individual's characteristic pattern of behaviour that persists across time and different contexts (McEvoy et al., 2015). Moule et al. (2016) observed a link between the active, exploratory and foraging behaviours of an Australian skink (*Lampropholis delicata*), leading to an active-explore behavioural syndrome that tend to increase in urban areas (Moule et al., 2016). In addition, behavioural syndromes such as boldness-tameness usually associated with the effect of island isolation (Blumstein & Daniel, 2005; Cabrera et al., 2017; Cooper et al., 2014; Stratton et al.,

2021), have been also related to occupation of urban areas. Indeed the predation pressures on urbanised habitats are thought to resemble island habitats as natural predators will either be absent (Candler & Bernal, 2015; Faeth et al., 2005) or shifted to novel food resources (Chapman & Jones, 2012; Chejanovski et al., 2017). Nevertheless, urbanisation not only implies the reduction of natural predators but also the introduction of invasive species, such as domestic cats (*Felis catus*)(Medina et al., 2014), and the lack of natural vegetation and shelters. The net impact might be higher predation for island native species that are slow to adapt or are unable to adapt (Audsley et al., 2006; Avilés-Rodríguez & Kolbe, 2019; Berger et al., 2007; Pellitteri-Rosa et al., 2017).

The Galápagos Archipelago is located approximately 960 km west of South America in the Pacific Ocean and supports over 1000 species of birds, reptiles, mammals, plants, and insects, with around half of them considered endemic (Parent et al., 2008). Although 97% of the land is protected as a National Park, factors like a growing human population, the introduction of over 1500 invasive species and a concurrence of more than 200,000 tourists per year, have jeopardised the conservation status of the Galápagos Islands (Benitez-Capistros et al., 2016; Gonzalez et al., 2008; Parent et al., 2008; Rivas-Torres et al., 2018). Due to these threatening processes, the Galápagos Islands were added by UNESCO to the list of World Heritage in Danger in June 2007 (Gonzalez et al., 2008). So far, several studies of Darwin finches species (*Geospiza fuliginosa* and *G. fortis*) (Gotanda, 2020; Grant et al., 2005; Knutie et al., 2019), giant tortoises (*Chelonoidis* spp.) (Benitez-Capistros et al., 2016), marine iguanas (*Amblyrynchus cristatus*) (Berger et al., 2007; French et al., 2010), sea lions (*Zalophus wollebaeki*) (Denkinger et al., 2015; Denkinger et al., 2014), lava lizards (*M. indefatigabilis*) (Tanner et al., 2007; Tanner & Perry, 2007) and marine life (Gonzales-Perez & Cubero-Pardo, 2010) have elucidated numerous negative impacts of urbanisation including modifications to foraging and antipredator behaviours, physiological changes (e.g. high stress-induced levels), introduced diseases and increased mortality from anthropogenic influences (e.g. road kill, introduced predators). However, until 2007, only 3% of

research undertaken on the Galápagos have been related to anthropogenic factors (Watkins, 2008), and these often overlooked groups of endemic Galápagos islands fauna that are equally susceptible to exponential human population growth and tourism activities on the Galápagos archipelago (Brewington et al., 2013; Watkins, 2008).

The first insight of negative human impact on lava lizard (*Microlophus* sp.) populations was reported 15 years ago and relates to roadways on Santa Cruz Island (Tanner et al., 2007; Tanner & Perry, 2007). This research demonstrated that roads reduce the population density of *M. indefatigabilis* and flagged the need for further research; however, little attention has been paid since. Thus, the goal of my study was to explore the impact of the increased anthropogenic influences and tourism on the Galápagos lava lizards. I studied six species from this group, which exhibit complex behavioural features (Carpenter, 1966, 1970). They are widely distributed across the archipelago, but only one species is present per island (Benavides et al., 2009). Importantly, lava lizards are relevant for other endemic species as they fill a variety of ecological roles including prey (Jaramillo et al., 2016), pollinators (Hervías-Parejo et al., 2020), and seed dispersers (Hervias-Parejo et al., 2019). Therefore, both the lava lizards and the Galápagos Islands represent an excellent opportunity to study the impact of urbanisation and wildlife tourism, as the islands present a gradient of urbanisation going from relatively highly populated to isolated islands. I hypothesised that Galápagos lava lizards exposed to high urbanisations levels will show human-induced behavioural shifts such as an increase in time spent active and vigilant. Although I demonstrated in Chapter 3 that this group is responding to their ecological and environmental context rather than being constrained by phylogenetic history, I can't avoid the potential confound that each island features a different species, thus, my results must be considered in that context. However, in an attempt to work around this issue, I took advantage of within island differences in human activity and examined three populations of *M. indefatigabilis* on Santa Cruz Island under varying levels of wildlife tourism. Research on the impact of human influence on the endemic fauna of the Galápagos Islands is still a growing field of interest but there are significant

knowledge gaps for non-emblematic species. My study is amongst the first targeting the responses of Galápagos lava lizards to the rapid human population growth, and provides a basis for future, more comprehensive conservation programs.

Methods

Subjects and study sites

The ten currently proposed Galápagos species of *Microlophus* are presumed to have an asymmetrical radiation after two independent colonisation events from the mainland (Benavides et al., 2009; Kizirian et al., 2004). As a result, two island clades have been recognised and include an eastern radiation consisting of two endemic species inhabiting San Cristobal (*M. bivittatus*) and Marchena (*M. habelii*) islands, and a western radiation of seven species that are located on the southern and western islands (Benavides et al., 2007; Benavides et al., 2009; Kizirian et al., 2004; Van Denburgh & Slevin, 1913). For the purpose of my research, I selected six Galápagos lava lizard species for behavioural observations that enabled me to consider different levels of human occurrence from high to absent (Figure 4.1). In addition, in an attempt to avoid a 'species effect', I selected multiple populations where possible to conduct within species comparisons. All selected species are characterised by strong sexual dimorphism, whereby males are larger than females and exhibit a well-developed dorsal crest (Carpenter, 1966). In addition, cryptic colour patterns with visible grey to bright tones are characteristic of both sexes, which intensify during the breading season starting in November till late April (Clark et al., 2017; Clark et al., 2015; Rowe et al., 2019; Watkins, 1998). All species also exhibit male territorial behaviour and female-defence polygyny due to sex ratios skewed towards females (Clark et al., 2019; Clark et al., 2017; Koening, 2017; Watkins, 1996).
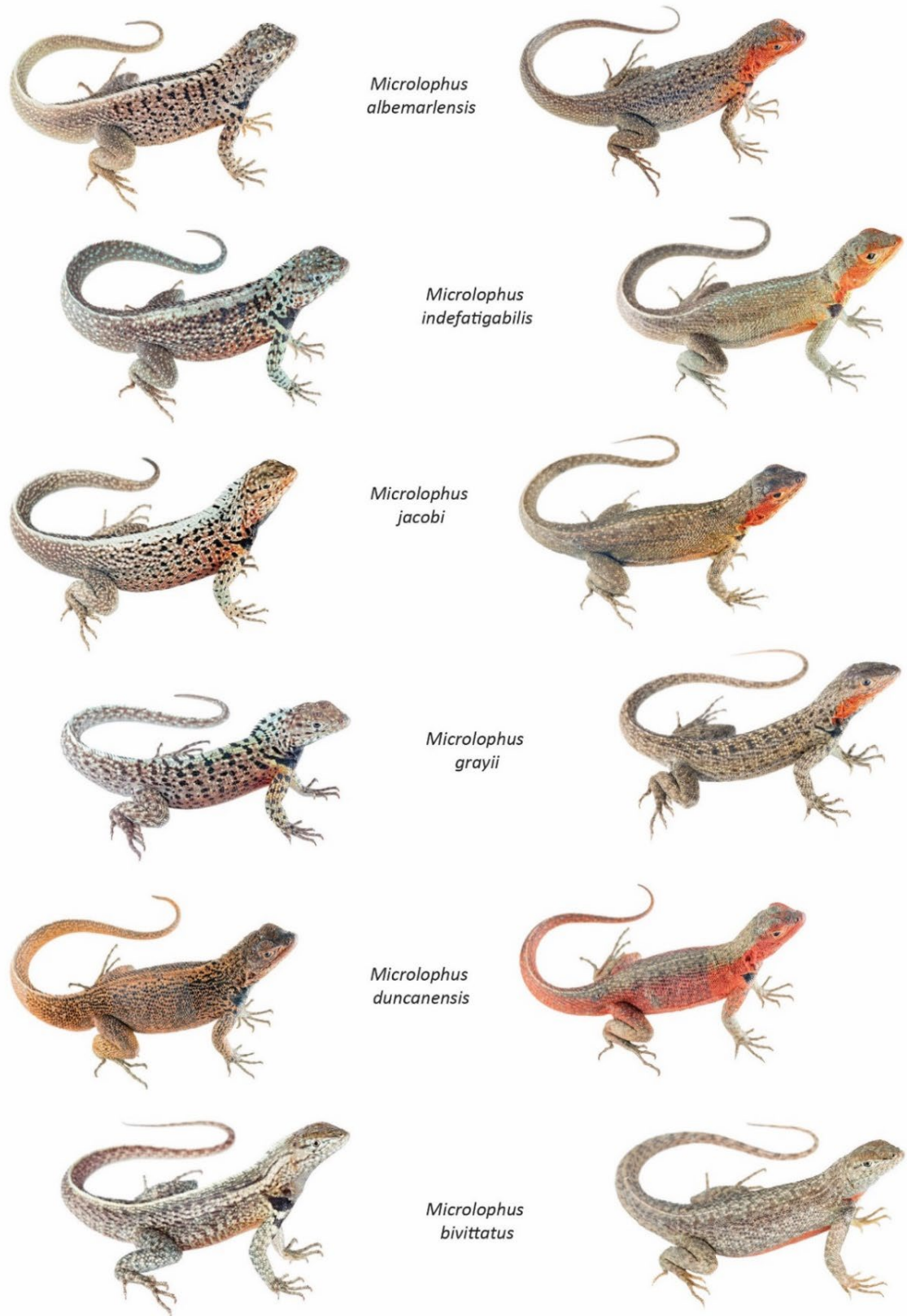
Figure 4.1 – Male (left) and female (right) *Microlophus* species sampled on the Galápagos Islands. Photography by Jose Vieira and Alejandro Artega-Tropical Herping (see https://www.tropicalherping.com) and used with permission.

