Functional significance of highly variable colouration in the shore skink (*Oligosoma smithi*)

A thesis presented in partial fulfilment of the requirements
for the degree of

Doctor in Philosophy

in

Ecology

at Massey University, Albany, New Zealand

Marleen Baling

2017

ABSTRACT

Variation in animal colouration is attributed to several biological functions, a key one being camouflage. Background-matching is a camouflage strategy where prey conceal themselves from predators by resembling their immediate backgrounds. Achieving optimal background-matching can be challenging, particularly in 1) visual backgrounds that form a mosaic caused by spatial variations in habitat characteristics, and 2) varying predator abundance or behaviour. Additionally, crypsis can be affected by alternative and potentially antagonistic functions, such as intraspecific signalling and thermoregulation. This thesis aimed to investigate the selective processes that affect prey colouration for background-matching in a heterogeneous environment. Specifically, I focused on the influence of habitat gradients, predator behaviour, and the potential conflict between camouflage requirements and thermoregulation or intraspecific signalling. Firstly, I conducted a detailed survey on the colour and colour patterns of a wild shore skink population (*Oligosoma smithi*) within a continuous heterogeneous habitat at Tāwharanui Regional Park. This population's body colouration showed a significant association with a vegetation gradient, consistent with selection for background-matching. However, field experiments also revealed that predation risk for the more common colour pattern variants was double that of the rarer variant's regardless of background type, consistent with predictions for apostatic selection (negative frequency-dependent selection). Secondly, I demonstrated that population colouration can respond to a change of habitat. One year after a translocation of shore skinks to an island habitat with a disjunct two-patch background, the population's colours matched the simple substrate type (bare rocky stones) more than the complex substrate (high vegetation cover on sand). Skinks were darker, less intense in colour, and had lower colour pattern diversity compared to the founder and source populations at Tāwharanui. This study highlighted the potential significance of considering camouflage requirements of a species in human-induced translocations. Thirdly, in an analysis of seasonal effects to camouflage, I found no evidence that background-matching in the Tāwharanui population was compromised by differences in body colours between breeding and non-breeding seasons. This is likely because colours associated with intraspecific signalling (i.e. that exhibited age-dependence and sexual dichromatism) were located in the ventral body regions of skinks that would typically be hidden from predators. Finally, across 17 populations, shore skink colouration showed patterns of spatial variation consistent with thermal melanism (thermoregulation) and island syndrome. Despite the strong correlation of maximum monthly temperature on colours and latitude on colour patterns, I suggest that the significantly darker island populations were caused by a combination of local adaptation (i.e. crypsis) and non-selective forces (e.g., genetic drift). Overall, my thesis provides new insight on how different selection processes maintain dramatic colouration within a species, and marks the first quantitative research on colouration in New Zealand reptiles.

ACKNOWLEDGEMENTS

The success of one person is never achieved by his or her own, and with this I am the same. I am humbled by the amount of support and opportunities that were given by many people along the way. First and foremost, I would like to thank my supervisors, Jim Dale, Devi Stuart-Fox and Dianne Brunton. Their continual encouragement, support, and advices have been extremely valuable. I feel like I have grown a lot professionally from the lessons I learned from them during this candidacy. I express my gratitude for the fees scholarship support from INMS (Gaven Martin) during my candidacy.

There are many (people and institutions) who gave a variety of support in different parts of my study:

Chapter Two: We thank field volunteers for help and support: Massey University (MU) Albany ecology group (C. Wedding, B. Barr, M. Barry, M. Delaney, D. van Winkel); Auckland Regional Council (ARC): G. Ussher, M. Maitland; Tāwharanui Open Sanctuary Society Inc.; Supporters Of Tiritiri Matangi; Department of Conservation (DOC); Ngäti Manuhiri; Ngäti Paoa; and Ngäti Whanaunga. We also thank J. Endler for Matlab scripts used for photo calibration. Work was approved under MU Animal Ethics (MUAE07/113), DOC wildlife translocation permit (DOCDM-73616) and ARC research permit 2005. This work was supported by the by Auckland Regional Council and Massey University. M. Baling was also funded by Supporters Of Tiritiri Matangi staff grant (2007), James-Sharon Watson Conservation Trust (2007), Lovell and Bery Clark Scholarship (2014) and Claude McCarthy Fellowship (2014).

Chapter Three: We thank for all help and support given by field volunteers, Massey University Albany ecology research group (C. Wedding, B. Barr, M. Barry, M. Delaney, D. van Winkel), Auckland Council (G. Ussher, M. Maitland); Tāwharanui Open Sanctuary Society Inc., Department of Conservation, Ngäti Manuhiri, & Ngäti Paoa. We also thank J. Endler for Matlab scripts used for photo calibration; T. Bowala, and Y. Yildrim for constructive comments. Project funding was provided by Auckland Council. M.B. was supported by James-Sharon Watson Conservation Trust, Lovell and Bery Clark Scholarship and Claude McCarthy Fellowship.

Chapter Four: We thank for all help and support from staff and volunteers in the field (B. Barr, M. Barry, D. H. Brunton, A. Harmer, C. Wedding, W. Ji, D. van Winkel), volunteers for creating the lizard models (L. Bütikofer, C. Chawla, B. Kreigenhofer, Y. Liu, Naren, O.

Ormano, Y. Yildrim, R. Yulo), D. Thomas for scanning 3D skink model, B. Dixon for 3D printing of the skink replicas, B. Reinke, Auckland Council (M. Maitland), Tāwharanui Open Sanctuary Society Inc, Ngäti Manuhiri, and New Zealand Department of Conservation. Wildlife and animal ethics permits were approved from New Zealand's Department of Conservation (DOCDM-73616, AK-33640-FAU), Auckland Regional Council (research permit 2005), Auckland Council (CS39A) and Massey University Animal Ethics Committee (MUAEC07/113, MUAEC12/26). MB was funded by the Society for Research on Amphibians and Reptiles in New Zealand (SRARNZ) Herpetological Research Award, Lovell and Berys Clark Scholarship, Claude McCarthy Fellowship and Auckland Regional Council. JD was funded by the College of Sciences, Massey University.

<u>Chapter Five</u>: We would like to thank for field volunteers and support: Massey University MU (M. Barry, D.H. Brunton, L. Bütikofer, M. Delaney, B. Evans, J. Laycock, M. Roper, M. Strickett, W. Webb), K. Corbett, D. Craddock, J. Fitter, R. Hallet, S. Hallet, J. Laffont, S. Sinclair, C. Wedding; New Zealand Department of Conservation DOC (L. Adams, G. Atkins, T. Bliss, N. Brown, R. Chappell, B. Kappers, P. Livingstone, J. Lucas, A. Kirk, G. Moorcroft, C. Moretti, K. Owens); Matakohe-Limestone Island (B. Buhler); Auckland Council (M. Maitland, M. Puckett); Bay of Plenty Regional Council; Bream Head Conservation Trust (C. Mitchell, P. Mitchell); EcoQuest Education Foundation (R. Longman-Sinclar, C. Longman-Sinclair); Ngätiwai Trust Board (C. Stone), Ngäti Whatua, Nga Rima O Kaipara, Ngäti Manuhiri, Ngäti Rehua, Ngäti Maru, Ngati Whanaunga, Ngäti Awa and Rurima Trust (B. Hughes, D. Hunia, TK Merito); NIWA (A. Tait, B. Liley); Ecogene (J. Allwood, R. Howitt, F. Molinia). We also thank D. Aguirre and L. Liggins for stats analyses advice; and Y. Yildrim and D. Pang for constructive comments. Work was approved under DOC permit AK-33640-FAU, Auckland Council Research Permit CS39, and MU Animal Ethics Committee no. 12/26. M. Baling was funded by Harriette Jenkins Award 2012, New Zealand Federation of Graduate Women Postgraduate Fellowship 2013, Lovell and Bery Clark Scholarship 2014, and the Institute of Natural and Mathematical Sciences.

--

I would like to give my thanks to others that gave alternate means of support, their company, the many talks and discussions through the years: Theresa Alipia, David Aguirre, Christophe Amiot, Pete Anderson, Daryl Andrews, Manuela Barry, Tharu Bowala, Luca Butikofer, Chavi Chawla, Elena Colombi, Cheryl Cross, Vanessa Cross, Vesna Davidovic, Catia Demilglio, Natasha Dougherty, Chaitanya Gokhale, Aaron Harmer, Heather Hendrickson, Weihong Ji, Colleen Keelty, Brigitte Kreigenhofer, Hayley Kim, Vicky Kim,

Jenny Laycock, Libby Liggins, Yunhao Liu, Anil Malhotra, Honour McCann, Freda McKisch, Naren, Luis Ortiz Catedral, Kevin Parker,Matt Pawley, Jo Peace, Philippe Remigi, Jessica Patino, Michelle Roper, Caroline Rose, Araceli Samaniego, Evelyn Sattlegger, Idan and Dana Shapira, Su Sinclair, Karen Stockin, Christina Straub, Daniel Thomas, Wesley Webb, Jacqui Wairepo, Annette Warbrooke, Chris Wedding, Anne Wignall, Mike Yap, Yeserin Yildrim, and Megan Young. Extra thank yous to Deborah Pang, Tharu Bowala and Yeserin Yildrim for all those last edits to the manuscripts!

Not forgetting the rock climbing crew who kept my sanity in check: Christie Ahn, Doug Atkinson, Gabriella Beans, Foo Hui Chien, Kenja Fyers, Micah Fyers, Peter Ham, Richard Kim, Brigitte Kreigenhofer; Manu Lange, Zhuowei Lim, Debra Pang, Geoffrey Shen, Victor Savelyev, Jenny Shim, James Speedy, Kyu Shim, Jung Hoo Shin, Yeserin Yildrim. Thank you for all the fun climbing/ bouldering sessions and unforgettable trips.

A special thank you to my family: my parents, Barling Layat Supen and Florence Leong, who have greatly influenced my curiosity of life, love of nature, science and education. Thank you for your unconditional support in everything that I do. My brothers, Robin Barling and Ewen Barling, what would I do without your company, and conversations on food and pop culture. Finally, to Richard Kim, the one who has been giving his support every other way that he can. Thank you for being on-belay: accompanying me during my late night writes, catching when I fall, and constantly checking that that I have enough to eat, exercise and rest, especially in the last legs of this journey.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1 INTRODUCTION

Typically we expect that under Darwinian natural selection, populations will express an optimal adaptive phenotypic state for any given characteristic. However, multiple phenotypes often occur within a single population. Body colouration is one example of a phenotypic trait that exhibits dramatic variation in many taxa (e.g., Bergstrom et al. 2012; Hanlon 2007; Lacey et al. 2010; Stuart-Fox et al. 2007). Variation in colour and colour patterns can occur continuously (e.g., different levels of intensities in feather or skin colour; Bergman and Beehner 2008; Chavez and Kenagy 2014; Tibbetts and Dale 2007) or as discrete morphs (e.g., distinct colour or colour patterns; Pérez i de Lanuza and Font 2015; Soria-Carrasco et al. 2014; Tate et al. 2016; Teasdale et al. 2013) across small or large spatial (e.g., between microhabitats, or large geographic distribution) and time scales (i.e. colour can vary rapidly within seconds to hours, or over days or months). The function and mechanism on how such multiple colouration states within a population or species arise have long fascinated many behavioural and evolutionary scientists.

In ectotherms such as lizards, body colouration are influenced by three major biological functions: concealment from predators, intraspecific signalling, and thermoregulation (Chen et al. 2012; Clusella-Trullas et al. 2007; Pearson 1977; Pérez i de Lanuza et al. 2013; Stevens and Merilaita 2011; Stuart-Fox et al. 2006; Stuart-Fox et al. 2004). Each of these biological functions can favour different phenotypes to increase overall population fitness. In the first function for colouration, the most common approach for lizards to conceal themselves from predators is via visual camouflage (Stevens and Merilaita 2011). This natural selection for camouflage favours prey colour and colour patterns that blend to their surroundings to reduce predator detection. In contrast, sexual selection for intraspecific signalling can produce conspicuous colouration to increase detection, and attract conspecifics to breed (Cooper Jr. and Greenberg 1992). Finally, lizards can use dark colouration (i.e. thermal melanism) to increase absorption of solar radiation for heat, and therefore, maintain their body thermoregulation (Clusella-Trullas et al. 2007). These functions are not mutually exclusive, and depending on the species, can either complement or be antagonistic with one another.

1.1 Camouflage: concealment from predators

Concealment via visual camouflage is the most common function for colour adaptation, particularly for prey species to avoid detection and recognition by predators (Stevens and

Merilaita 2011). Stevens and Merilaita (2009) defined several strategies of visual camouflage, broadly categorised in two main forms: 1) crypsis or preventing detection (e.g., background-matching, disruptive colouration, self-shadow concealment); and 2) preventing recognition even when presence is detected (i.e. masquerade, motion dazzle, motion camouflage). Crypsis, especially background-matching, is one of the more basic and ubiquitous strategies, and will be the focus of this thesis. Background-matching, defined by Endler (1978, 1984), is achieved by prey resembling a random sample of the background that it is normally seen in by its predators. This selection is maximised over space and time, which should result in a highly accurate matching in colour and colour patterns between prey and its background. In many cases however, optimal background-matching does not occur in natural populations — instead we usually see a wide variation of cryptic colouration within a species and also within a population.

Merilaita et al. (2001; 1999) and Houston et al. (2007) suggested that prey colouration will occur within a specialisation-compromise continuum if their environments are composed of two or more distinct habitat types (either in colour, structure or complexity). Prey will either adapt to favour specialisation to match one of the distinct patch types (specialist), or alternatively display a compromised phenotype that matches general characteristics of several patch types (generalist)(Merilaita and Dimitrova 2014). Such compromise represents a trade-off that can be influenced by three aspects: i) the differences in visual colour, structure and complexity of the habitat patches; ii) predator density, visual system and behaviour; and iii) the prey's biological ability to adapt to the environment.

Firstly, the degree of disparity in colour, structure and complexity between habitat patches can affect the diversity of colour and colour pattern variants, and their background-matching in a prey population. Much research have shown that within disjunct two-patch type habitat (e.g., green vs. brown, or uniform vs. complex backgrounds), prey matched more to one patch over the other, resulting in disruptive selection for colour patterns within population (e.g., Bond and Kamil 2006; Houston et al. 2007; Merilaita et al. 2001; Morey 1990; Nilsson and Ripa 2010). In particular, simple habitats generally favour selection for optimal background-matching, so populations in these backgrounds would show low variation in colour and colour patterns. In contrast, complex environments are less stringent on the degree of background-matching because the high level of visual noise from background patterning should afford sufficient protection for different variants from predator detection (Merilaita 2003; Merilaita and Dimitrova 2014).

Less research have been done on investigating population colouration within more continuous mixed habitat types, where these backgrounds form a continuum in colour, structure or complexity (e.g., a vegetation gradient across a sand dune). Particularly, more studies using natural systems are needed to substantiate predictions from theoretical modelling and studies using virtual environments on background-matching in continuous heterogeneous habitats (Houston et al. 2007; Merilaita et al. 2001; Merilaita et al. 1999). For example, where do prey population living in continuous heterogeneous habitat fit within the specialise-compromise continuum of background-matching? Do generalists vary in levels of conspicuousness within the habitat's various backgrounds? I explored these questions of background-matching in heterogeneous habitats in Chapter 2 and Chapter 3.

Secondly, predator diversity, intensity, and behaviour can strongly influence the degree of background-matching of prey (e.g., Bond 2007; Calsbeek and Cox 2012; Endler 1978; Stuart-Fox et al. 2008; Troscianko et al. 2013). Different types of predators will have different visual acuities or colour visions that can affect how prey colouration is perceived in its environment (Bowmaker 1998; Defrize et al. 2010; Kelber et al. 2003; Lind and Kelber 2009; Osorio et al. 1999; Théry et al. 2004). For example, snakes and birds differ in their colour discrimination, and rapid colour-changing chameleons have been shown to exhibit different colour responses depending on whether they are exposed to avian or snake predators (Stuart-Fox et al. 2008). Bird predators often have high colour discrimination and acuity (Aidala et al. 2012; Olsson et al. 2015), so in general these predator types select for accurate background-matching in prey. High intensity of predation on a population may also promote accurate background-matched colouration (Endler 1978). Lastly, predators are capable of learning and optimising their search for cryptic prey (Bond 1983; Bond 2007; Troscianko et al. 2009). For example, predators can use search images to optimise their detection for highly cryptic prey, and impose another selective pressure, apostatic selection, onto the prey population (Bond 2007; Merilaita and Dimitrova 2014). This negative frequency-dependent selection favours survival of rare variants, and has been linked to the maintenance of high variation in population colouration (Bond and Kamil 2002, 2006; Merilaita 2006). However, few data have compared these two selective processes (crypsis and apostatic selection) in wild populations, and the visual cues for detecting cryptic prey (e.g., colour vs. colour pattern) are often unclear. For my study, I approached this knowledge gap by experimentally testing the predation risk of different colour patterns observed in a naturally occurring prey population (Chapter 4).

The third aspect that can influence background-matching in a heterogeneous habitat is the prey species' ability to adapt to their environment (Bergstrom et al. 2012; Cortesi et al. 2015; Tyrie et al. 2015; Westley et al. 2013). For example, a lack of genetic variation or heritability could reduce the range of phenotypes, and thus the population's capability to adapt or spread to available neighbouring habitat (Morgans and Ord 2013; Westley et al. 2013). Even different variants within a population or species can have different strategies, survivorship or thermoregulatory needs that can affect their spatial and temporal distribution (Allen et al. 2013; Chapple et al. 2008; Forsman and Shine 1995; Halperin et al. 2017; King 2003; Tanaka 2005). Furthermore, prey may be adaptive behaviourally to respond to changes in their environments. Several species can actively choose background colours to match their body colouration (Cooper Jr. and Sherbrooke 2012; Gilis 1982; Kang et al. 2013; Karpestam et al. 2012; Merilaita et al. 1999), and some can even orientate their body positions on their background until crypsis is optimised (Kang et al. 2014; Kang et al. 2012), while others elicit facultative camouflage where they can change colour over time to conceal themselves from visual predators (see below, on physiological and morphological colour changes).

1.2 Conflicting signals: camouflage, thermoregulation and intraspecific signalling

Thermoregulation is important for the maintenance of body functions such as digestion, egg production, locomotion, and growth rate. That is, it critically affects an animal's survival and reproductive success (Cooper Jr. and Greenberg 1992; Girons 1980; Norris and Kunz 2012; Pearson 1977; Rowe et al. 2016). For ectotherms, variation in body colouration may represent a selection for thermal melanism (Bittner et al. 2002; Clusella-Trullas et al. 2008; Clusella-Trullas et al. 2007; Tanaka 2009). The thermal melanism hypothesis predicts that dark-pigmented individuals have an advantage over light-pigmented individuals during low temperature conditions because darker colours can increase the rate of absorption of solar radiation. (Clusella-Trullas et al. 2007). Clusella-Trullas et al. (2007) found strong support for two predictions of the hypothesis: 1) dark-coloured species will occupy cooler areas compared to light-coloured species because the ability to increase body temperature faster will provide an advantage over species that are not melanistic; and 2) melanism increases fitness in cold climates, due to its higher efficiency in attaining preferred body temperature and performance. Thermal melanism may complement the need for camouflage, particularly if the local habitat colour coincides with local climate (e.g., cold, rainy forest habitats are darker compared to warm white sandy beaches).

For intraspecific signalling, there are different kinds of information that colour-based signals can broadcast, including individual quality, attractiveness, social or breeding status, kinship, sex or species recognition (Cooper Jr. and Greenberg 1992; Dale 2006; Fox et al. 2003). Therefore, most colouration for intraspecific signalling functions to attract attention of conspecifics, while colouration for camouflage serves to avoid detection. As a consequence, intraspecific signalling may carry a high cost to fitness, with higher risk of exposure to predator detection. Given this, then how do lizards adapt colouration to fit the need for complex visual intraspecific signalling or thermoregulation while simultaneously concealing themselves from predators? In general, there are two basic strategies, and both potentially reflect a compromise (i.e. trade-off) between survival and reproductive success.

First there is compelling evidence for colour division on the body regions of lizards to suit the opposing functions for crypsis versus intraspecific signalling. For example, the high complexity of colouration in male Australian dragon lizards (*Ctenophorus* spp.) was attributed to social signalling, but the males still had some level of compromise for both camouflage and intraspecific signalling by body colour partitioning (Chen et al. 2012). The dorsal regions of the body 'exposed' to visual predators were found to be more cryptic than the hidden body regions. In addition, the level of contrast to the background can also differ between sexes, where females are generally more cryptic than males (Runemark et al. 2010; Stuart-Fox et al. 2004; Stuart-Fox and Ord 2004). The energetic cost of this strategy in body colour partitioning should be low (cf. physiological colour change, below) and is likely widespread in many species (Norris and Lowe 1964).

An alternative strategy for potential trade-off between camouflage and the other two functions is the ability to change colour. Colour change can be observed either through 'morphological colour change', which can occur over days to months, or via 'physiological colour change' that occurs rapidly within seconds to hours (Cooper Jr. and Greenberg 1992; Fan et al. 2014; Hanlon 2007; Kang et al. 2016; Stuart-Fox et al. 2008) The most common research is on physiological colour change (Hanlon 2007; Josef et al. 2012; Stuart-Fox and Moussalli 2009; Wente and Phillips 2003; Zylinski et al. 2011). For example, physiological colour change in chameleon species occurs dramatically and rapidly for both intraspecific signalling and concealment from visual predators (Stuart-Fox et al. 2008; Stuart-Fox et al. 2006). Less dramatic physiological colour changes (e.g., change from light to dark) is also observed in many other lizard species, including nocturnal animals (e.g., Fulgione et al. 2014; Hernández-Gallegos and Domínguez-Vega 2012; Ito et al. 2013; Zucker 1989).

Morphological colour change is common in many species, where individuals are conspicuous during the breeding and more cryptic during the non-breeding seasons (Cooper Jr. and Greenberg 1992). This seasonal colour change will ensure maximum use of colour for mate attraction during the breeding season, and a reduced probability of being detected by predators outside the breeding season. Few studies have quantified this, and in this thesis (Chapter 3) my study site provided the opportunity to monitor colour pattern changes not only on a spatial scale but also across time.

1.3 Geographical variation in colour among populations

Body colouration can exhibit population-level variation, where evolutionary forces such as natural selection, gene flow, founder effects and genetic drift result in phenotypic variation across different populations (Brakefield 1990; McLean and Stuart-Fox 2014). At a geographic scale, there are two predictions for selection for thermoregulation and crypsis. First, large spatial positional gradients (latitude, elevation) and environmental conditions (e.g., temperature, humidity, solar radiation, predator type and pressure) will affect geographic colour variation for thermal melanism. Here, we expect populations will be darker at colder climates or at higher latitudes to increase thermoregulatory efficiency (Castella et al. 2013; Clusella-Trullas et al. 2007; Fielding and Defoliart 2005; Fischer and Lindenmayer 2005; Lacey et al. 2010). Second, selection for crypsis predicts that body colour within a population will be more similar to the local habitat (local adaptation for crypsis) compared to another population in a different habitat type (Brown and Thorpe 1991; Gvoždík 1999; Macedonia et al. 2003). Therefore, these naturally-selected phenotypic traits among populations will co-vary with the level of environmental heterogeneity among populations (Brown et al. 1991; Dale 2006; Thorpe 1991). In addition, we also expect body patterns to undergo a similar selective pressure for local adaptation (Allen et al. 2015; Bechtel 1978; Chapple et al. 2008; Dimitrova and Merilaita 2014).

However, observed body colour variation does not always indicate functional adaptation. Non-selective forces such as genetic drift and founder effects can cause stochastic fluctuations of a population’s phenotypes. These random, non-selective forces occur within all populations (Runemark et al. 2010) but are most influential in smaller populations (Gray and McKinnon 2006). Populations in insular systems (e.g., islands) are likely to undergo genetic drift, especially if the founder population size is low, resulting in observed higher variance between populations, and lower variance within populations (Brakefield 1990; King 1988; Runemark et al. 2010; Uy and Vargas-Castro 2015).

These evolutionary forces are not mutually exclusive, and so I expect that observe variation among populations will be the outcome of a combination of processes. In Chapter 5, I look at the degree of influence that both camouflage and thermoregulation may have on the geographical variation of colour patterns among populations.

1.4 *Oligosoma smithi* as a model species

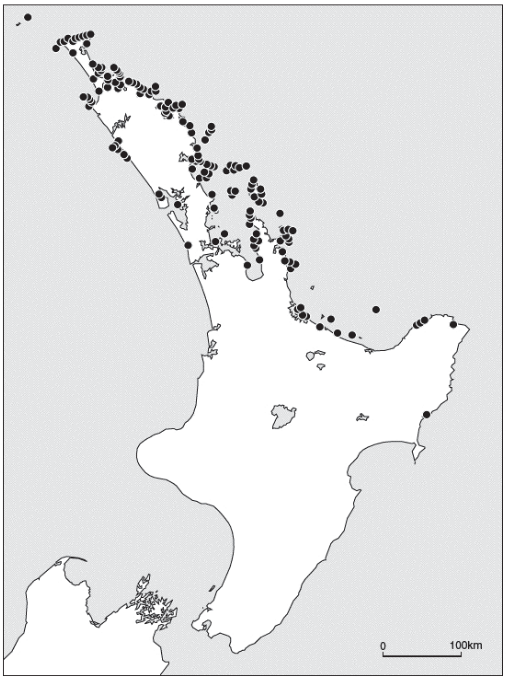


Figure 1. Geographic distribution of the shore skink, *Oligosoma smithi* (Towns et al. 2002)

The shore skink, *Oligosoma smithi*, is endemic to New Zealand, listed as “Not Threatened” under the Department of Conservation of New Zealand (DOC) Threatened List (Hitchmough et al. 2010) and is managed under the *Oligosoma* spp. Recovery Plan (Towns et al. 2002). This diurnal, active species has a wide geographic distribution, covering the northern coasts of the mainland North Island, and includes offshore islands (Figure 1; Towns et al. 2002). Despite being restricted to the coast, shore skink can still be found between 20 – 100 m (up to 2 km inland) from the high tide, occurring over highly disturbed, heterogeneous habitats (sand dunes, rocky stone beaches, vegetation scrub; Baling et al. 2016; Towns et al. 2002). This species matures relatively fast (in two years) and produces 2 – 6 offspring per clutch annually in the beginning of the year, peaking in February (M. Baling unpublished data).

Figure 2. Example of shore skink colouration.

Shore skinks have amongst the greatest variations in colour and colour pattern New Zealand skinks (Figure 2; Hardy 1977). There is continuous colouration within and among populations, but there are also populations that consist of only dark-coloured individuals, particularly on islands (McCallum 1980, 1982; Towns 1972; Towns and Hayward 1973). The dorsal colour variation seems to coincide with habitat types; pale skinks found in pale sand dunes, speckled and dark (sometimes with green structural colours) individuals in vegetation, and uniform, dark-coloured skinks in dark boulder or stone gravel beaches; all indicating the traits' potential role for crypsis. The ventral body region also exhibit colouration from pale white to orange-brown within the species, and is present in both sexes, and to some extent in juveniles (pers obs; Hardy 1977; Hare et al. 2008).

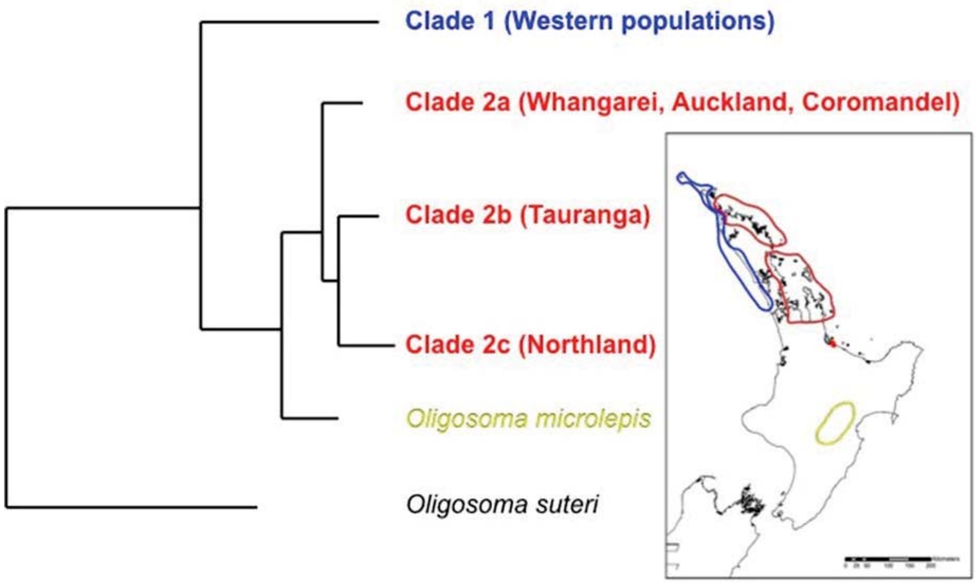


Figure 3. Shore skink phylogeny consisting of two clades. Clade 1 (blue) and 2 (red) are shore skinks and the third clade (yellow) is another species, small-scaled skink, *O. microlepis*. Adapted from Hare et al. (2008)

A phylogeograhic study has split shore skinks into two main clades (Figure 3); the first is the western population (Three Kings and the western Northland coastline of North Island) and the second clade is the eastern population consisting of three subclades (eastern coastline covering Northland, Auckland, and its surrounding regions, East-Coast Bay of Plenty) (Hare et al. 2008). A third clade was identified and is a different species, *O. microlepis*, the small-scaled skink. This species occurs in very different locations to shore skinks: in the middle of North Island Central Plateau. Hare et al. (2008) suggested the sister lineage to *O. microlepis* may have been a recent split from shore skink that occurred during the North Island submergence in the Pliocene period. The authors also suggested that that shore skink may constitute a species complex; however, taxonomy for the new species (western shore skink) has not been resolved.

Overall, shore skink is an ideal model species due to the characteristics that matches the intent of the study: i) it has a relatively wide geographic distribution, ii) high variation in colour patterns, iii) relatively fast breeding and rate of maturation, iv) accessibility to many populations; and v) availability of recent phylogenetic data. The functional significance for colour patterns in the shore skinks was unknown and unquantified, so as with many other New Zealand reptiles.

1.5 Aims and objectives

I investigated the function and evolution of body colouration in a highly variable lizard species. In particular, I focused on the selective processes that may affect colouration for crypsis (background-matching), and the degree of influence the interactions between camouflage and the other two biological functions (thermoregulation and intraspecific signalling) have on the expression of colour and colour patterns. My objectives are to:

1. Test two factors that can influence effective background-matching in continuous heterogeneous habitat: i) habitat colour, structure and complexity; and ii) predation risk on colour pattern variants.
2. Determine variation in colouration and background-matching of a population following translocation to a disjunct two-patch habitat type.
3. Investigate if there is a trade-off between the need for crypsis and intraspecific signalling in population colouration over a spatial and temporal scale.
4. Determine the degree of influence thermal melanism and crypsis have on the geographic body colouration among populations.

1.6 Thesis structure and outline

This thesis is structured as ‘PhD by Publication’, where the main chapters were written as scientific articles ready for submission. The content of the thesis consists of four research chapters, with an introductory chapter, and overall discussion section at the end. The graphics page at the beginning of each data chapter (i.e. Chaper Two to Five) represents the graphical abstract for each study.

<u>Chapter One</u>: This first chapter introduces the biological functions for animal colouration (with particular focus on colouration for crypsis), and factors that can affect the selective processes for variation in prey colouration in heterogeneous environments.

<u>Chapter Two</u>: This is a field study that investigated how a change in visual habitat characteristics can alter prey colouration for crypsis. It was an opportunistic observation to document the changes in shore skink colouration following re-location of a subpopulation from a mainland site (continuous heterogeneous habitat) to an island that

differed in background colour and substrate (disjunct two-patch habitat). This chapter was written from a conservation management perspective to highlight the potential significance of habitat characteristics for prey crypsis, and ultimately survival of a translocated species. It has been published in *Biological Conservation*.

Chapter Three: This research chapter is a field observation study that documented the spatial and temporal variation in shore skink colouration within a continuous heterogeneous habitat. The study site was also the source location (Tāwharanui Regional Park) for the translocated population in Chapter Two. I investigated where this population fits within the background-matching specialise-compromise continuum across a vegetation gradient (sand to vegetation). Additionally, I evaluated how the role of colouration was divided between the different body regions of the skink, and whether population colouration varies across seasons (breeding and non-breeding) to fit within the requirements for crypsis and intraspecific signalling. I plan to submit this chapter to *Ecology and Evolution*.

Chapter Four: For this third research chapter I investigated the second factor that can affect background-matching in heterogeneous habitat: predation risk. Based on the results of the observational field study in Chapter Three, here I determined the relative risk of different colour and colour pattern variants for avian attacks at different background types. I used 3D-printed skink replicas that were painted according to the spectral reflectance of shore skinks. This chapter has been submitted to, and is currently under review at *Proceedings of the Royal Society B*.

Chapter Five: This fifth chapter examined the effect of camouflage and thermoregulation on shore skink colouration at a larger spatial scale: between both island and mainland populations across the North Island. Here, I looked at large scale effects, such as environmental gradients, latitudinal cline, phylogeny, island syndrome or local adaptation for crypsis that can affect skink colour and colour pattern diversity (with a particular focus on thermal melanism).

Chapter Six: This last chapter summarises the findings of the four research chapters, with discussions on the contributions of my research to the field of animal colouration, the strengths, and limitations of each study. I also suggest potential directions for future work on this topic.

1.6.1 Terminology

In this thesis, I assigned particular terms to the following:

Term	Description
Colour	Overall body colour – hue, saturation and brightness of the animals.
Colour patterns	Body patterning, usually on the dorsal body region of the animals
Colouration	Both colour and colour patterns of the animal, population or species

1.7 References

Aidala, Z., Huynen, L., Brennan, P.L.R., Musser, J., Fidler, A., Chong, N., Machovsky Capuska, G.E., Anderson, M.G., Talaba, A., Lambert, D., Hauber, M.E., 2012. Ultraviolet visual sensitivity in three avian lineages: paleognaths, parrots, and passerines. *Journal of Comparative Physiology A* 98: 495. doi:10.1007/s00359-012-0724-3

Allen, J.J., Akkaynak, D., Sugden, A.U., Hanlon, R.T., 2015. Adaptive body patterning, three-dimensional skin morphology and camouflage measures of the slender filefish *Monacanthus tuckeri* on a Caribbean coral reef. *Biological Journal of the Linnean Society* 2: 377-396. doi:10.1111/bij.12598

Allen, W.L., Baddeley, R., Scott-Samuel, N.E., Cuthill, I.C., 2013. The evolution and function of pattern diversity in snakes. *Behavioral Ecology* 24: 1237-1250. doi:10.1093/beheco/art058

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. *Biological Conservation* 203: 298-305. doi:10.1016/j.biocon.2016.10.002

Bechtel, H.B., 1978. Color and pattern in snakes (Reptilia, Serpentes). *Journal of Herpetology* 12: 521-532. doi:10.2307/1563357

Bergman, T.J., Beehner, J.C., 2008. A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas (*Theropithecus gelada*). *Biological Journal of the Linnean Society* 94: 231-240. doi:10.1111/j.1095-8312.2008.00981.x

Bergstrom, C.A., Whiteley, A.R., Tallmon, D.A., 2012. The heritable basis and cost of colour plasticity in coastrange sculpins. *Journal of Evolutionary Biology* 25: 2526-2536. doi:10.1111/j.1420-9101.2012.02624.x

Bittner, T.D., King, R.B., Kerfin, J.M., 2002. Effects of body size and melanism on thermal biology of garter snakes (*Thamnophis sirtalis*). *Copeia* 2002: 477-782.

Bond, A.B., 1983. Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. *Journal of Experimental Psychology* 9: 292-306.

Bond, A.B., 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* 8: 489-514. doi:10.1146/annurev.ecolsys.38.091206.095728

Bond, A.B., Kamil, A.C., 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* 415: 609-613. doi:10.1038/415609a

Bond, A.B., Kamil, A.C., 2006. Spatial heterogeneity, predator cognition, and the evolution fo color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences* 103: 3214-3219. doi:10.1073pnas.0509963103

Bowmaker, J.K., 1998. Evolution of colour vision in vertebrates. *Eye* 12: 541-547. doi:10.1038/eye.1998.143

Brakefield, P.M., 1990. Genetic drift and patterns of diversity among colour-polymorphic populations of the homopteran *Philaenus spumarious* in an island archipelago. *Biological Journal of the Linnean Society* 39: 219-237. doi:10.1111/j.1095-8312.1990.tb00513.x

Brown, R.P., Thorpe, R.S., 1991. Within-island microgeographic variation in the colour pattern of the skink, *Chalcides sexlineatus*: Pattern and cause. *Journal of Evolutionary Biology* 4: 557-574. doi:10.1046/j.1420-9101.1991.4040557.x

Brown, R.P., Thorpe, R.S., Báez, M., 1991. Parallel within-island microevolution of lizards on neighbouring islands. *Letters to Nature* 352: 60-62. doi:10.1038/352060a0

Calsbeek, R., Cox, R.M., 2012. An experimental test of the role of predators in the maintenance of a genetically based polymorphism. *Journal of Evolutionary Biology* 25: 2091-2101. doi:10.1111/j.1420-9101.2012.02589.x

Castella, B., Golay, J., Monney, J.-C., Golay, P., Mebert, K., Dubey, S., 2013. Melanism, body condition and elevational distribution in the asp viper. *Journal of Zoology* 290: 273-280. doi:10.1111/jzo.12037

Chapple, D.G., Hutchinson, M.N., Maryan, B., Plivelich, M., Moore, J.A., Keogh, J.S., 2008. Evolution and maintenance of colour pattern polymorphism in *Liopholis* (Squamata : Scincidae). *Australian Journal of Zoology* 56: 103-115. doi:10.1071/zo08040

Chavez, A.S., Kenagy, G.J., 2014. Clinical colour variation within panmictic population of tree squirrels, *Tamiasciurus douglasii* (Rodentia: Sciuridae), across an ecological gradient. *Biological Journal of the Linnean Society* 113: 536-546. doi:10.1111/bij.12361

Chen, I.-P., Stuart-Fox, D., Hugall, A.F., Symonds, M.R.E., 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution* 66: 3605-3614. doi:10.1111/j.1558-5646.2012.01698.x

Clusella-Trullas, S., Terblanche, J.S., Backburn, T.M, Chown, S.L., 2008. Testing the thermal melanism hypothesis: a macrophysiological approach. *Functional Ecology* 22: 232-238. doi:10.1111/j.1365-2435.2007.01377.x

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2007. Thermal melanism in ectotherms. *Journal of Thermal Biology* 32: 235-245. doi:10.1016/j.jtherbio.2007.01.013

Cooper Jr., W.E., Greenberg, N., 1992. Reptilian coloration and behavior, In Biology of the Reptilia: Hormones, brain and behavior. eds C. Gans, D. Crews. *The University of Chicago Press*, USA.

Cooper Jr., W.E., Sherbrooke, W.C., 2012. Choosing between a rock and a hard place: camouflage in the round-tailed horned lizard *Pherynosoma modestum*. *Current Zoology* 58: 541-548. doi:10.1093/czoolo/58.4.543

Cortesi, F., Feeney, W.E., Ferrari, M.C.O., Waldie, P.A., Phillips, G.A.C., McClure, E.C., Sköld, H.N., Salzburger, W., Marshall, N.J., Cheney, K.L., 2015. Phenotypic plasticity confers multiple fitness benefits to a mimic. *Current Biology* 25: 949-954. doi:10.1016/j.cub.2015.02.013

Dale, J., 2006. Intraspecific variation in coloration, In Bird coloration: Function and Evolution. eds G.E. Hill, K.J. McGraw. *Harvard University Press*, USA.

Defrize, J., Théry, M., Casas, J., 2010. Background colour matching by a crab spider in the field: a community sensory ecology perspective. *The Journal of Experimental Biology* 213: 1425-1435. doi:10.1242/jeb.039743

Dimitrova, M., Merilaita, S., 2014. Hide and seek: properties of prey and background patterns affect prey detection by blue tits. *Behavioral Ecology* 25: 402-408. doi:10.1093/beheco/art130

Endler, J.A., 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11: 319-364. doi:10.1007/978-1-4615-6956-5_5

Endler, J.A., 1984. Progressive background in moths, and a quantitative measure of crypsis. *Biological Journal of Linnean Society* 22: 187-231. doi:10.1111/j.1095-8312.1984.tb01677.x

Fan, M., Stuart-Fox, D., Cadena, V., 2014. Cyclic colour change in the bearded dragon Pogona vitticeps under dfferent photoperiods. *PLoS ONE* 9: e111504. doi:10.1371/journal.pone.0111504

Fielding, D.J., Defoliart, L.S., 2005. Density and temperature-dependent melanization of fifth-instar *Melanoplus sanguinipes*: interpopulation comparisons. *Journal of Orthoptera Research* 14: 107-113. doi:10.1665/1082-6467(2005)14[107:DATMOF]2.0.CO;2

Fischer, J., Lindenmayer, D.B., 2005. The sensitivity of lizards to elevation: A case study from south-eastern Australia. *Diversity and Distributions* 11: 225-233. doi:10.1111/j.1366-9516.2005.00139.x

Forsman, A., Shine, R., 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of the Linnean Society* 55: 273-291. doi:10.1111/j.1095-8312.1995.tb01066.x

Fox, S.F., Kelly, M.J., Baird, T.B. eds., 2003. Lizard social behavior. *The John Hopkins University Press*, Baltimore, Maryland.

Fulgione, D., Trapanese, M., Maselli, V., Rippa, D., Itri, F., Avallone, B., Van Damme, R., Monti, D.M., Raia, P., 2014. Seeing through the skin: dermal light sensitivity provides cryptism in moorish gecko. *Journal of Zoology* 294: 122-128. doi:10.1111/jzo.12159

Gilis, J.E., 1982. Substrate color-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn & Hebard). *Animal Behaviour* 30: 113-116. doi:10.1016/S0003-3472(82)80244-3

Girons, H.S., 1980. Thermoregulation in reptiles with special reference to the tuatara and its ecophysiology. *Tuatara* 24: 59-80.

Gray, S.M., McKinnon, J.S., 2006. Linking color polymorphism maintenance and speciation. *Trends in Ecology and Evolution* 22: 71-79. doi:10.1016/j.tree.2006.10.005

Gvoždík, L., 1999. Colour polymorphsim in a population of the common lizard, *Zootoca vivipara* (Squamata: Lacertidae). *Folia Zoologica* 48: 131-136.

Halperin, T., Carmel, L., Hawlena, D., 2017. Movement correlates of lizards' dorsal pigmentation patterns. *Functional Ecology* 31: 370-376. doi:10.1111/1365-2435.12700

Hanlon, R., 2007. Cephalopod dynamic camouflage. *Current Biology* 17: 400-404. doi:10.1016/j.cub.2007.03.034

Hardy, G.S., 1977. The New Zealand Scincidae (Reptilia: Lacertilia); a taxanomic and zoogeographic study. *New Zealand Journal of Zoology* 4: 221-325. doi:10.1080/03014223.1977.9517956

Hare, K.M., Daugherty, C.H., Chapple, D.G., 2008. Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. *Molecular Phylogenetics and Evolution* 46: 303-315. doi:10.1016/j.ympev.2007.08.012

Hernández-Gallegos, O., Domínguez-Vega, H., 2012. Seasonal changes in the dorsal coloration in the lizard *Apidoscelis costata costata* (Squamata: Teiidae) [Cambio estacional en la coloracion dorsal de la lagartija Apidoscelis costata costata (Squamata: Teiidae)]. *Revista de la Biología Tropical* 60: 405-412.

Hitchmough, R.A., Hoare, J.M., Jamieson, H., Newman, D., Tocher, M.D., Anderson, P.J., Lettink, M., Whitaker, A.H., 2010. Conservation status of New Zealand reptiles, 2009. *New Zealand Journal of Zoology* 37: 203-224. doi:10.1080/03014223.2010.496487

Houston, A.I., Stevens, M., Cuthill, I.C., 2007. Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral Ecology* 18: 769-775. doi:10.1093/beheco/arm039

Ito, R., Ikeuchi, I., Mori, A., 2013. A day gecko darkens is body color in response to avian alarm calls. *Current Herpetology* 21: 26-33. doi:10.5358/hsj.32.26

Josef, N., Amodio, P., Fiorito, G., Shashar, N., 2012. Camouflaging in a complex environment - octopuses use specific features of their surroundings for background matching. *PLoS ONE* 7: e37579. doi:10.1371/journal.pone.0037579

Kang, C., Kim, Y.E., Jang, Y., 2016. Colour and pattern change against visually heterogenous backgrounds in the tree frog *Hyla japonica*. *Scientific Reports* 6: 22601. doi:10.1038/srep22601

Kang, C., Stevens, M., Moon, J.-y., Lee, S.-I., Jablonski, P.G., 2014. Camouflage through behavior in moths: the role of background matching and disruptive coloration. *Behavioral Ecology* 26: 45-54. doi:10.1093/beheco/aru150

Kang, C.-K., Moon, J.-Y., Lee, S.-I., Jablonski, 2012. Camouflage through an active choice of a resting spot and body orientation in moths. *Journal of Evolutionary Biology* 25: 1695-1702. doi:10.1111/j.1420-9101.2012.02557.x

Kang, C.-K., Moon, J.-Y., Lee, S.-I., Jablonski, P.G., 2013. Moths on tree trunks seek out more cryptic positions when their current crypticity is low. *Animal Behaviour* 86: 587-594. doi:10.1016/j.anbehav.2013.06.014

Karpestam, E., Wennersten, L., Forsman, A., 2012. Matching habitat choice by experimentally mismatches phenotypes. *Evolutionary Ecology* 26: 893-907. doi:10.1007/s10682-011-9530-6

Kelber, A., Vorobyev, M., Osorio, D., 2003. Animal colour vision — behavioural tests and physiological concepts. *Biological Reviews* 78: 81-118. doi:10.1017/S1464793102005985

King, R.B., 1988. Polymorphic populations of the garter snake *Thamnophis sirtalis* near Lake Erie. *Herpetologica* 44: 451-458.

King, R.B., 2003. Mendelian inheritance of melanism in the garter snake *Thamnophis sirtalis*. *Herpetologica* 59: 484-489. doi:10.1655/02-93

Lacey, E.P., Lovin, M.E., Richter, S.J., Herington, D.A., 2010. Floral reflectance, color, and thermoregulation: what really explains geographic variation in thermal acclimation ability of ectotherms? *The American Naturalist* 175: 335-349. doi:10.1086/650442

Lind, O., Kelber, A., 2009. Avian colour vision: effects of variation in receptor sensitivity and noise data on model predictions as compared to behavioural results. *Vision Research* 49: 1939-1947. doi:10.1016/j.visres.2009.05.003

Macedonia, J.M., Echternacht, A.C., Walguarnery, J.W., 2003. Color variation, habitat light and background contrast in *Anolis carolinensis* along a geographical transect in Florida. *Journal of Herpetology* 37: 467-478.

McCallum, J., 1980. Reptiles of the northern Mokohinau Group. *Tane* 26: 53-60.

McCallum, J., 1982. Reptiles of the Hauraki Gulf, New Zealand. *Herpetofauna* 10: 35-41.

McLean, C.A., Stuart-Fox, D., 2014. Geographic variation in animal colour polymorphisms and its role in speciation. *Biological Reviews* 89: 860-873. doi:10.1111/brv.12083

Merilaita, S., 2003. Visual background complexity facilitates the evolution of camouflage. *Evolution* 57: 1248-1254. doi:10.1554/03-011

Merilaita, S., 2006. Frequency-dependent predation and maintenance of polymorphism. *Journal of Evolutionary Biology* 19: 2022-2030. doi:10.1111/j.1420-9101.2006.01137.x

Merilaita, S., Dimitrova, M., 2014. Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Functional Ecology* 28: 1208-1215. doi:10.1111/1365-2435.12248

Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B* 268: 1925-1929. doi:10.1098/rspb.2001.1747

Merilaita, S., Stevens, M., 2011. Crypsis through background matching, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 17-33. *University Press*, Cambridge, UK.

Merilaita, S., Tuomi, J., Jormalainen, V., 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* 67: 151-161. doi:10.1111/j.1095-8312.1999.tb01858.x

Morey, S.R., 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. *Journal of Herpetology* 24: 292-296. doi:10.2307/1564396

Morgans, C.L., Ord, T.J., 2013. Natural selection in novel environments: predation selects for background matching in the body colour of a land fish. *Animal Behaviour* 86: 1241–1249. doi:10.1016/j.anbehav.2013.09.027

Nilsson, J., Ripa, J., 2010. The origin of polymorphic crypsis in a heterogenous environment. *Evolution* 64: 1386-1394. doi:10.1111/j.1558-5646.2009.00918.x

Norris, A.L., Kunz, T.H., 2012. Effects of solar radiation on animal thermoregulation, In Solar radiation. ed. E.B. Babatunde, pp. 195-220. *InTech*, http://www.intechopen.com/books/solar-radiation/effects-of-solar-radiation-on-animal-thermoregulation.

Norris, K.S., Lowe, C.H., 1964. An analysis of background matching in amphibians and reptiles. *Ecology* 45: 565-580. doi:10.2307/1936109

Olsson, P., Lind, O., Kelber, A., 2015. Bird colour vision: behavioural thresholds reveal receptor noise. *Journal of Experimental Biology* 218: 184-193. doi:10.1242/jeb.111187

Osorio, D., Vorobyev, M., Jones, C.D., 1999. Colour vision of domestic chicks. *Journal of Experimental Biology* 202: 2951-2959.

Pearson, O.P., 1977. The effect of substrate and of skin color on thermoregulation of a lizard. *Comparative Biochemistry and Physiology Part A: Physiology* 58: 353-358. doi:10.1016/0300-9629(77)90154-2

Pérez i de Lanuza, G., Font, E., 2015. Differences in conspicuousness between alternative color morphs in a polychromatic lizard. *Behavioral Ecology* 26: 1432-1446. doi:10.1093/beheco/arv075

Pérez i de Lanuza, G., Font, E., Carazo, P., 2013. Color-assortative mating in a color-polymorphic lacertid lizard. *Behavioral Ecology* 24: 273-279. doi:10.1093/beheco/ars164

Rowe, J.W., Clark, D.L., Mortensen, R.A., Commissaris, C.V., Wittle, L.W., Tucker, J.K., 2016. Thermal and substrate color-induced melanization in laboratory reared red-eared sliders (*Trachemys scripta elegans*). *Journal of Thermal Biology* 61: 125-132. doi:10.1016/j.jtherbio.2016.09.005

Runemark, A., Hansson, B., Pafilis, P., Valakos, E.D., Svensson, E.I., 2010. Island biology and morphological divergence in the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC Evolutionary Biology* 10: 269. doi:10.1186/1471-2148-10-269

Soria-Carrasco, V., Gompert, Z., Comeault, A.A., Farkas, T.E., Parchman, T.L., Johnston, J.S., Buerkle, C.A., Feder, J.L., Bast, J., Schwander, T., Egan, S.P., Crespi, B.J., Nosil, P., 2014. Stick insect genomes reveal natural selection's role in parallel speciation. *Science* 344: 738-742. doi:10.1126/science.1252136

Stevens, M., Merilaita, S., 2009. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B* 364: 423-427. doi:10.1098/rstb.2008.0217

Stevens, M., Merilaita, S. eds., 2011. Animal camouflage: mechanisms and function. *University Press*, Cambridge.

Stuart-Fox, D., Moussalli, A., 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London B* 364: 463-470. doi:0.1098/rstb.2008.0254

Stuart-Fox, D., Moussalli, A., Whiting, M.J., 2007. Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *The American Naturalist* 170: 916-930. doi:10.1086/522835

Stuart-Fox, D., Moussalli, A., Whiting, M.J., 2008. Predator-specific camouflage in chameleons. *Biology Letters* 4: 326-329. doi:10.1098/rsbl.2008.0173

Stuart-Fox, D., Whiting, M.J., Moussalli, A., 2006. Camouflage and colour change: antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. *Biological Journal of Linnean Society* 88: 437-446. doi:10.1111/j.1095-8312.2006.00631.x

Stuart-Fox, D.M., Moussalli, A., Johnston, G.R., Owens, I.P.F., 2004. Evolution of color variation in dragon lizards: Quantitative tests of the role of crypsis and local adaptation. *Evolution* 58: 1549-1559. doi:10.1554/03-448

Stuart-Fox, D.M., Ord, T.J., 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B* 271: 2249-2255. doi:10.1098/rspb.2004.2802

Tanaka, K., 2005. Thermal aspect of melanistic and striped morphs of the snake *Elaphe quadrivirgata*. *Zoological Science* 22: 1173-1179. doi:10.2108/zsj.22.1173

Tanaka, K., 2009. Some like it cool? Intermorph comparison of preferred body temperature in a colour-dimorphic snake. *Animal Biology* 59: 31-39. doi:10.1163/157075609X417071

Tate, G.J., Bishop, J.M., Amar, A., 2016. Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morph in a polymorphic bird. *Ecology Letters* 19: 679-686. doi:10.1111/ele.12606

Teasdale, L.C., Stevens, M., Stuart-Fox, D., 2013. Discrete colour polymorphism in the tawny dragon lizard (*Ctenophorus decresii*) and differences in signal conspicuousness among morphs. *Journal of Evolutionary Biology* 26: 1035-1046. doi:10.1111/jeb.12115

Théry, M., Debut, M., Gomez, D., Casas, J., 2004. Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology* 16: 25-29. doi:10.1093/beheco/arh130

Thorpe, R.S., 1991. Clines and cause: Microgeographic variation in the Tenerife gecko (*Terentola delalandii*). *Systematic Zoology* 40: 172-187. doi:10.2307/2992255

Tibbetts, E.A., Dale, J., 2007. Indivdual recognition: it is good to be different. *Trends in Ecology and Evolution* 22: 529 - 537. doi:10.1016/j.tree.2007.09.001

Towns, D.R., 1972. The reptiles of Mercury Island. *Tane* 18: 95-106.

Towns, D.R., Hayward, B.W., 1973. Reptiles of Aldermen Islands. *Tane* 19: 93-104.

Towns, D.R., Neilson, K.A., Whitaker, A.H., 2002. North Island *Oligosoma* spp. Skink Recovery Plan. *Department of Conservation*, Wellington.

Troscianko, J., Lown, A.E., Hughes, A.E., Stevens, M., 2013. Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* 8: e73733. doi:10.1371/journal.pone.0073733

Troscianko, T., Benton, C.P., Lovell P George, Tolhurst, D.J., Pizlo, Z., 2009. Camouflage and visual perception. *Philosophical Transactions of the Royal Society B* 364: 449-461. doi:10.1098/rstb.2008.0218

Tyrie, E.K., Hanlon, R.T., Siemann, L.A., Uyarra, M.C., 2015. Coral reef flounders, *Bothus lunatus*, choose substrates on which they can achieve camouflage with their limited body pattern repertoire. *Biological Journal of the Linnean Society* 114: 629-638. doi:10.1111/bij.12442

Uy, J.A.C., Vargas-Castro, L.E., 2015. Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneivenris* of the Solomon Islands. *The Auk* 132: 787-794. doi:10.1642/AUK-14-284.1

Wente, W.H., Phillips, J.B., 2003. Fixed green and brown color morphs and novel color-changing morph of the Pacific tree frog *Hyla regilla*. *The American Naturalist* 162: 461-473. doi:10.1086/378253

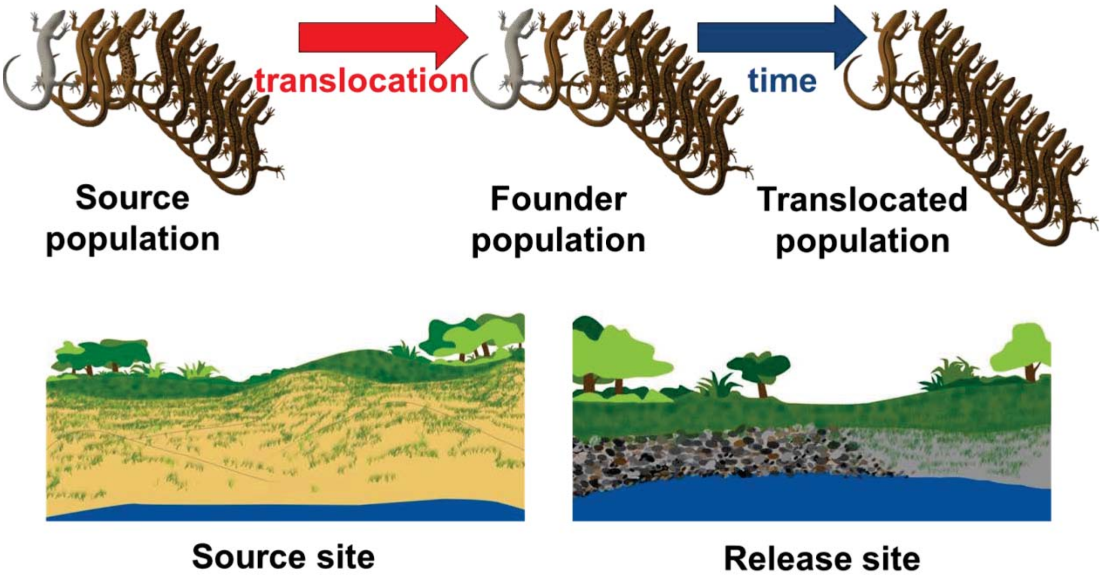
Westley, P.A.H., Stanley, R., Fleming, I.A., 2013. Experimental tests for heritable morphological color plasticity in non-native brown trout (*Salmo trutta*) populations. *PLoS ONE* 8: e80401. doi:10.1371/journal.pone.0080401

Zucker, N., 1989. Dorsal darkening and territoriality in a wild population of the tree lizard, *Urosaurus ornatus*. *Journal of Herpetology* 23: 1989. doi:10.2307/1564050

Zylinski, S., How, M.J., Osorio, D., Hanlon, R.T., Marshall, N.J., 2011. To be seen or hide: visual characteristics of body patterns for camouflage and communication in the Australian giant cuttlefish *Sepia apama*. *The American Naturalist* 177: 681-690. doi:1086/659626

CHAPTER 2

HABITAT SUITABILITY FOR CONSERVATION TRANSLOCATION: THE IMPORTANCE OF CONSIDERING CAMOUFLAGE IN CRYPTIC SPECIES



Published article:

Baling M, Stuart-Fox D, Brunton DH & Dale J 2016. Habitat suitability for conservation translocation: the importance of considering camouflage in cryptic species. *Biological Conservation*. 203: 298-305. doi: 10.1016/j.biocon.2016.10.002 (see Appendix 10)

2 HABITAT SUITABILITY FOR CONSERVATION TRANSLOCATION: THE IMPORTANCE OF CONSIDERING CAMOUFLAGE IN CRYPTIC SPECIES

2.1 Abstract

Habitat suitability is a critical aspect for the successful establishment of a translocated population. Past studies have identified multiple factors that contribute to habitat suitability, including resource availability, presence of invasive species, landscape connectivity and climate. However, visual camouflage — colouration that conceals individuals from predators or prey — is another important ecological requirement that has been largely overlooked. We provide a case study to illustrate how colouration in a prey species can change from that of the source site following translocation. Shore skinks (*Oligosoma smithi*) were moved from a coastal sand dune ecosystem to an offshore island beach that differed in substrate and colour. Within one year following release, the translocated population's colour pattern variation had reduced to mostly one type. The high match in colour between the skinks and release site (including a new substrate type) may have contributed to the observed colouration shift. This reduced variation in population colouration implies that not all founders survived, potentially decreasing the genetic diversity in the population. Our study highlights the importance of considering a species' camouflage requirements when selecting habitat for release, not only to maximise founder survival and establishment success, but also to maintain phenotypic and genotypic diversity in the long-term.

2.2 Introduction

In conservation translocations, habitat suitability is of critical importance for the successful establishment of a population (Germano and Bishop 2008; Wolf et al. 1998). A suitable, good quality habitat promotes survival and breeding of a newly founded population. In contrast, poor habitat quality at release sites has been shown to incur significant post-translocation losses; for example, 16% – 50% of failed cases are associated with poor habitat quality (Brichieri-Colombi and Moehrenschlager 2016; Germano and Bishop 2008; Moehrenschlager et al. 2013; Wolf et al. 1996). However, what constitutes habitat quality, and the specific reasons of translocation failure, are often unclear (Ewen and Armstrong 2007; Fischer and Lindenmayer 2000; Wolf et al. 1996). Therefore, identifying the ultimate causes for translocation failure due to a 'poor quality' site can be challenging.

Factors that determine habitat suitability or 'quality' are species-specific (Ewen et al. 2014). Selecting a suitable habitat will depend on understanding the critical ecological requirements for the species in question, as well as the species function within the ecosystem or food web. Previous studies have looked at habitat or landscape characteristics that fit species' requirements for foraging, refuge use, egg-laying sites (Castilla and Swallow 1995; Ebrahimi and Bull 2012; Ortiz-Catedral and Brunton 2009), dispersal or other behaviours (Armstrong and Ford 2015; Gobiel and Villard 2008; Parlato and Armstrong 2013; Richardson et al. 2015; Stamps and Swaisgood 2007), effect of invasive or anthropogenic threats (e.g., removal of introduced predators, or isolation from the public; Atkinson 2002; Moseby et al. 2015; Norbury et al. 2014; Towns 2011; Towns et al. 1997), and climatic differences between sites (e.g., climate change, Fordham et al. 2012; Schwartz and Martin 2013). In addition to the above, for some species the need for camouflage may be critical for survival, either to avoid predators or to successfully capture prey. The efficacy of visual camouflage is often dependent on the matching of the animal's body colouration to its immediate background (Merilaita and Stevens 2011; Stevens and Merilaita 2011a). Therefore, a potential mismatch between the animals and their new environment may increase their conspicuousness to predators or prey.

Three main factors influence effective background-matching in cryptic animals (Houston et al. 2007; Merilaita et al. 2001): 1) phenotypic plasticity and genetic variation of the focal species (e.g., Bergstrom et al. 2012; Cortesi et al. 2015; Morgans and Ord 2013; Rosenblum 2005; Tyrie et al. 2015; Westley et al. 2013); 2) the abundance and species composition of predators or prey (e.g., Defrize et al. 2010; Llandres et al. 2011; Rohwer and Paulson 1987;

Stankowich and Coss 2007; Théry et al. 2004; Troscianko et al. 2013); and 3) the colour, structure and complexity of the habitat (e.g., Kekäläinen et al. 2010; Nafus et al. 2016; Nafus et al. 2015). Because each factor influences an animal's conspicuousness across time and space, any change in these factors due to translocation could impact the population at different levels. For example, a population that mismatches with their release site can have lower establishment of founders through reduced individual fitness (inability to hide from predators or to capture prey). Lower founder size will affect recruitment rate, and the phenotypic and genotypic diversity of the translocated population (Armstrong and Wittmer 2011; Forsman 2014; Miller et al. 2009; Thrimawithana et al. 2013).

How significant a problem can ineffective camouflage be on the outcome of conservation translocations? We cannot currently assess this quantitatively for human-mediated translocations due to a lack of relevant data from the translocation outcomes, although the potential effects of human-induced disturbances on threatened-species' camouflage was raised within a recent literature review (Delhey and Peters 2016). Nevertheless, a few studies have highlighted the potential effect of camouflage on the fitness of translocated species. One study on Atlantic salmon (*Salmo salar*) translocated for economic purposes showed a significant decrease in individual survival and higher predation scars on salmon at mismatched background sites (Donnelly and Whoriskey Jr 1993). The authors noted the importance of colour-matching to minimise likelihood of individual loss to predators. Additionally, experimental and field studies on desert tortoises (*Gopherus agassizii*) found that the availability of rocks at a site contributed to reduced predator detection and lowered the dispersal of juveniles from the release site, thereby increasing individual fitness of the tortoises (Nafus et al. 2016; Nafus et al. 2015). The authors emphasised the importance of linking habitat to camouflage behaviour (i.e. individual fitness) when selecting suitable habitat for species conservation management.

Here, we present a case study that illustrates how body colouration, and therefore the degree of background-matching of a population, can change post-translocation without population management. We quantified population colouration and background-matching of a cryptic prey species before and after translocation. We also observed the degree of matching of the population when released to a site that included novel substrates. Our case study shows that colour and colour patterns of a translocated population can significantly differ from the source, even within one generation, and highlights the potential significance of camouflage on the phenotypic diversity of a translocated population.