Fieldwork was carried out from December 2018 to January 2019 (Santa Cruz and Isabella islands) and December 2019 to January 2020 (San Cristobal, Floreana, Santiago and Pinzon islands). Overall, nine localities were surveyed, eight for the Western radiation and one for the Eastern radiation (Figure 4.2 and Table 4.1). The vegetation of the study sites can be classified as deciduous forest and shrubland, which covers around 42% of the archipelago (Ministerio del Ambiente del Ecuador, 2013; Rivas-Torres et al., 2018). However, use of other microhabitats were also recorded including urban areas, coastal humid forest, shrubland and mangrove (Santa Cruz, Santiago, Floreana: see Rivas-Torres et al. (2018); Figure 4.1, Figure S4.1). The timing of the present study coincided with the breeding season (November till July), also known as the hot season on the Galápagos Islands. It is characterised by mean temperatures 5°C warmer than the minima and receive approximately 200mm of rain through the last days of December until May (Rivas-Torres et al., 2018).
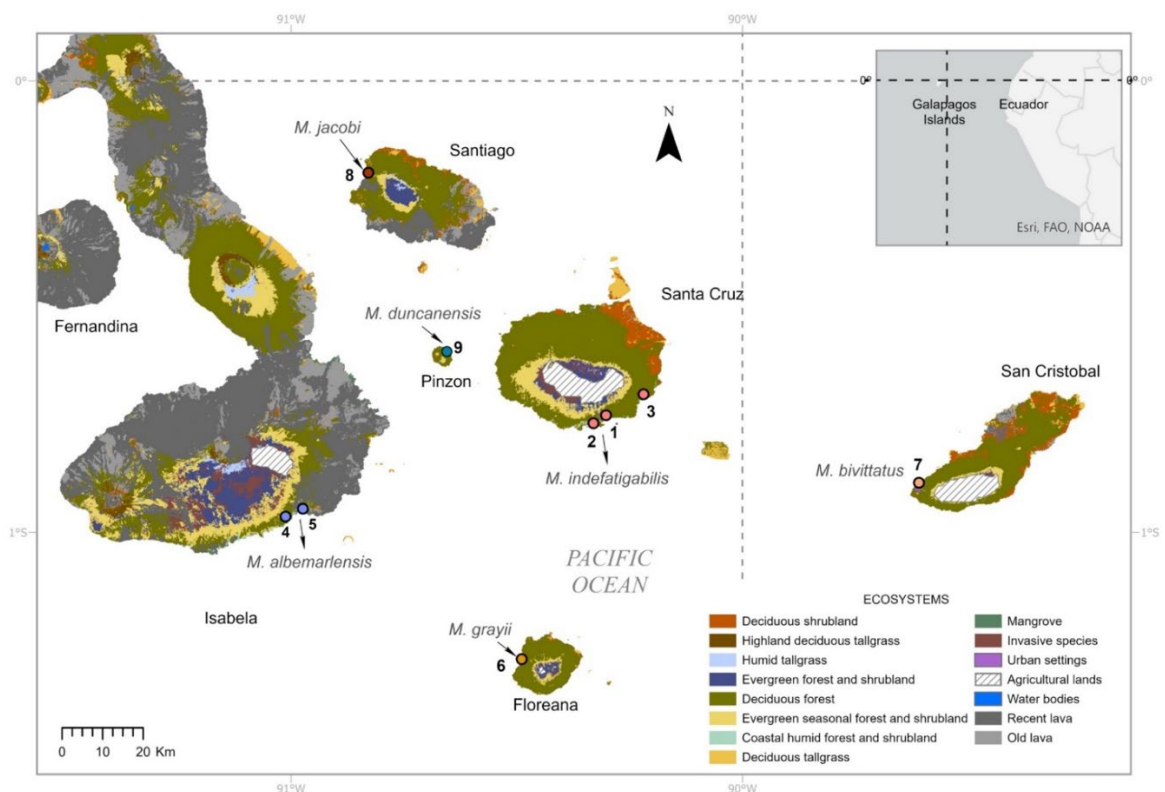
Figure 4.2 – Sampled sites for the six *Microlophus* species on the Galápagos archipelago. Refer Table 4.1 for localities details and Rivas et al (2018) for Galápagos islands vegetation coverage classification map.

Table 4.1 – Sampling locations of *Microlophus* species from the Western and Eastern clade on the Galápagos archipelago.

Map Ref	Island (Urbanisation)	Species (Clade)	Locality	Coordinates	Habitat*
1	Santa Cruz *(High)*	*M. indefatigabilis* (Western clade)	Parque Nacional Galápagos (PNG)[1]	0° 44' 19.3056'' S, 90° 18' 9.0108'' W	Deciduous forest and urban settings
2	Santa Cruz *(High)*	*M. indefatigabilis* (Western clade)	El Garrapatero beach[2]	0° 41' 37.374'' S, 90° 13' 9.7572'' W	Coastal humid forest and shrubland
3	Santa Cruz *(High)*	*M. indefatigabilis* (Western clade)	Tortuga Bay[3]	0° 45' 29.5128'' S, 90° 19' 48.9468'' W	Coastal humid forest, evergreen seasonal forest and shrubland
4	Isabela *(Medium)*	*M. albemarlensis* (Western clade)	Muro de Lágrimas	0° 57' 53.7696'' S, 91° 0' 44.3952'' W	Deciduous forest
5	Isabela *(Medium)*	*M. albemarlensis* (Western clade)	Centro de Crianza "Arnaldo Tupiza Chamaidan"	0° 56' 50.8956'' S, 90° 58' 26.6592'' W	Deciduous forest and urban settings
6	Floreana *(Low)*	*M. grayii* (Western clade)	La Lobería	1° 16' 49.3356'' S, 90° 29' 20.9364'' W	Deciduous forest
7	San Cristobal *(Medium)*	*M. bivittatus* (Eastern clade)	Centro de Interpretación Ambiental Gianni Arismendy	0° 53' 24.3168'' S, 89° 36' 33.6564'' W	Deciduous forest
8	Santiago *(Isolated)*	*M. jacobi* (Western clade)	Playa Espumilla	0° 12' 12.3516'' S, 90° 49' 43.464'' W	Deciduous forest, mangrove, and deciduous tallgrass
9	Pinzon *(Isolated)*	*M. duncanensis* (Western clade)	Playa Escondida	0° 35' 57.8112'' S, 90° 39' 17.8056'' W	Old lava, deciduous tallgrass, and deciduous forest

Numbers represent tourism activity levels where (1) not touristic, (2) mild – 16,000/year, and (3) high – 65,000/year.
*Habitats are classified based on Rivas et al (2018).

Data collection

The data collection strategy consisted of sub-dividing each study site into three non-overlapping linear transects of 4m by 120m, which were located at the edges to enhance the probability of locating lizards in dense vegetation (Maura et al., 2011). Sampling consistency among sites was accomplished by standardising my activities beginning with population size estimation along each transect at the beginning of the day, followed by behavioural observations of adult lizards, which were undertaken across intervening days. Lastly, vegetation assessments surveying the same transect lines were conducted after all other activities.

I estimated the population size by registering all individuals on the left of the path, as well as on the transect itself. This process was carried out by one observer at each transect for three consecutive days during the early morning (0800-0900) (Ruiz de Infante Anton et al., 2013). Age class (adult or juvenile) and sex were also registered during the surveys. To quantify behaviour, I used a partial ethogram of the behavioural repertoire of Galápagos *Microlophus* species (Carpenter, 1966, 1970; Chamorro et al., 2012; Coelho et al., 2018) and personal observations (see Table S4.1). For three to four consecutive days, I undertook focal sampling of adult lizards of both sexes for three hours during the morning (0900-1200) and afternoon (1400-1700), focusing on one transect per day. During focal observations, the activity of a selected individual was registered at two-minute intervals, with both female and male focal lizards observed separately by two trained observers per session. For each morning and afternoon session, different focal animals were chosen and a total of 90 behavioural observations were registered per adult individuals sampled at each locality. In addition to focal observations, environmental conditions including air temperature were measured using a Kestrel-4000 weather meter (Nielsen Kellerman Australia Pty Ltd) every 10 minutes and at the start of each session.

I surveyed the vegetation composition of each sample site using forty points distributed in a zig-zag pattern across each transect at 3 m intervals. This allowed me to characterise the habitat

by placing a touching pole in odd-numbered points located near to the transect edge and even-numbered points positioned 5 m away from the transect path. At each point the substrate type was registered and classified based on the life form: ground cover, herb and forbs, shrubs, woody plants, cactus, and non-vegetation. In addition, the height was scored at 0.1 m increments to 2m height, with vegetation greater than 2m categorized as woody plant.

Statistical Analysis

All statistical analyses were performed in the R statistical environment (RCoreTeam, 2018). I estimated the species encounter rate per population by summing individuals across transects within a given session and using the maximum value across sessions per site (Table S4.1). To compare habitats I computed a non-metric multivariate analysis with Bray-Curtis similarities using the VEGAN package (Oksanen et al., 2010). The ordination depicted habitat structure differences between sample sites, which were compared using an analysis of similarity (ANOSIM). The NMDS analysis showed two-levels of ordinations (stress value: 0.1763) to explain variation among sites in vegetation. Ground cover and shrub were positively correlated with NMDS1, while herbs and forbs were negatively correlated (Figure 4.3). For NMDS2, woody plant and 'nil' correlated negatively, and cactus positively (Figure 4.3).
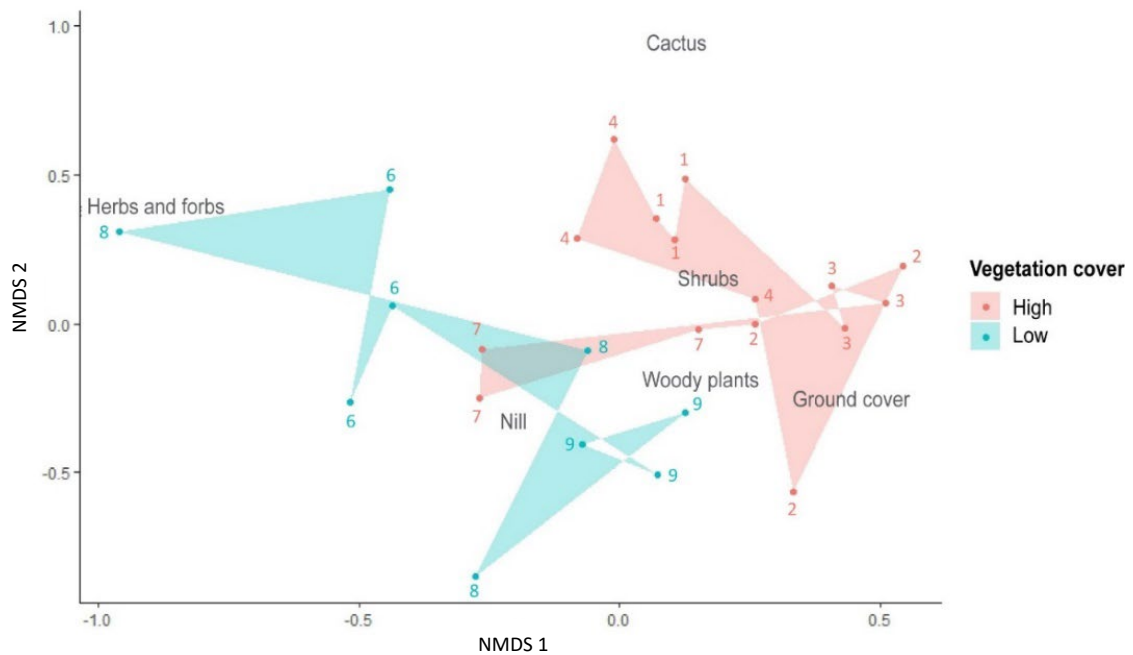
Figure 4.3 – Non-metric multidimensional scaling (NMDS) analysis for vegetation composition on Galápagos islands sampled sites. Site numbers correspond to localities listed on Table 4.1. Vegetation cover levels correspond to shrubs, woody plants, and ground cover as high, and herbs and forbs and 'nil' (absent vegetation) as low based on the background noise environment each vegetation type exerts.