2.3 Methods

2.3.1 Study species and study site

The shore skink (*Oligosoma smithi*) is a New Zealand endemic (national conservation status: Not Threatened, Hitchmough et al. 2013) with a relatively wide geographic distribution, inhabiting the northern half of the North Island. This species is present in diverse coastal habitats, from sand dunes, sandy, rocky pebbles or boulder beaches to vegetated cliffs on the mainland and offshore islands (Towns et al. 2002). There is extensive variation in body colouration in this species among populations, with island populations having less variation overall compared to the mainland (McCallum and Harker 1982; Towns 1972). It is not known if shore skink colouration is genetically determined. Within their coastal habitat, shore skinks are found close to high tide mark of the coastline to > 1 km inland; (Towns 1975). Their home range and dispersal behaviour is unknown, but because of the small size of the skinks (i.e. adult snout-vent length, SVL = 50 — 70 mm), we expect movement to be small. Similar to other New Zealand native reptile species, natural predators for shore skinks are birds (van Winkel and Ji 2012), and populations are also affected by introduced mammals such as cats, rats, hedgehogs and mice (Jones et al. 2005; Lettink and Cree 2006; Norbury et al. 2014; Wedding 2007). Some populations are able to persist in non-predator controlled sites (M. Baling personal observation; Towns 1996). As part of a conservation effort to restore reptile diversity at an island reserve in the Auckland region (Baling et al. 2013), shore skinks were translocated from the nearest mainland population.

We sourced skinks from Tāwharanui Regional Park (hereafter 'Tāwharanui'), a 550 ha peninsula protected by predator-proof fencing erected in 2004. All introduced mammal species were eradicated following an aerial drop of poison in the park except for three species (house mice *Mus musculus*, European rabbits *Oryctolagus cuniculus* and European hedgehogs *Erinaceus europaeus*, Maitland 2011). As a consequence, the population size of the resident shore skinks increased dramatically. The park also has a mixture of introduced (e.g., Australian magpie *Cracticus tibicen*, common myna *Acridotheres tristis*) and native (e.g., pukeko *Porphyrio melanotus*, sacred kingfisher *Todiramphus sanctus*) predatory birds. In 2006, we collected 40 skinks (14 males and 26 females) from a coastal sand dune system that had a gradient of light-coloured sand at the foreshore to 100% vegetation cover at the back of the dunes. Nine out of the 26 females were recorded gravid at the time of capture. We captured skinks using an existing pitfall trap grid at the site, and also hand-searches by public volunteers, and staff and students of Massey University.

We then released these 40 shore skinks to Tiritiri Matangi Island Scientific Reserve (hereafter 'Tiri') in the Hauraki Gulf, Auckland (Baling et al. 2010). Tiri is a 220 ha public community-led island restoration that has had a highly successful history of translocation of threatened endemic birds, and more recently, reptiles (Baling et al. 2013; Galbraith and Cooper 2013; Parker 2013). The island is free of introduced mammals (Graham and Veitch 2002), and has high densities of bird species, including known native predators of lizards (e.g., sacred kingfisher and morepork *Ninox novaeseelandiae*, van Winkel and Ji 2012). The island had three extant resident reptile species, two skinks and one gecko (Baling et al. 2013). Shore skinks were recorded in the 1970's but subsequent surveys failed to detect their presence, and so the species was declared locally extinct (Baling et al. 2013).

Shore skinks were released on a small north-facing beach comprised of areas of dark-coloured sand at the west and a mix of small and boulder rocks on the east part of the beach. Where the sand and rocks met (in the mid-section of the beach), there was accumulated driftwood and seaweed. Both substrates were mainly bare at the front of beach (with some seaweed and driftwood), and had varying levels of vegetation cover at the back. Vegetation consisted of exotic grasses, followed by thicker bush and trees towards the back of the beach. There were two other resident species present at the site: copper (*Oligosoma aeneum*) and moko skinks (*O. moco*), both are known to co-exist with shore skinks at other sites (Towns 1972; Towns et al. 2002).

2.3.2 Population surveys

Between February 2007 and March 2008, we monitored populations at Tāwharanui and Tiri every three months. At Tāwharanui, we used three existing pitfall trap grids set at the sand dunes by a previous study (Wedding 2007; Wedding et al. 2010). The grids were spaced 75 m and 120 m apart along the coastline, with each grid containing 40 4 L-sized plastic pitfall traps spaced every 20 m × 25 m, for a total of 120 traps for all three grids. At Tiri, we set up two 6 × 3 grids within the sand and rock sections of the beach. The grids had alternating pitfall traps and artificial refuges, spaced c. 5 m apart. These two grids were connected to a line of six pitfall traps in the middle of the beach, where the sand and rock met. For both sites we baited pitfall traps with fish-based cat food, and checked all traps and refuges every 24 h for three trap-nights at Tāwharanui and six trap-nights at Tiri for each survey. We temporarily marked all captured skinks with a xylene-free pen to avoid individual resampling during each survey. After processing, individuals were released at their point of capture.

During surveys, we took standardised digital photographs of the dorsal side of skinks and habitat backgrounds (1 × 1 m) where the skinks were caught using an Olympus mju 770SW (Olympus, Japan). Each photograph (dorsal or background) included a photographic grey standard (QPcard 101, Sweden) with 18% reflectance. We also photographed founder individuals when animals were caught for translocation in December 2006. Due to the nature of the translocation (i.e. public volunteers were used on the day of captures) not all backgrounds for the founder individuals were recorded or photographed. Overall, we had three groups of skinks: the source, a subset of the founders, and the translocated population (i.e. a mix of survived founders and their offspring).

2.3.3 Quantifying colour pattern complexity

Figure 4. The four dorsal body pattern types assigned to shore skinks at Tāwharanui Regional Park. From left to right: *plain*, *midplain*, *spot*, and *midspot*.

We used the photographs to score individuals according to the degree of dorsal pattern complexity. We quantified complexity according to pattern elements that are known to influence camouflage: i.e. pattern shapes, number of shapes (diversity) and density of each shape (Dimitrova and Merilaita 2011; Merilaita and Dimitrova 2014). Based on these criteria, we assigned individuals to one of four pattern types: (1) *plain*: no patterns or very weakly patterned; (2) *midplain*: no or very weak speckling combined with the presence of a mid-dorsal line on > 50% of the body length; (3) *spot*: distinctive dense speckling and no (or < 50%) mid-dorsal line on length of body; and (4) *midspot*: distinctive dense speckling and presence of mid-dorsal line in > 50% of the body length (Figure 4).

2.3.4 Quantifying vegetation cover

We quantified the proportion of vegetation cover within a 1 × 1 m plot of each habitat background where skinks were caught. We divided each photograph into four sections and estimated the proportion of vegetation cover by eye.

2.3.5 Quantifying colour from photograph

To quantify colour, we scored digital photographs, which capture the majority of the visible spectrum (400 – 700 nm) but not the ultraviolet (300 – 400 nm). These are appropriate for shore skinks because they showed minimal ultraviolet reflectance (see Appendix 1). Additionally, the distribution of lizard colours within a RGB colour space has been shown to be significantly similar in the avian or lizard visual colour space (Smith et al. 2016).

In each photograph, we extracted the averaged mean red (R), green (G), blue (B), and brightness (V) values (ranging from 0 to 255) from 400 random points selected within areas of the body or habitat, and the grey standards. Within each background photograph, we selected two polygon areas similar to the size of skinks and extracted values as above, and averaged the values of the two areas. We then calibrated all values for skink and background using linearisation and equalisation protocols described in Stevens (2007). Firstly, we determined the relationship between the camera responses to all values (R, G, and B) by photographing a set of grey standards (ColourChecker Classic, X-Rite, USA) with measured reflectance values. We applied a biexponential function (Garcia et al. 2013), to linearise R, G, B and V values to reflectance:

$$y = a * \exp(b * x) + c * \exp(d * x),$$

where, y is the linearised value, and a, b, c, d are empirically derived constants specific to a given camera. Finally, we equalised R, G, B, V values relative to the grey standard in each photographs to remove any effect of variation in lighting.

We calculated the standardised differences between the calibrated R and G channels as $x = (R - G)/(R + G + B)$, and between G and B channels as $y = (G - B)/(R + G + B)$ to obtain a two-dimensional representation of colour space, where the distance from origin represents saturation, and the angle relative to the axis is hue (Endler 1990). We calculated saturation (S) as $S = (x^2 + y^2)^{1/2}$, where x and y represents the standardised difference of R-G and G-B channels, respectively.

2.3.6 Statistical analyses

We investigated colour pattern variation by comparing the proportions of each colour pattern type between three populations: source (Tāwharanui), the subset of founders from Tāwharanui, and translocated (Tiri). We used Fisher's exact test to determine whether the proportion of the colour pattern types in the founder and translocated populations differed significantly more than expected by chance. We conducted *post-hoc* binomial tests to identify the specific colour patterns that differed between the populations.

To ascertain the baseline association between colour pattern complexity of skinks and vegetation cover, we plotted 95% confidence intervals (CI) of means for the percentages of vegetation cover (arc-sin transformed) against colour patterns of the source population. We used the degree of overlap between CI of the colour patterns as a measure of significant differences from one another ($p < 0.05$). Additionally, we calculated the magnitude of effect sizes between colour patterns using a standardised mean difference, unbiased Cohen's d (Morgans and Ord 2013). These values and their CI were then converted to r values (Nakagawa and Cuthill 2007; Ord et al. 2011; Ord and Stamps 2009) to provide a familiar effect size metric ($r = -1$ to 1) that functions similarly to correlation coefficient (Ord and Stamps 2009). Any CI of r that did not overlap with zero was considered to be a biological effect. We also applied this approach for comparison within the founder and translocated populations. Due to the occurrence of two different substrate types at the Tiri population, rock and sand, we analysed data for the two substrates separately.

As the skinks varied primarily in saturation and brightness of colour, we only assessed matching between skinks and their backgrounds of these two values. We conducted a power transformation for brightness ($\lambda = -0.5$) and saturation ($\lambda = 0.5$) to achieve normalisation of data. For the source population, we determined the association between skink brightness or saturation and vegetation cover or background brightness and saturation using linear regressions.

To measure if there was an overall difference in habitat colour (brightness and saturation) between Tāwharanui and Tiri, we compared the mean, CI and standardised mean difference (using r-values, Morgans and Ord 2013; Ord and Stamps 2009) between the backgrounds occupied by skinks. We looked at the difference between background and skink to determine the degree of background-matching for each pattern type at source population to the backgrounds of Tāwharanui. Due to the dominance of one colour pattern type in the translocated population, we only compared background-matching for type *midspot* between all populations.

2.4 Results

2.4.1 Colour pattern variation and habitat use

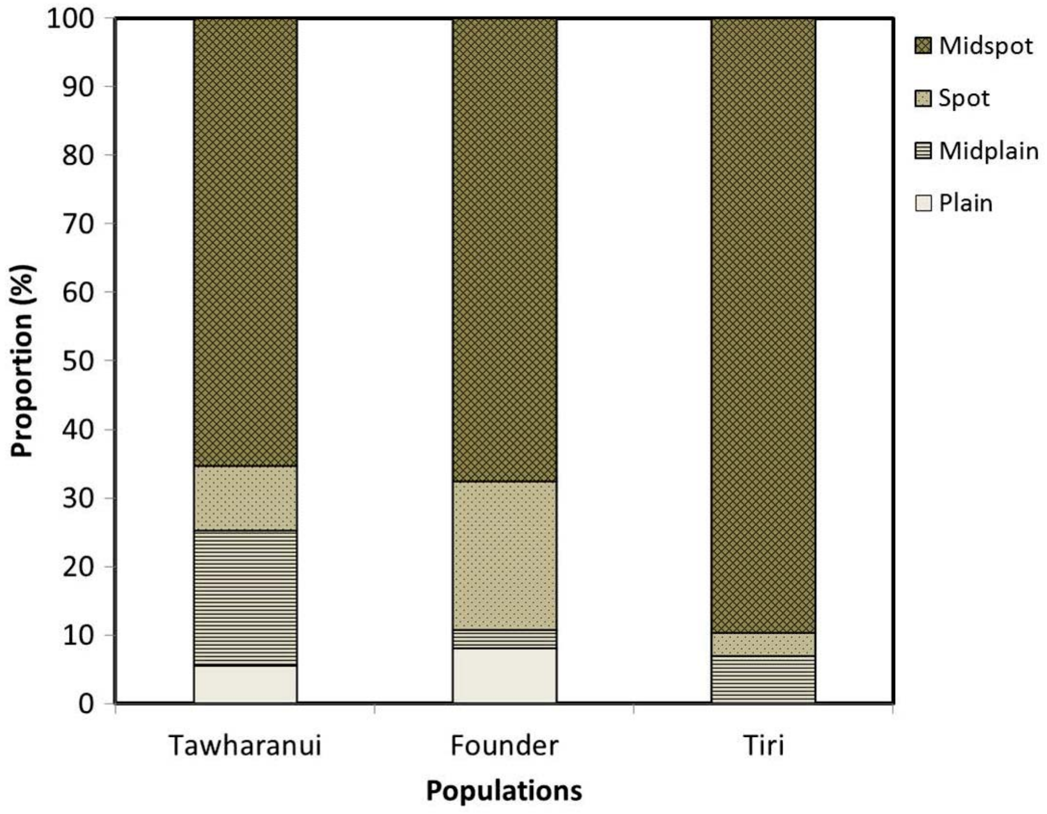


Figure 5. Proportion of four colour patterns (*plain*, *midplain*, *spot*, *midspot*) in three shore skink populations: Tāwharanui Regional Park (n = 337), subset of the founders (n = 37), and translocated populations at Tiritiri Matangi Island (n = 29).

The founder population had *midspot* as the most common colour pattern (67.6%, n = 25), followed by *spot* (21.6%, n = 8). The proportions of founders with the other two colour patterns were low (Figure 5). When compared to the founder, the distribution of colour patterns in the translocated population at Tiri was significantly different than expected by chance (Fisher's exact test, $p = 0.03$, n = 37, 29). Specifically, the proportion of *midspot* was higher (89.7% vs. 67.6%, binomial test, $p < 0.01$, n = 26, 25) while *spot* was lower (3.4%, vs. 21.6%, binomial test, $p = 0.03$, n = 1, 8) at Tiri than expected given the observed proportions in the founder population (Figure 5). *Plain* was not present at the translocated population.

The distribution of the colour patterns varied in relation to vegetation cover at the source population (Figure 6). *Plain* individuals occupied habitats with significantly lower vegetation cover (< 70%) compared to the other three types (*plain-midplain* r = 0.33, *plain-spot* r = 0.36, *plain-midspot* r = 0.38; vs. *midplain-spot* r = 0.02, *midplain-midspot* r = 0.22). *Midspots* were primarily found in over 90% vegetation cover. We observed a difference in occupancy for colour patterns between the two substrates at Tiri (translocated population). The majority of individuals (i.e. *midspot*) caught on sand were in over 90% vegetation cover (Figure 6c), similar to the source population. However, it was the opposite for the novel substrate, rock, where all *midspots* were caught in < 20% vegetation cover. Full comparisons of vegetation cover occupied between pattern types for each population (effect sizes) are provided in Appendix 2.

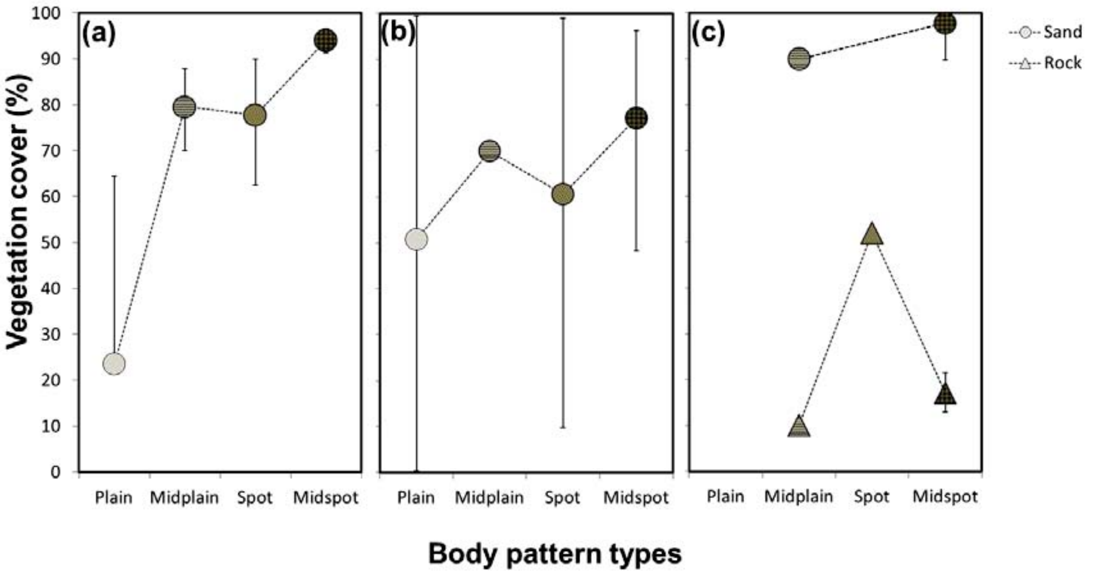


Figure 6. Dorsal colour patterns of shore skinks (*plain*, *midplain*, *spot*, *midspot*) occupying different percentages of vegetation cover (mean and 95% CI) at three populations: (a) source at Tāwharanui Regional Park (n = 337), (b) subset of founders from Tāwharanui (n = 19), and (c) translocated population at Tiritiri Matangi Island (sand n = 15, rock n = 14).

At Tāwharanui, background saturation of colour increased ($r^2 = 0.091$, $p < 0.01$) while brightness decreased with increasing vegetation cover ($r^2 = 0.605$, $p < 0.01$). Therefore, high vegetation cover had most intense and darkest background colour compared to low vegetation covers. The habitats occupied by skinks at Tāwharanui and Tiri differed significantly in saturation but not in brightness. Saturation was greater at the highly vegetated Tiri sand (S = 0.37, CI 0.309 – 0.439) and less in more open areas of Tiri rock (S = 0.09, CI 0.061 – 0.119) compared to the source population at Tāwharanui. The mean difference for saturation was greatest within Tiri, between sand and rock (r = 0.87). Full comparisons of effect sizes for colour between sites are provided in Appendix 3.

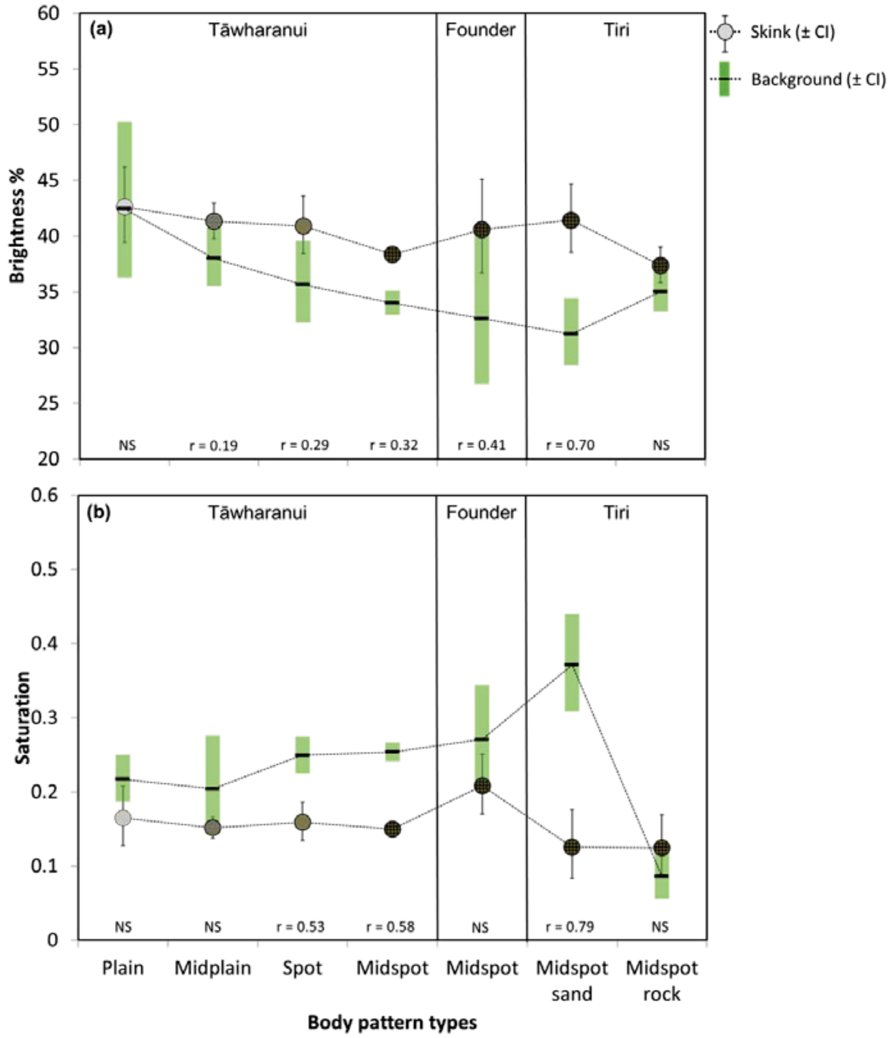


Figure 7. Mean brightness (a) and saturation (b) of colour (mean and 95% CI) for each colour patterns of shore skinks (*plain*, *midplain*, *spot*, *midspot*) and habitat background of source population at Tāwharanui Regional Park, compared to *midspots* in the founder population, and translocated population at Tiritiri Matangi Island. *r* is the effect size for standard mean difference between dorsal and background colours. Difference was not significant ($p > 0.05$) when CI of means for skink and background overlap (NS).

2.4.2 Background-matching of shore skinks

The colour of skinks was generally lighter ($r^2 = 0.09$, $p < 0.01$) and less saturated ($r^2 = 0.074$, $p < 0.01$) than that of the available backgrounds (Figure 6). There was an increase in the discrepancy between the brightness of skinks and their background as pattern complexity increased (Table 1; Figure 6a), with *midspots* showing the greatest mismatch to the background at Tāwharanui and on the sand background at Tiri. *Midspots* were most matched to their background at Tiri rock, and least matched at Tiri sand in terms of both brightness and saturation (Table 1; Figure 7).

Table 1. The standard mean differences in colour (brightness and saturation) between three shore skink populations: source and subset of founder populations from Tāwharanui Regional Park, and translocated populations at Tiritiri Matangi Island (two substrate types).

Population	**Comparison with background**	**Effect size, *r* (lower CI, upper CI)**	***n* body, background**
Brightness			
Tāwharanui	*Plain*	0.01 (-0.307, 0.322)	19, 16
	Midplain	0.19 (0.014, 0.347) *	65, 58
	Spot	0.29 (0.043, 0.495) *	31, 27
	Midspot	0.32 (0.228, 0.401) *	218, 177
Founder	*Midspot*	0.41 (0.031, 0.662) *	13, 9
Tiri – sand	*Midspot*	0.70 (0.444, 0.826) *	13, 12
Tiri – rock	*Midspot*	0.38 (-0.014, 0.635)	12, 12
Saturation			
Tāwharanui	*Plain*	0.32 (-0.007, 0.560)	19, 16
	Midplain	0.15 (-0.023, 0.316)	65, 58
	Spot	0.53 (0.326, 0.673) *	31, 27
	Midspot	0.58 (0.517, 0.636) *	218, 177
Founder	*Midspot*	0.40 (-0.010, 0.655)	13, 9
Tiri – sand	*Midspot*	0.79 (0.588, 0.874) *	13, 12
Tiri – rock	*Midspot*	0.30 (-0.096, 0.578)	12, 12

* CI's that do not overlap with zero are significantly different at $p < 0.05$.

2.5 Discussion

Our study provides evidence that when habitat differs from the source location, colour and colour patterns of cryptic prey can alter within a short period of time following translocation. Overall, we saw a marked effect on the colouration in shore skinks translocated to Tiri, where there was reduced variation in colour patterns favouring almost exclusively one type. This shift in colouration did not seem to have an apparent negative effect on habitat use of the Tiri population because within one year, individuals were able to adapt and utilise a new substrate (rock) that was not present at the source coastal sand dunes of Tāwharanui. The high match (in terms of brightness and saturation) between the surviving skinks to rock (with low vegetation cover) may have contributed to the successful transition to the new substrate. But we also suspect a reduced number of founder individuals survived, and discuss the consequences (i.e. reduced genetic diversity) of this strong selection for inconspicuous colouration.

2.5.1 Change in colour pattern diversity

Out of the four colour pattern types from the mainland source population, only one was dominant at the island release site. *Midspots* had the most complex colour pattern, and were the darkest variant of the four types, so it may have had an advantage in the darker and highly vegetated environment at Tiri (see below). But *midspot* was also the most abundant type within the source and founder populations, so we cannot rule out a founder effect, with the *midspot* variant being fixed (and the rare *plain* pattern type lost) in the founder population due to chance. As yet, we do not know the degree of heritability, survivorship, alternative functions (e.g., thermoregulation, social signalling), or whether there are breeding or behavioural differences between the colour patterns (e.g., Clusella-Trullas et al. 2007; Keren-Rotem et al. 2016; Olsson et al. 2013; Scali et al. 2012; Stuart-Fox and Moussalli 2009).

Nevertheless, we still expected to observe higher variation at Tiri because the population surveyed was a mix of founder and first generation island-born individuals. At least 35% of the founder females, consisting of all four colour pattern types, were gravid at the time of capture at the source. As captive wild-born females give birth to an average of four live young (2 – 6 young) annually (M. Baling unpublished data), we estimated about 36 neonates to be born within the first three months following release. Therefore, we expected that the first generation offspring born on Tiri (but sired by males from Tāwharanui) would contribute a higher variation in colouration within the translocated population. Despite this, our field observations showed higher than expected occurrence of *midspot* within one generation.

Interestingly, the presence of a single colour pattern type at Tiri corresponds to other naturally-occurring shore skink populations on offshore islands with rocky or boulder shorelines bordered by vegetation (M. Baling personal observation; McCallum 1980; McCallum and Harker 1982; Towns 1972; Towns and Hayward 1973). These populations have no or very low phenotypic variation (e.g., *plain* dark to almost black, with sparse speckling). The reason for this low variation on offshore islands is unknown, but for our one-year study, we suggest as likely causes bird predation pressure (van Winkel and Ji 2012) coupled with specific habitat characteristics.

2.5.2 Habitat occupancy of shore skinks

Shore skinks at Tiri occupied both highly vegetated sand areas (similar to the Tāwharanui population), and novel rock substrates, mainly in areas of low vegetation cover (< 50%). Despite the availability of rocky stones with high vegetation cover (up to 100%) we did not sight or catch shore skinks within that part of the survey grid. This distribution in pattern types among substrates could also be influenced by behavioural preference of the skinks. Habitat choice to improve camouflage has been observed in other species (e.g., Ahnesjö and Forsman 2006; Cooper Jr. and Sherbrooke 2012; Marshall et al. 2016; Morey 1990; Nafus et al. 2015), but needs to be confirmed for shore skinks.

Another potential influence on the occupancy of shore skinks at the release site is competition with resident species. Moko and copper skinks have been seen or caught in the survey grid, including in highly vegetated rock areas. Interspecific competition (either through territorial aggression or spatial displacement) between shore skinks and resident species at the release site is unknown but possible (Baling et al. 2013). However, anecdotal observation of the general distribution of the three species at the site during our surveys did not appear to differ from populations on other islands with rocky beaches (McCallum and Harker 1982; Towns 1972). Shore skinks at these islands have been recorded using rock or boulder beaches edged by vegetation.

2.5.3 Background-matching of shore skinks

The degree of background-matching for *midspot* was dependent on substrate type. Individuals mismatched with the dark, saturated 'brown-green' of highly vegetated habitat with sand substrate at both source and release sites. This mismatch could be compensated by the high vegetation cover, which provides greater visual complexity (in shape diversity, size and spatial density; Dimitrova and Merilaita 2010; Dimitrova and Merilaita 2011, 2014; Sherratt et al. 2007; Xiao and Cuthill 2016) and visual obstruction or physical protection, thus making detection more difficult. In contrast, *midspots* were highly matched to the dark grey and simpler backgrounds of rock. Similarly, *plain* patterned individuals matched the low or no vegetation sand dunes of Tāwharanui. The low visual complexity of low vegetation cover habitats is likely to increase reliance on background-matching. Other studies have also suggested that such simple or uniform backgrounds promote the evolution of accurate colour background-matching in prey (Houston et al. 2007; Merilaita et al. 2001; Sherratt et al. 2007).

Due to the small sample size of the other three colour pattern types, we are unable to determine if their degree of background-matching was related to survivorship at Tiri. However, we suggest that *midspot* had a higher probability of survival compared to the other colour pattern types for two reasons: 1) likelihood of background-matching at the release site, and 2) habitat availability. Firstly, of all colour patterns at Tāwharanui, *midspot* provided the closest colour and pattern match to the Tiri backgrounds. Secondly, the lack of bare sand may have considerably reduced the chances of survival of *plain* at Tiri. We did not quantify habitat availability in this study but areas with < 20% vegetation cover occurred in 20% of our survey grid (4.15 ha) at Tāwharanui (C. Wedding unpublished data; Wedding 2007). Compared to the smaller-sized beach at Tiri (0.15 ha), vegetation covered most of the sand area down to high-tide level, so there was a lot less bare ground area available at Tiri compared to Tāwharanui.

2.5.4 Diversity in translocated populations

The shore skink founders have successfully survived to produce offspring on the island, but the diversity of the population appears reduced based on the observed colouration in the survived individuals. If we assume that the shore skink colouration are inherited, the observed biased frequency of *midspot* in the population may indicate reduced genetic diversity, due to poor survival of mismatched founders or their offspring. This loss in diversity for one population may not be significant for a widely distributed species like the shore skink, but may be detrimental to a rare species. The importance of maintaining diversity will depend on the management objectives for the species; whether conservation priority is to increase the number of individuals, or to maintain their genetic diversity (e.g., Towns et al. 2016). This can then influence the management decisions for both population and release site selections (Ewen and Armstrong 2007; Ewen et al. 2014).

Ideally for cryptic species, the range of substrate colour and complexity of habitat at the release site should match that in the source population to maintain effective camouflage. This is particularly important for cases of populations living in low complexity habitats, where accurate background-matching is critical for founder survival. If the options for habitat choice are limited and if variation in population colouration is high at the source, a larger founder population size (i.e. high phenotypic and genotypic diversity) should be released at the site. This is because high phenotypic diversity such as prey colouration can provide protection against predators at both individual and population levels (Forsman 2014; Karpestam et al. 2016). However, if the population size at the source is low (e.g., rare or highly threatened species), losing valuable individuals can have significant negative impact. For such species, the conservation objectives generally include increasing the number of breeding animals, and high survival of individuals during and post-translocation. To this end, healthy animals, representing genetic diversity are often selected. We suggest that conservation translocations of cryptic species also consider the phenotypes of the founder individuals that would best match habitat available at the release area. This will ensure minimal disruption of the relationship between released founder individuals and their environment at the establishment phase of the translocation.

2.6 Authors' contributions

MB: obtained permits, conducted the translocations, planned the experimental design, collected field data, statistical analyses and wrote the manuscript. DSF: contributed to statistical analyses and edited the manuscript. DHB: conceived, obtained permits, and conducted and translocations, and edited the manuscript. JD: contributed to statistical analyses and editing of the manuscript (also see Appendix 10).

2.7 References

Ahnesjö, J., Forsman, A., 2006. Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology* 20: 235-257. doi:10.1007/s10682-006-6178-8

Armstrong, D.P., Ford, H.A., 2015. Using reintroduction to compensate for isolation in fragmented landscapes, In Advances in reintroduction biology of Australian and New Zealand fauna. eds D.P. Armstrong, M.W. Hayward, D. Moro, P.J. Seddon, pp. 155-166. *CSIRO Publishing*, Victoria, Australia.

Armstrong, D.P., Wittmer, H.U., 2011. Incorporating Allee effects into reintroduction strategies. *Ecological Research* 26: 687-695. doi:10.1007/s11284-011-0849-9

Atkinson, I.A.E., 2002. Recovery of wildlife and restoration of habitats in New Zealand. *Pacific Conservation Biology* 8: 27-35. doi:10.1071/PC020027

Baling, M., van Winkel, D., Rixon (née Habgood), M., Ruffell, J., Ji, W., Ussher, G., 2013. A review of reptile research and conservation management on Tiritiri Matangi Island, New Zealand. *New Zealand Journal of Ecology* 37: 272-281.

Baling, M., Wedding, C., Barry, M., Ji, W., Brunton, D.H., 2010. Re-introduction of shore skinks to offshore islands in the Auckland region, New Zealand, In Global re-introduction perspectives: additional case-studies from around the globe. ed. P.S. Soore, pp. 88-91. *IUCN/ SSC Re-introduction Specialist Group*, Abu Dhabi, UAE.

Bergstrom, C.A., Whiteley, A.R., Tallmon, D.A., 2012. The heritable basis and cost of colour plasticity in coastrange sculpins. *Journal of Evolutionary Biology* 25: 2526-2536. doi:10.1111/j.1420-9101.2012.02624.x

Brichieri-Colombi, T.A., Moehrenschlager, A., 2016. Alignment of threat, effort, and perceived success in North American conservation translocations. *Conservation Biology* 30: 1159-1172. doi:10.1111/cobi.12743

Castilla, A.M., Swallow, J.G., 1995. Artificial egg-laying sites for lizards: a conservation strategy. *Biological Conservation* 72: 387-391. doi:10.1016/0006-3207(94)00060-4

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2007. Thermal melanism in ectotherms. *Journal of Thermal Biology* 32: 235-245. doi:10.1016/j.jtherbio.2007.01.013

Cooper Jr., W.E., Sherbrooke, W.C., 2012. Choosing between a rock and a hard place: camouflage in the round-tailed horned lizard *Pherynosoma modestum*. *Current Zoology* 58: 541-548. doi:10.1093/czoolo/58.4.543

Cortesi, F., Feeney, W.E., Ferrari, M.C.O., Waldie, P.A., Phillips, G.A.C., McClure, E.C., Sköld, H.N., Salzburger, W., Marshall, N.J., Cheney, K.L., 2015. Phenotypic plasticity confers multiple fitness benefits to a mimic. *Current Biology* 25: 949-954. doi:10.1016/j.cub.2015.02.013

Defrize, J., Théry, M., Casas, J., 2010. Background colour matching by a crab spider in the field: a community sensory ecology perspective. *The Journal of Experimental Biology* 213: 1425-1435. doi:10.1242/jeb.039743

Delhey, K., Peters, A., 2016. Conservation implications for conservation of anthropogenic impacts on visual communication and camouflage. *Conservation Biology* 31: 30-39. doi:10.1111/cobi.12834

Dimitrova, M., Merilaita, S., 2010. Prey concealment: visual background complexity and prey contrast distribution. *Behavioral Ecology* 21: 176-181. doi:10.1093/beheco/arp174

Dimitrova, M., Merilaita, S., 2011. Prey pattern regularity and background complexity affect detectability of background-matching prey. *Behavioral Ecology* 23: 384-390. doi:10.1093/beheco/arr201

Dimitrova, M., Merilaita, S., 2014. Hide and seek: properties of prey and background patterns affect prey detection by blue tits. *Behavioral Ecology* 25: 402-408. doi:10.1093/beheco/art130

Donnelly, W.A., Whoriskey Jr, F.G., 1993. Transplantation of Atlantic salmon (*Salmo salar*) and crypsis breakdown, In Production of Juvenile Atlantic Salmon, Salmo salar, in Natural Waters eds R.J. Gibson, R.E. Cutting, pp. 25-34. *National Research Council of Canada*, Canada.

Ebrahimi, M., Bull, C.M., 2012. Food supplementation reduces post-release dispersal during simulated translocation of the endangered pygmy bluetongue lizard *Tiliqua adelaidensis*. *Endangered Species Research* 18: 169-178. doi:10.3354/esr00446

Endler, J.A., 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of Linnean Society* 41: 315-352. doi:10.1111/j.1095-8312.1990.tb00839.x

Ewen, J.G., Armstrong, D.P., 2007. Strategic monitoring of reintroductions in ecological restoration programmes. *Ecoscience* 14: 401-409.

Ewen, J.G., Soorae, P., Canessa, S., 2014. Reintroduction objectives, decisions and outcomes: global perspectives from the herpetofauna. *Animal Conservation* 17: 74-81. doi:10.1111/acv.12146

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. *Biological Conservation* 96: 1-11. doi:10.1016/S0006-3207(00)00048-3

Fordham, D.A., Watts, M.J., Delean, S., Brook, B.W., Heard, L.M.B., Bull, C.M., 2012. Managed relocation as an adaptation strategy for mitigating climate change threats to the persistence of an endangered lizard. *Global Change Biology* 18: 2743-2755. doi:10.1111/j.1365-2486.2012.02742.x

Forsman, A., 2014. Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. *Proceedings of the National Academy of Sciences* 111: 302-307. doi:10.1073/pnas.1317745111

Galbraith, M., Cooper, H., 2013. Tiritiri Matangi — an overview of 25 years of ecological restoration. *New Zealand Journal of Ecology* 37: 258-260.

Garcia, J.E., Dyer, A.G., Greentree, A.D., Spring, G., Wilksch, P.A., 2013. Linearisation of RGB camera responses for quantitative image analysis of visible and UV photography: a comparism of two techniques. *PLoS ONE* 8: e79534. doi:10.1371/journal.pone.0079534

Germano, J.M., Bishop, P.J., 2008. Suitability of amphibians and reptiles for translocation. *Conservation Biology* 23: 7-15. doi:10.1111/j.1523-1739.2008.01123.x

Gobiel, J.-F., Villard, M.-A., 2008. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98: 447-458. doi:10.1034/j.1600-0706.2002.980309.x

Graham, M.F., Veitch, C.R. eds., 2002. Changes in bird numbers on Tiritiri Matangi Island, New Zealand, over the period of rat eradication. *IUCN SSC Invasive Specialist Group*, IUCN, Gland, Switzerland and Cambridge, UK.

Hitchmough, R., Anderson, P., Barr, B., Monks, J., Lettink, M., Reardon, J., Tocher, M., Whitaker, T., 2013. Conservation status of New Zealand reptiles, 2012. *New Zealand Department of Conservation*, Wellington.

Houston, A.I., Stevens, M., Cuthill, I.C., 2007. Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral Ecology* 18: 769-775. doi:10.1093/beheco/arm039

Jones, C., Moss, K., Sanders, M., 2005. Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: implications for conservation. *New Zealand Journal of Ecology* 29: 29-35.

Karpestam, E., Merilaita, S., Forsman, A., 2016. Colour polymorphism protects prey individuals and populations against predation. *Scientific Reports* 6: 22122. doi:10.1038/srep22122

Kekäläinen, J., Huuskonenm, H., Kiviniemi, V., Taskinen, J., 2010. Visual conditions and habitat shape the coloration of the Eurasian perch (*Perca fluviatilis* L.): a trade-off between camouflage and communication? *Biological Journal of Linnean Society* 99: 47-59. doi:10.1111/j.1095-8312.2009.01339.x

Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A., Geffen, E., 2016. Male preference for sexual signalling over crypsis is associated with alternative mating tactics. *Animal Behaviour* 117: 43-49. doi:10.1016/j.anbehav.2016.04.021

Lettink, M., Cree, A., 2006. Predation by feral house mouse (*Mus musculus*) of Mccann's skinks (*Oligosoma maccani*) constrained in pitfall trap. *Herpetofauna* 36: 61-62.

Llandres, A.L., Gawryszewski, F.M., Heiling, A.M., Herberstein, M.E., 2011. The effect of colour variation in predators on the behaviour of pollinators: Australian crab spiders and native bees. *Ecological Entomology* 36: 72-81. doi:10.1111/j.1365-2311.2010.01246.x

Maitland, M., 2011. Tawharanui Open Sanctuary — detection and removal of pest incursions, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 441-444. *IUCN*, Gland, Switzerland.

Marshall, K.L.A., Philpot, K.E., Stevens, M., 2016. Microhabitat choice in island lizards enhances camouflage against avian predators. *Scientific Reports* 6: 19815. doi:10.1038/srep19815

McCallum, J., 1980. Reptiles of the northern Mokohinau Group. *Tane* 26: 53-60.

McCallum, J., Harker, F.R., 1982. Reptiles of Little Barrier Island. *Tane* 28: 21-136.

Merilaita, S., Dimitrova, M., 2014. Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Functional Ecology* 28: 1208-1215. doi:10.1111/1365-2435.12248

Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B* 268: 1925-1929. doi:10.1098/rspb.2001.1747

Merilaita, S., Stevens, M., 2011. Crypsis through background matching, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 17-33. *University Press*, Cambridge, UK.

Miller, K.A., Nelson, N.J., Smith, H.G., Moore, J.A., 2009. How do reproductive skew and founder group size affect genetic diversity in reintroduced population? *Molecular Ecology* 18: 3792-3802. doi:0.1111/j.1365-294X.2009.04315.x

Moehrenschlager, A., Shier, D.M., Moorhouse, T.P., Stanley Price, M.R., 2013. Righting past wrongs and ensuring the future: challenges and opportunities for effective reintroductions amidst a biodiversity strategy, In Key topics in conservation biology. eds D.W. Macdonald, K.J. Willis, pp. 405-429. *John Wiley & Sons Ltd*.

Morey, S.R., 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. *Journal of Herpetology* 24: 292-296. doi:10.2307/1564396

Morgans, C.L., Ord, T.J., 2013. Natural selection in novel environments: predation selects for background matching in the body colour of a land fish. *Animal Behaviour* 86: 1241–1249. doi:10.1016/j.anbehav.2013.09.027

Moseby, K.E., Carthey, A., Schroeder, T., 2015. The influence of predators and prey naivety on introduction success: current and future directions, In Advances in reintroduction biology of Australian and New Zealand fauna. eds D.P. Armstrong, M.W. Hayward, D. Moro, P.J. Seddon, pp. 29-42. *CSIRO Publishing*, Victoria, Australia.

Nafus, M.G., Esque, T.C., Averill-Murray, R.C., Nussear, K.E., Swaisgood, R.R., 2016. Habitat drives dispersal and survival of translocated juvenile desert tortoises. *Journal of Applied Ecology*. doi:10.1111/1365-2664.12774

Nafus, M.G., Germano, J.M., Perry, J.A., Todd, B.D., Walsh, A., Swaisgood, R.R., 2015. Hiding in plain sight: a study on camouflage and habitat selection in a slow-moving desert herbivore. *Behavioral Ecology* 26: 1389-1394. doi:10.1093/beheco/arv096

Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a parctice guide for biologists. *Biological Reviews* 82: 591-605. doi:10.1111/j.1469-185X.2007.00027.x

Norbury, G., van den Munckhof, M., Neitzel, S., Hutcheon, A., Reardon, J., Ludwig, K., 2014. Impacts of invasive house mice on post-release survival of translocated lizards. *New Zealand Journal of Ecology* 38: 322-327.

Olsson, M., Stuart-Fox, D., Ballen, C., 2013. Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology* 24: 529-541. doi:10.1016/j.semcdb.2013.04.001

Ord, T.J., King, L., Young, A.R., 2011. Contrasting theory with the empirical data on species recognition. *Evolution* 65: 2572-2591. doi:10.1111/j.1558-5646.2011.01319.x

Ord, T.J., Stamps, J.A., 2009. Species identity cues in animal communication. *The American Naturalist* 174: 585-593. doi:10.1086/605372

Ortiz-Catedral, L., Brunton, D.H., 2009. Nesting sites and nesting success of reintroduced red-crowned parakeets (*Cyanoramphus novaezelandiae*) on Tiritiri Matangi Island, New Zealand. *New Zealand Journal of Zoology* 36: 1-10. doi:10.1080/03014220909510133

Parker, K.A., 2013. Avian translocations to and from Tiritiri Matangi 1974–2013. *New Zealand Journal of Ecology* 37: 282-287.

Parlato, E.H., Armstrong, D.P., 2013. Predicting post-release establishment using data from multiple reintroductions. *Biological Conservation* 160: 97-104. doi:10.1016/j.biocon.2013.01.013

Richardson, K.M., Doerr, V., Ebrahimi, M., Lovegrove, T.G., Parker, K.A., 2015. Considering dispersal in reintroduction and restoration planning, In Advances in reintroduction biology of Australian and New Zealand fauna. eds D.P. Armstrong, M.W. Hayward, D. Moro, P.J. Seddon, pp. 59-72. *CSIRO Publishing*, Victoria, Australia.

Rohwer, S., Paulson, D.R., 1987. The avoidance-image hypothesis and color polymorphism in Buteo hawks. *Ornis Scandinavica* 18: 285-290.

Rosenblum, E.B., 2005. The role of phenotypic plasticity in color variation of Tularosa Basin lizards. *Copeia* 2005: 586-596. doi:10.1643/CP-04-154R1

Scali, S., Sacchi, R., Azzusi, M., Daverio, S., Oppedisano, T., Mangiacotti, M., 2012. Homeward bound: factors affecting homing ability in a polymorphic lizard. *Journal of Zoology* 289: 196-203. doi:10.1111/j.1469-7998.2012.00977.x

Schwartz, M.W., Martin, T.G., 2013. Translocation of imperiled species under changing climates. *Annals of the New York Academy of Science* 1286: 1-14. doi:10.1111/nyas.12050

Sherratt, T.N., Pollitt, D., Wilkinson, D.M., 2007. The evolution of crypsis in replicating populations of web-based prey. *Oikos* 116: 449-460. doi:10.1111/j.0030-1299.2007.15521.x

Smith, K.R., Cadena, V., Endler, J.A., Kearney, M.R., Porter, W.P., Stuart-Fox, D., 2016. Color change for thermoregulation versus camouflage in free-ranging lizards. *The American Naturalist* 188: 668-678. doi:10.1086/688765

Stamps, J.A., Swaisgood, R.R., 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102: 392-409. doi:10.1016/j.applanim.2006.05.038

Stankowich, T., Coss, R.G., 2007. The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proceedings of the Royal Society B* 274: 175-182. doi:10.1098/rspb.2006.3716

Stevens, M., Merilaita, S., 2011. Animal camouflage: an introduction, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 1-16. *Cambridge University Press*, Cambridge, UK.

Stevens, M., Párraga, C.A., Cuthill, I.C., Partridge, J.C., Troscianko, T.S., 2007. Using digital photography to study animal coloration. *Biological Journal of Linnean Society* 90: 211-237. doi:10.1111/j.1095-8312.2007.00725.x

Stuart-Fox, D., Moussalli, A., 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London B* 364: 463-470. doi:0.1098/rstb.2008.0254

Théry, M., Debut, M., Gomez, D., Casas, J., 2004. Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology* 16: 25-29. doi:10.1093/beheco/arh130

Thrimawithana, A.H., Ortiz-Catedral, L., Rodrigo, A., Hauber, M.E., 2013. Reduced total genetic diversity following translocations? A metapopulation approach. *Conservation Genetics* 14: 1043-1055. doi:10.1007/s10592-013-0494-7

Towns, D.R., 1972. The reptiles of Mercury Island. *Tane* 18: 95-106.

Towns, D.R., 1975. Ecology of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in boulder beach habitats. *New Zealand Journal of Ecology* 2: 389-407.

Towns, D.R., 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. *Pacific Conservation Biology* 2: 286-292. doi:10.1071/PC960286

Towns, D.R., 2011. Eradications of vertebrate pests from islands around New Zealand: what have we delivered and what have we learned?, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 364-371. *IUCN*, Gland, Switzerland.

Towns, D.R., Hayward, B.W., 1973. Reptiles of Aldermen Islands. *Tane* 19: 93-104.

Towns, D.R., Miller, K.A., Nelson, N.J., Chapple, D.G., 2016. Can translocations to islands reduce extinction risk for reptiles? Case studies from New Zealand. *Biological Conservation* 204: 120-127. doi:10.1016/j.biocon.2016.04.024

Towns, D.R., Neilson, K.A., Whitaker, A.H., 2002. North Island *Oligosoma* spp. Skink Recovery Plan. *Department of Conservation*, Wellington.

Towns, D.R., Simberloff, D., Atkinson, I.A.E., 1997. Restoration of New Zealand islands: readdressing the effects of introduced species. *Pacific Conservation Biology* 3: 99-124. doi:10.1071/PC970099

Troscianko, J., Lown, A.E., Hughes, A.E., Stevens, M., 2013. Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* 8: e73733. doi:10.1371/journal.pone.0073733

Tyrie, E.K., Hanlon, R.T., Siemann, L.A., Uyarra, M.C., 2015. Coral reef flounders, *Bothus lunatus*, choose substrates on which they can achieve camouflage with their limited body pattern repertoire. *Biological Journal of the Linnean Society* 114: 629-638. doi:10.1111/bij.12442

van Winkel, D., Ji, W., 2012. Evidence of lizard predation by New Zealand kingfishers (*Todiramphus sanctus vagans*) and potential implications for threatened species translocations. *New Zealand Journal of Zoology* 39: 201-208. doi:10.1080/03014223.2011.638309

Wedding, C.J., 2007. Aspects of the impacts of mouse (*Mus musculus*) control on skinks in Auckland, New Zealand, In Institute of Natural Sciences. p. 146. *Massey University*, Auckland.

Wedding, C.J., Ji, W., Brunton, D.H., 2010. Implications of visitation by shore skinks *Oligosoma smithi* to bait stations containing brodifacoum in a dune system in New Zealand. *Pacific Conservation Biology* 16: 86-91. doi:10.1071/PC100086

Westley, P.A.H., Stanley, R., Fleming, I.A., 2013. Experimental tests for heritable morphological color plasticity in non-native brown trout (*Salmo trutta*) populations. *PLoS ONE* 8: e80401. doi:10.1371/journal.pone.0080401

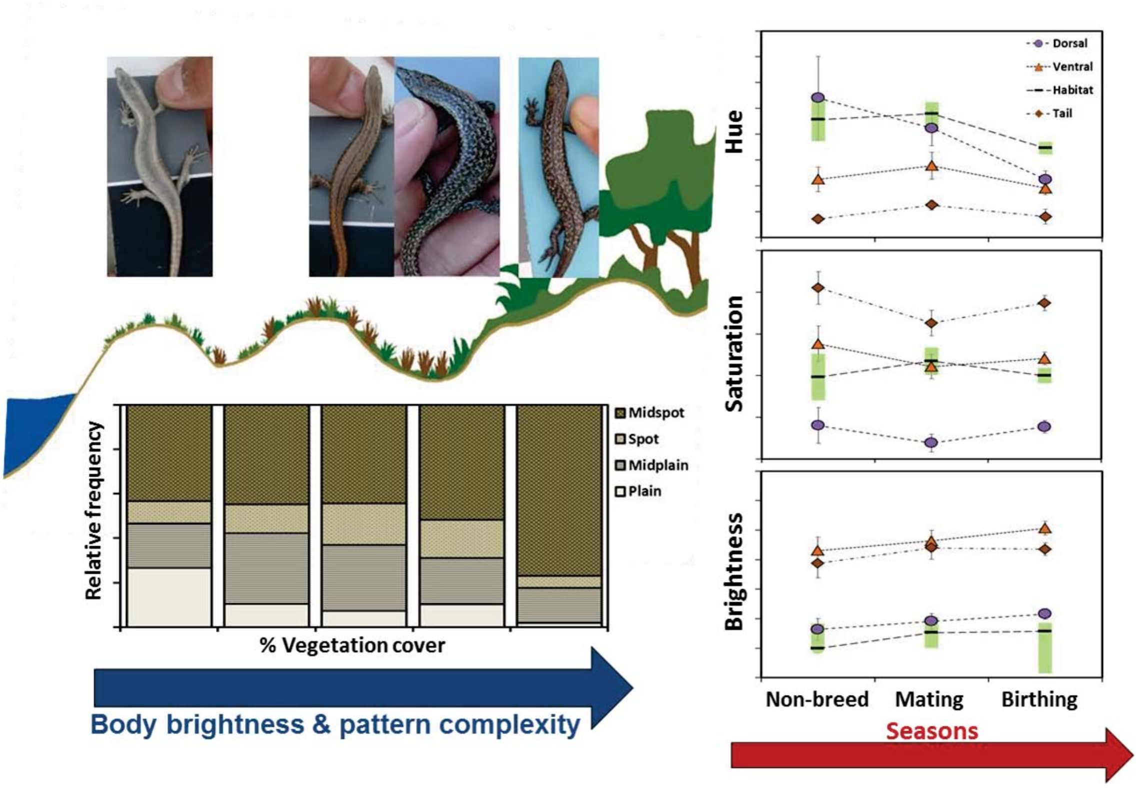
Wolf, C.M., Garland Jr, T., Griffith, B., 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation* 86: 243-255. doi:10.1016/S0006-3207(97)00179-1

Wolf, C.M., Griffith, B., Reed, C., Temple, S.A., 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* 10: 1142-1154. doi:10.1046/j.1523-1739.1996.10041142.x

Xiao, F., Cuthill, I.C., 2016. Background complexity and the detectability of camouflaged targets by birds and humans. *Proceedings of the Royal Society B* 283: 20161527. doi:10.1098/rspb.2016.1527

CHAPTER 3

SPATIAL AND TEMPORAL VARIATION IN PREY COLOURATION FOR BACKGROUND-MATCHING ACROSS A CONTINUOUS HETEROGENEOUS ENVIRONMENT



Article in prep:

Baling M, Stuart-Fox D, Brunton DH & Dale J. Spatial and temporal variation in prey colouration for background-matching across a continuous heterogeneous environment. *Ecology and Evolution*.

3 SPATIAL AND TEMPORAL VARIATION IN COLOURATION FOR BACKGROUND-MATCHING ACROSS A CONTINUOUS HETEROGENEOUS ENVIRONMENT

3.1 Abstract

Background-matching is one of the most widespread forms of animal camouflage, and its effectiveness depends on how well an animal blends into its background. In heterogeneous habitats, matching can be challenging because visual characteristics can vary dramatically across spatial scale. In such situations, background-matching can either be optimised for a specific habitat type (specialists), or represent a compromise for several habitats (generalists). Additionally, temporal variations can also affect crypsis, especially when animals use colouration for intraspecific signalling during certain times of the year (e.g., mate selection). We currently have a poor understanding of how wild animals optimise background-matching within continuously heterogeneous habitats, and whether this is affected by requirements of intraspecific signalling across biological seasons. Here, we quantified colour and colour patterns of a wild population of shore skink (*Oligosoma smithi*) 1) to investigate whether background-matching varies across a vegetation gradient; 2) to assess potential signalling functions of colour; and 3) to determine whether there is a trade-off between the need for crypsis and intraspecific signalling in colouration across seasons. We found that background-matching of skinks was similar along the vegetation gradient for brightness (achromatic contrast), whereas matching for colour values showed a negative correlation (i.e. increase in chromatic contrast). Colour pattern complexity increased with a vegetation gradient, but all pattern types occurred throughout the site. Adult skinks were more matched to background for colour only during the birthing season. Saturation of the ventral body colour differed between juveniles and adults, and between sexes. The dorsal hue values of adults were weakly correlated with body size and condition only during the birthing season. Our study suggests that selection favours a compromised background-matching strategy in wild populations across continuously heterogeneous habitats. Despite the evidence for intraspecific signalling, the crypsis did not greatly differ across seasons.

3.2 Introduction

Many animals that are under selective pressure of visually-oriented predators use body colouration to reduce their probability of being detected (e.g., Endler 1980; Hanlon 2007; Marshall et al. 2015; Rojas 2016; Stevens and Merilaita 2011b). The success of visual camouflage can depend on how effectively the animal blends into its background, (Endler 1978; Merilaita and Stevens 2011; Troscianko et al. 2016; Zimova et al. 2016), and therefore, we expect that under stabilising natural selection, prey populations will exhibit an optimal colouration that accurately matches their habitat (Dale 2006). However, optimising background-matching can be challenging for populations living in heterogeneous habitats, where visual characteristics of the background can vary across space and time.

How habitats vary in colour, structure, and complexity can influence the extent and distribution of variation in colouration within a population. In addition, the degree of mobility of individuals in a population across a heterogeneous habitat can also exert a strong influence. For example, disjunct background types (e.g., rock vs. vegetation) are expected to cause disruptive selection in distinctive colouration (e.g., brown vs. green morphs), especially if movement of individuals is limited to within either one or another background (Dale 2006; Houston et al. 2007; Merilaita et al. 2001; Merilaita et al. 1999; Nilsson and Ripa 2010). In such conditions, animals can achieve optimal background-matching only in one background type, and will be conspicuous in the other (specialist strategy). In contrast, populations where individuals can range over two or more different background types (e.g., a gradient from open to highly vegetated areas) can exhibit a range of colouration (e.g., different degrees of body lightness or colour pattern complexity) that may match the general habitat characteristics. Despite being an inaccurate match to the entire occupied range, a compromised background-matching strategy (generalists) is expected to reduce predation risk within the population (Houston et al. 2007; Merilaita et al. 2001; Merilaita et al. 1999). Many studies on background-matching have looked at disjunct habitat patches (e.g., Merilaita 2003; Merilaita and Dimitrova 2014; Merilaita et al. 2001; Merilaita et al. 1999), but few have quantified variation in background-matching along a continuum of a habitat's visual characteristics, particularly for wild populations.

In addition to spatial differences within a habitat, temporal variations can also affect background-matching. First, predation risk itself can vary over time due to changes in composition of the predator species, their population density or even their behavioural activity, which consequently, can alter the selection on prey colouration for background-matching (Bond 2007; Caro et al. 2016; Endler 1978). Secondly, seasonal changes in habitat structure and colour (e.g., white snow in winter and green vegetation in summer), can also affect the selection of phenotypic characteristics for crypsis (Mills et al. 2013; Rojas 2016; Steen et al. 1992; Tullberg et al. 2008; Zimova et al. 2014). Finally, colour can also have other biological functions that may vary across time, such as the need for intraspecific signalling during the breeding season. Because conspecific interactions such as aggression, territoriality, and mate attraction often involve conspicuous colouration, these functions can increase the risk of being detected by predators. There are several strategies that species can use to compensate for these potentially opposing functions (i.e. crypsis vs. intraspecific signalling). These include 1) changing their colouration within seconds to hours (i.e. physiological colour change), or across seasons (morphological colour change) (e.g., Bohórquez-Alonso and Molina-Borja 2014; Cooper Jr. and Greenberg 1992; Cuervo and Belliure 2013; King and King 1991); and 2) exhibiting cryptic colouration on body regions ‘exposed’ to visually-oriented predators, and conspicuous signals on the body regions that are ‘hidden’ from predators (LeBas and Marshall 2000; Marshall and Stevens 2014; Martin et al. 2013; Norris and Lowe 1964; Pérez i de Lanuza and Font 2015; Runemark et al. 2010; Stuart-Fox et al. 2004; Stuart-Fox and Ord 2004). This balance between potentially antagonistic selection for crypsis and conspicuous signalling is expected to affect the degree of background-matching.

We quantified the colouration of the highly variable shore skink (*Oligosoma smithi*) across time and space. Our observational study had three objectives: 1) to investigate the spatial variation in colour and colour patterns for background-matching across a vegetation gradient; 2) to assess the potential signalling functions of colour variation by testing for correlations with age, sex and quality, and 3) to determine if there is a trade-off between the need for crypsis and intraspecific signalling in colouration across seasons along the vegetation gradient. For the first objective, we predicted that a) background-matching should be greater for dorsal than ventral body regions because the latter is not typically exposed to predators, and b) that dorsal colour- and pattern-matching to the background are consistent across the vegetation gradient because of selection for effective crypsis. For the second objective, we expected that if colours are also used for intraspecific signalling, there should be differences between age (breeding adult vs. juveniles) or sex; or condition-dependence of colour (body condition or size) as a signal of individual quality. For the third objective, we predicted that if colour or colour patterns for intraspecific signalling varies across seasons, the degree of background-matching will be lower during the breeding seasons compared to the non-breeding season. Alternately, background-matching may not be significantly affected if colouration for intraspecific signalling is only found on ventral regions.

3.3 Methods

3.3.1 Study population

Tāwharanui Regional Park (Tāwharanui) is a 550 ha mainland open sanctuary located at a peninsula within the Hauraki Gulf of Auckland, New Zealand (Maitland 2011). The sand dune system at Tāwharanui consists of pale sand and a vegetation gradient of low proportion of vegetation cover in the foreshore to 100% vegetation cover at the back of the dunes (Wedding 2007). Shore skink population at our study site has a high variance of dorsal colour and colour patterns. In addition, early *ad-hoc* observations suggested differences in colouration among body regions (i.e. paler ventral colouration).

3.3.2 Population surveys

Between November 2006 and May 2008, we monitored the shore skink population at Tāwharanui every three months. We used three existing pitfall trap grids at the sand dunes as described in (Baling et al. 2016, and Chapter 2). We checked traps every 24 hours for 3 trap-nights per survey. For each captured skink, we used an Olympus mju 770SW (Olympus, Japan) to take three photographs: dorsal side, ventral side, and the habitat background (1 × 1 m) where the skink was caught. We included a photographic grey standard (QPcard 101, Sweden) with 18% reflectance within each photograph, and saved the photographs as standardised digital JPG-file. We also recorded the sex, body mass and length (snout to vent length, SVL) of each skink.

3.3.3 Quantifying colour patterns and habitat from photographs

We scored skinks according to the degree of their dorsal colour pattern complexity as described in (Baling et al. 2016, or Chapter 2). We assigned individuals to one of four colour pattern types: (1) *plain*: no patterns or very weakly patterned; (2) *midplain*: no or very weak speckling combined with the presence of a mid-dorsal line on more than 50% of the body length; (3) *spot*: distinctive dense speckling and no (or less than 50%) mid-dorsal line on length of body; and (4) *midspot*: distinctive dense speckling and presence of mid-dorsal line in more than 50% of the body length (Figure 8). For the assessments of the habitats, we estimated the amount of vegetation in the photographs. This was quantified as the proportion of vegetation cover, where by each habitat photograph was divided into a 2 × 2 grid and proportion was estimated by eye for each grid section (minimum 5%, maximum 25% each). We then summed the four section scores for a final score.

Figure 8. From left to right: Four dorsal colour pattern types assigned to the shore skink population at Tāwharanui Regional Park.: *plain*, *midplain*, *spot*, and *midspot*; and examples of ventral body colours of shore skinks, ranging from both extremes with an intermediate in the middle.

3.3.4 Quantifying colour from photographs

Our study species shows minimal ultraviolet (UV, 300 – 400 nm) reflectance (see Appendix 1). Therefore, we used photographs rather than a spectrophotometer (Endler 1990; Montgomerie 2006) to quantify the colours because digital photography can provide information on variations for both colour and colour patterns. Additionally, the distribution of lizard colours within RGB (see below) colour space has been shown to be highly correlated with the distribution of colours in avian or lizard visual colour space (Smith et al. 2016). For each photograph, we used the R package *colorZapper* (Dale et al. 2015; Valcu and Dale 2014) to extract the mean values of the red (R), green (G), blue (B), and brightness (V) from 400 random points within selected areas of the grey standard, three areas of the body (dorsal body; ventral body and base of ventral tail), and habitat background. For background, we selected two polygon areas similar to the size of the skinks within each photograph, extracted values as above, and averaged the values of the two areas. We then calibrated the colours according to Baling et al. (2016; Chapter 2). For hue and saturation values, we acquired these from a two-dimensional representation of colour space, where the distance from origin represents saturation, and the angle relative to the axis is hue (Endler 1990). This entailed first calculating the standardised differences between the calibrated R and G channels as, $x = (R - G)/\ (R + G + B)$, and between G and B channels as, $y = (G - B)/(R + G + B)$. We then calculated saturation (S) as:

$$S = (x^2 + y^2)^{\frac{1}{2}},$$

and hue (H) as:

$$H = tan^{-1}\left(\frac{y}{x}\right),$$

where x and y represent the standardised difference of R-G and G-B channels, respectively.

3.3.5 Calculating colour contrasts (background-matching)

For an index of background-matching, we calculated the degree of achromatic and chromatic contrasts between each body area (dorsal, ventral and ventral tail) and backgrounds using the calibrated RGB values (Cadena et al. 2017). Achromatic contrast was calculated as relative differences in brightness between skink and its background:

$$achromatic\ contrast\ = \frac{(R_s + G_s + B_s)\ -\ (R_b + G_b + B_b)}{(R_s + G_s + B_s) +\ (R_b + G_b + B_b)},$$

where subscripts s and b represent skink and background, respectively.

We estimated chromatic contrast by calculating the Euclidean distance of each body area and its respective background using the proportions of each of the calibrated values of RGB (e.g., $R/(R + G + B)$, where the sum of R, G and B equals to 1 $(R + G + B) = 1$

$$chromatic\ contrast = \sqrt{\left(R_{ps} - R_{pb}\right)^2 + \left(G_{ps} - G_{pb}\right)^2 + (B_{ps} - B_{pb})^2},$$

where subscripts ps and pb represent the proportions for skink and background, respectively. We assumed that lower contrast values indicate higher similarities between body and background (i.e. high background-matching).