This significant habitat dissimilitude observed among sites on the ordination graph (ANOSIM: r=0.5331, p=0.001) were combined with the Galápagos Islands' vegetation coverage classification published by Rivas-Torres et al. (2018) along with published records of human population for the Galápagos islands (Moncayo Rosero, 2015) to classify my study sites into four levels of urbanisation (*isolated*, *low*, *medium*, and *high* human influence) and two levels of vegetation composition (*high* and *low* vegetation). Santa Cruz, the most populated island (15,000 residents; *high* human influence) was characterised by the presence of various habitats (deciduous forest, urban settings, coastal humid forest, evergreen seasonal forest and shrubland, Table 4.1) with shrubs, woody plants, and ground cover (*high* vegetated, Figure 4.2-4.3). While the next most populated islands, San Cristobal, and Isabela (7,200 and 2,350 residents respectively; *medium* human influence), featured deciduous forest and urban settings mostly with shrubs (*high* vegetated, Table 4.1, Figure 4.2-4.3). Floreana (250 residents; *low* human influence) showed a dominant deciduous forest with herbs and forbs (*low* vegetated, Table 4.1, Figure 4.2-4.3). The uninhabited islands of Santiago and Pinzon (*isolated*) were also characterised by mixed habitats

(Table 4.1). Santiago featured deciduous forest, mangrove, and deciduous tallgrass dominated mostly by woody plants (*low* vegetated, Figure 4.2-4.3). In contrast, Pinzon featured old lava, deciduous tallgrass, and deciduous forest dominated by herbs and forbs (*low* vegetated, Figure 4.2-4.3). Also, for *M. indefatigabilis* on Santa Cruz, I characterised my three study sites based on tourism activity (Caisaguano et al., 2020) to allow me to consider a within island effect: Tortuga Bay is a popular tourist site welcoming 65,000 visitors annually, El Garrapatero receives roughly a quarter of the number of visitors (16,000/year) while the Galápagos National Parks offices is not a tourist destination and has the lowest human visitation (numbers are not available).

My objective was to consider behaviour as a function of human population, as well as environmental influences (ambient temperature) and in the context of ecological differences (population size). I choose to focus on 25 behaviours scored across the sessions based on frequency of occurrence, and as they have been related to possible behavioural syndromes caused by human influence (Moule et al., 2016; Pellitteri-Rosa et al., 2017). I then allocated these behaviours to one of four categories: passive, active, vigilance and interspecific interactions (see Table S4.1). I converted to proportions the data for time spent in each behaviour category and used beta regression models using the *betareg* function from the BETAREG package (Cribari-Neto & Zaileis, 2010). Each behaviour category was analysed separately and individuals that did not exhibit a given behaviour were assigned a score of zero. Values exactly equal to 0 or 1 were adjusted as per Smithson and Verkuilen (2006) using the formula:

$$p\ transformed = \frac{p(n-1) + 0.5}{n}$$

where *p* was the proportion value, and *n* was the sample size. I fitted the regression model with urbanisation levels (i.e., high, medium, low, isolated), temperature, and number of individuals as factors. I report the significance of coefficients in the model, including all six pairwise contrasts for

population level. To analyse within species variation, the same procedure was followed yet only

for *M. indefatigabilis* populations and exploring behaviour as a function of tourism activity (i.e.,

negligible, moderate, and high for PNG, Garrapatero and Tortuga Bay respectively); temperature

and number of individuals were excluded from this model as they were very similar across sites

(Table S4.1).

Results

The proportion of time engaged in active and passive behaviours is shown in Figure 4.4. Beta

regression analysis indicated that there was variation between levels of urbanisation for both

active and passive behaviours, but no effect of temperature and number of lizards in the

population (Table 4.2). The proportion of time engaged in active behaviours was significantly

higher on the island with high levels of urbanisation (Santa Cruz) compared with medium, low,

and isolated islands (Table 4.2, Figure 4.4a). In contrast, the proportion of time engaged in passive

behaviours was significantly lower where there is high human influence compared with isolated

islands (Table 4.2, Figure 4.4b).

Table 4.2 – Outcome from beta regression models examine variation in passive and active behaviour as a function of urbanisation levels, temperature, and abundance.

Parameter		Estimate	SE	z score	p value
Passive Behaviour					
Urbanisation factor					
Isolated v	**High**	**-0.515**	**0.221**	**-2.328**	**0.020**
Isolated v	Moderate	-0.251	0.198	-1.270	0.204
Isolated v	Low	-0.082	0.318	-0.258	0.796
Low v	High	-0.433	0.252	-1.716	0.086
Low v	Moderate	-0.169	0.290	-0.583	0.560
Moderate v	High	0.264	0.189	1.397	0.163
Temperature		-0.034	0.044	-0.769	0.442
Abundance		0.000	0.011	-0.043	0.966
Active Behaviour					
Urbanisation factor					
Isolated v	**High**	**0.433**	**0.191**	**2.273**	**0.023**
Isolated v	Moderate	0.010	0.174	0.056	0.955
Isolated v	Low	-0.153	0.287	-0.534	0.593
Low v	**High**	**0.586**	**0.228**	**2.572**	**0.010**
Low v	Moderate	0.163	0.263	0.619	0.536
Moderate v	**High**	**-0.423**	**0.162**	**-2.613**	**0.009**
Temperature		0.017	0.037	0.458	0.647
Abundance		0.003	0.010	0.322	0.747
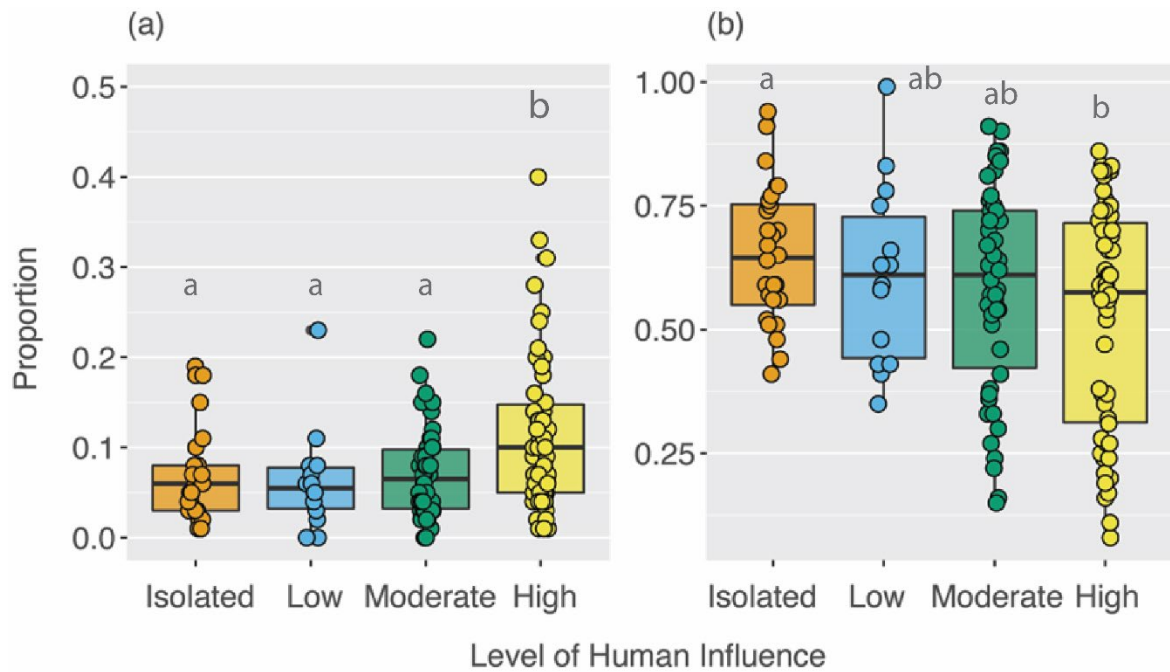
Figure 4.4 – Proportion of time engaged in (a) active and (b) passive behaviours as a function of level of human influence (urbanisation levels). Letters above bars indicate pairwise differences between levels of human influence (a-b).

The proportion of time engaged in social interactions and vigilance behaviours is shown in Figure 4.5. Beta regression analysis suggested that social interactions did not vary among urbanisation levels (Figure 4.5a), while the proportion of time engaged in vigilance behaviours showed some effect of human influence, along with an effect of lizard abundance (Table 4.4). Regression coefficients for vigilance behaviour suggested that lizards on the highly populated island were significantly less vigilant than those on the low populated island (Figure 4.5b). Vigilance was also found to vary with the number of lizards in the population with vigilance levels increasing as population size increased (Figure 4.6a); this relationship was also observed for temperature (Figure 4.6b), although temperature did not quite reach significance (Table 4.4).
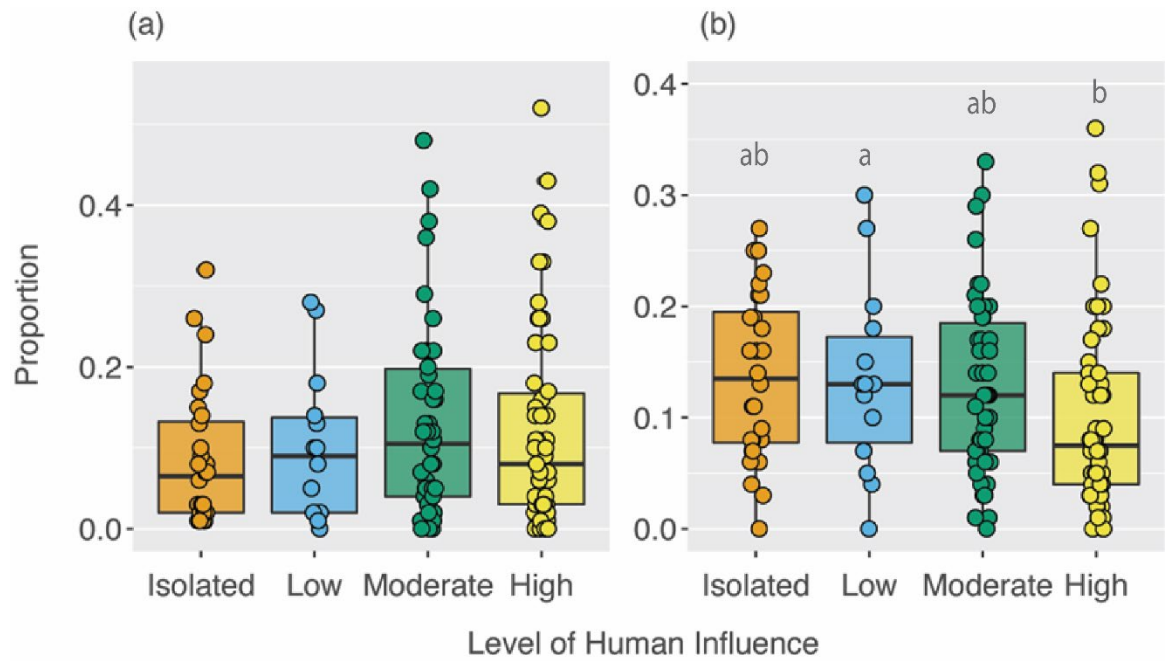
Figure 4.5 – Proportion of time engaged in (a) social interactions and (b) vigilance behaviours as a function of level of human influence (urbanisation levels). Letters above bars indicate pairwise differences between levels of human influence (b). No significant differences were found in social interactions behaviour.
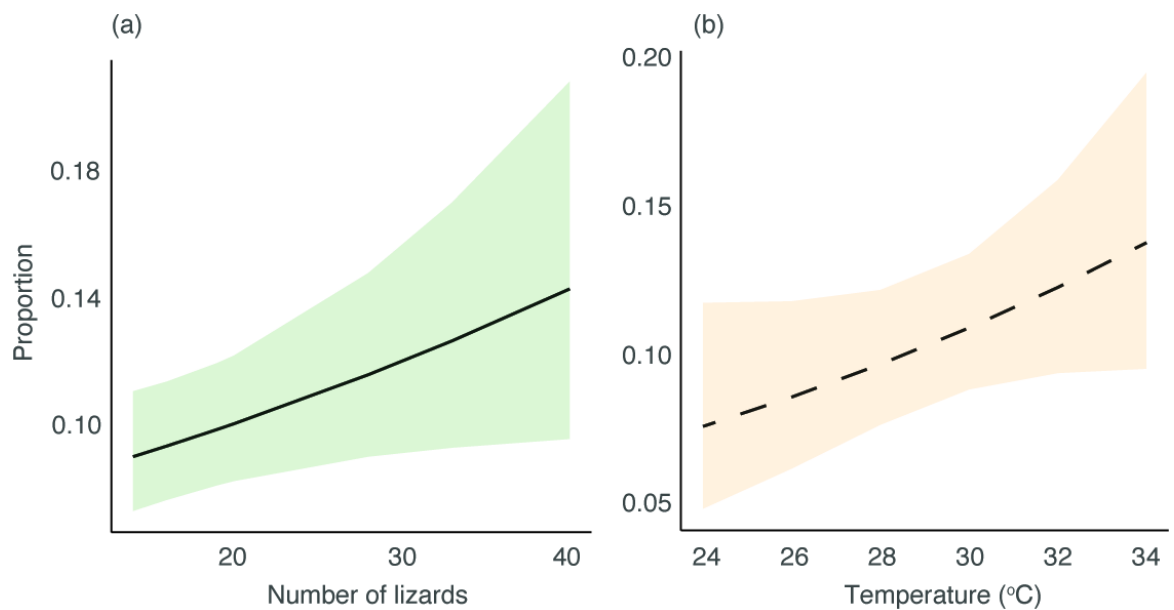
Figure 4.6 – Proportion of time engaged in vigilance behaviour as a function of (a) the number of lizards in the population and (b) ambient temperature. The solid regression line represents a significant relationship while the dashed line is not significant. Ribbons represent 95% confidence intervals.