3.3.6 Statistical analyses

3.3.6.1 Colour and colour pattern background-matching

First, we tested if background-matching for colour was higher for any one body region. We calculated the differences between the colour contrasts against the background of the three body areas (dorsal, ventral and ventral tail) using paired Wilcox signed rank test. Based on these results, we later focused on the body region most 'exposed' to predators — the dorsal region. We determined if variation in dorsal background-matching was influenced by population structure (age, sex), pattern types, local spatial distance, and season. We used achromatic and chromatic contrasts as our separate response variables:

age (juvenile vs. adult), sex (male vs. female), pattern type (*plain*, *midplain*, *spot* and *midspot*), vegetation gradient (proportion of vegetation cover) and biological seasons as fixed effects; and surveyed years (2006 – 2008) as a random effect. We categorised seasons based on observations of breeding activity in the field and in captivity (M. Baling unpublished data) as: 1) non-breeding (nb, April – September), 2) breeding/mating season (bm, October – December), and 3) breeding/birthing season (bb, January – March). All statistical analyses were conducted using R v. 3.2.3 (R Foundation for Statistical Computing). We performed model comparison using Akaike's information criterion with a correction for finite sample sizes (AICc) to select the linear mixed effects (LME) models (via maximum likelihood) with the lowest AICc values (R packages *lme4* and *AICcmodavg*). We further examined the fixed variables in these models using likelihood ratio tests to confirm the best model fit, and used Tukey contrast tests (R package *multcomp*) *post-hoc* to conduct multiple pairwise comparisons of the fixed variables and their interactions. Regressions were used *post-hoc* for vegetation cover.

To assess colouration independently of background-matching, we determined if body colours, colour pattern types, and habitat background varied in relation to population structure, vegetation gradient and season. We conducted a stepwise procedure to select the lowest AICc values for LME and general linear mixed effects (GLME) models. We used hue, saturation and brightness of the dorsal body, ventral body, ventral tail and background as separate response variables; sex, pattern type, season and percentage of vegetation cover as fixed effects; and year of surveys as a random effect for the LME models. When using pattern type as response variable, we used GLME models (family = binomial). We only used sex, season and percentage of vegetation cover for fixed effects, and year as random effects for these models. All *post-hoc* analyses for multiple comparisons were conducted as described above.

3.3.6.2 Seasonal variation in colours for intraspecific signalling in adults

In adult shore skinks, we looked for evidence of sex, and condition-dependence of colour patterns between the seasons. We first tested for differences between gravid and non-gravid females to rule out colour differences due to reproductive status (Cooper Jr. 1983; Cuervo and Belliure 2013; Ferguson 1976; Forsman and Shine 1995; Vercken et al. 2008; Weiss 2006). Because there was no significant differences, we pooled all females in subsequent analyses (ANOVA, hue: p = 0.19, saturation: p = 0.06, brightness: p = 0.65, n = 171). We then used hue, saturation and brightness of dorsal, ventral and ventral tail as separate response variables; sex, pattern, season, body size (SVL), and body condition (scaled mass index; for methods see Peig and Green 2009) as fixed effects; and year of surveys as a random effect for the LME models. For colour patterns, we only used sex, season and percentage of vegetation cover for fixed, and year as random effects for the GLME models. Model comparisons and *post-hoc* analyses were conducted similarly as previously described.

3.4 Results

3.4.1 Colour contrasts among body regions

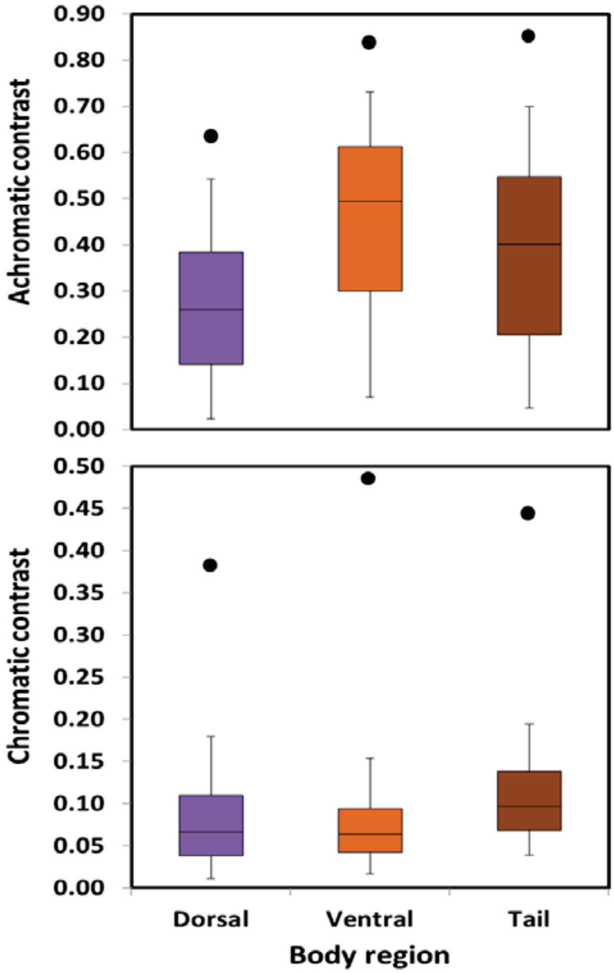


Figure 9. Median colour (achromatic and chromatic) contrast between body and habitat background for dorsal, ventral, and ventral tail regions of the shore skinks. Dots represent outliers.

Overall, shore skinks at Tāwharanui were more camouflaged on the dorsal region than the other areas. The dorsal region had the lowest achromatic contrast compared to the ventral tail and ventral areas (Wilcox test, $p < 0.01$ for all, n=352; Figure 9). Chromatic contrast values were similar between the dorsal and ventral regions, and both were significantly lower compared to the ventral tail (Wilcox test, dorsal vs. ventral $p = 0.45$; $p < 0.01$ for others, n=352).

3.4.2 Body colouration and background-matching across the vegetation gradient

Skinks were less matched in colour (chromatic contrast) as vegetation cover increased, but achromatic contrast remained consistent throughout (linear regression, achromatic contrast: linear regression, $p = 0.14$, $r^2 = 0.004$; chromatic contrast: $p < 0.01$, $r^2 = 0.218$). When we looked at background and skink brightness separately, skinks were on average, darker than their background at low vegetation cover. This shifted when background brightness steeply declined with increasing vegetation cover, resulting in backgrounds being darker than skinks at locations with high vegetation cover (linear regression, $p < 0.01$ for all; dorsal: $r^2 = 0.20$; background $r^2 = 0.60$; Figure 10b). For chromatic contrast, there was a significant increase in background colour (both hue and saturation) across vegetation cover resulted in the observed higher contrast values between skinks and their backgrounds (linear regression, background: $p < 0.01$ for all; H: $r^2 = 0.23$; S: $r^2 = 0.12$; Figure 10b). Dorsal saturation values were consistently low (Figure 10b), hence, we described the skink dorsal colours as grey-tones. Dorsal hue value increased with vegetation cover only during the nonbreeding and mating seasons (brown-grey to green-grey; linear regression, nb: $p < 0.01$, $r^2 = 0.16$; bm: $p = 0.01$, $r^2 = 0.06$; bb: $p = 0.17$, $r^2 = 0.01$).

Shore skink colour patterns were spatially structured across the vegetation gradient, where complex dorsal patterning occurred more at locations with higher vegetation cover (Figure 10a). There were also multiple overlaps in distribution of the colour pattern types. *Plain* type had the lowest abundance within the population, and was found more often at locations with low vegetation cover. Alternately, *midspot*, the most complex patterned type (and most commonly found in the population), was observed at high vegetation cover (t-test, plain: $p = < 0.01 - 0.02$, df = 23 – 43; midspot: $p < 0.01$, df = 23 – 98). The occurrence of *midplain* and *spot* did not differ in relation to vegetation cover (t-test, $p = 0.77$, df = 56).

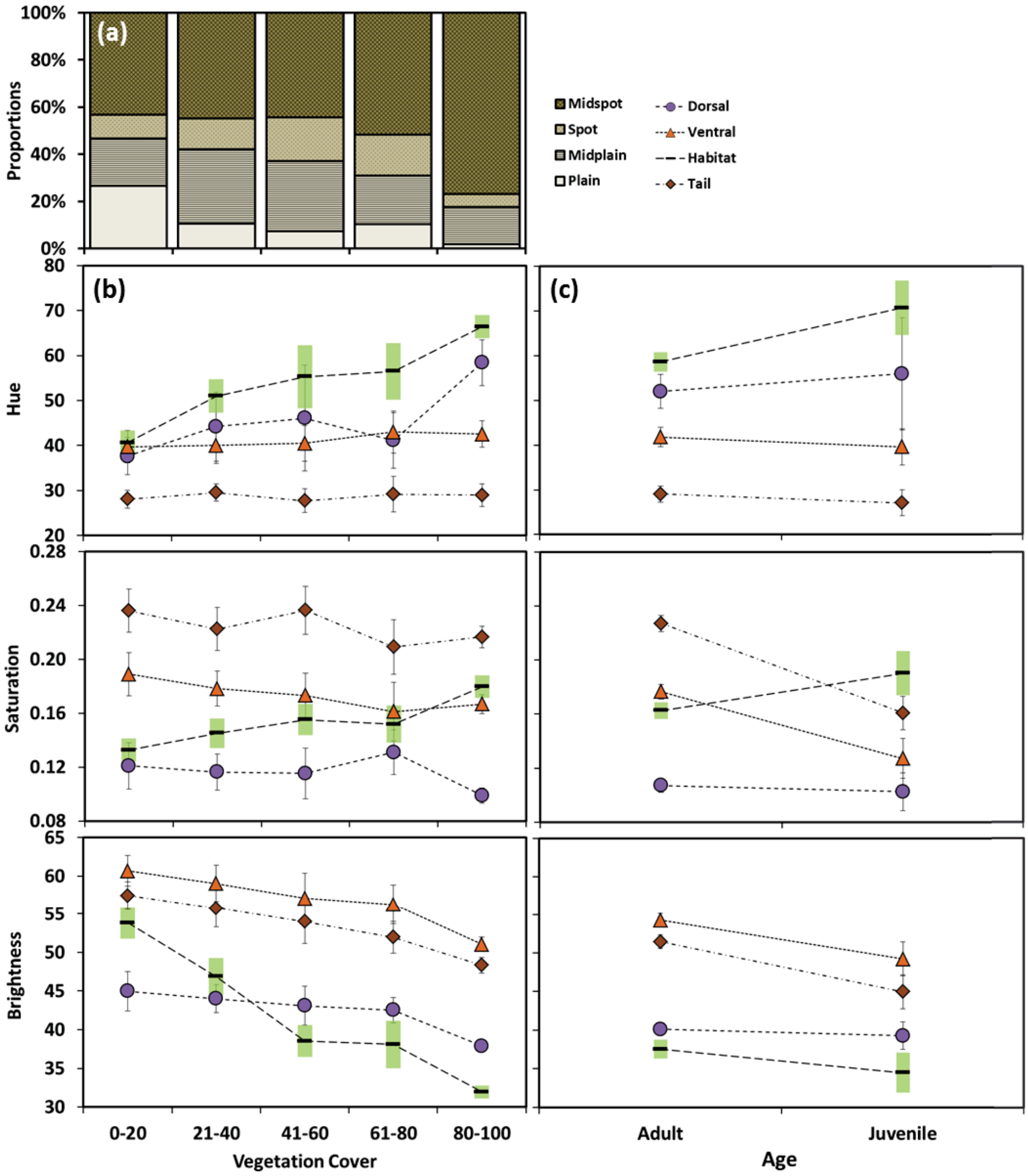


Figure 10. a) Frequency of four colour patterns of shore skinks across the categorical percentage of vegetation cover; and b) mean body (dorsal, ventral and ventral tail) and habitat background colour (hue, saturation and brightness) across categorical percentage of the vegetation cover; and c) between age classes (adult and juvenile). Bars represent 95% confidence intervals.

3.4.3 Association of colour to age, sex and quality

There were differences in colour between age classes and sexes at the ventral regions. Adult shore skinks' ventral body and ventral tail were lighter and more intensely orange-brown than juveniles (Tukey contrast tests; $p < 0.01$ for all; Figure 10c). Within adults, ventral regions of male shore skinks were more intensely orange-brown, and tails were more red-brown in colour compared to females (Tukey contrast tests, ventral saturation: $p = <0.01 – 0.02$; ventral tail hue: $p < 0.01$; Figure 11c). There was also some evidence of condition dependence of colour. Dorsal hue values of adult shore skinks were weakly correlated to body size and body condition, where larger or better-conditioned skinks were more orange-grey in colour during the birthing season (linear regression, size: p = 0.03, r^2 = 0.02; condition: p = 0.04, r^2 =0.02).

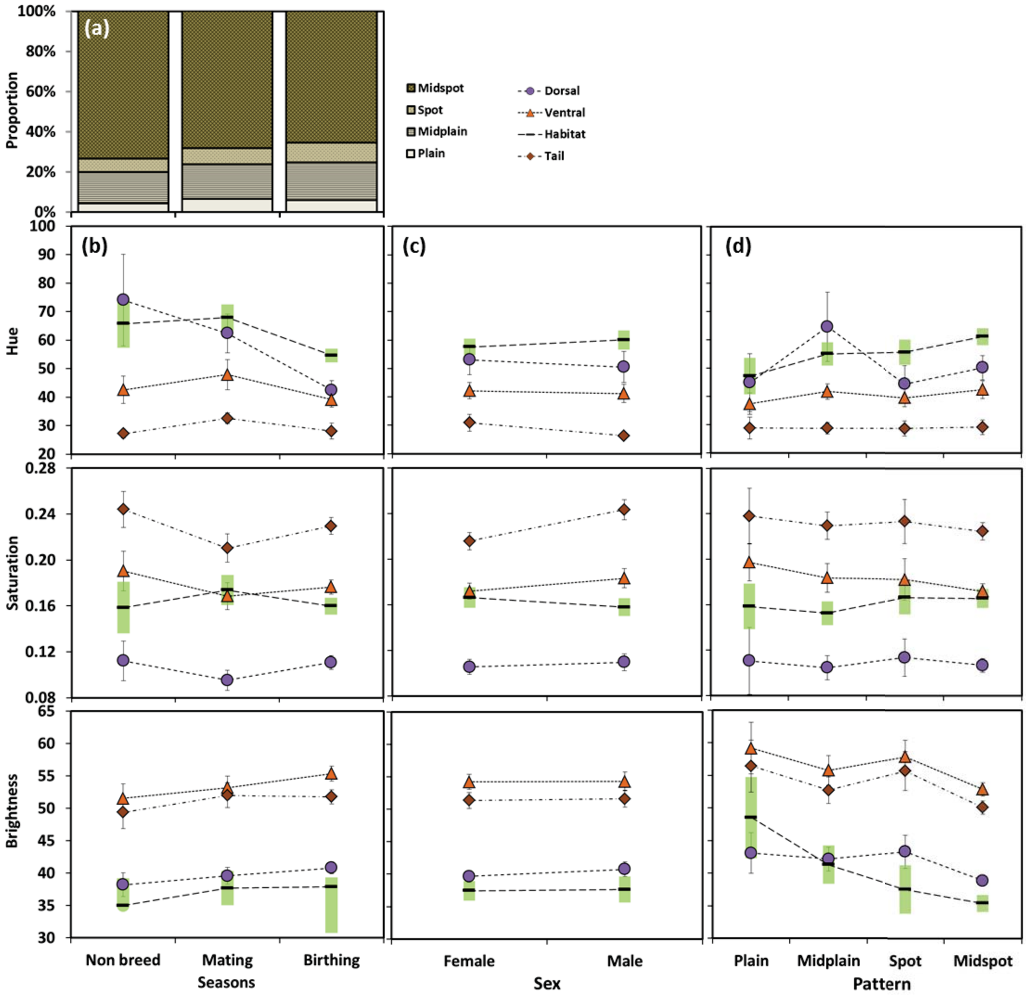


Figure 11. a) Frequency of four colour patterns in adult shore skinks across seasons; and b) mean body (dorsal ventral, and ventral tail) and habitat background colour (hue, saturation and brightness) across seasons, c) between sexes, and d) between colour pattern types. Bars represent 95% confidence intervals.

3.4.4 Seasonal variation of body colouration and background-matching

Overall, the degree of background-matching was not significantly different between seasons (Tukey contrast test, achromatic contrast between seasons: p = 0.41 – 0.57; chromatic contrast: nb vs. bm p = 0.07). The only exception was for chromatic contrast, where adult shore skinks were more camouflaged in colour during the birthing season compared to non-breeding and mating seasons (Tukey contrast test, $p < 0.01$; bb = 0.055 ±0.00003 SE; nb = 0.110 ±0.00007 SE; bm = 0.074 ±0.00004 SE).

During the birthing season, both males and females had the lowest dorsal hue values, being more brown-grey compared to other seasons (Tukey contrast tests, male: $p < 0.01$ for all comparisons; female: bb vs. nb, $p < 0.01$). In the mating season, all adults were least intense in yellow-grey, and were more yellow-brown ventrally. During this time, ventral hue value was significantly higher compared to other seasons (Tukey contrast tests, $p = < 0.01 – 0.01$; Figure 11b). During the non-breeding season, skinks had the most intense green-grey dorsal colouration and dark orange-brown ventral colouration. Specifically, saturation values were significantly high for all body regions compared to other seasons (Tukey contrast tests, dorsal: $p = < 0.01 – 0.01$ ventral: $p < 0.01 – 0.05$; ventral tail: $p < 0.01 – 0.06$; Figure 11b), while ventral body and ventral tail were darkest (Tukey contrast test, ventral: nb vs. bb, $p = 0.03$; ventral tail: nb vs. bm, $p = 0.06$).

3.5 Discussion

Shore skink colouration at the coastal sand dunes of Tāwharanui showed spatial and temporal variation that is consistent with both crypsis and intraspecific signalling requirements. The constant background-matching of colour (i.e. brightness) across the vegetation gradient and structured but overlapping spatial distribution of all four colour pattern types suggests a compromised (generalist) rather than specialist background-matching strategy in this population. Body saturation of colour may not be as important for camouflage compared to brightness and colour patterns. Instead, saturation may be more important for intraspecific signalling. There was evidence of partitioning of body colours where saturation differed among age classes (adults and juveniles) and sexes on the 'hidden' ventral body regions. Adult shore skinks also showed morphological colour change on both dorsal and ventral regions between seasons; being dark and rich in colour (dorsal green-grey, ventral orange-brown) during the non-breeding season, becoming less intense in colour (ventral orange-brown) during the mating season, to dorsal turning brown-red during the birthing season. Hue values were also weakly associated with body size and body condition only during the birthing season. These changes, however, do not seem to affect the degree of background-matching over time.

3.5.1 Background-matching across a continuous heterogeneous habitat

As predicted, within continuous heterogeneous habitats, background-matching for colour (achromatic contrast) remained constant across the vegetation gradient. However, it was how the shore skinks contrasted with their background that had changed, where skinks were darker than their background at low vegetation cover and lighter than their background at high vegetation cover. This spatial change in background-matching was primarily due to changes in background colours, rather than by variation in skink colour *per se*. It is likely that the dominant colour pattern variant (i.e. *midspot*) affected the overall dorsal colour of the population, reducing the average body brightness across the spatial gradient.

Overall, the colour patterns of the shore skinks matched the vegetation gradient, as expected. These colour patterns could be reflective of the vegetation type or structure (in shape or patterns) at their corresponding backgrounds. Other studies have observed associations of dorsal colour pattern types to vegetation types, such as striped dorsal individuals are found more often in grasses (Chen et al. 2013; Woolbright and Stewart 2008). Similarly, we noted *midplain* (i.e. striped) individuals in areas of different grasses (e.g., pīngao *Ficinia spiralis*, spinifex *Spinifex sericeus*) at the low to intermediate vegetation cover areas in the foredunes. At higher vegetation cover in the back of the dunes, speckled patterns of the *midspots* complemented the thicker ground vegetation cover such as rushes and tangled, dense vines (e.g., sand coprosma *Coprosma acerosa*, pohuehue *Muehlenbeckia complexa*; Wedding 2007).

Although this population showed a structured distribution in colour pattern-matching, it is still unclear why particular colour patterns such as *midspot* were in high frequency at low vegetation cover (cf. *plain*), where we would expect colour pattern-matching to be low for this type. Possible explanations for the observed relative frequencies of colour pattern types include different predation risk, behavioural traits, and biological functions among colour pattern types. Resident predators may have behavioural preferences for specific prey variants (e.g., apostatic selection) or specific habitat patches that select for particular pattern types (Bond 2007; Endler 1978; Moyen et al. 2006; Tate et al. 2016). Additionally, the different colour pattern types of shore skinks may have different behavioural traits (e.g., background choice for optimal camouflage; Ahnesjö and Forsman 2006; Cooper Jr. and Sherbrooke 2012; Marshall et al. 2016; Morey 1990; Nafus et al. 2015) or alternative antipredator strategies (e.g., disruptive colouration, flicker fusion; Cooper Jr. and Greenberg 1992; Endler 1978; Halperin et al. 2017; Hogan et al. 2016; Merilaita and Lind 2005; Stevens and Merilaita 2011a) that affect the distribution of the skinks. Finally, there might be additional biological functions to colour such as thermoregulation that can affect skink colouration (e.g., thermal melanism; Clusella-Trullas et al. 2007; Stuart-Fox and Moussalli 2009).

3.5.2 Body colours for intraspecific signalling

Shore skinks showed evidence of colour differences with respect to age (juveniles vs. adults), sex and quality. Individuals advertising their maturity and sex through body colours can reduce conspecific aggression, determine social hierarchy, identify competitors, determine the condition or quality of potential mates, and indicate reproductive status (Booth 1990; Cooper Jr. 1983; Cuervo and Belliure 2013; Cuervo and Shine 2007; Ferguson 1976; Forsman and Shine 1995; Martín and Forsman 1999; Martin et al. 2013; McLean et al. 2010; Takahashi et al. 2012; Vercken and Clobert 2008; Vercken et al. 2008; Weiss 2006). There are anecdotal observations of captive wild-born adult shore skinks that have died due to conspecific aggression (including among females; M. Baling unpublished data), but it is unknown whether the variation in colouration co-varies with these behaviours in shore skinks.

3.5.3 Variation of colour patterns across seasons

As we expected, shore skinks showed morphological colour change between non-breeding and breeding seasons. The largest variance was observed in dorsal hue, changing from green-grey during the nonbreeding season, to yellow-grey in the mating season, to brown-grey during the birthing season. Contrary to our expectations, however, the degree of background-matching was relatively consistent across the vegetation gradient over the seasons, implying that colours for intraspecific signalling did not negatively affect skink camouflage. The lack of differences in the degree of background-matching between seasons is likely due to body partitioning in colouration. Although, coloration at the hidden body regions is often argued to function in mate attraction (e.g., Cuervo and Shine 2007; Martin et al. 2013), shore skinks have not been observed to behaviourally display their ventral side to conspecifics (e.g., Meyers et al. 2006; Whiting et al. 2006). Overall, the fine-scale changes in dorsal colour were subtle, and whether they are conspicuous enough to be perceived by conspecifics or predators requires further investigation.

Many studies of colour change in animals involve rapid physiological colour changes (within seconds or hours), such as observed in predator-prey and intraspecific interactions in chameleons or cuttlefish (Hanlon 2007; Keren-Rotem et al. 2016; Stuart-Fox and Moussalli 2008; Stuart-Fox et al. 2008), or in circadian rhythms in crabs (Stevens 2016). There are, however, a limited number of studies that investigated whether colour changes across habitats and seasons, particularly for crypsis versus intraspecific signalling. Our study integrated these aspects, and showed how crypsis could play an important role in generating fine-scale variations in dorsal colouration of shore skinks in spatially heterogeneous habitats. Although the degree of background-matching did not vary greatly between seasons, particular aspects of colour (e.g., saturation) and the colours of the ventral body region (i.e. not exposed to predators) can still deviate from the expectations of crypsis that would otherwise confer protection.

3.6 Authors' contributions

MB: obtained permits, conducted the translocations, planned the experimental design, collected field data, statistical analyses and wrote the manuscript. DSF: contributed to statistical analyses and edited the manuscript. DHB: conceived, obtained permits, and conducted and translocations, and edited the manuscript. JD: contributed to statistical analyses and editing of the manuscript.

3.7 References

Ahnesjö, J., Forsman, A., 2006. Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology* 20: 235-257. doi:10.1007/s10682-006-6178-8

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. *Biological Conservation* 203: 298-305. doi:10.1016/j.biocon.2016.10.002

Bohórquez-Alonso, M.L., Molina-Borja, M., 2014. Reflectance of sexually dichromatic UV-blue patches varies during the breeding season and and between two subspecies of *Gallotia galloti* (Squamata: Lacertidae). *Biological Journal of the Linnean Society* 113: 556-569. doi:10.1111/bij.12345

Bond, A.B., 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* 8: 489-514. doi:10.1146/annurev.ecolsys.38.091206.095728

Booth, C.L., 1990. Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* 40: 125-163. doi:10.1111/j.1095-8312.1990.tb01973.x

Cadena, V., Smith, K.R., Endler, J.A., Stuart-Fox, D., 2017. Geographic divergence and colour change in response to visual backgrounds and illumination intensity in bearded dragons. *Journal of Experimental Biology* 220: 1048-1055. doi:10.1242/jeb.148544

Caro, T., Sherratt, T.N., Stevens, M., 2016. The ecology of multiple colour defences. *Evolutionary Ecology* 30: 797-809. doi:10.1007/s10682-016-9854-3

Chen, I.-P., Symonds, M.R.E., Melville, J., Stuart-Fox, D., 2013. Factors shaping the evolution of colour patterns in Australian agamid lizards (Agamidae): a comparative study. *Biological Journal of Linnean Society* 109: 101-112. doi:10.1111/bij.12030

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2007. Thermal melanism in ectotherms. *Journal of Thermal Biology* 32: 235-245. doi:10.1016/j.jtherbio.2007.01.013

Cooper Jr., W.E., 1983. Female color change in the keeled earless lizard, *Holbrookia propinqua*: relationship to reproductive cycle. *The Southwestern Naturalist* 28: 275-280.

Cooper Jr., W.E., Greenberg, N., 1992. Reptilian coloration and behavior, In Biology of the Reptilia: Hormones, brain and behavior. eds C. Gans, D. Crews. *The University of Chicago Press*, USA.

Cooper Jr., W.E., Sherbrooke, W.C., 2012. Choosing between a rock and a hard place: camouflage in the round-tailed horned lizard *Pherynosoma modestum*. *Current Zoology* 58: 541-548. doi:10.1093/czoolo/58.4.543

Cuervo, J.J., Belliure, J., 2013. Exploring the function of red colouration in female spiny-footed lizards (*Acanthodactylus erythrurus*): patterns of seasonal colour change. *Amphibia-Reptilia* 34: 525-538. doi:0.1163/15685381-00002912

Cuervo, J.J., Shine, R., 2007. Hues of a dragon's belly: morphological correlates of ventral coloration in water dragons. *Journal of Zoology* 273: 298-304. doi:10.1111/j.1469-7998.2007.00328.x

Dale, J., 2006. Intraspecific variation in coloration, In Bird coloration: Function and Evolution. eds G.E. Hill, K.J. McGraw. *Harvard University Press*, USA.

Dale, J., Dey, C.J., Delhey, K., LKempenaers, B., Valcu, M., 2015. The effects of life history and sexual selection on male and female plumage colouration. *Nature* 527: 367-370. doi:10.1038/nature15509

Endler, J.A., 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11: 319-364. doi:10.1007/978-1-4615-6956-5_5

Endler, J.A., 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34: 76-91.

Endler, J.A., 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of Linnean Society* 41: 315-352. doi:10.1111/j.1095-8312.1990.tb00839.x

Ferguson, G.W., 1976. Color change and reproductive cycling in female collared lizards (*Crotaphytus collaris*). *Copeia* 3: 491-494.

Forsman, A., Shine, R., 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of the Linnean Society* 55: 273-291. doi:10.1111/j.1095-8312.1995.tb01066.x

Halperin, T., Carmel, L., Hawlena, D., 2017. Movement correlates of lizards' dorsal pigmentation patterns. *Functional Ecology* 31: 370-376. doi:10.1111/1365-2435.12700

Hanlon, R., 2007. Cephalopod dynamic camouflage. *Current Biology* 17: 400-404. doi:10.1016/j.cub.2007.03.034

Hogan, B.G., Scott-Samuel, N.E., Cuthill, I.C., 2016. Contrast, contours and the confusion effect in dazzle camouflage. *Royal Society Open Science*. doi:10.1098/rsos.160180

Houston, A.I., Stevens, M., Cuthill, I.C., 2007. Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral Ecology* 18: 769-775. doi:10.1093/beheco/arm039

Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A., Geffen, E., 2016. Male preference for sexual signalling over crypsis is associated with alternative mating tactics. *Animal Behaviour* 117: 43-49. doi:10.1016/j.anbehav.2016.04.021

King, R.B., King, B., 1991. Sexual differences in color and color change in wood frogs. *Canadian Journal of Zoology* 69: 1963-1968. doi:10.1139/z91-271

LeBas, N.R., Marshall, N.J., 2000. The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society B* 267: 445-452. doi:10.1098/rspb.2000.1020

Maitland, M., 2011. Tawharanui Open Sanctuary — detection and removal of pest incursions, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 441-444. *IUCN*, Gland, Switzerland.

Marshall, K.L.A., Philpot, K.E., Damas-Moreira, I., Stevens, M., 2015. Intraspecific colour variation among lizards in distinct island environments enhances local camouflage. *PLoS ONE* 10: e0135241. doi:10.1371/journal.pone.0135241

Marshall, K.L.A., Philpot, K.E., Stevens, M., 2016. Microhabitat choice in island lizards enhances camouflage against avian predators. *Scientific Reports* 6: 19815. doi:10.1038/srep19815

Marshall, K.L.A., Stevens, M., 2014. Wall lizards display conspicuous signals to conspecifics and reduce detection by avian predators. *Behavioral Ecology* 25: 1325-1337. doi:10.1093/beheco/aru126

Martín, J., Forsman, A., 1999. Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: an experiment *Behavioral Ecology* 27: 396-400. doi:10.1093/beheco/10.4.396

Martin, M., Meylan, S., Gomez, D., Le Galliard, J.-F., 2013. Ultraviolet and carotenoid-based coloration in the viviparous lizard *Zootoca vivipara* (Squamata: Lacertidae) in relation to age, sex, and morphology. *Biological Journal of the Linnean Society* 110: 128-141. doi:10.1111/bij.12104

McLean, C.A., Moussalli, A., Stuart-Fox, D., 2010. The predation cost of female resistance. *Behavioral Ecology* 21: 861-867. doi:10.1093/beheco/arq072

Merilaita, S., 2003. Visual background complexity facilitates the evolution of camouflage. *Evolution* 57: 1248-1254. doi:10.1554/03-011

Merilaita, S., Dimitrova, M., 2014. Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Functional Ecology* 28: 1208-1215. doi:10.1111/1365-2435.12248

Merilaita, S., Lind, J., 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings of the Royal Society B* 272: 665-670. doi:10.1098/rspb.2004.3000

Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B* 268: 1925-1929. doi:10.1098/rspb.2001.1747

Merilaita, S., Stevens, M., 2011. Crypsis through background matching, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 17-33. *University Press*, Cambridge, UK.

Merilaita, S., Tuomi, J., Jormalainen, V., 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* 67: 151-161. doi:10.1111/j.1095-8312.1999.tb01858.x

Meyers, J.J., Irschick, D.J., Vanhooydonck, B., Herrel, A., 2006. Divergent roles for multiple sexual signals in a polygynous lizard. *Functional Ecology* 20: 709-716. doi:10.1111/j.1365-2435.2006.01152.x

Mills, L.S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T., Lukacs, P.M., 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences* 110: 7360-7365. doi:10.1073/pnas.1222724110

Montgomerie, R., 2006. Analyzing colors, In Bird coloration: mechanisms and measurements. eds G.E. Hill, K.J. McGraw, pp. 90-147. *Harvard University Press*, USA.

Morey, S.R., 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. *Journal of Herpetology* 24: 292-296. doi:10.2307/1564396

Moyen, F., Gomez, D., Doutrelant, C., Pierson, J., Théry, M., 2006. Interacting effects of signalling behaviour, ambient light and plumage colour in a temperate bird, the blue tit *Parus caeruleus*. *Revue D Ecologie-La Terre Et La Vie* 61: 367-382.