Table 4.4 – Outcome from beta regression models examine variation in social interactions and vigilance behaviour as a function of urbanisation levels, temperature, and abundance.

Parameter		Estimate	SE	z score	p value
Social Interactions					
Urbanisation factor					
Isolated v	High	0.251	0.240	1.047	0.295
Isolated v	Moderate	0.301	0.212	1.418	0.156
Isolated v	Low	0.240	0.343	0.701	0.484
Low v	High	0.011	0.270	0.041	0.968
Low v	Moderate	0.060	0.310	0.194	0.846
Moderate v	High	0.049	0.201	0.245	0.807
Temperature		0.058	0.047	1.237	0.216
Abundance		0.004	0.012	0.377	0.706
Vigilance Behaviour					
Urbanisation factor					
Isolated v	High	-0.167	0.201	-0.831	0.406
Isolated v	Moderate	-0.010	0.171	-0.057	0.954
Isolated v	Low	0.313	0.281	1.115	0.265
Low v	**High**	**-0.481**	**0.224**	**-2.151**	**0.031**
Low v	Moderate	-0.323	0.252	-1.281	0.200
Moderate v	High	0.158	0.171	0.924	0.355
Temperature		0.066	0.039	1.691	0.091
Abundance		**0.020**	**0.009**	**2.135**	**0.033**

As human activity on Santa Cruz varied across my sampling sites, I conducted additional analyses to compare *M. indefatigabilis* populations on active, passive and vigilance behaviours (Figure 4.7). There was no evidence for variation as a function of visitation level for active and passive behaviours, but there was for vigilance behaviour (Table 4.3). Lizards from the Parque Nacional Galápagos (PNG), which is not a tourism destination, were significantly less vigilant than lizards from Tortuga Bay which has high visitation (Figure 4.7c).

Table 4.3 – Outcome from beta regression models examine variation in passive, active and vigilance behaviour as a function of tourism activity on Isla Santa Cruz.

Parameter		Estimate	SE	z score	p value
Passive Behaviour					
PNG v	Garrapatero	0.438	0.233	1.880	0.060
PNG v	Tortuga Bay	0.302	0.237	1.275	0.202
Garrapatero v	Tortuga Bay	0.137	0.223	0.613	0.540
Active Behaviour					
PNG v	Garrapatero	-0.083	0.285	-0.291	0.771
PNG v	Tortuga Bay	-0.203	0.285	-0.713	0.476
Garrapatero v	Tortuga Bay	-0.120	0.285	-0.422	0.673
Vigilance Behaviour					
PNG v	**Tortuga Bay**	**0.538**	**0.260**	**2.074**	**0.038**
PNG v	Garrapatero	0.063	0.272	0.232	0.817
Garrapatero v	Tortuga Bay	-0.475	0.257	-1.848	0.065
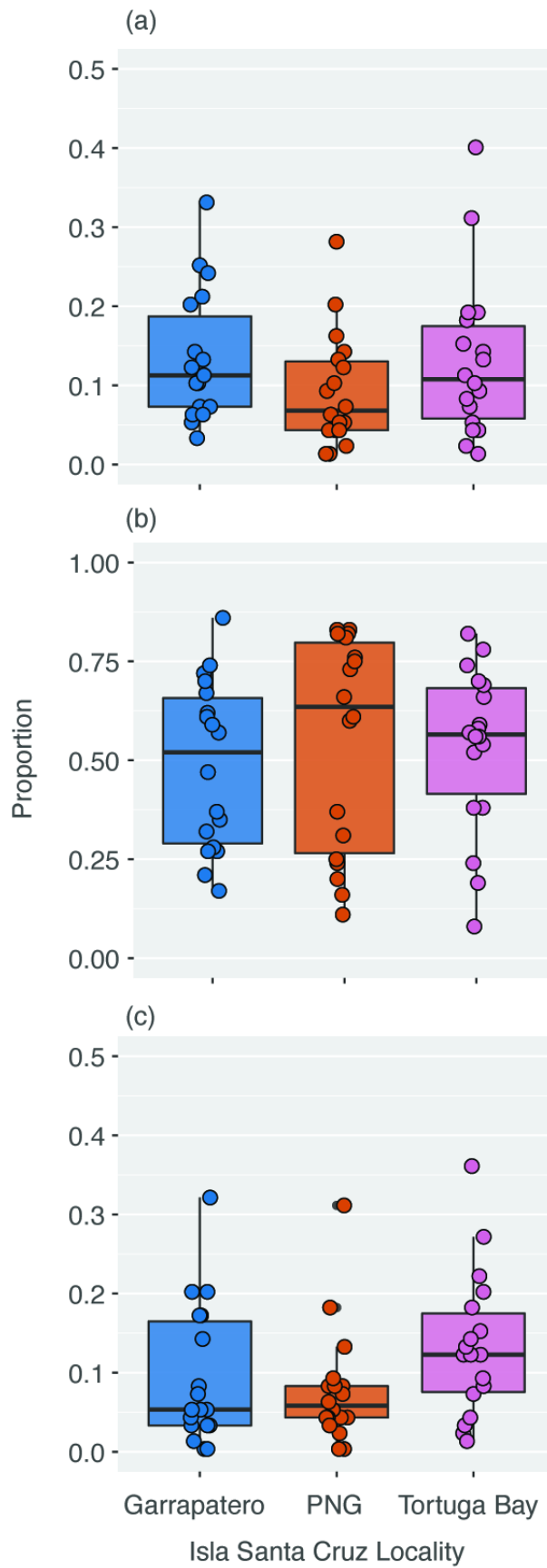
Figure 4.7 – Proportion of time engaged in (a) active, (b) passive and (c) vigilance behaviours as a function of tourism activity on the island of Santa Cruz.

Discussion

Numerous studies have demonstrated that urbanisation has substantially altered or even degraded species ecosystems to the point of unbalancing the natural life cycle (Chapman et al., 2012; De Meester et al., 2018; Dylewski et al., 2020; Luther & Baptista, 2010; Tyne et al., 2017). My study suggests that urbanisation might be a determining factor for Galápagos lava lizard behaviour. Species that occur on the highly populated island of Santa Cruz spent more time active than species living on islands with medium, low, and isolated levels of urbanisation. Santa Cruz lizards also showed overall lower levels of vigilance. Interestingly, when I explored vigilance across populations on Santa Cruz, it was actually higher in Tortuga Bay that experience the highest levels of tourism. Levels of vigilance here were generally still lower than on the other islands and might actually reflect the positive relationship with population abundance. As I am unable to distinguish between vigilance for predators and scanning for conspecifics, lizards at the highest tourism site that also happens to have high population numbers, might be surveying for conspecifics. In general, isolated species showed an opposite trend and spent more time being vigilant and passive. Social interactions seem to be unaffected by urbanisation level, with variation reflecting ecological factors not considered here (see Chapter 3). Result of my broad sweeping study hints at an effect of anthropogenic disturbance on Galápagos *Microlophus* sp. behaviour and reinforces the need for more research.

Animal decision making often reflects a balance between the cost and benefits of different behavioural strategies (De Meester et al., 2018). Extrinsic factors such as predation risk and resource availability may determine the frequency and strategy for exploring and foraging behaviours (Chapman et al., 2012; Chejanovski et al., 2017; Ditchkoff et al., 2006; Engelhardt & Weladji, 2011; Lee & Thornton, 2021). Previous studies have suggested that insular species usually face low levels of predatory threat and food availability leading to an increase in boldness as a strategy to fulfil their needs (Blumstein & Daniel, 2005; De Meester et al., 2018). Therefore, we

might anticipate that species inhabiting island ecosystems spend more time active, yet my results

suggest that human influence is a mediating factor for Galápagos lava lizards, such that species

inhabiting highly urbanised sites were more active than species on islands with lower levels of

urbanisation. Tanner and Perry (2007) reported similar results for lava lizards on Santa Cruz (*high*

urbanisation level), reporting that lizards were active around roads and even using them as

basking sites. Often animals living in urban areas can become more active due to the absence of

natural selective pressures (Candler & Bernal, 2015), which contrasts with natural environments

exhibiting higher occurrence of natural predators and competition (Moule et al., 2016). Although

the increase of activity on highly urbanised areas has been associated with a better exploitation of

new resources, it might not be totally beneficial for lava lizards. A clear decrease in population

density associated with road development on Santa Cruz Island points to a negative impact of

heavily transited roads threating the status of lava lizards' populations (Tanner et al., 2007;

Tanner & Perry, 2007).

On the other hand, variation in the type and availability of food resources in urban areas

can also change species food preferences and increase the time required to forage effectively

(Candler & Bernal, 2015; Chapman & Jones, 2012; Chejanovski et al., 2017). For generalist species

such as the Galápagos lava lizards (Hervias-Parejo et al., 2019; Kohlsdorf et al., 2008), it is possible

that the exposure to new prey types increase the availability of food. In fact, prey analysis of

faeces collected during my fieldwork elucidated the consumption of invasive ants previously

reported on the Galápagos islands (Causton et al., 2006), supporting the idea of changes to their

diet preferences (unpublished work; see Chapter 5). Such diet shifts may reduce antagonistic

foraging strategies like cannibalism, which has been previously reported for a few species of

Galápagos lava lizards (Moore et al., 2017). This highlights an interesting and important field for

future research as Galápagos lava lizards play an important role in ecosystem function (Chamorro

et al., 2012; Hervías-Parejo et al., 2020), such that variation in their diet preferences could disrupt

important ecological relationships among Galápagos species.

A shift in activity associated with high levels of urbanisation (Santa Cruz Island) might be connected with a reduction in vigilance behaviours by lava lizards as reported for other species (Blumstein & Daniel, 2005; Chapman et al., 2012; Gotanda, 2020). In fact, evolutionary theory predicts that costly antipredator behaviours will be selected against when predation risk diminishes (Brock et al., 2015). As fleeing or vigilant behaviours can be energetically costly and reduce the opportunities for fitness-enhancing activities such as foraging or thermoregulation (Cooper et al., 2015). Therefore, because islands generally host fewer predators an increase on species tameness is expected as a way to balance the cost of antipredation behaviours (Brock et al., 2015). In the case of the Galapagos islands, the habitat alteration has become an important issue since the first human migration in 1970, specially in Santa Cruz Island where the exponential population growth has led to 2.81 km^{2}of urban areas and 54.91 km^2 of agricultural lands altering the natural habitat and life cycles of resident species (Brewington et al., 2013; Shao et al., 2020; Watkins, 2008). These significant habitat alterations, might lead to decreased exposure to, or even the loss of, natural predators such as the Galápagos hawk (*Buteo galapagoensis*), which is the only diurnal raptor on the Galápagos archipelago and is almost extinct on Santa Cruz island (Bollmer et al., 2006). Thus, it is possible that the loss of natural predators on Santa Cruz Island is shifting vigilance behaviours in *M. indefatigabilis*, and another example of the most common consequence of urbanisation in animals (Chapman et al., 2012; Dammhahn et al., 2020; Diego-Rasilla, 2003; Duchateau et al., 2007). Gotanda (2020) showed that Darwin finches (*Geospiza fuliginosa*) exhibited lower levels of antipredator behaviour in urban areas than individuals on pristine island. Consequently, it is possible that lava lizards also might be adapting their behaviour to live in urban areas as a result of a decrease in natural predation risk, and thus attempting to successfully exploit the available resources in these new altered environments by being more active than vigilant.

Notwithstanding, intraspecific comparisons of *M. indefatigabilis* populations in Santa Cruz Island showed an opposite trend for vigilance behaviour in highly visited touristic places.

Galápagos islands are among the most famous destinations for wildlife tourism welcoming over 150,000 tourists per year (Brewington et al., 2013; Caisaguano et al., 2020). The effect of focused human wildlife interactions for recreational purposes have been associated with negative impacts on animal welfare leading to chronic stress, decreased reproduction, increased aggression, disease susceptibility and more (Bhattacharjee et al., 2015; Moorhouse et al., 2015; Reynolds & Braithwaite, 2001; Szott et al., 2019). Vigilance plays an extremely important role in an animal's survival as it allows them to scan and survey their surroundings to monitor potential threats or conspecifics (Li et al., 2017). However, significant increments in vigilance behaviours might be detrimental for animals as they could become more visible to predators and reduce their foraging efficiency (Dyck & Baydack, 2004; Merrall & Evans, 2020; Treves, 2000). Gonzales-Perez and Cubero-Pardo (2010) demonstrated that multiple tourism activities on water and land influenced the behaviour of six emblematic species on the Galápagos Islands, where vigilance and evasiveness were the most commonly observed (Gonzales-Perez & Cubero-Pardo, 2010). Because Tortuga Bay annually records over 65,000 visitors (Caisaguano et al., 2020), it is possible that lizards inhabiting this site might be engaging more in vigilant behaviours not only due to the higher presence of humans, but also because Tortuga Bay habitat has been altered to human needs thereby disturbing the natural environment and forcing lava lizards to modify microhabitat preferences. Indeed, lizards at Tortuga Bay utilised man-made rock walls near to walking paths that featured less vegetation (personal observations), which could increase their visibility to predators and human encounters. Further research is needed to identify whether these specific factors are leading to behavioural changes in lava lizards living in touristic sites.

Vigilance behaviour of Galápagos lava lizards was also influenced by relative abundance. Consequently, results for Tortuga Bay, which had one of the highest number of lizards of any population studied, might reflect scanning for conspecifics rather than potential predators. As lava lizards are highly territorial (Carpenter, 1966), populations of greater size are expected to exhibit more conspecific encounters (Butler, 1980; De Boer, 1981; Jirotkul, 1999). Thus, scanning serves

to identify potential rivals and initiate appropriate behavioural strategies to avoid costly interactions (Lanham & Bull, 2004). Nevertheless, Tanner and Perry (2007) reported that lava lizard population densities in Santa Cruz might be lower near roads (i.e. 40km road in Puerto Ayora) and that animals occupying territories near them are more exposed to feral animals, human foot traffic, and other risks. Similarly, Tortuga Bay has a 2.5 km trail that connects the town with the beach and lizards are highly visible here because they seem to prefer this rocky trail for thermoregulation (personal notes). It is possible that lava lizards might be more vigilant as a consequence of the direct and constant human contact related to the high number of visitors reported on this site (Caisaguano et al., 2020). Although this outcome contrasts the overall time spent vigilant for lava lizards on highly populated sites, it also suggests that direct human contact could represent a major threat to population levels. Unfortunately, there are no data for my study sites on population sizes before recent human expansion, so it is difficult to know whether numbers are stable or have changed, and if so, in which direction. Clearly, we need to know the trajectory of change from a conservation perspective to know if they are under threat (Piano et al., 2020), and my data provides at least one reference point.

In contrast to heavily populated islands, lava lizards inhabiting isolated islands spent more time passive and vigilant. Prior studies of *M. albemarlensis* living in the Plaza Sur islet, which is free of human inhabitants, have associated an increase in wariness, endurance, and speed with inhabiting sparsely vegetated habitats (Jordan et al., 2005; Miles et al., 2001; Snell et al., 1988). Pinzon and Santiago islands featured low vegetated habitats where the presence of patches of woody plants and herbs and forbs increase the individuals' visibility to predators. Indeed, the occurrence of natural predators such as the Galápagos Hawk (*Buteo galapagoensis*) was evident for both islands, where the successful elimination of invasive species have allowed the population of these Galápagos endemic species to grow (Jaramillo et al., 2016). Thus, it is possible that species on isolated islands might be under higher predation risk leading to an increase in awareness necessitated by fewer hiding spots and longer periods of exposure (Miles et al., 2001).

This might also be related to the time spent in passive behaviours, as the time exposed to the sun influences lizard metabolism and performance on other behaviours such as vigilance (Carrascal et al., 2010). In addition, as lizards living on isolated islands show awareness as a natural behaviour, it is possible that the loss of it might be a consequence of urbanisation on the Galápagos Archipelago.

Behavioural differences between highly urbanised and isolated islands provide insight into the effect of human activity on Galápagos lava lizards. The increase in activity at sites with high urbanisation levels is consistent with previous findings from a range of species and might be an advantage to exploit urban areas. Nevertheless, my results also suggest that it could be a disadvantage by increasing the vulnerability of native species, especially on island ecosystems, as urbanisation can alter the selective pressures in various ways. Recent studies on *M. albemarlensis* suggests a high impact of roads on their survival rates and abundance (Tanner et al., 2007; Tanner & Perry, 2007), exposing a direct impact of human growth on the Galápagos islands. Human development represents a threat to wildlife around the world, and Galápagos lava lizards are no exception. My study demonstrates the influence of urbanisation and tourism on a non-emblematic species of the Galápagos islands, yet one that is extremely important in the natural ecosystem. Authorities must be mindful of the potential impact of urbanisation and wildlife tourism, and I encourage further research in the Galápagos to understand the behavioural strategies that animals use to adapt to urban areas.

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Appendix

Table S4.1 – Behaviour grouping and proportions per species.

Behaviour	Definition
Passive	
Basking	Individual positioned in the sun on different substrates, not displaying other behaviour.
Buried	Hide the whole body under soft soil or sand using the limbs and remains in the same place.
Shade sites	Individual position away from the sun, not displaying other behaviour.
Hiding	Move to a bush or crack.
Rain	Heavy rain conditions
Active	
Foraging	Looking for prey items or capturing them.
Walk	Forward movement of fore and hindlimbs on different substrates.
Climb	Moving upwards in a vertical substrate.
Jump	Lift complete body from the ground
Dig	Forward and back movements of forelimbs on the ground removing substrate.
Drinking	Using tong or snout to drink water from a small pond or water body.
Leg movement	Move of hindlimbs up or down for a short period
Scratch	Moving fore or hindlimbs forward and back against a specific part of the body.
Spins	Moving ole body in circles in the same place.
Lick	Using tongue to touch a part of the body
Vigilance	
Predation	An individual is captured and eaten.
Scan high level	Side to side head movement on a high substrate.
Scan low level	Side to side head movement on a low substrate.

Behaviour	Definition
	Interactions
Display	For the statistical analysis the head bobs and push ups behaviours were combined to avoid observer error.
Head bobs (display)	Vertical up and down movement of an individual's head independent from the body. Motion repeated several times without a visual individual near.
Push ups (display)	Vertical up and down movement of an individual's head accompanied with the flexion of hind limbs. Motion repeated several times without a visual individual near.
Tail movement	Ventral part of the body Up and down or looped movement of the tail.
Social interactions	Any interaction with an individual of the same species that could not be defined as feeding or predation.
Territorial	Display including a sequence of head bobs, push ups, persecution, intimidation, biting and aggressive attack from and individual to another regardless the sex.
Mating	Male and female engaging mating display.
Interaction with other species	Any interaction with an individual of the different species that could not be defined as feeding or predation.
Chase	Follow a conspecific in a fast pace

Table S4.2 – Temperature and abundance features for each Galapagos lava lizard species sampled during the fieldwork.