Nafus, M.G., Germano, J.M., Perry, J.A., Todd, B.D., Walsh, A., Swaisgood, R.R., 2015. Hiding in plain sight: a study on camouflage and habitat selection in a slow-moving desert herbivore. *Behavioral Ecology* 26: 1389-1394. doi:10.1093/beheco/arv096

Nilsson, J., Ripa, J., 2010. The origin of polymorphic crypsis in a heterogenous environment. *Evolution* 64, 1386-1394. doi:10.1111/j.1558-5646.2009.00918.x

Norris, K.S., Lowe, C.H., 1964. An analysis of background matching in amphibians and reptiles. *Ecology* 45: 565-580. doi:10.2307/1936109

Peig, J., Green, J., 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118: 1883-1891. doi:10.1111/j.1600-0706.2009.17643.x

Pérez i de Lanuza, G., Font, E., 2015. Differences in conspicuousness between alternative color morphs in a polychromatic lizard. *Behavioral Ecology* 26: 1432-1446. doi:10.1093/beheco/arv075

Rojas, B., 2016. Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biological Reviews*. doi:10.1111/brv.12269

Runemark, A., Hansson, B., Pafilis, P., Valakos, E.D., Svensson, E.I., 2010. Island biology and morphological divergence in the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC Evolutionary Biology* 10: 269. doi:10.1186/1471-2148-10-269

Smith, K.R., Cadena, V., Endler, J.A., Kearney, M.R., Porter, W.P., Stuart-Fox, D., 2016. Color change for thermoregulation versus camouflage in free-ranging lizards. *The American Naturalist* 188: 668-678. doi:10.1086/688765

Steen, J.B., Erikstad, K.E., Høidal, K., 1992. Cryptic behaviour in moulted hen willow *Ptarmigan lagopus l. lagopus* during snow melt. *Ornis Scandinavica* 23: 101-104.

Stevens, M., 2016. Color change, phenotypic plasticity and camouflage. *Frontiers in Ecology and the Environment* 4: 51. doi:10.3389/fevo.2016.00051

Stevens, M., Merilaita, S., 2011a. Animal camouflage: an introduction, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 1-16. *Cambridge University Press*, Cambridge, UK.

Stevens, M., Merilaita, S. eds., 2011b. Animal camouflage: mechanisms and function. *University Press*, Cambridge.

Stuart-Fox, D., Moussalli, A., 2008. Selection for social signalling drives the evolution of chameleon colour change. *PLoS Biology* 6: e25. doi:10.1371/journal.pbio.0060025

Stuart-Fox, D., Moussalli, A., 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London B* 364: 463-470. doi:0.1098/rstb.2008.0254

Stuart-Fox, D., Moussalli, A., Whiting, M.J., 2008. Predator-specific camouflage in chameleons. *Biology Letters* 4: 326-329. doi:10.1098/rsbl.2008.0173

Stuart-Fox, D.M., Moussalli, A., Johnston, G.R., Owens, I.P.F., 2004. Evolution of color variation in dragon lizards: Quantitative tests of the role of crypsis and local adaptation. *Evolution* 58: 1549-1559. doi:10.1554/03-448

Stuart-Fox, D.M., Ord, T.J., 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B* 271: 2249-2255. doi:10.1098/rspb.2004.2802

Takahashi, Y., Morimoto, G., Watanabe, M., 2012. Ontogenic colour changes in females as a function of antiharassment strategy. *Animal Behaviour* 84: 685-692. doi:10.1016/j.anbehav.2012.06.025

Tate, G.J., Bishop, J.M., Amar, A., 2016. Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morph in a polymorphic bird. *Ecology Letters* 19: 679-686. doi:10.1111/ele.12606

Troscianko, J., Wilson-Aggarwal, J., Stevens, M., Spottiswoode, C.N., 2016. Camouflage predicts survival in ground-nesting birds. *Scientific Reports* 6: 19966. doi:10.1038/srep19966

Tullberg, B.S., Gamberale-Stille, G., Bohlin, T., Merilaita, S., 2008. Seasonal ontogenetic colour plasticity in the adult striated shieldbug *Graphosoma lineatum* (Heteroptera) and its effect on detectability. *Behavioral Ecology and Sociobiology* 62: 1389-1396. doi:10.1007/s00265-008-0567-7

Valcu, M., Dale, J., 2014. colorZapper: color extraction utilities. R package version 1.0, https://github.com/valcu/colorZapper.

Vercken, E., Clobert, J., 2008. Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*). *Ecoscience* 15: 320-326. doi:10.2980/15-3-3135

Vercken, E., Massot, M., Sinervo, B., Clobert, J., 2008. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* 20: 221-232. doi:10.1111/j.1420-9101.2006.01208.x

Wedding, C.J., 2007. Aspects of the impacts of mouse (*Mus musculus*) control on skinks in Auckland, New Zealand, In Institute of Natural Sciences. p. 146. *Massey University*, Auckland.

Weiss, S.L., 2006. Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology* 17: 726-732. doi:10.1093/beheco/arl001

Whiting, M.J., Stuart-Fox, D., O'Connor, D., Firth, D., Bennett, N.C., Blomberg, S.P., 2006. Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour* 72: 353-363. doi:10.1016/j.anbehav.2005.10.018

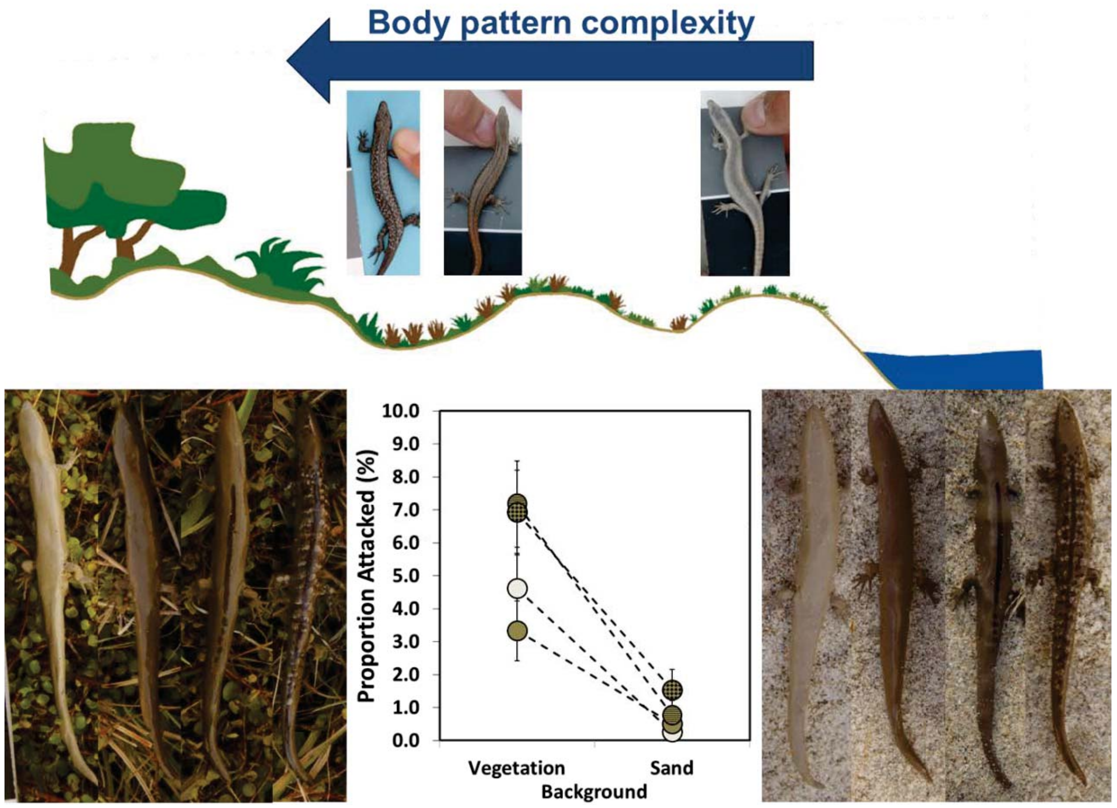
Woolbright, L.L., Stewart, M.M., 2008. Spatial and temporal variation in color pattern morphology in the tropical frog, *Eleutherodactylus coqui*. *Copeia* 2008: 431-437. doi:10.1643/CG-06-092

Zimova, M., Mills, L.S., Lukacs, P.M., Mitchell, M.S., 2014. Snowshoe hares display limited phenotypic plasticity to mismatch in seasonal camouflage. *Proceedings of the Royal Society B* 281: 20140029. doi:10.1098/rspb.2014.0029

Zimova, M., Mills, L.S., Nowak, J.J., 2016. High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters* 19:s 299-307. doi:10.1111/ele.12568

CHAPTER 4

BACKGROUND-MATCHING AND APOSTATIC SELECTION MAINTAIN PREY COLOUR PATTERN VARIATION IN A HETEROGENEOUS ENVIRONMENT



Article in review:

Baling M, Stuart-Fox D & Dale J. Background-matching and apostatic selection maintain prey colour pattern variation in a heterogeneous environment. *Proceedings of the Royal Society B*.

4 BACKGROUND-MATCHING AND APOSTATIC SELECTION MAINTAIN PREY COLOUR PATTERN VARIATION IN A HETEROGENEOUS ENVIRONMENT

4.1 Abstract

Two important predator-driven mechanisms maintaining variation colouration within natural prey populations are selection for matching different backgrounds, and frequency-dependent (apostatic) selection resulting from predators' search image for the most common variants. However, evaluating the relative role of these selection mechanisms in wild populations, and how they affect colour vs. colour pattern on backgrounds with differing complexity, is an enduring challenge. We used data on colouration in a wild population of shore skink (*Oligosoma smithi*), and a field experiment with realistic replicas to test whether predators are more likely to 1) attack prey that show a poorer match to the background; or 2) attack prey that are more abundant in the population, irrespective of their conspicuousness. Our results show that the proportion of different colour pattern variants was consistent over time, and had a non-random distribution that strongly corresponded to the vegetation gradient. However, our experiment with prey replicas revealed that predators preferentially attacked the more common patterned variants, regardless of their brightness- and pattern-matching on different backgrounds. Our study provides evidence that both selection for background-matching and apostatic selection (particularly on pattern elements) may play an important role in maintaining colour pattern variation in a wild population.

4.2 Introduction

The evolution of colouration in cryptic prey populations is often attributed to predator-driven selection (Endler 1978; Hargeby et al. 2004; Nilsson and Ripa 2010; Nosil and Crespi 2006). Visually-oriented predators can detect individuals based on either 1) the conspicuousness of prey against their immediate background (e.g., selection for background-matching), or 2) an acquired cognitive search image, which depends on the variant's relative frequency in the population (frequency-dependent, or apostatic selection). These two, non-mutually exclusive mechanisms of selection can each generate substantial variation in colour and colour patterns within populations, particularly in habitats with highly heterogeneous or complex backgrounds (Bond 2007; Bond and Kamil 2006; Dimitrova and Merilaita 2010).

In the case of selection for background-matching, spatial or temporal variation in background colour (e.g., overall brightness or range of hues) and complexity (e.g., shape, diversity or density of pattern elements) can generate and maintain variation in colour and colour patterns (e.g., Dimitrova and Merilaita 2014; Endler 1978; Merilaita and Stevens 2011). Specifically, disruptive selection on prey colouration will occur if individuals primarily remain only within one of the disjunct background types, either due to restricted movement or active background choice (Bond and Kamil 2006; Merilaita et al. 1999; Sandoval 1994). In the case of apostatic selection, predators form a search image for the most abundant variants (Bond 2007; Karpestam et al. 2014). Thus, rare variants can be overlooked irrespective of their conspicuousness, thereby maintaining variation within the population (Allen 1988; Bond 2007). Apostatic selection is expected to be strongest in populations occupying very complex backgrounds (Bond and Kamil 2006; Cooper 1984; Franks and Oxford 2011). This is because higher complexity in habitat texture or pattern requires predators to conduct slower, more selective searches for prey, such that either 1) all untargeted variants have lower probability of detection because predators focus only on the most common variant, or 2) only rare variants that are sufficiently distinct from the most common variant are overlooked (Allen 1988; Bond and Kamil 2006; Raymond 1984; Troscianko et al. 2009).

Numerous studies have compared predation risk of prey with different colours or colour pattern phenotypes on different backgrounds using both virtual environments (Bond and Kamil 2006; Dimitrova and Merilaita 2010, 2011; Merilaita et al. 2001; Merilaita and Ruxton 2009), and captive or field experiments on real or artificial prey (e.g., Bittner 2003; Farallo and Forstner 2012; Kusche and Meyer 2014; Mochida et al. 2015; Stuart-Fox et al.

2003; Torres-Dowdall et al. 2014). However, there are few data on whether or how different mechanisms of selection act on colour versus colour pattern. Furthermore, because differentiating between selection for background-matching and apostatic selection in natural systems can be challenging, spatial and temporal information about the relative frequencies of colour pattern variants in wild populations is ultimately essential (Bond and Kamil 2006; Farallo and Forstner 2012), but this information is often lacking (e.g., Hegna et al. 2013; Stuart-Fox et al. 2003; Torres-Dowdall et al. 2014).

Here, we investigate selection for background-matching and apostatic selection on prey colouration in a visually heterogeneous habitat using the highly colour variable shore skink, *Oligosoma smithi*. First, we assessed the frequency of colour pattern variants in a wild population spanning seven years. Under selection for background-matching, we expected the frequencies of variants to be higher in areas where they match their immediate background more closely, and to be stable over time. In contrast, under apostatic selection we expected the frequencies of particular variants to be unrelated to background-matching, and possibly fluctuate over time (Bond and Kamil 1998). Second, using highly realistic 3D-printed replicas in the field, we compared predation risk on naturally occurring variants that differed in 1) brightness (light vs. dark), and 2) pattern (uniform vs. intermediate patterning vs. highly complex patterns). Each variant was placed on two different backgrounds (sand with < 20% vegetation cover or dune vegetation with > 80% cover). Under selection for background-matching, we expected higher predation risk for variants with a poor match to a given background (e.g., dark variants on sand or light variants in vegetation), irrespective of their natural frequency. Under apostatic selection, we expected predation risk to be negatively associated with the frequency of variants in the natural population, particularly in the more complex, vegetated habitat.

4.3 Methods

4.3.1 Study site

We studied shore skinks at the coastal sand dunes of Tāwharanui Regional Park (hereafter "Tāwharanui"), in Auckland, New Zealand. These dunes consist of pale sand and a gradient of low vegetation cover in the foreshore to 100% vegetation at the back of the dunes. Tāwharanui is free from all introduced mammals except for three species (house mice *Mus musculus*, European rabbits *Oryctolagus cuniculus* and European hedgehog *Erinaceus europaeus*) (Maitland 2011). The park has both native (e.g., pukeko *Porphyrio melanotus*, sacred kingfisher *Todiramphus sanctus*) and introduced (e.g., Australian magpie *Cracticus tibicen*, common myna *Acridotheres tristis*) predatory bird species.

4.3.2 Population survey

We conducted yearly surveys of shore skinks at Tāwharanui in 2006 – 2008 and 2012 (see Baling et al. 2016 or Chapter 2, for further details on survey design). For each skink, we took digital photographs of the lizard and the habitat background (1 × 1 m) where the skink was caught (Figure 12). We used these photographs to score individual patterns as 1) *plain* (no patterns or very weakly patterned), 2) *simple* (no or very weak speckling combined with a mid-dorsal line on > 50% of the body length), or 3) *complex* (distinctive dense speckling and the presence of mid-dorsal line in > 50% of the body length). We quantified vegetation cover of habitat background by overlaying a 2 × 2 grid over each habitat photograph, and estimated the proportion of vegetation by eye. We binned all backgrounds into 5 categories, from 0 – 20% to 80 – 100% vegetation cover.

4.3.3 Predation experiment

We developed a highly realistic skink model using a combination of 3D-printed skink replicas (http://www.nzfauna.ac.nz/nzfauna---skink) and clay (Figure 12c; for further details on model design, see Appendix 4). Shore skinks at Tāwharanui varied in brightness and colour patterns, where the lightest coloured skinks tended to be unpatterned and darker skinks had a range of colour patterns (Baling et al. 2016). We mixed acrylic paints to reproduce colour similar to the spectral reflectance of live shore skinks, and painted the models based on the natural variation in colour pattern complexity: no pattern (*plain*), single mid-dorsal line (*simple*) and mid-dorsal line and speckling (*complex*). These colour patterns were sufficiently distinct from one another in pattern shape diversity, contrast, size and densities (Dimitrova and Merilaita 2011; Hanlon 2007; Merilaita and Dimitrova 2014). In total, there were four types of models (Figure 12c): *plain*-light, *plain*-dark, *simple*-dark and *complex*-dark. We created 60 models for each type, totalling 240 models.

We placed models along two backgrounds, one in vegetation (> 80% vegetation cover) and the other on sand (< 20% cover). In each background type, six grids were spaced 150 m apart where five of each model type (20 models in total) were set within the 4 × 3 m grid. Models were anchored by tying the fishing line to vegetation, or to a U-shaped wire pinned into the sand. We checked all models twice a day for signs of predation made by either birds or rodents (see Appendix 5, for more details on identification of bite marks), and replaced any model that was attacked. Checks were conducted in the morning (09:00 -

12:00 hrs local time), and afternoon (16:00 – 18:00 hrs). Checks were repeated for six days, with a total of 12 checks.

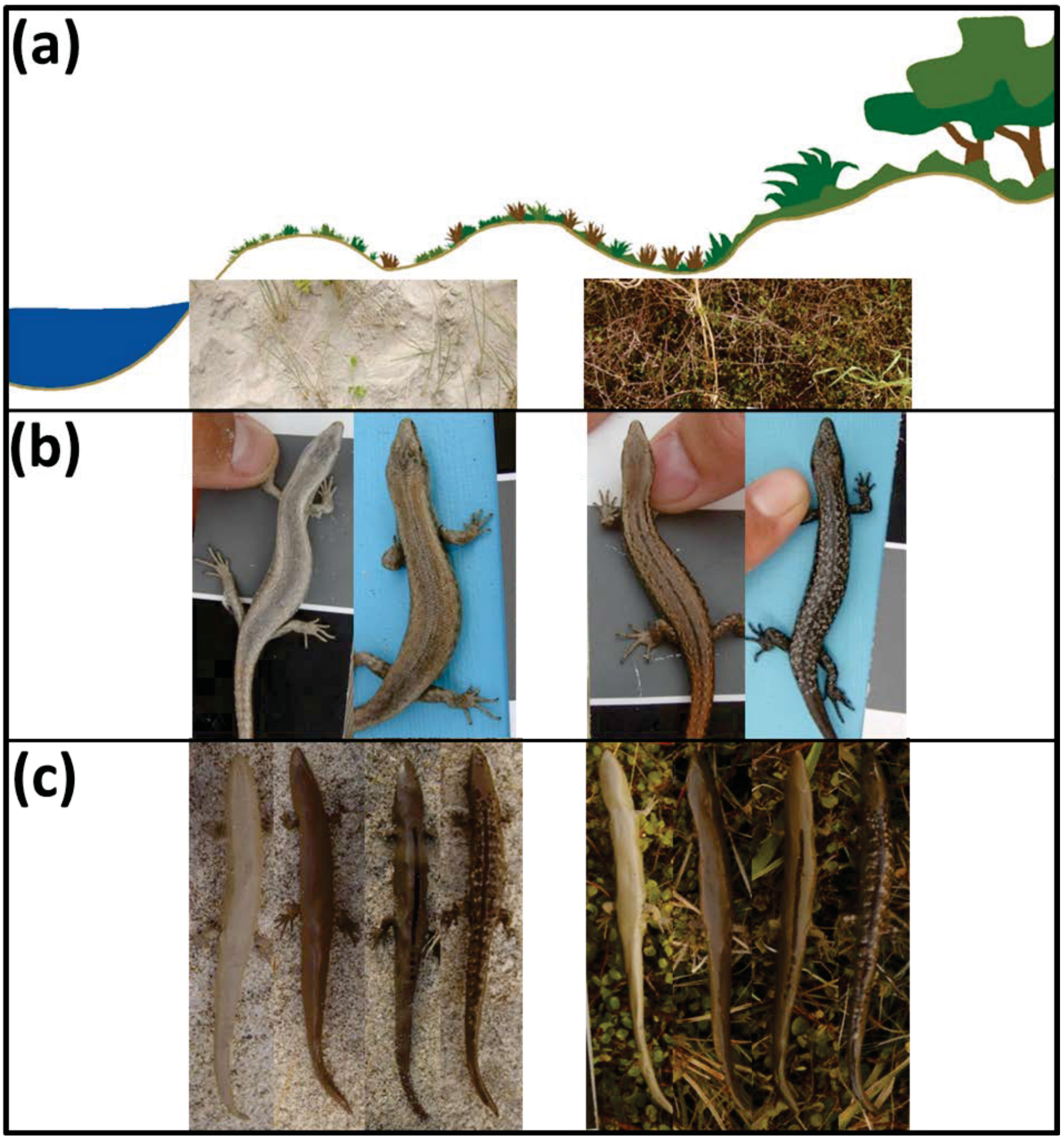


Figure 12. (a) New Zealand coastal sand dune, the fore-dune is sand with low vegetation cover (left) and back dunes has high vegetation (right); (b) shore skink colour pattern variants at Tāwharanui Regional Park; and (c) 3D-printed skink models (covered in soft clay), in sand and vegetation backgrounds. From left to right: *plain*-light, *plain*-dark, *simple*-dark, *complex*-dark.

4.3.4 Predicted attack scenarios

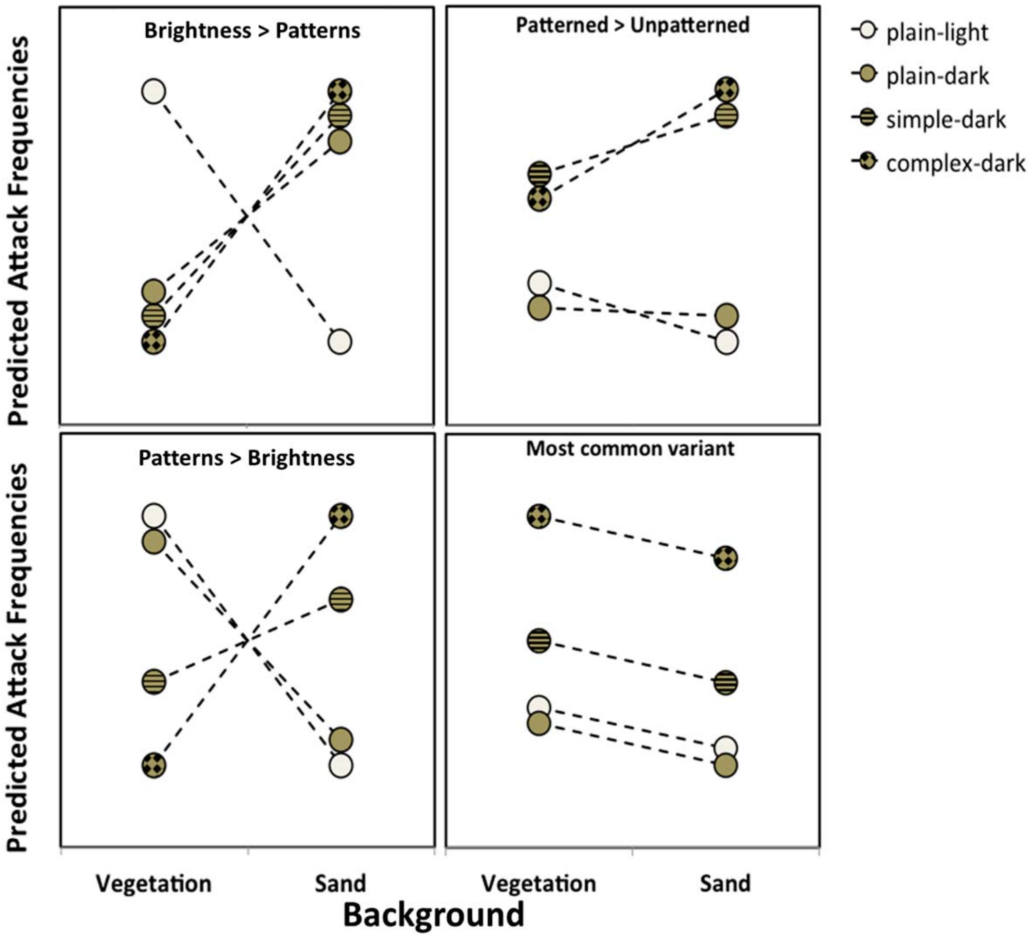


Figure 13. Predicted avian attack frequencies on shore skink clay models under four scenarios.

For the predation experiment, we evaluated predictions based on four scenarios that differed in the relative importance on predation risk of 1) brightness contrast against the background, 2) pattern-matching, 3) presence of body patterns, or 4) relative frequency of colour pattern variants. First, if overall brightness contrast is the most important factor affecting predation risk (Brightness > Patterns scenario, Figure 13), we expected *plain*-light models to be attacked more frequently in vegetation than sand backgrounds, and the reverse trend for darker (including the patterned) models. Second, if pattern-matching is the most important factor influencing predation risk (Patterns > Brightness scenario, Figure 13), attack frequencies should be higher on *simple*-dark, followed by *complex*-dark in the vegetation, and the opposite for sand areas. Third, if the presence of body patterning is the primary determinant of predation risk because variants similar to the most common variant are attacked more frequently than rare, distinct variants (Patterned > Unpatterned scenario, Figure 13), we expected the patterned models to be attacked most in both backgrounds. Finally fourth, if predators target the most common variant in the population (Most common variant scenario, Figure 13), we expected attack rates to be positively correlated to relative abundance in the natural population, regardless of background type; that is, *complex*-dark models to be attacked the most, followed by *simple*-dark and *plain*.

4.3.5 Statistical analysis

From the population survey, we evaluated whether the proportion of the pattern types differed significantly between years (Fisher's exact test), and in relation to (binned) vegetation cover (chi-squared test).

For the predation experiment, we fitted mixed effect logistic regressions (MELR) with a binomial distribution for the response (attacked or not attacked) to determine the effect of model type (*plain*-light, *plain*-dark, *simple*-dark and *complex*-dark), background type (sand vs. vegetation), sequential days (Days 1 – 7), time of day (morning and afternoon) and grid (Grids 1 – 6) on avian predation attacks (rodent attacks were excluded). For the predictor variables, we assigned model type, background and time of day as fixed effects, while grid and sequential days were random effects. The four model types enabled us to examine the effect of brightness (light vs. dark) and colour pattern (*plain* vs. *simple* vs. *complex*) on bird attack frequencies. When testing for an effect of brightness, we pooled all dark models if initial analysis showed no significant difference in attack frequencies between the three (*plain*-dark, *simple*-dark and *complex*-dark). Similarly, all *plain* models were grouped to examine the effect of body patterning if there was no difference between *plain*-light and *plain*-dark. We further pooled model types into unpatterned and patterned groups. Additionally, we investigated the variation in attack frequencies separately for each vegetation background (sand vs. vegetated).

All statistical analyses were conducted using R v. 3.1.2 (R Foundation for Statistical Computing). We conducted a stepwise procedure for all analyses, using Akaike's information criterion with a correction for finite sample sizes (AICc) to select the models with the lowest AICc values (R packages *lme4* and *AICcmodavg*). In these models we further examined the fixed effects using likelihood ratio tests (chi-square) to confirm the best model fit, and used Tukey contrast tests (R package *multcomp*; Hothorn et al. 2008) *post-hoc* to conduct pairwise comparisons.

4.4 Results

4.4.1 Pattern type frequencies in the population

The proportion of pattern types (*plain, simple*-dark and *complex*-dark) in the shore skink population at Tāwharanui did not differ between years (Fisher's exact test, $p = 0.55$, Figure 14a). *Complex*-dark was the most common variant, with > 70% occurrence in the population each year. This was followed by *simple*-dark (5 – 20%) and then *plain* as the rarest variant (< 8%). These colour patterns varied significantly in their spatial distribution across the vegetation cover gradient (Chi square test, $p < 0.01$, df = 8, Figure 14b). *Plain* occurred much more frequently in low vegetation cover compared to high cover (low vegetation: 26.7%, n = 8; high vegetation: 1.3%, n = 3). It was the opposite for *complex*-dark, with highest occurrences in high vegetation cover (82.3%, n = 186) compared to low cover (53.3%, n = 16). However, *complex*-dark was still the dominant type even at lowest vegetation cover. *Simple*-dark occurred more frequently than expected in areas containing 21 – 40% vegetation cover (28.6%, n = 12) compared to other areas (16.4 – 26.7%, n = 6 – 37).

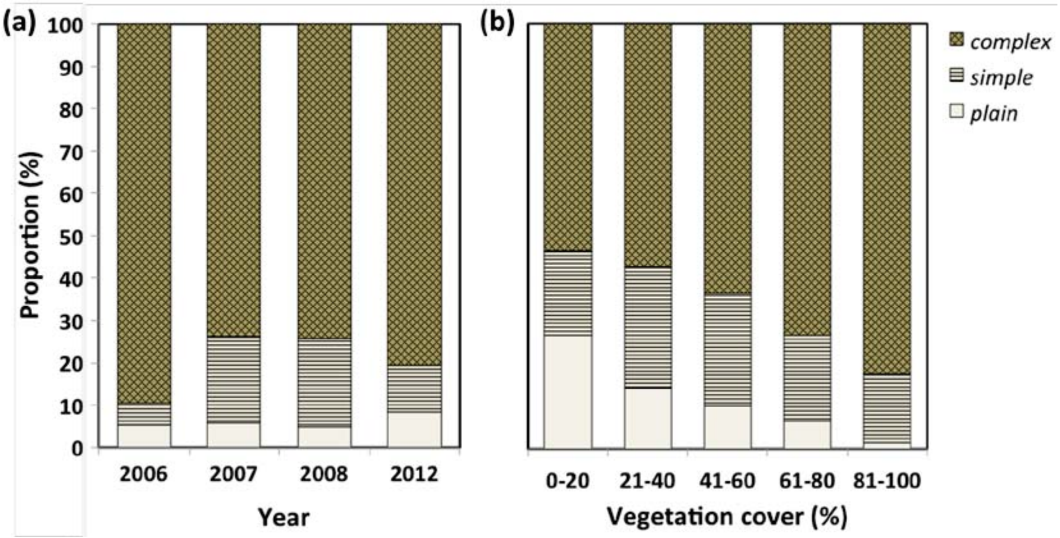


Figure 14. (a) Proportion of shore skink colour patterns across four years, and (b) across vegetation cover.

4.4.2 Predation experiment

In each of the 12 checks (twice per day), there were 240 models presented at once in the field, giving a total of 2,880 individual model half-days exposed to predation. We saw rodent predation attempts on five models and avian attacks on 97 models in total.

Overall, there was no significant difference in avian attack frequencies in relation to the brightness of models (light: 2.44%, n = 19; pooled dark: 3.38%, n = 79; Tukey contrast test, *p* = 0.13), so this result is contrary to the predicted Brightness >Patterns scenario (Figure 13). Similarly, there was no association with pattern-matching (Patterns > Brightness scenario), where *simple*-dark (4.28%, n = 32, Tukey contrast test, *p* = 0.01) and *complex*-dark (4.28%, n = 32, Tukey contrast test, *p* = 0.01) were twice as likely to be attacked compared to *plain* (pooled: 2.16%, n = 33; Figure 14a). This difference was stronger (Tukey contrast test, *p* < 0.01) when models were binned as unpatterned (*plain*) vs. patterned (4.27%, n = 64). Results were also consistent within each background (Figure 14b), where attacks were higher for patterned (sand: 1.17%, n = 9; vegetation: 7.59%, n = 55) than the rarer unpatterned models (sand: 0.39%, n = 3, *p* = 0.09; vegetation: 4.00%, n = 30, Tukey contrast test, *p* < 0.01). Therefore, observed results are consistent with the Patterned > Unpatterned scenario. See Appendix 6, for table of models.

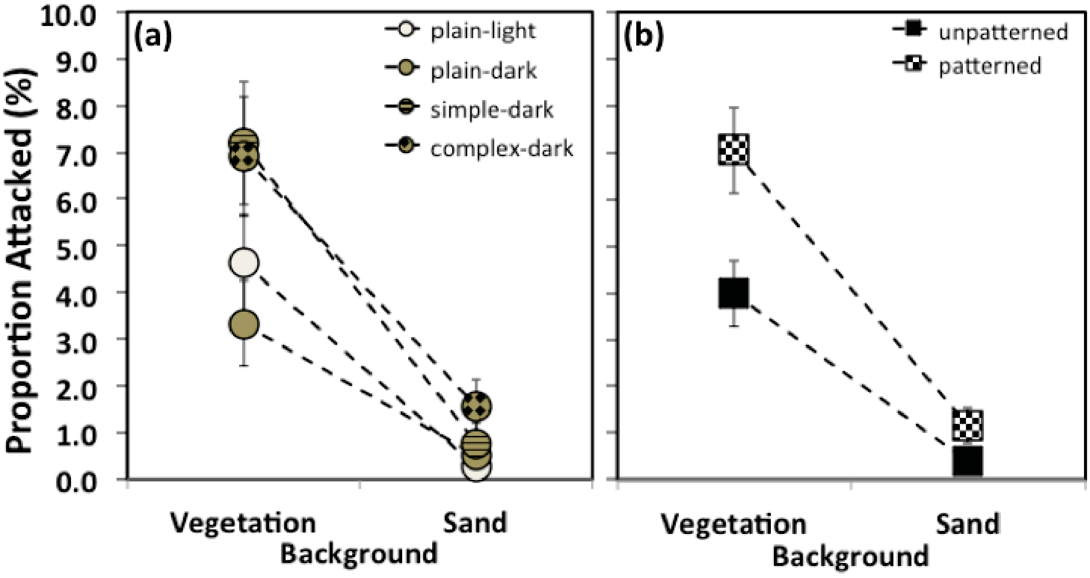


Figure 15. Observed attack frequencies (±SE) of (a) four clay model types, and (b) combined models of shore skinks.

Avian predators attacked 0.77% (n = 12) of the models on the sand background, and considerably more (5.45%, n = 85) of the models in vegetation. However, because there was an interaction between background and time of day, the difference in overall attack frequencies between backgrounds was not statistically significant (MELR, *p* = 0.07). In vegetation, avian attacks were higher during the morning compared to the afternoon (7.69%, n = 60 vs. 3.60%, n = 25, Tukey contrast test, *p* = 0.02). Additionally, attacks were only higher in vegetation compared to sand (7.69%, n = 60 vs. 0.36%, n = 3; Tukey contrast test, *p* < 0.01) during the morning. There was no difference in attack frequencies between times of day for sand (0.36%, n = 3 vs. 1.27%, n = 9, Tukey contrast test, *p* = 0.19), or between backgrounds during the afternoon (1.27% vs. 1.27%, Tukey contrast test, p = 0.24). See Appendix 6 for more details.

4.5 Discussion

Selection for matching different backgrounds in heterogeneous habitats and apostatic selection are two important predator-driven evolutionary mechanisms generating and maintaining colour pattern variation. Our study provides evidence for both mechanisms, suggesting that a complex interaction between them may maintain colouration in shore skinks. Our field observations showed that proportions of *complex*, *simple* and *plain* colour pattern variants corresponded to the vegetation gradient such that the proportion of *complex* variants increased with increasing vegetation cover while the proportion of *plain* increased with decreasing vegetation cover (i.e. increasing bare sand). Furthermore, the proportions of colour pattern variants were relatively stable over seven years, although this time period may have been insufficient to detect longer term temporal variation in colour pattern frequencies given the long generation time of these skinks (two years to reach sexual maturity and longevity > 10 years) (Bond and Kamil 2006). However, contrary to selection for background-matching, attack frequency in the predation experiment was unrelated to conspicuousness. Based on background-matching, we expected attack frequency to be higher on *plain* variants in the vegetation background and higher on *complex* variants in the sand background. Instead, we observed the opposite, with higher attacks on *complex* variants in the vegetation background. *Complex* variants were by far the most common in the population so the higher attack frequency on this pattern type is consistent with apostatic selection (Bond 2007).

Although *simple* variants were far less frequent than *complex* variants in the natural population, they were nonetheless attacked at similarly high frequencies (Patterned > Unpatterned scenario, Figure 13). Several studies have shown that prey variants similar to the most common varieties in a population are more likely to be attacked by predators (Allen 1988; Gorbunova 2017; Raymond 1984; Reid and Shettleworth 1992). For predators that encounter many prey variants unpredictably in one background type or within complex backgrounds, using general features or a combination of features may enable them to more reliably detect multiple variants (Reid and Shettleworth 1992; Troscianko et al. 2013). Therefore, predators may attack patterned variants (*simple* and *complex*) at similar frequencies because body patterning is a salient detection cue (Allen 1988). In our population, both dark and light *plain* models (< 8% in wild population) were attacked less frequently than the two dark models of different colour patterns (*simple* and *complex*). These results suggest that body patterning may be more important for detection than brightness (at least for static models, see below) and that apostatic selection may act primarily through reduced detection of the rarest variant.

Brightness contrast against the background had little effect on predation risk at our study site despite the apparent conspicuousness (to human eyes) of both light and dark models on their corresponding mis-matched backgrounds. This result is surprising because brightness matching is common in many cryptic prey, particularly melanic species (Forsman et al. 2011; Kettlewell 1955; Stevens et al. 2013). Brightness contrast between prey and background can be an important visual cue for predators (Defrize et al. 2010; Endler 1978; Stuart-Fox et al. 2003; Troscianko et al. 2016), particularly for detecting small (Lind and Kelber 2011; Osorio et al. 1999) or moving prey, because the achromatic visual channel is associated with the perception of movement (Kelber et al. 2003; Osorio and Vorobyev 2005). However, the replicas in our predation experiment were static. It is possible that brightness contrast may be important, but mainly for moving prey.

Alternatively, brightness contrast may not be a reliable visual cue for predators at Tāwharanui because of the high exposure and intensity of sunlight at the sand dunes during the day. Full sunlight exposure in an open environment can create extreme contrasts between intense light and dark patches of vegetation and coastal debris at the dunes. The light-coloured sand at the low vegetated areas will also reflect sunlight, and create glare for the observer. This dramatic lighting could impair discrimination between background and object, including prey that are highly patterned (Endler 1978). Consequently, the amount of exposure and position of the sun during the day could influence the visibility of skinks to predators (Dimitrova et al. 2009; Endler 1978).

Prey of various colouration should be harder to detect on complex or patterned backgrounds (Dimitrova and Merilaita 2010, 2011; Troscianko et al. 2009; Xiao and Cuthill 2016). Therefore, we expected skinks on a uniform (sand) background to have higher predation risk than those in vegetation. However, attack frequencies were higher in vegetation (in the morning). This is likely because predators focus their foraging efforts on more vegetated habitats, which had a much higher abundance of skinks (n = 226 in vegetation cover > 80%, compared to n = 30 in vegetation cover < 20%, Figure 14b). Additionally, predator abundances may differ between habitat types (Endler 1978; Troscianko et al. 2009), although this explanation seems less likely for avian predators at the spatial scale of our study site.

In conclusion, our results indicate that both selection for background-matching and apostatic selection may contribute to maintaining colour pattern variation in shore skinks at Tāwharanui. Although there was observed spatial structuring of colour pattern variants in relation to vegetation cover, which consistent with selection for background-matching, our predation experiment suggests that apostatic selection may also be important, by reducing predation risk for the least common (*plain*) variant. Additionally, our results provide empirical evidence for selection on colour pattern variation, to some extent independent of brightness. More generally, this study highlights that predator-driven selection processes may not be mutually exclusive, and that the importance of one or the other could be underestimated if only one method of investigation (observational or experimental study) is used.

4.6 Authors' contributions

MB: obtained permits, planned the experimental design, collected field data, produced the clay models, carried out predation experiment, statistical analyses and wrote the manuscript. DSF: conceived of the study, trained MB on mixing paint for the models, contributed to experimental design, statistical analyses and editing the manuscript. JD: participated in the experimental design, production of the 3D replicas, statistical analyses and editing the manuscript.

4.7 References

Allen, J.A., 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society B* 319: 485-503. doi:10.1098/rstb.1988.0061

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. *Biological Conservation* 203: 298-305. doi:10.1016/j.biocon.2016.10.002

Bittner, T.D., 2003. Polymorphic clay models of *Thamnophis sirtalis* suggest patterns of avian predation. *Ohio Journal of Science* 103: 62-66.

Bond, A.B., 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* 8: 489-514. doi:10.1146/annurev.ecolsys.38.091206.095728

Bond, A.B., Kamil, A.C., 1998. Apostatic selection by blue jays produce balanced polymorphism in virtual prey. *Letters to Nature* 395: 594-596. doi:10.1038/26961

Bond, A.B., Kamil, A.C., 2006. Spatial heterogeneity, predator cognition, and the evolution fo color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences* 103: 3214-3219. doi:10.1073pnas.0509963103

Cooper, J.M., 1984. Apostatic selection on prey that match the background. *Biological Journal of Linnean Society* 23: 221-228. doi:10.1111/j.1095-8312.1984.tb00140.x

Defrize, J., Théry, M., Casas, J., 2010. Background colour matching by a crab spider in the field: a community sensory ecology perspective. *The Journal of Experimental Biology* 213: 1425-1435. doi:10.1242/jeb.039743

Dimitrova, M., Merilaita, S., 2010. Prey concealment: visual background complexity and prey contrast distribution. *Behavioral Ecology* 21: 176-181. doi:10.1093/beheco/arp174

Dimitrova, M., Merilaita, S., 2011. Prey pattern regularity and background complexity affect detectability of background-matching prey. *Behavioral Ecology* 23: 384-390. doi:10.1093/beheco/arr201

Dimitrova, M., Merilaita, S., 2014. Hide and seek: properties of prey and background patterns affect prey detection by blue tits. *Behavioral Ecology* 25: 402-408. doi:10.1093/beheco/art130

Dimitrova, M., Stobbe, N., Schaefer, H.M., Merilaita, S., 2009. Concealed by conspicuousness: distractive prey markings and backgrounds. *Proceedings of the Royal Society B* 276: 1905-1910. doi:10.1098/rspb.2009.0052

Endler, J.A., 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11: 319-364. doi:10.1007/978-1-4615-6956-5_5

Farallo, V.R., Forstner, M.R.J., 2012. Predation and the maintenance of color polymorphism in a habitat specialist squamate. *PLoS ONE* 7: e30316. doi:10.1371/journal.pone.0030316

Forsman, A., Karisson, M., Wennersten, L., Johansson, J., Karpestam, E., 2011. Rapid evolution of fire melanism in replicated populations of pygmy grasshoppers. *Evolution* 65: 2530-2540. doi:10.1111/j.1558-5646.2011.01324.x

Franks, D.W., Oxford, G.S., 2011. The interrelationship between crypsis and colour polymorphism. *Ecology Letters* 14: 295-300. doi:10.1111/j.1461-0248.2010.01583.x

Gorbunova, E.S., 2017. Perceptual similarity in visual search for multiple targets. *Acta Psychologica* 173: 46-54. doi:10.1016/j.actpsy.2016.11.010

Hanlon, R., 2007. Cephalopod dynamic camouflage. *Current Biology* 17: 400-404. doi:10.1016/j.cub.2007.03.034

Hargeby, A., Johansson, J., Ahnesjö, J., 2004. Habitat-specific pigmentation in a freshwater isopod: adaptive evolution over a small spatiotemporal scale. *Evolution* 58: 81-94. doi:10.1111/j.0014-3820.2004.tb01575.x

Hegna, R.H., Saporito, R.A., Donnelly, M.A., 2013. Not all colors are equal: predation and color polytypism in the aposematic poison frog *Oophaga pumilio*. *Evolutionary Ecology* 27: 831-845. doi:10.1007/s10682-012-9605-z

Hothorn, T., Brezt, F., Westfall, P., Heiberger, R.M., 2008. multcomp: simultaneous inference in general parametric models. http://CRAN.R-project.org R package version 1.4-6.

Karpestam, E., Merilaita, S., Foraman, A., 2014. Natural levels of colour polymorphism reduce performance of visual predators searching for camouflaged prey. *Biological Journal of the Linnean Society* 112: 546-555. doi:10.1111/bij.12276

Kelber, A., Vorobyev, M., Osorio, D., 2003. Animal colour vision - behavioural tests and physiological concepts. *Biological Reviews* 78: 81-118. doi:10.1017/S1464793102005985

Kettlewell, H.B.D., 1955. Selection experiments on industrial melanism in the *Lepidoptera*. *Heredity* 9: 323-342. doi:10.1038/hdy.1955.36

Kusche, H., Meyer, A., 2014. One cost of being gold: selective predation and implications for maintenance of the Midas cichlid colour polymorphism (Perciformes: Cichlidae). *Biological Journal of the Linnean Society* 111: 350-358. doi:10.1111/bij.12205

Lind, O., Kelber, A., 2011. The spatial tuning of achromatic and chromatic vision in budgerigars. *Journal of Vision* 11: 1-9. doi:10.1167/11.7.2

Maitland, M., 2011. Tawharanui Open Sanctuary — detection and removal of pest incursions, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 441-444. *IUCN*, Gland, Switzerland.

Merilaita, S., Dimitrova, M., 2014. Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Functional Ecology* 28: 1208-1215. doi:10.1111/1365-2435.12248

Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B* 268: 1925-1929. doi:10.1098/rspb.2001.1747

Merilaita, S., Ruxton, G.D., 2009. Optimal apostatic selection: how should predators adjust to variation in prey frequencies? *Animal Behaviour* 77: 239-245. doi:10.1016/j.anbehav.2008.09.032

Merilaita, S., Stevens, M., 2011. Crypsis through background matching, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 17-33. *University Press*, Cambridge, UK.

Merilaita, S., Tuomi, J., Jormalainen, V., 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* 67: 151-161. doi:10.1111/j.1095-8312.1999.tb01858.x

Mochida, K., Zhang, W.-Y., Toda, M., 2015. The function of body coloration of the hai coral snake *Sinomicrurus japonicus boettgeri*. *Zoological Studies* 54: 33. doi:10.1186/s40555-015-0110-2

Nilsson, J., Ripa, J., 2010. The origin of polymorphic crypsis in a heterogenous environment. *Evolution* 64: 1386-1394. doi:10.1111/j.1558-5646.2009.00918.x

Nosil, P., Crespi, B.J., 2006. Experimental evidence that predation promotes divergence in adaptive radiation. *Proceedings of the National Academy of Sciences* 103: 9090-9095. doi:10.1073/pnas.0601575103

Osorio, D., Miklósi, A., Gonda, Z., 1999. Visual ecology and perception of coloration patterns by domestic chicks. *Evolutionary Ecology* 13: 673+689. doi:10.1023/A:1011059715610

Osorio, D., Vorobyev, M., 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings of the Royal Society B* 272: 1745-1752. doi:10.1098/rspb.2005.3156

Raymond, D.L., 1984. Wild birds prefer the familiar striped and unstriped artificial prey. *Biological Journal of Linnean Society* 23: 229-235. doi:10.1111/j.1095-8312.1984.tb00141.x

Reid, P.J., Shettleworth, S.J., 1992. Detection of cryptic pey: search image or search rate? *Journal of Experimental Psychology* 18: 273-286. doi:10.1037/0097-7403.18.3.273

Sandoval, C.P., 1994. The effects of the relative geographic scales of gene flow and selection on morph frequencies in the walking-stick *Timema cristinae*. *Evolution* 48: 1866-1879.

Stevens, M., Rong, C.P., Todd, P.A., 2013. Colour change and camouflage in the horned ghost crab *Ocypode ceraphthalamus*. *Biological Journal of Linnean Society* 109: 257-270. doi:10.1111/bij.12039

Stuart-Fox, D.M., Moussalli, A., Marshall, N.J., Owens, I.P.F., 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour* 66: 541-550. doi:10.1006/anbe.2003.2235

Torres-Dowdall, J., Machado-Schiaffino, G., Kautt, A.F., Kusche, H., Meyer, A., 2014. Differential predation on the two colour morphs of Nicaraguan Crater lake Midas cichlid fish: implications for the maintenance of its gold-dark polymorphism. *Biological Journal of Linnean Society* 112: 123-131. doi:10.1111/bij.12271

Troscianko, J., Lown, A.E., Hughes, A.E., Stevens, M., 2013. Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* 8: e73733. doi:10.1371/journal.pone.0073733

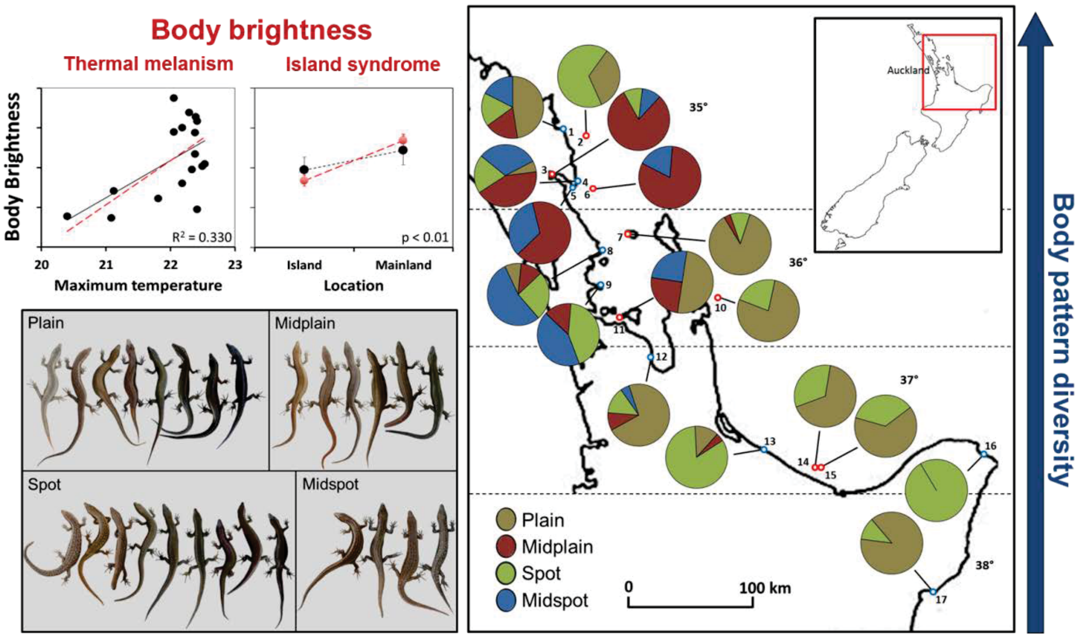
Troscianko, J., Wilson-Aggarwal, J., Stevens, M., Spottiswoode, C.N., 2016. Camouflage predicts survival in ground-nesting birds. *Scientific Reports* 6: 19966. doi:10.1038/srep19966

Troscianko, T., Benton, C.P., Lovell P George, Tolhurst, D.J., Pizlo, Z., 2009. Camouflage and visual perception. *Philosophical Transactions of the Royal Society B* 364: 449-461. doi:10.1098/rstb.2008.0218

Xiao, F., Cuthill, I.C., 2016. Background complexity and the detectability of camouflaged targets by birds and humans. *Proceedings of the Royal Society B* 283: 20161527. doi:10.1098/rspb.2016.1527

CHAPTER 5

GEOGRAPHIC VARIATION IN COLOUR AND PATTERNS IS ASSOCIATED WITH CLIMATE AND MICROHABITAT IN A LIZARD



Article in prep:

Baling M, Stuart-Fox D & Dale J. Geographic variation in colour and patterns is associated with climate and microhabitat in a lizard*:* evidence for thermoregulation and camouflage.

5 GEOGRAPHIC VARIATION IN COLOUR AND PATTERNS IS ASSOCIATED WITH CLIMATE AND MICROHABITAT IN A LIZARD

5.1 Abstract

In ectotherms, body colouration can serve three biological functions: visual camouflage, thermoregulation, and intraspecific signalling. The degree of influence these functions have on colour and colour pattern diversity within a species can vary across a large spatial scale, especially when environmental clines strongly affect biological processes. Here, we evaluate whether variation in colour and colour patterns across populations of a colour-variable skink species from a temperate region is affected by thermal melanism (thermoregulation) or crypsis (camouflage). First, if skink colours are selected for thermal melanism, we predicted skinks to be darker with increasing latitude or climatic gradient. Second, if skink colour pattern diversity is driven by local adaptation for crypsis, we predicted that colouration would correlate with local habitat. We compared colours and colour patterns in 17 skink populations across both offshore islands and the mainland New Zealand. We found that brightness decreased with mean monthly maximum temperatures, suggesting a role of thermal melanism. However, of four distinct colour patterns, only one (*plain*) was associated with microhabitat (i.e. proportion of rock), and another (*midspot*) decreased in frequency across latitude. Additionally, islands had increased melanism, higher frequency of *plain* types, and less *midspots* compared to mainland sites, despite no apparent differences in environmental conditions measured between the two locations. We concluded that high level of colouration in this species is driven by complex interactions between various selective processes for both thermoregulation and camouflage, while not ruling out the potential influence of stochastic processes in some of the populations.

5.2 Introduction

Animals can exhibit a range of colouration — from uniform, monomorphic colouration within a species, to diverse colours and colour patterns within and among populations. For ectotherms, variation in a population colouration can have three main biological functions: visual camouflage, thermoregulation, and intraspecific signalling (Cooper Jr. and Greenberg 1992; Stuart-Fox and Moussalli 2009). First, selection for camouflage (to avoid predator detection) typically results in prey matching its body to its background. This function predicts that prey colouration will vary according to its immediate habitat background (see Stevens and Merilaita 2009). Second, selection for colouration that facilitates thermoregulation will favour dark-coloured individuals in cold environments where the body can heat up faster through increased absorption of solar radiation (thermal melanism; Clusella-Trullas et al. 2007; Smith et al. 2016b). Finally, social selection via female preference or rival competition can result in sexual dichromatism or polymorphic colouration (e.g., Baird et al. 2013; Bastiaans et al. 2013; Pérez i de Lanuza et al. 2013; Sinervo and Lively 1996). Because all three biological functions are important for individual fitness via both survival (e.g., reduced predation risk, improved growth rate; Rowe et al. 2016; Stevens and Merilaita 2009) and breeding success (e.g., access to good quality mates, improved embryo growth; Azócar et al. 2014) they are not mutually exclusive. Nevertheless, these alternate functions can be antagonistic with respect to optimal colouration. A significant challenge for evolutionary biologists is to determine how multiple and potentially conflicting functions affect colouration.

At the population level, body colouration can vary across large spatial scales, and this can be the outcome of selection for thermoregulation, selection for crypsis, or the result of non-adaptive evolutionary changes. Firstly, in many species colouration follows altitudinal, latitudinal and other environmental gradients such as temperature, solar radiation, UV and aridity (e.g., Castella et al. 2013; Harris et al. 2012; McLean et al. 2015; Rajabizadeh et al. 2015; Reguera et al. 2014; Schweiger and Beierkuhnlein 2015). These trends are often attributed to thermal melanism, where darker animals at higher latitudes or lower temperatures have increased fitness from effective thermoregulation (Castella et al. 2013; Clusella-Trullas et al. 2007; Fischer and Lindenmayer 2005). Climatic gradients may also affect other characteristics such as body size, clutch size and growth (e.g., Pincheira-Donoso et al. 2008; Rowe et al. 2016; Schweiger and Beierkuhnlein 2015), but for ectotherms these traits are linked to thermoregulation (Azócar et al. 2014). Secondly, when predation selection for prey is strong at some sites, colouration can vary spatially within populations through adaptation of colour patterns for crypsis (either via prey conspicuousness, or predator search behaviour; Bond 2007; Stevens and Merilaita 2011). In this case, population colouration should be tightly linked to the background of the local habitat (Marshall et al. 2015). Finally, non-adaptive forces, such as gene flow between populations, or genetic drift within populations, can potentially influence geographic variation of colour and colour patterns. Small and/or isolated populations (particularly those on islands) are susceptible to founder effects or genetic drift, hence colouration could also be influenced by stochastic processes (McLean and Stuart-Fox 2014). In addition, populations on islands are often under the effect of 'island syndrome', and melanism has been shown to occur more frequently in populations on islands compared to its mainland counterparts (Boback and Siefferman 2010; Novosolov et al. 2013; Runemark et al. 2010). However, the selective processes underlying island syndrome effect may include local adaptation and/ or stochastic processes (Brakefield 1990; Runemark et al. 2010; Uy and Vargas-Castro 2015).

Here, we quantify the geographic variation in colour and colour pattern diversity of the shore skink, *Oligosoma smithi*, and using phylogenetic comparative methods, we test whether colouration among populations is consistent with trends expected by thermal melanism or camouflage. This species is widely distributed across several latitudes of the New Zealand temperate region, and has one of the highest levels of variation in colour patterns among New Zealand skinks (Hardy 1977). Both colour and colour patterns of shore skinks vary among populations, and also between sites in islands and mainland. Lizards in temperate regions can often be active at low temperatures (e.g., Cree 1994), thus we expect that selection of colour for thermoregulation will be strong and detectable across the latitudinal or climatic gradients. We also expect local adaptation for crypsis occurring among the populations because an earlier study on shore skinks revealed a clear association between colour patterns and habitat background (Baling et al. 2016). Most studies on geographic variation in colouration in ectotherms have focused either only on colour (melanism), or between uniform versus patterned morphs (e.g., Azócar et al. 2014; Castella et al. 2013; Clusella-Trullas et al. 2007; Forsman and Shine 1995; Harris et al. 2012; McLean et al. 2015; Rajabizadeh et al. 2015; Reguera et al. 2014; Zapletalová et al. 2016). Our study provides a needed field investigation on geographical diversity on both colour and colour patterns within a species. This allows us to evaluate whether different selective pressures act on colour versus colour patterns. More specifically, we expected that variation in colour would have occurred under a stronger influence of thermal melanism, whereas colour pattern diversity would be a reflection of adaptation for camouflage.

5.3 Methods

5.3.1 Study sites and population surveys

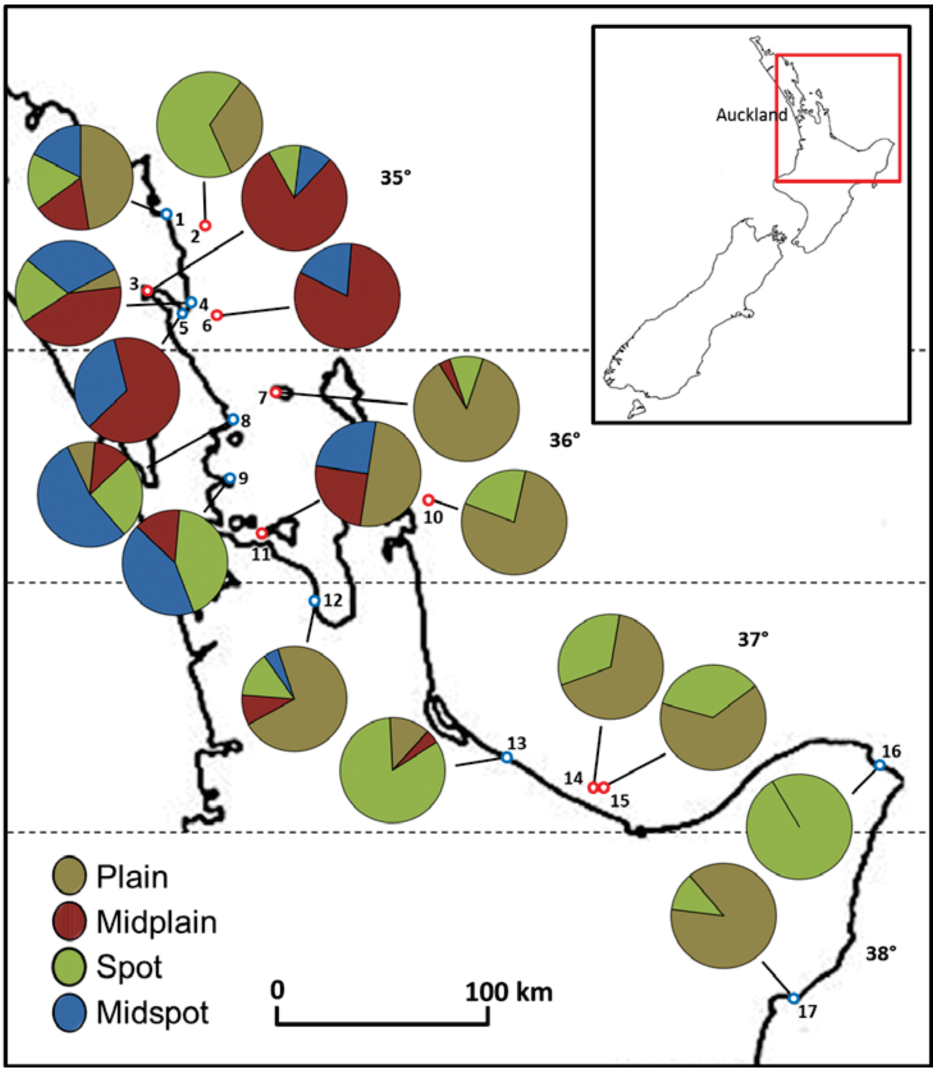


Figure 16. The proportion of colour pattern types for each surveyed population, at latitudes 35° to 38°, New Zealand. 1. Mimiwhangta (n = 40); 2. Aorangi Island (n = 15); 3. Matakohe-Limetsone Island (n = 10); 4. Ocean Beach (n = 36); 5. Smuggler's Bay (n = 3); 6. Lady Alice Island (n = 17); 7. Hauturu Island (n = 31); 8. Tāwharanui Regional Park (n = 35); 9. Shakespear Regional Park (n = 14); 10. Korapuki Island (n = 63); 11. Crusoe Island (n = 4); 12. Whakatiwai (n = 44); 13. Maketu (n = 24); 14. Rurima Island (n = 3); 15. Motouki Island (n = 17); 16. Te Araroa (n = 5); 17. Kaiti Beach (n = 17). Red and blue circles represent islands and mainland sites, respectively.

We surveyed 17 populations of shore skinks between latitudes 35°– 38° in the North Island, New Zealand (Figure 16). These surveyed areas represent approximately 80% of the geographical distribution of the species (latitudes 34° – 38°). The populations sampled consisted of almost equal numbers of islands and mainland sites within each latitudinal range, totalling eight islands and nine mainland sites (Figure 16). Each site was visited once (ranging 3 – 7 days) within Austral summer and autumn seasons between 2012 and 2014. We captured skinks using a combination of live pitfall traps and funnel traps, baited with fish-based cat food. We photographed all captured skinks and their habitat backgrounds (1 × 1 m) using a Pentax Optio W60 (Pentax, Japan). Each photograph (dorsal or background) included a photographic grey standard (Digital Gray Card DGC-100, Robin Myers Imaging, USA) with 30% reflectance. Skinks were marked with non-permanent, xylene-free pen upon release to avoid resampling. We collected 10 – 70 background photographs from each site, and the sample size was dependend on the size of the area surveyed for skinks (e.g., large sand dune, narrow rocky beach).

5.3.2 Skink colour and pattern from photographs

We quantified colour using digital photographs. The distribution of lizard colours within a RGB (red, green blue) colour space is significantly similar to its distribution within avian or lizard visual colour space (Smith et al. 2016b). Although photographs capture the majority of the visible spectrum (400 – 700 nm) but not ultraviolet (300 – 400 nm), this was suitable for shore skinks because they showed minimal ultraviolet reflectance (see Appendix 1). In each image, we extracted the averaged mean red (R), green (G), blue (B), and brightness (V) values from each photograph and calibrated them according to methods in Baling et al. (2016). We acquired values for hue and saturation from a two-dimensional representation of colour space, where the distance from origin represents saturation, and the angle relative to the axis is hue (Endler 1990). We first calculated the standardised differences between the calibrated R and G channels as, $x = (R - G)/(R + G + B)$, and between G and B channels as, $y = (G - B)/(R + G + B)$. We then determined saturation (S) as:

$$S = (x^2 + y^2)^{\frac{1}{2}},$$

and hue (H) as:

$$H = tan^{-1}\left(\frac{y}{x}\right),$$

where x and y represents the standardised difference of R-G and G-B channels, respectively. Each of the colour variables, hue, saturation and brightness were averaged for each population.

We scored dorsal colour pattern complexity as described in (Baling et al. 2016, or Chapter 2). Briefly, we assigned individuals to one of four types: (1) *plain*: no patterns or very weakly patterned; (2) *midplain*: no or very weak speckling combined with the presence of a mid-dorsal line on more than 50% of the body length; (3) *spot*: distinctive dense speckling and no (or less than 50%) mid-dorsal line on length of body; and (4) *midspot*:

distinctive dense speckling and presence of mid-dorsal line in more than 50% of the body length (Figure 17). For each population, we quantified the relative frequency of each colour pattern.