Species	Population	Temperature (°C)	Encounter rates		
			Males	Females	Maximum individuals
Microlophus indefatigabilis	Parque Nacional Galápagos (PNG)	29.45	9	10	30
Microlophus indefatigabilis	El Garrapatero beach	29.7	9	15	34
Microlophus indefatigabilis	Tortuga Bay	31.01	10	26	55
Microlophus albemarlensis	Muro de Lágrimas	31.58	6	14	32
Microlophus albemarlensis	Centro de Crianza "Arnaldo Tupiza Chamaidan"	29.18	11	22	39
Microlophus grayii	La Lobería	28.52	9	5	28
Microlophus bivittatus	Centro de Interpretación Ambiental Gianni Arismendy	28.59	10	18	35
Microlophus jacobi	Playa Espumilla	30.66	9	7	27
Microlophus duncanensis	Playa Escondida	29.46	17	25	47

Figure S4.1 – Habitat photos for the sample sites on the Galápagos Archipelago.

1) Parque Nacional Galápagos - Santa Cruz Island (*Microlophus indefatigabilis*)

1) Parque Nacional Galápagos - Santa Cruz Island (*Microlophus indefatigabilis*)

2) El Garrapatero beach

3) Tortuga Bay

4) Muro de Lágrimas - Isabela Island (*Microlophus albemarlensis*)
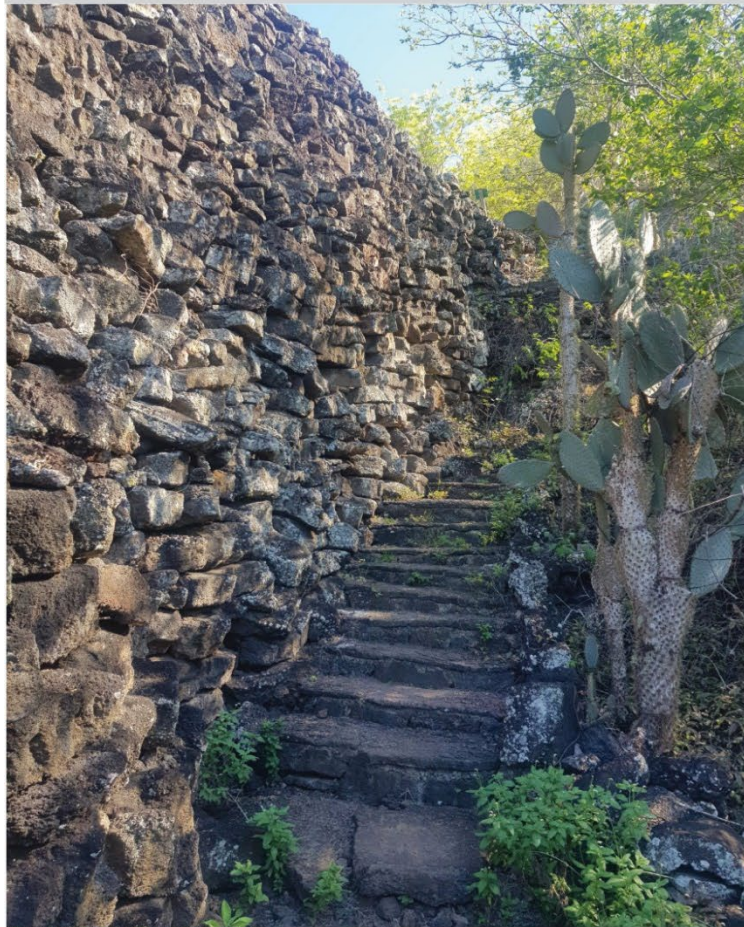
5) Centro de Crianza

6) La Lobería - Floreana (*Microlophus grayii*)

7) Centro de Interpretación Ambiental - San Cristobal Island (*Microlophus bivittatus*)

8) Playa Espumilla - Santiago Island (*Microlophus jacobi*)

9) Playa Escondida - Pinzon Island (*Microlophus duncanensis*)

CHAPTER FIVE

General Discussion

Thesis overview: further directions and recommendations.

Behavioural ecology is an active field of research that employs integrative approaches to study behaviour in the context of ecology and evolution. This research field has certainly changed from descriptive topics to understand more complex processes influencing animal behaviour including competition, demographic consequences of behaviour variation, ecological basis of differences in behaviour among species, and the role of sexual selection in speciation (Owens, 2006). Along with this have also evolved the tools to investigate animal behaviour which include the application of modern molecular (Campbell et al., 2009; Rittschof & Robinson, 2014) and phylogenetic comparative techniques (Hernández et al., 2021), facilitating the study of cryptic and closely related species. The complexity of behaviour and communication signals of many species of lizards have seen them become model organisms within the field of behavioural ecology (Anderson & Poe, 2018; Baird et al., 2013; Camargo et al., 2010; Eloy De Amorim et al., 2017; Patton et al., 2021). A vast number of studies worldwide have focused on characterising and describing visually conspicuous displays, and aggressive and thermoregulatory behaviours (Abram et al., 2017; Angilletta et al., 2002; Baird et al., 2013; Carpenter, 1983). Many researchers have also explored the possible proximate causes that influenced animal behaviour, contributing to knowledge of the relationships between behaviour and ecology (Asbury & Adolph, 2007; Fleishman, 1986, 1992; Ord et al., 2002; Ord & Garcia-Porta, 2012; Ord et al., 2007; Ord & Stamps, 2017; Peters, 2008).

In **Chapter 1**, I presented an overview of the factors that have been reported to influence animal behaviour. In addition, I explored the use of lizards as model systems for behavioural ecology before I summarised the behavioural research on South American lizards with a particular focus on Ecuador, including my study system of Ecuadorian lava lizards (*Microlophus* sp.). Lava lizards and have been the centre of few ecological and behavioural research projects in the last 10 years, beginning with descriptive studies by Carpenter (1966, 1970, 1977) and Watkins (1996,

1997, 1998) on island and mainland species, which reported species differences in territorial displays repertories between males. Relatively recent research has considered processes that lead to behavioural divergence on lava lizard's species (Clark et al., 2016; Clark et al., 2017; Clark et al., 2015; Rowe et al., 2020; Rowe et al., 2019). The fact that lava lizards are distributed on the mainland and the Galápagos Islands suggest the influence of diverse selective pressures driving their speciation and evolution (Benavides et al., 2009; Clark et al., 2015). My dissertation investigated the role that behaviour plays in ecological specialisations and niche delimitation of the *Microlophus* species from Ecuador. It used a consistent approach that comprises assessment of encounter rates and habitat composition along with focal behavioural observations and improved filming techniques for characterising motion displays. This allowed me to examine the influence of extrinsic ecological and environmental constraints on species phenotypes on the extent of species interactions, ecological influence in the context of phylogenetic relatedness, and anthropogenic factors (Figure 5.1).
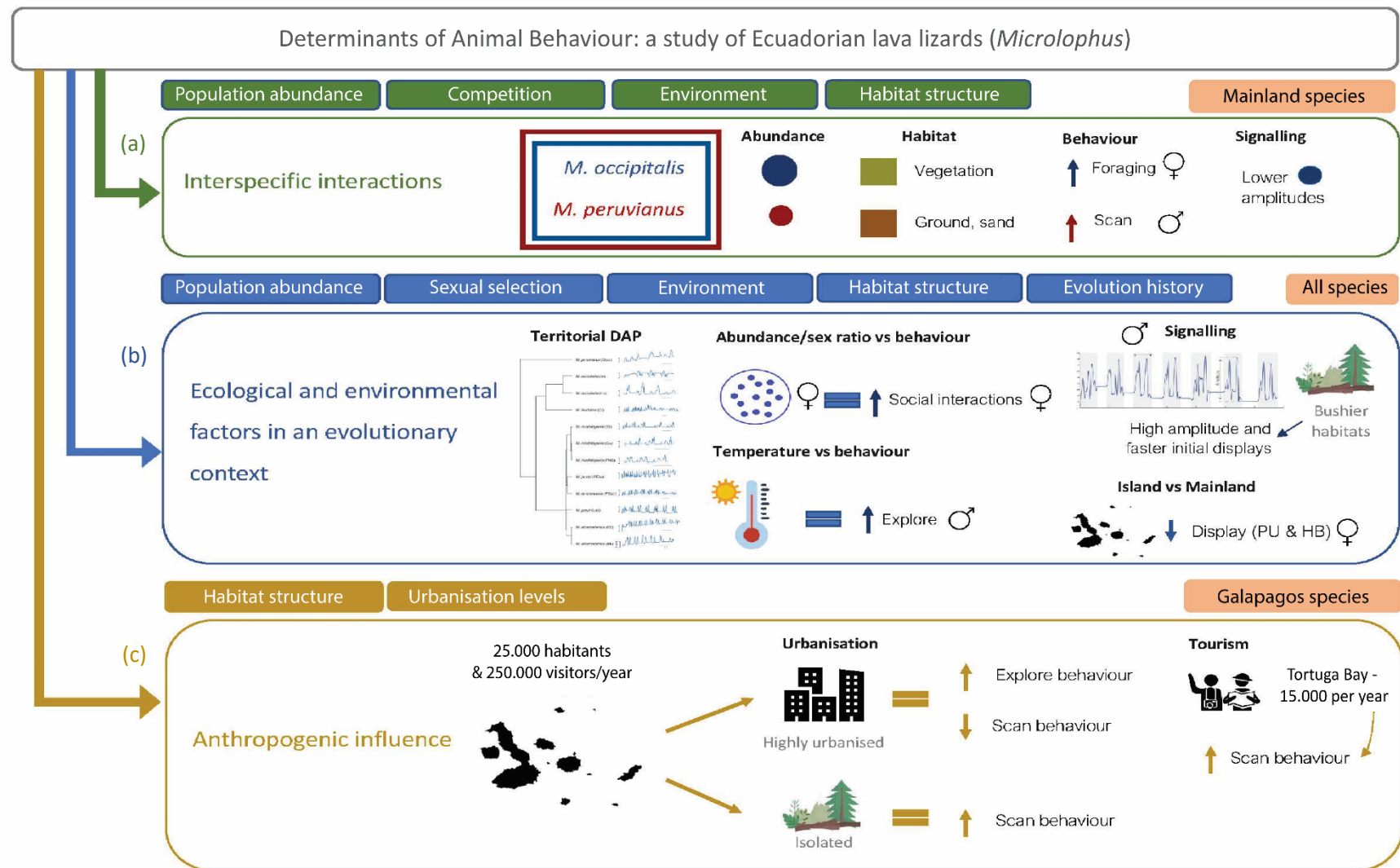
Figure 5.1 – This dissertation has examined variation in the behaviour of Ecuadorian lava lizards as a function of multiple factors. (a) The role of interspecific interactions was considered in Chapter 2 (green) and indicated shifts in mainland lava lizards (*Microlophus occipitalis* and *M. peruvianus*) abundance, habitat selection, foraging and scanning behaviours, as well as signal structure. (b) In Chapter 3 (blue), I considered the influence of multiple ecological and environmental factors in an evolutionary context, elucidating the relevance of extrinsic factors on lava lizards' social, exploring and signalling behaviours, as well as the influence of habitat structure on territorial displays. (c) Chapter 4 (beige) considered the impact of human development on the Galápagos lava lizards' behaviour, showing variation in vigilance and exploring behaviours on highly urbanised and touristic islands.

Species coexistence can often determine resource partitioning along multiple ecological niche dimensions. In **Chapter 2**, I attempted to assess the effect of different levels of inter-specific competition (sympatry and allopatry) on *Microlophus occipitalis* and *M. peruvianus* populations along the Ecuadorian west coast. In so doing I recorded the relative abundance and ecological features (habitat composition and environmental factors) for both species among different levels of competition, along with focal behavioural observations and filming of territorial displays of adults. I found variations in encounter rates across competition levels with higher abundance in allopatric populations, which provided relatively more suitable environments (Chávez-Villavicencio et al., 2018; Rowe et al., 2019). In addition, both species exhibited shifts to their foraging, exploring, and scanning behaviours as an intent to, potentially, avoid overlapping of their temporal niche axis with the other species. Likewise, microhabitat use preferences of *M. occipitalis* and *M. peruvianus* in sympatry relative to allopatry shifted to different microhabitat heights based on the new microhabitats available. Along with the microhabitat shifts in *M. occipitalis* in sympatry, smaller limbs and slender bodies were recorded, which is thought to enhance climbing performance and increase stability on smooth surfaces (Herrel, 2001; Vanhooydonck et al., 2007). In addition, I recorded variation in the territorial display action patterns of *M. occipitalis*, though I suggested these are consistent with habitat differences rather than competition. This species might also prove to be useful for consideration of ecological effects on display structure. I would also recommend recording and analysing territorial displays of *M. peruvianus* so that we can compare and contrast differences between levels of competition for both species. I anticipate this will help to disentangle the effect of competition and local conditions.

Although my approach targeted an understanding of the role of interspecific interactions in niche partitioning, it is clear that many interacting factors are relevant. A lack of detailed ecological research on both Ecuadorian lava lizard species has hindered interpretation of my study outcomes, and so the ecological preferences of both species require more detailed study before

we can truly consider the role of interspecific competition. Furthermore, my project was designed

to sample two levels of competition (allopatry and sympatry), so the discovery that one site

featured parapatric populations rather than an allopatric population was interesting but

presented me with unexpected complication. I chose to present data for this population for

completeness but focussed my discussion on comparisons between allopatry and sympatry as per

my original plan. Nevertheless, I believe this other level of species' interaction is worthy of further

consideration. The very existence of adjacent populations, which was unknown to local

researchers, is worthy of investigation. There were also interesting behavioural observations, such

as an increase in aggression behaviours in parapatric males of *M. occipitalis*. Population structure

was somewhat different here (fewer females) and would be interesting to consider this particular

location, and potentially other parapatric populations, in more detail.

Notwithstanding the aforementioned limitations, my results propose for the first time

that the coexistence of both species might be influencing their temporal and spatial niche axis in

several ways. Also, as one of the first projects on Ecuadorian mainland lava lizards' behaviour

since Watkins (1996, 1997, 1998), I am laying the groundwork for further research not only on the

effect of competition, but also on the influence of sexual selection and habitat composition on

species niches. I expect that this will help to elucidate clear future fields of research and generate

interest on this relatively neglected lava lizard's species in Ecuador.

Lava lizards are closely related species, so it is important to account for their shared

evolutionary history when establishing possible drivers of behavioural divergence. In **Chapter 3**, I

aimed to test alternative evolutionary models of behaviours, including territorial signals, of

Ecuadorian lava lizards. I employed several phylogenetic comparative methods (i.e., phylogenetic

signal analysis and phylogenetic regressions) to assess phenotypical traits under relevant

ecological and environmental conditions, as well as biogeographical settings, within the context of

phylogenetic relatedness. As mentioned earlier, the methodology developed in Chapter 2 allowed

for considerations of behaviour and signal performance under diverse ecological conditions.

Combining results presented in Chapters 2 and 3 I have identified relevant behaviours that might

be under strong selection pressures. I predicted that the behaviour of Ecuadorian lava lizards will

be influenced by external factors to varying degrees, and that island and mainland behaviour

patterns will differ due to their markedly different ecological circumstances. Results showed that

evolutionary history has not constrained lava lizards' behaviour and has demonstrated an

important role of extrinsic ecological, environmental, and social factors in their behavioural

evolution. As my study species have only relatively recently diverged, and I restricted the effect of

their evolutionary history, my research provides further evidence that behaviour can be plastic

and related to local conditions. I propose that population structure affects social interactions,

which also impacted exploratory behaviour. In addition, females of island populations spent

significantly less time signalling than mainland females. In terms of environmental factors, it was

not a surprise that temperature was a strong predictor of behaviour performance, with a

reduction in exploration by males under high temperature conditions. Interestingly, the time

spent signalling by males also presented the same trend under high temperatures, which could be

a by-product of lower exploration leading to fewer conspecific encounters. Yet, a reduction in

signalling by males was also observed in populations with greater male-biased size dimorphism

suggesting a role of sexual selection. In the case of signal structure, vegetation type played a

determinant role. Species in shrub dominated habitats were found to commence displays at

higher speeds and amplitudes, reducing as the displays progress, which supports previous

research that has demonstrated signal structure is influenced by the plant environment (Peters et

al., 2007). In addition, signal structure was also predicted by the number of lizards present, with

males increasing speed and amplitude of display movements over the course of the display as the

population size increased.

The aforementioned traits represent characteristics that appear to have shifted

independently of their phylogenetic history. Therefore, I propose them as ideal candidates to

understand behavioural divergence among species. However, the lack of statistical strength for

some of the behaviours analysed suggest that increasing the samples size by adding more

populations, including the remaining four species from the Galápagos Islands, must be done to

understand the processes influencing lava lizards behavioural and signal divergence. As the

relationship between behaviour and phylogenetic constraints can be complex to measure, I

quantified the phylogenetic signal on Ecuadorian lava lizard behavioural traits with no implications

as to the mechanisms that might cause this resemblance. Nevertheless, detecting the

phylogenetic signal for a given trait is a function of the sample size, the power of the statistical

analysis, the accuracy of the phylogenetic tree and the trait data (Blomberg et al., 2003).

Therefore, further research must target to include not only a bigger data set but also all

Microlophus species. This was a limitation of my research that I was not able to overcome due to

budget and fieldwork limitations. However, I consider that the substantial sampling effort, in

conjunction with a robust analytical approach, allowed me to extract some novel and important

outcomes and lay valuable groundwork for future research.

My dissertation includes research on almost half of the recognised species for the

Microlophus group, and more than 70% of the Ecuadorian lava lizard species. Thus, I am in a

somewhat unique position to propose new fields of research. Additional data gathered during my

fieldwork, particularly for this chapter, has allowed me to start adjacent projects on the Galápagos

lava lizards. The first project includes a comprehensive update of the diet of the six species of

Galápagos lava lizards. Preliminary results suggest a consumption of diverse prey items including

insects, vegetation, and moult (Figure 5.2). Also, fieldwork observations allow us to witness a male

lava lizard (*Microlophus albemarlensis*) eating a small gecko (unidentified species) supporting prior

research although related to cannibalism (Moore et al., 2017). A second project is focused on

chest patterns, which caught my attention when photographing individuals (Figure 5.3). This

project examines the relationship between chest patterns and morphology, particularly the head,

to determine whether they provide cues on dominance and/or fighting ability. Whereas both

projects are conducted in collaboration with local Ecuadorian institutions, a third project

considers the thermal ecology of lizards worldwide and brings together researchers from multiple

countries to consider the effect of temperature on lizard activity for over 100 species from 17

countries. Therefore, my research activities extend beyond these empirical thesis chapters, and

taken together will help to consider behavioural responses of lizards to changing environmental

conditions.
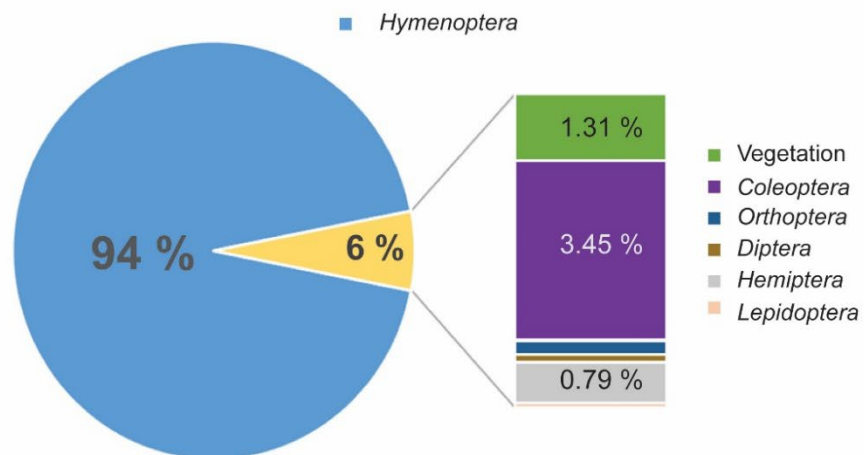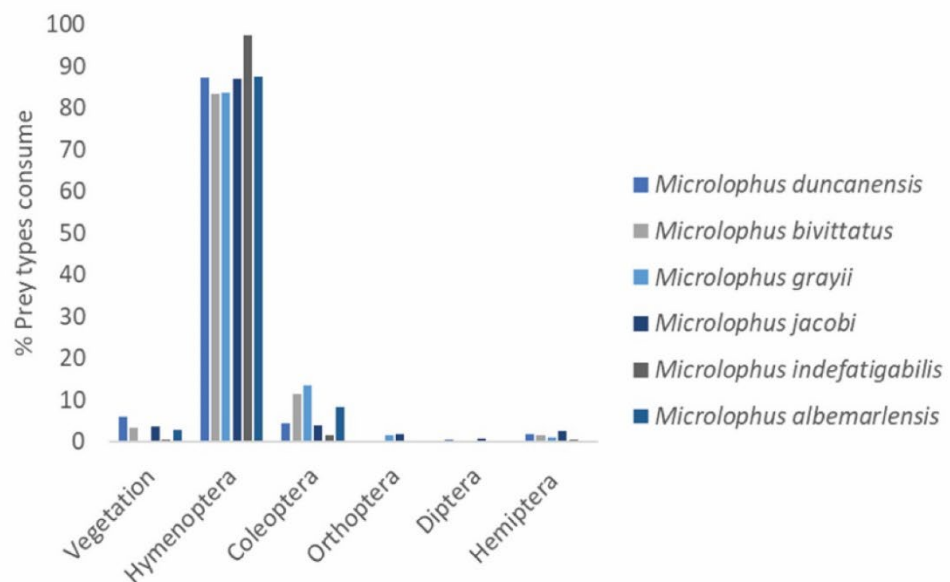
Figure 5.2 – Preliminary results of the Galápagos lava lizards diet analysis carried out in collaboration with other members of the Animal Behaviour Group at La Trobe University and collaborators from Ecuadorian universities. a) Adult male foraging on a cricket (Order: *Orthoptera*) and female foraging on a caterpillar (Order: *Lepidoptera*). b) Global prey type consumption by six Galápagos lava lizard species. c) Detailed prey consumption for six Galápagos lava lizard species.
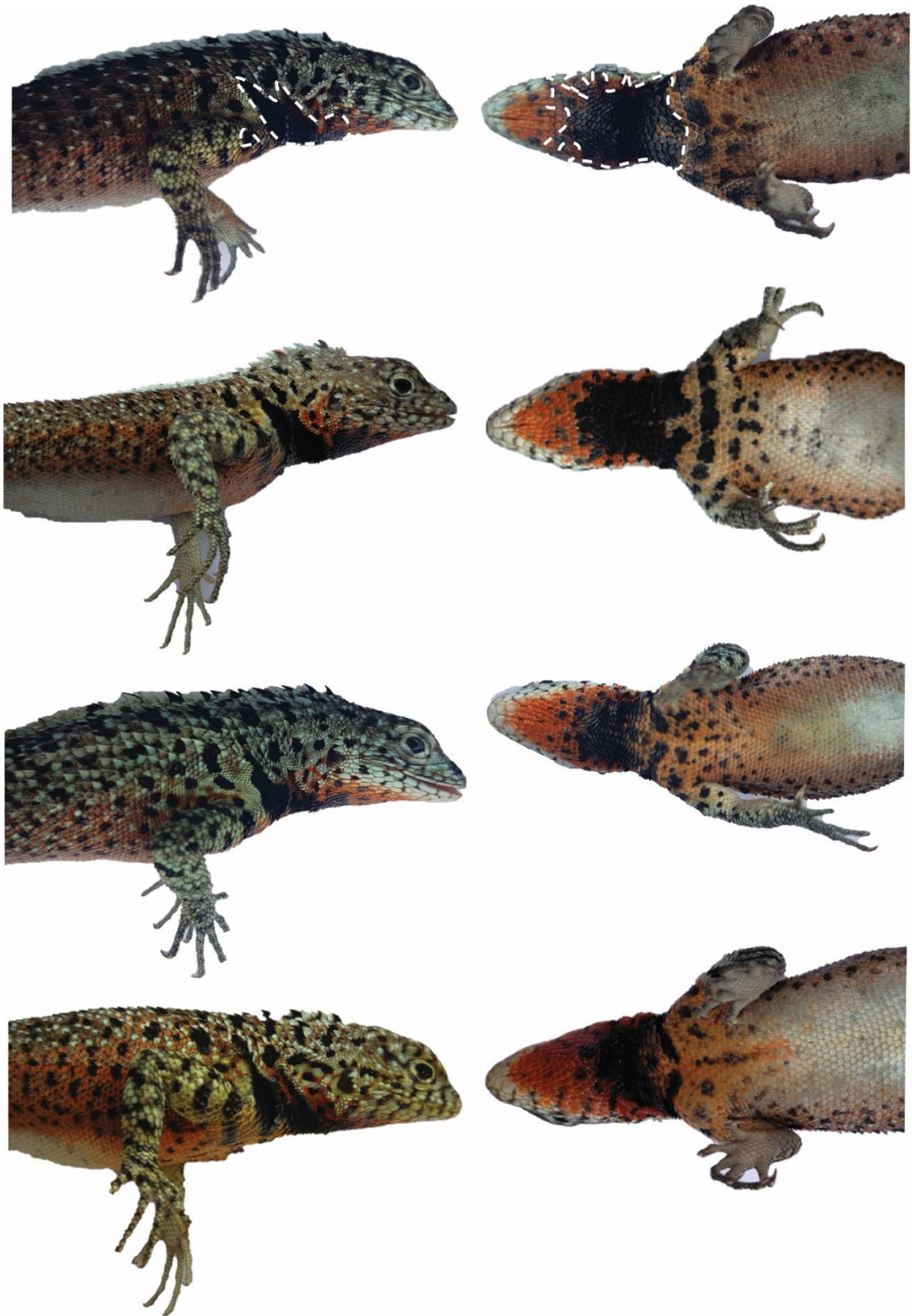
Figure 5.3 – Colour chest patterns on the side and middle throat (white dashed lines) of adult males of Santa Cruz lava lizards (*Microlophus indefatigabilis*). Note the variation in pattern size between different individuals.

To complement information presented on lava lizards' behavioural adaptations, in

Chapter 4, I aimed to estimate the impact of exponential human development on the behaviour

of Galápagos lava lizards. Here I focused on islands that represent a gradient of urbanisation from

highly urbanised to isolated. Urbanisation is among the major causes for natural habitat

modification and is introducing new challenges to native species. The Galápagos Islands have

faced a significant increase in urbanisation and wildlife tourism in the past 30 years, jeopardising

the natural balance of its ecosystem (Benitez-Capistros et al., 2016). In addition, the effect of

urbanisation on lava lizards has previously been reported by Tanner et al. (2007), suggesting high

impact arising from main roads on Santa Cruz. My results support this earlier work, as species

inhabiting highly urbanised islands spent more time active than species on islands with lower

levels of urbanisation. At the same time, lizards also showed a reduction in vigilance behaviours in

urban areas. I also demonstrated within-species differences on the Santa Cruz lava lizard (*M.*

*indefatigabilis*) that showed increased vigilance in highly touristic sites. Clearly, lava lizards are

responding in interesting ways to anthropogenic influences. Many of these behavioural shifts are

consistent with previous findings from a range of species (Amdekar et al., 2018; Kaiser et al.,

2018; Thompson & McLachlan, 2007), and so further research is certainly necessary.

My results suggest that the constant human development on the Galápagos Islands might

be having a negative impact on lava lizards' behaviour by increasing their vulnerability to new

threats. In addition, I am flagging the urgent need to fill relevant knowledge gaps on non-

emblematic Galápagos species to be able to develop more comprehensive conservation projects.

Island ecosystems are among the most vulnerable to the negative impacts of human

development, and the Galápagos Islands are not the exception. Therefore, authorities must be

mindful of the potential impact of urbanisation and wildlife tourism, and I encourage further

research in the Galápagos not only to understand the behavioural strategies that animals use to

adapt to urban areas, but also to implement educational projects focussed on involving the local

community to be able to protect and preserve the unique species and ecosystems of the

Galápagos Archipelago.

Contributions to South American behavioural ecology.

Behavioural ecology is still a developing field in South America and is relatively skewed towards

the study of birds, mammals and insects (Jaffe et al., 2020). The leading countries in this field are

Brazil, Argentina, and Chile, which often tend to carry out descriptive research. Research on

lizards has considered thermoregulatory (Corbalán & Debandi, 2013; Dias & Rocha, 2004; Maia-

Carneiro & Rocha, 2013; Medina et al., 2009), antipredator (Constanzo-Chávez et al., 2018; Jaksić

& Núñez, 1979; Santoyo-Brito et al., 2020; Schulte et al., 2004; Vaz E Nunes et al., 2012) and social

(Costa Caldeira et al., 2010; Lisboa et al., 2017; Robles & Halloy, 2008; Trigosso-Venario et al.,

2002) behaviours, along with studies into the use of chemical and visual signals (Labra et al., 2001;

Martins et al., 2004). The model organisms for these studies have been mostly highly diverse

groups from the Iguanidae family such as the genus *Liollaemus*.

Groups with lower diversity such as the lava lizards (*Microlophus* genus) have been

relatively neglected. It is for this reason that I have undertaken a comprehensive study of

Ecuadorian lava lizard behaviour. My project is the first in South America to utilise three-

dimensional reconstruction of the territorial display pattern of a South American lizard and

allowed me to identify differences associated with environmental and social factors (**Chapter 2**

and **Chapter 3**). This is an important contribution to the Ecuadorian scientific community as I

present the first graphical representation of *M. peruvianus* territorial display along with updates

on the previously described display patterns reported by Carpenter (1966, 1977) for *M. occipitalis*

and six species of Galápagos lava lizards (**Chapter 3**). Since Carpenter (1966, 1977) there has been

only modest additional descriptions of the territorial display of *Microlophus* species. A few studies

have used Carpenter's graphical depictions (DAPs) to consider possible causes related to the

display diversification (Clark et al., 2016; Clark et al., 2017; Clark et al., 2015; Macedonia et al.,

2019), while Macedonia et al. (2019) represents the only other attempt to provide new characterisations of display structure. By providing a more accurate representation of the communication signals of lava lizards, I have been able to consider signals in an ecological and evolutionary context, which yielded significant outcomes that were not realised in a comparable study that used very restricted display data (Clark et al. 2015).

I have also made valuable contributions to the ecological and behavioural knowledge of lava lizards. I presented substantial information that hopefully will increase interest on the *Microlophus* group as a model system for ecological, behavioural, and evolutionary studies. In fact, I made a significant contribution to basic ecological knowledge of mainland lava lizards in Ecuador, presenting detailed data of their habitat preferences, population abundance, behavioural patterns, and interspecific interactions (**Chapter 2**). Also, I have contributed new locality records for *M. peruvianus,* clarifying their distribution along the Ecuadorian coast. I have also recorded morphological and photographic information for adult males and females of both mainland species updating the information available to local Ecuadorian institutions (**Chapter 2**). Hence, I am laying the ground for future research on mainland lava lizard species by providing a broad set of data and encouraging future research. I believe that mainland species offer an excellent opportunity to explore the effect of competition and species interactions for their overlap distribution along the west coast of South America (**Chapter 2**). In addition, they can provide valuable information that can be contrasted with island congeners to look for insights on the processes influencing the evolution of island species specially on these closely related species (**Chapter 3**).

Another aspect where I am laying the foundation for future research is on the role of sexual selection within species and populations. It was clear from my outcomes that factors such as sexual dimorphism and sex ratio are determinants of behaviour (**Chapter 2** and **3**), corroborating earlier work by Watkins (1996, 1997, 1998) and Clark et al. (2017). Thus, I am

offering more insights into the effect of sexual selection that is worthy of future research and could explain further diversification of Ecuadorian lava lizards. My research activities have provided meaningful information on thermal ecology of lava lizards as part of global efforts to understand thermal biology of lizards across the globe, morphological and photographic records of island species to local authorities, and diet preferences and tissue samples in collaboration with local institutions. The collection of tissues samples for local collaborators is specifically important as the last update of the phylogenetic relationships within the *Microlophus* group was undertaken almost 15 years ago by Benavides et al. (2007). Equally important are my contributions on the effect of urbanisation on Galápagos lava lizards that will be required for conservation and management (**Chapter 4**). After Tanner et al. (2007), my research is the second to demonstrate the effect of human urbanisation on the behaviour of the Galápagos lava lizards. Differences in behaviour can be linked with relative human impact, but it is difficult to know in which direction the change is going given the group has been mostly neglected. My work has cast a spotlight on lava lizards and serves as a wake-up call to pay attention to all species, particularly at a place of such international significance as the Galápagos Islands.

I believe it is extremely important for the Ecuadorian scientific community for the work described herein to be led by a local, as the few publications available in ecology and behaviour are mostly led by international researchers. At the same time, my work showcases South American behavioural research and I hope will help to bring about recognition that Latin American countries can be sources of abundant behavioural data for local and international scientists. Ultimately, I hope my contributions will catch the attention of Latin American scientists and encourage them to consider the field of behavioural ecology – to the benefit of all South America, including Ecuador. Admittedly, I consider myself as one of the Ecuadorian biologists inspired by prior behavioural research in my home country. My research and fieldwork experience studying the behavioural ecology of Ecuadorian lava lizards over the last few years has reinforced my passion to study and protect the diversity featured in my home country, Ecuador.

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