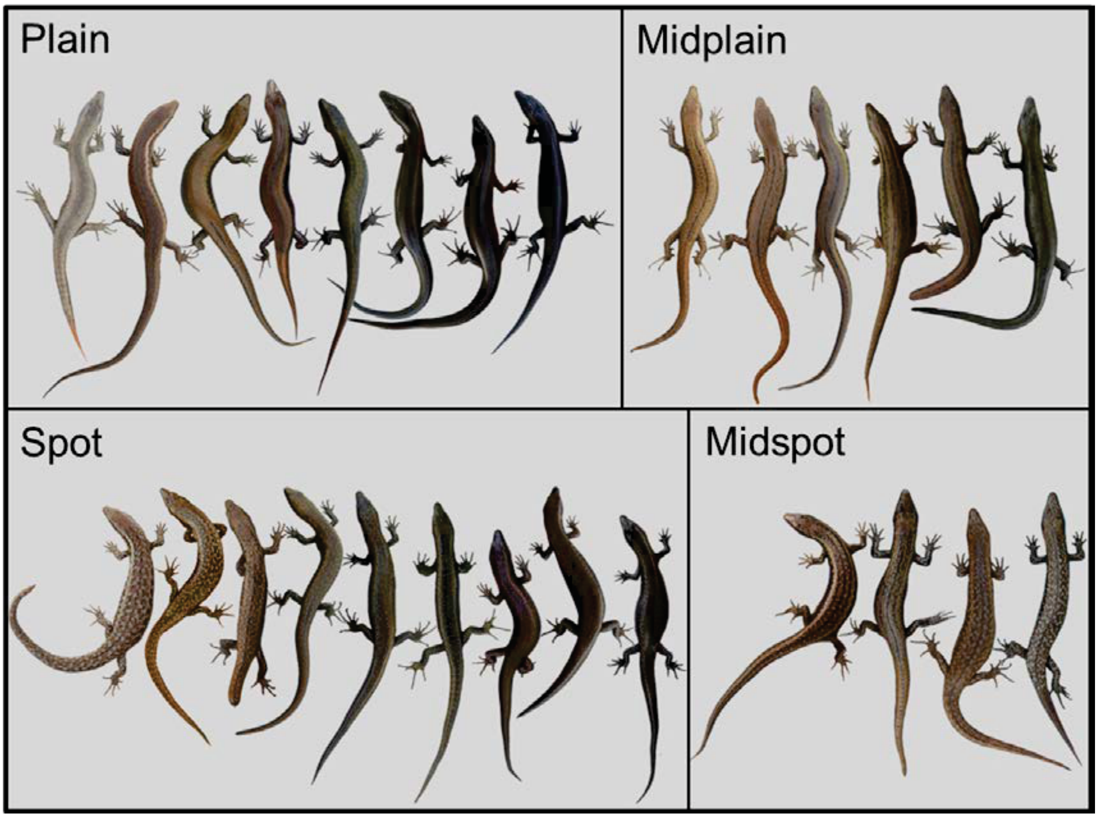


Figure 17. An example of variation in colour for the four colour patterns in 17 shore skink populations.

5.3.3 Environmental data

We selected environmental variables that were predicted to affect colouration in shore skinks: i.e. habitat background and climate indices. Due to the sample size of our study, we minimised the number of variables in our analyses. In our previous study (Chapter 2), habitat colour and microhabitat (vegetation cover in the immediate vicinity where skinks were captured) were shown to correlate to shore skink colouration (Baling et al. 2016). So we quantified background colour as detailed above, and for the microhabitat, we estimated by eye the proportion of vegetation, sand and rock cover of the backgrounds from photographs (minimum 5%, maximum 100% of each; see Chapter 3 for details). Proportions of microhabitat types were averaged for each population. Due to the collinearity of proportion of rock to the other two variables, we conducted a principal components analysis (PCA) to determine the variable that explained the most variance in the data (see Appendix 7, for extended methods). We selected proportion of rock, but for our colour models we used proportion of vegetation as our microhabitat predictor because rock was correlated to mean monthly maximum temperature (see below).

We acquired climate data for all 17 study sites from the National Institute of Water and Atmospheric Research (NIWA) virtual climate station data (Cichota et al. 2008) and UV Atlas v. 2.2 (NIWA, New Zealand). Because most climate variables (e.g., temperature, UV index, maximum UV index, and radiation) were correlated with latitude, we only used the latitudinal cline (coordinates) for our models (see Appendix 8, for extended methods). We also selected monthly maximum temperature as another environmental predictor because it co-varied independently to the latitudinal range or other climate data. We calculated the mean monthly maximum temperature (thereafter "maximum temperature") for each study site using data from October to April (Austral summer and autumn seasons) over six years (2010-2016).

5.3.4 Phylogenetic tree

We obtained ND2 sequences of shore skinks and four outgroup species (*O. microlepis*, *O. suteri*, *O. moco* and *Lampropholis guichenoti*; Hare et al. 2008); from GenBank. Sequence data for six of our shore skink populations were not available (Tāwharanui Regional Park, Shakespear Regional Park, Maketu, Rurima Island, Te Araroa and Kaiti Beach), so we sent tissue samples collected from these sites to Ecogene (Auckland, New Zealand), where sequencing data were generated based on the methods outlined in Hare et al. (2008). We first aligned all sequences using MEGA7 (Kumar et al. 2016), and then determined the best-fit model of evolution for our dataset by comparing different mutation models using the Akaike's information criterion with a correction for finite sample sizes (AICc), which is implemented in MEGA7, to select the maximum likelihood (ML) models with the lowest AICc values. We constructed a ML tree using Hasegawa-Kishino-Yano (+Gamma) model, and used 1000 bootstrap replicates to assess branch support. All other shore skink populations and outgroup species in the original tree (Hare et al. 2008) were removed from the final tree (see Appendix 9, for phylogenetic trees).

5.3.5 Statistical analyses

We used phylogenetic generalised least squares (PGLS) regressions to account for phylogenetic independence between the populations (Garamszegi 2014). First, we predicted that if shore skink colour was strongly selected for thermoregulation, then brightness (which is negatively related to melanism) between populations will negatively correlate with maximum temperature or latitudinal cline (Figure 18a). Alternately, if camouflage has a significant influence on colour, we expected to see a stronger association between body colour (especially brightness) and background colour or microhabitat cover (Figure 18b). We used hue, saturation and brightness separately as our response variables, and latitudinal cline (coordinates), maximum temperature, background colour, and proportion of vegetation cover (arc-sin transformed) as predictors. We also included location of where populations were from (mainland vs. island sites) as another predictor to take into account potential island syndrome for melanism (Uy and Vargas-Castro 2015). Secondly, for skink colour patterns (in contrast to colour) we predicted that if dorsal patterning is selected for camouflage, we should find a significant association between relative frequency of each colour pattern and background (either microhabitat cover or background colour). Here, we used proportion of colour pattern (*plain*, *midplain*, *spot* and *midspot*) in separate models as response variables, and latitudinal cline, location, background brightness and proportion of rock cover as predictor variables.

We carried out PGLS multiple regressions using *ape* and *nlme* packages in R v. 3.2.3 (R Foundation for Statistical Computing). Models were compared using Akaike's information criterion (R package *AICcmodavg*) with a correction for finite sample sizes (AICc) to select the models with the lowest AICc and high AICc weight (> 0.90) values. Phylogenetic signal associated to the residual errors of the fitted model was reported as λ with 95% confidence intervals. A low value in λ (close to 0) suggests that phylogeny has little influence on the error structure of data in the fitted model, whereas high λ (close to 1) assumes strong influence of phylogeny on the data (Garamszegi 2014). We took the best model and a subset of the competing models that added up at least 0.95 of the total AICc weight. This gave us 95% confidence that predictors in the selected models were important for the response variables (Symonds and Moussalli 2011). We summed the AICc weights of each predictor (aAICc weight) from the selected models to determine the degree of influence (between 0 and 1) each predictor had on the response variable. To further interpret the relationship between the response variables and the predictors, we conducted separate linear regressions in R.

Finally, we further investigated if there was any difference between mainland and island sites in habitat background colour, microhabitat (vegetation and rock cover) and climate (mean monthly temperature, mean monthly maximum temperature, solar radiation, mean monthly UVI and mean maximum UVI) using t-test and linear regression.

5.4 Results

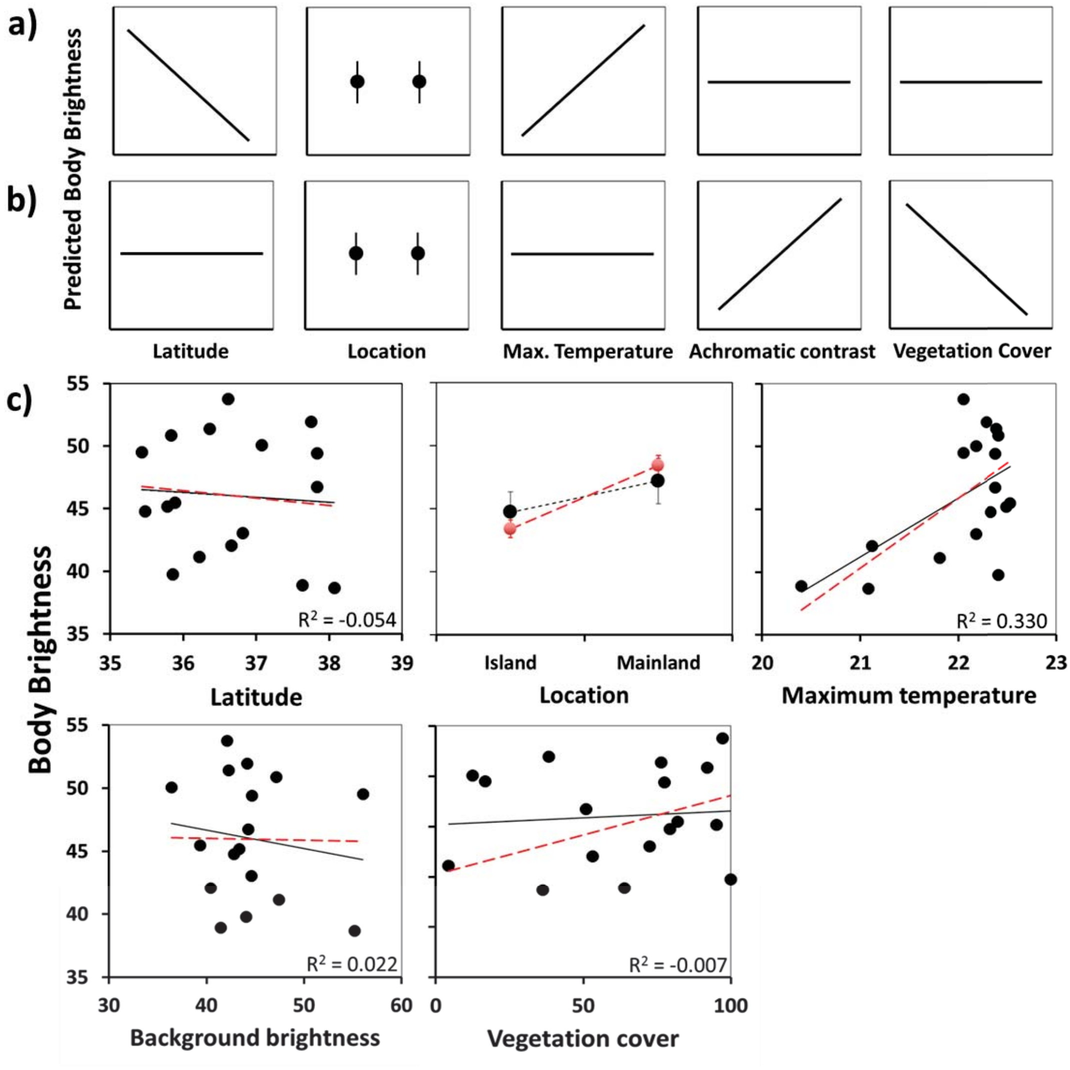


Figure 18. a) Predicted body brightness across latitude (coordinates), location (island vs. mainland), maximum temperature (°C), habitat colour (brightness) and microhabitat cover (vegetation) if shore skink colour was strongly selected for thermoregulation; b) predicted body brightness if shore skink colour was under selection for camouflage; and c) the trends observed in body brightness (raw data) for each independent variable. Black lines are linear regression using raw data (with r^2 values shown) and red lines are values predicted from PGLS brightness model 1. Circles are mean brightness with standard error bars, with black circles representing values from raw data and red from data predicted from PGLS brightness model 1.

For colouration, we found that maximum temperature and location (i.e. mainland versus island) were the strongest predictors for shore skink colour in terms of hue and brightness, but not saturation (Table 2). Because body saturation was consistently low among populations (mean = 0.09 ±0.007 SE, possible range 0 to 1), the overall colour for skinks were more towards grey tones. Shore skink populations were lighter and more brown-grey in colour at sites with higher maximum temperatures (PGLS, hue: $p < 0.01$; brightness: $p < 0.01$; Figure 18c, Table 2). Although latitudinal cline was an important predictor for the models, skink colour did not significantly vary according to latitude (PGLS, hue $p = 0.06 - 0.18$; saturation $p = 0.24 - 0.35$; brightness $p = 0.13 - 0.88$). Background colour and microhabitat (vegetation cover) were not selected for most of the best-fit models, therefore, not considered as important predictors for colour variation. These combined results when compared to our predicted scenarios (Figure 18), confirmed that climate strongly affects shore skink colour. We also observed mainland populations being lighter and more brown-grey than island populations (PGLS, hue: $p < 0.01$, brightness: $p < 0.01$), despite the similarities in habitat colour or maximum temperature between island and mainland sites (t-test island vs. mainland, habitat hue: $p = 0.87$, means = 86.8 ± 6.74 SE, 88.3 ± 5.88 SE; saturation: $p = 0.48$, means = 0.15 ± 0.02 SE, 0.18 ± 0.03 SE; brightness: $p = 0.60$, means =43.2 ± 208.6 SE, 44.3 ± 149.5 SE; temperature: p =0.43, means= 22.2°C ± 0.17 SE, 21.9°C ± 0.23 SE).

For skink colour patterns, habitat type was a strong predictor for only one colour pattern type (Table 2). The occurrence for *plain* in populations increased as the proportion of rock cover increased in backgrounds (PGLS $p < 0.01$, linear regression, $p < 0.01$, $r^2 = 0.326$). Rock cover was not a strong predictor for other colour patterns(PGLS aAICc weights, *midplain* = 0.07, *spot* = 0.05, *midspot* = 0.05). Overall, the frequency of each colour pattern varied between populations, with higher occurrences in colour pattern diversity observed in the lower latitudes (Figure 16). When phylogeny was taken into account, latitude was a significant predictor for all colour patterns, but only the frequency of *midspot* significantly reduced with increasing latitude (PGLS *midspot* $p = 0.02$; Table 2). Additionally, *midspot* occurred less while *plain* more on islands compared to mainland populations (PGLS *plain* $p = 0.02$, *midspot* $p < 0.01$).

Table 2. Best fit PGLS models (lowest AICc) and their associated subset competing models that had AICc weight summed to at least 0.95 for shore skink colour (hue, saturation and brightness) and colour patterns (*plain*, *midplain*, *spot* and *midspot*). Table lists the coefficient values for latitude (coordinates), location (mainland vs. island sites), maximum temperature (for colour only), background colour, microhabitat (proportion for vegetation for colour models, and proportion of rock cover for colour pattern models). aAICc is the summed value of AICc weights for each predictor variable to determine their degree of influence on the response variables. λ is phylogenetic signal associated to the residual errors of each fitted model, with 95% confidence interval.

Response variables		**n**	**Latitude**	**Location**	**Max. Temp**	**Background**	**Microhabitat**	**λ (95% CI)**	**AICc**	**AICc weight**
Hue	aAICc	17	0.99	0.99	0.99	0.04				
model 1			-8.06	-38.86**	-48.63***			1.15 (0.866 – 1.429)	145.28	0.95
model 2			-13.30	-51.50***	-64.17***	0.16		2.16 (0.492 – 3.819)	151.40	0.04
Saturation	aAICc	17	1.00	0.01						
model 1			0.008					-0.38 (-0.721 – -0.048)	-47.86	0.99
model 2			0.006	0.019				-0.22 (-0.286 – -0.153)	-38.70	0.01
Brightness	aAICc	17	1.00	1.00	1.00					
model 1			1.04	5.04**	7.07***			-0.32 (-0.323 – -0.312)	93.28	1.00
model 2			-0.18	2.84				-0.20 (-0.220 – -0.182)	106.52	0.00
Plain	aAICc	17	0.99	0.99		0.37	0.64			
model 1			13.34*	-20.77*				1.15 (0.987 – 1.311)	147.89	0.35
model 2			14.86**	-8.05		1.18	0.75**	-0.20 (-0.206 – -0.202)	148.40	0.27
model 3			10.22*	-8.54			0.89***	-0.43 (-0.491 – -0.363)	148.43	0.27
model 4			27.45*	985.60**		0.79	0.26	1.12 (0.911 – 1.326)	154.40	0.10
Midplain	aAICc	17	0.95	0.71			0.07			
model 1			-12.08	-0.91				1.06 (0.645 – 1.470)	143.42	0.62
model 2			-12.18					1.07 (0.729 – 1.404)	145.06	0.27
model 3			-15.22*	-1.16			-0.37	0.09 (-1.007 – 1.189)	147.93	0.07
Spot	aAICc	17	0.97	0.86			0.05			
model 1			7.11	13.17				0.53 (-0.362 – 1.415)	147.42	0.81
model 2			9.09					0.38 (-0.412 – 1.181)	151.41	0.11
model 3			6.75	13.82			0.05	0.56 (-0.376 – 1.503)	153.06	0.05
Midspot	aAICc	16	0.98	0.98			0.05			
model 1			-8.62*	14.73 **				1.41 (0.412 – 2.417)	124.96	0.93
model 2			-8.39*	11.35**			-0.14	1.22 (0.045 – 2.403)	130.99	0.05

5.5 Discussion

The colour and colour pattern diversity of shore skinks varied significantly with both climate and habitat. As predicted, skink colour, particularly brightness and hue, was mainly related to maximum temperature, where skinks were lighter and more brown-grey at sites with higher maximum temperatures. This suggests a potential role for selection of colour for thermoregulation. For shore skink colour patterns however, overall trends were more complex, and their relative frequency in the populations differed depending on the type of colour pattern. *Plain* individuals were more frequent in backgrounds with high amounts of rock, and this result is consistent with a colouration function for camouflage. Surprisingly, the frequency of *midspot* types was lower at sites located at higher latitudes, which suggests a possible link to thermoregulation. Between mainland and island populations, both colour and colour pattern of shore skinks differed despite no differences in the measured environmental variables (e.g., habitat colour and maximum temperature). Here, island populations had more *plain* but less *midspot* individuals, and skinks were darker and green-grey compared to mainland populations, which had lighter brown-grey skinks.

Overall, maximum temperature was the most influential factor for variation across populations of body brightness in shore skinks. However, brightness did not vary according to latitudinal cline, implying that the climatic gradients correlated with latitude, namely temperature, solar radiation and UVI gradients may not be important influences on colouration. Shore skinks often live in open, exposed coastal habitats where environmental conditions can be extreme. Darker colouration at sites with low maximum temperatures can increase absorption efficiency and reduce the time required for animals to achieve preferred body temperatures (Clusella-Trullas et al. 2009; Forsman 1995; Heath 1975; Smith et al. 2016b). Conversely, a lighter coloured body would reduce solar energy absorption that could cause the body to overheat at high temperatures (Tattersall et al. 2006).

For shore skink colour patterns, we expected that variation in colour patterns across populations would show a signature of strong selection for crypsis because a detailed analysis of within-population variability showed a high association between the distribution of colour pattern types and vegetation cover (Baling et al. 2016). Other studies also had similar observations of colour patterns matching their microhabitat types (Chen et al. 2013; Farallo and Forstner 2012; Woolbright and Stewart 2008). However in this cross-population study, only one colour pattern type, *plain*, was found more often in backgrounds with a high proportion of rock (such as island sites). These rock microhabitats are generally smooth stone pebbles, approximately 10 to 20 cm in diameter (M. Baling unpublished data; Towns 1996). Both *plain* and rock background habitat are similar in that they lack any complexity in overall shape, diversity and density of markings (cf. *spot* and *midspot* patterns versus vegetation background). That is, *plain* is likely the better match in this uniform background compared to other colour patterns.

In contrast to *plain*, *midspot* varied with latitudinal gradient even when shore skink phylogeny was taken into account. Apart from its function as camouflage, body patterning on prey (e.g., longitudinal stripes) has been suggested to aid in escape behaviours (e.g., flicker fusion, motion dazzle; Allen et al. 2013; Cooper Jr. and Greenberg 1992; Endler 1978; Halperin et al. 2017; Hogan et al. 2016). At lower temperatures, such active behaviours require higher thermoregulatory effort to reach optimal temperature (e.g., basking longer or in more exposed habitats). Studies have also seen patterned morphs to have lower measures of crypsis, survival, and reproduction than uniform or darker individuals (Forsman and Shine 1995; Tanaka 2005, 2007, 2009; Woolbright and Stewart 2008). Forsman and Shine (1995) documented lower amounts of body patterning in garden skinks (*Lampropholis delicata*) as latitude increased, and have attributed it to increased predation risk. Therefore, we hypothesise that different colour pattern variants within a species is likely to have alternative anti-predation strategies that could influence their fitness across a large spatial scale.

The mainland populations of shore skinks were lighter brown-grey compared to island populations. Even though our measurements showed no significant difference in climate variables between island and mainland locations (e.g., monthly temperature, monthly maximum temperature, UVI), islands may still differ from the mainland at a microclimate level. Indeed, New Zealand islands are characterised as having a temperate marine climate, and islands have slightly higher temperatures, less cloud cover and less rain compared to the mainland (Daugherty et al. 1990; Meurk and Blaschke 1990). Therefore, further investigations incorporating climate variables at a smaller scale would be useful to confirm the association of body colouration to local island climate. Another possibility is that island and mainland sites may differ in predator density. All islands we surveyed were free from introduced mammalian predators, so these locations are likely to have a higher density of native predators (mainly birds) compared to mainland sites (e.g., Graham et al. 2013; Towns 2002, 2011). Higher predator pressure on islands may select for darker-coloured skinks to better match their background. Even though differences in predation pressure between islands and mainland still needs to be confirmed, support for the background-matching hypotheses comes from our study of translocated shore skinks (from mainland to an offshore island), where the population became darker, and more closely matched the backgrounds of the release site within one generation (Baling et al. 2016). The lower body brightness on islands observed in our current study is consistent with the former study, but also corresponds to "island syndrome" (Boback and Siefferman 2010; Uy and Vargas-Castro 2015). Here, genetic drift or founder effect could have some degree of influence on the skink populations on islands (Bittner and King 2003; King 2003), but it is likely to be weak at the larger scale in this comparative study (i.e. we have a high number of replicates for island vs. mainland populations, and we controlled for phylogeny).

In conclusion, our study demonstrates how different environmental factors have varying degrees of influence on the overall variation of colour and colour pattern diversity within a species. We mainly provided additional support to other studies on how thermal melanism can shape the intraspecific colour and colour pattern variation among populations. Although selection of colouration for camouflage may seem to have a higher immediate cost to survival than thermoregulation (Smith et al. 2016a), the ability to attain preferred body temperature faster is also strongly linked to reduced predation risk (e.g., less time exposed to predators while basking, higher sprint speed, faster growth; Castilla et al. 1999; Clusella-Trullas et al. 2007; Rowe et al. 2016). The degree of selective pressure on body colouration can also be location-specific; where local adaptation for crypsis (e.g., predator diversity, density or adaptive behaviour) or island syndrome (e.g., combination of microclimate, predator density, and genetic drift or founder effect) will be more prevalent in insular populations. High variation in colouration among wild populations is therefore a product of complex combination of selective pressures acting on the species.

5.6 Authors' contributions

MB: obtained permits, planned the experimental design, collected field data, statistical analyses and wrote the manuscript. DSF: contributed to experimental design, statistical analyses and editing the manuscript. JD: contributed in the experimental design, genetic analyses, statistical analyses and editing the manuscript.

5.7 References

Allen, W.L., Baddeley, R., Scott-Samuel, N.E., Cuthill, I.C., 2013. The evolution and function of pattern diversity in snakes. *Behavioral Ecology* 24: 1237-1250. doi:10.1093/beheco/art058

Azócar, D.L.M., Perotti, M.G., Bonino, M.F., Schulte II, J.A., Abdala, C.S., Cruz, F.B., 2014. Variation in body size and degree of melanism within a lizards clade: is it driven by latitudinal and climatic gradients? *Journal of Zoology* 295: 243-253. doi:10.1111/jzo.12193

Baird, T.A., Baird, T.D., Shine, R., 2013. Showing red: male coloration signals same-sex rivals in an Australian water dragon. *Herpetologica* 69: 436-444.

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. *Biological Conservation* 203: 298-305. doi:10.1016/j.biocon.2016.10.002

Bastiaans, E., Morinaga, G., Gamaliel, J., Gaytán, C., Marshall, J.C., Sinervo, B., 2013. Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behavioral Ecology* 24: 968-981. doi:10.1093/beheco/art010

Bittner, T.D., King, R.B., 2003. Gene flow and melanism in garter snakes revisited: a comparison of molecular markers and island vs. coalescent models. *Biological Journal of the Linnean Society* 79: 389-399. doi:10.1046/j.1095-8312.2003.00199.x

Boback, S.M., Siefferman, L.M., 2010. Variation in color and color change in island and mainland boa constrictor (*Boa constrictor*). *Journal of Herpetology* 44: 506-515. doi:10.1670/09-026.1

Bond, A.B., 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* 8: 489-514. doi:10.1146/annurev.ecolsys.38.091206.095728

Brakefield, P.M., 1990. Genetic drift and patterns of diversity among colour-polymorphic populations of the homopteran *Philaenus spumarious* in an island archipelago. *Biological Journal of the Linnean Society* 39: 219-237. doi:10.1111/j.1095-8312.1990.tb00513.x

Castella, B., Golay, J., Monney, J.-C., Golay, P., Mebert, K., Dubey, S., 2013. Melanism, body condition and elevational distribution in the asp viper. *Journal of Zoology* 290: 273-280. doi:10.1111/jzo.12037

Castilla, A.M., Van Damme, R., Bauwens, D., 1999. Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in Lacertid lizards. *Natura Croatica* 8: 253-274.

Chen, I.-P., Symonds, M.R.E., Melville, J., Stuart-Fox, D., 2013. Factors shaping the evolution of colour patterns in Australian agamid lizards (Agamidae): a comparative study. *Biological Journal of Linnean Society* 109: 101-112. doi:10.1111/bij.12030

Cichota, R., Snow, V.O., Tait, A.B., 2008. A functional evaluation of virtual climate station rainfall data. *New Zealand Journal of Agricultural Research* 51: 317-329. doi:10.1080/00288230809510463

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2007. Thermal melanism in ectotherms. *Journal of Thermal Biology* 32: 235-245. doi:10.1016/j.jtherbio.2007.01.013

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2009. Thermal benefits of melanism in cordylid lizards: a theoretical and field test. *Ecology* 90: 2297-2312.

Cooper Jr., W.E., Greenberg, N., 1992. Reptilian coloration and behavior, In Biology of the Reptilia: Hormones, brain and behavior. eds C. Gans, D. Crews. *The University of Chicago Press*, USA.

Cree, A., 1994. Low annual reproductive output in female reptiles from New Zealand. *New Zealand Journal of Zoology* 21: 351-372. doi:10.1080/03014223.1994.9518005

Daugherty, C.H., Towns, D.R., Atkinson, I.A.E., Gibbs, G.W., 1990. The significance of the biological resources of New Zealand islands for ecological restoration, In Ecological restoration of New Zealand islands. eds D.R. Towns, C.H. Daugherty, I.A.E. Atkinson, pp. 9-21. *Department of Conservation*, Wellington.

Endler, J.A., 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11: 319-364. doi:10.1007/978-1-4615-6956-5_5

Endler, J.A., 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of Linnean Society* 41: 315-352. doi:10.1111/j.1095-8312.1990.tb00839.x

Farallo, V.R., Forstner, M.R.J., 2012. Predation and the maintenance of color polymorphism in a habitat specialist squamate. *PLoS ONE* 7: e30316. doi:10.1371/journal.pone.0030316

Fischer, J., Lindenmayer, D.B., 2005. The sensitivity of lizards to elevation: A case study from south-eastern Australia. *Diversity and Distributions* 11: 225-233. doi:10.1111/j.1366-9516.2005.00139.x

Forsman, A., 1995. Heating rates and body temperature variation in melanistic and zigzag *Vipera berus*: does colour make a difference? *Annales Zoologici Fennici* 32: 365-374.

Forsman, A., Shine, R., 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of the Linnean Society* 55: 273-291. doi:10.1111/j.1095-8312.1995.tb01066.x

Garamszegi, L.Z. ed., 2014. Modern phylogenetic comparative methods and their application in evolutionary biology: concepts and practice. *Springer*, Heidelberg.

Graham, M., Veitch, D., Aguilar, G., Galbraith, M., 2013. Monitoring terrestrial bird populations on Tiritiri Matangi Island, Hauraki Gulf, New Zealand, 1987–2010. *New Zealand Journal of Ecology* 37: 359-369.

Halperin, T., Carmel, L., Hawlena, D., 2017. Movement correlates of lizards' dorsal pigmentation patterns. *Functional Ecology* 31: 370-376. doi:10.1111/1365-2435.12700

Hardy, G.S., 1977. The New Zealand Scincidae (Reptilia: Lacertilia); a taxanomic and zoogeographic study. *New Zealand Journal of Zoology* 4: 221-325. doi:10.1080/03014223.1977.9517956

Hare, K.M., Daugherty, C.H., Chapple, D.G., 2008. Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. *Molecular Phylogenetics and Evolution* 46: 303-315. doi:10.1016/j.ympev.2007.08.012

Harris, R., McQuillan, P., Hughes, L., 2012. Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper, *Phaulacridium vittatum*. *Journal of Biogeography* 39: 1450-1461. doi:10.1111/j.1365-2699.2012.02710.x

Heath, D.J., 1975. Colour, sunlight and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia* 19: 29-38. doi:10.1007/BF00377587

Hogan, B.G., Scott-Samuel, N.E., Cuthill, I.C., 2016. Contrast, contours and the confusion effect in dazzle camouflage. *Royal Society Open Science*. doi:10.1098/rsos.160180

King, R.B., 2003. Mendelian inheritance of melanism in the garter snake *Thamnophis sirtalis*. *Herpetologica* 59: 484-489. doi:10.1655/02-93

Kumar, S., Stecher, G., Tamura, K., 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870-1874. doi:10.1093/molbev/msw054

Marshall, K.L.A., Philpot, K.E., Damas-Moreira, I., Stevens, M., 2015. Intraspecific colour variation among lizards in distinct island environments enhances local camouflage. *PLoS ONE* 10: e0135241. doi:10.1371/journal.pone.0135241

McLean, C.A., Stuart-Fox, D., 2014. Geographic variation in animal colour polymorphisms and its role in speciation. *Biological Reviews* 89: 860-873. doi:10.1111/brv.12083

McLean, C.A., Stuart-Fox, D., Moussalli, A., 2015. Environment, but not genetic divergence, influences geographic variation in colour morph frequencies in a lizard. *BMC Evolutionary Biology* 15: 156. doi:10.1186/s12862-015-0442-x

Meurk, C.D., Blaschke, P.M., 1990. How representative can restored islands really be? An analysis of climo-edaphic environments in New Zealand, In Ecological restoration of New Zealand islands. eds D.R. Towns, C.H. Daugherty, I.A.E. Atkinson, pp. 52-72. *Department of Conservation*, Wellington.

Novosolov, M., Raia, P., Meiri, S., 2013. The island syndrome in lizards. *Global Ecology and Biogeography* 22: 184-191. doi:10.1111/j.1466-8238.2012.00791.x

Pérez i de Lanuza, G., Font, E., Carazo, P., 2013. Color-assortative mating in a color-polymorphic lacertid lizard. *Behavioral Ecology* 24: 273-279. doi:10.1093/beheco/ars164

Pincheira-Donoso, D., Hodgson, D.J., Tregenza, T., 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology* 8: 68. doi:10.1186/1471-2148-8-68

Rajabizadeh, M., Adriaens, D., Kaboli, M., Sarafraz, J., Ahmadi, M., 2015. Dorsal colour pattern variation in Eurasian mountain vipers (genus *Montivipera*): a trade-off between thermoregulation and crypsis. *Zoologischer Anzeiger* 257: 1-9. doi:10.1016/j.jcz.2015.03.006

Reguera, S., Zamora-Camacho, F.J., Moreno-Rueda, G., 2014. The lizard *Psammodromus algirus* (Squamata: Lacertidae) is darker at high altitudes. *Biological Journal of the Linnean Society* 112: 132-141. doi:10.1111/bij.12250

Rowe, J.W., Clark, D.L., Mortensen, R.A., Commissaris, C.V., Wittle, L.W., Tucker, J.K., 2016. Thermal and substrate color-induced melanization in laboratory reared red-eared sliders (*Trachemys scripta elegans*). *Journal of Thermal Biology* 61: 125-132. doi:10.1016/j.jtherbio.2016.09.005

Runemark, A., Hansson, B., Pafilis, P., Valakos, E.D., Svensson, E.I., 2010. Island biology and morphological divergence in the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC Evolutionary Biology* 10: 269. doi:10.1186/1471-2148-10-269

Schweiger, A.H., Beierkuhnlein, C., 2015. Size dependency in colour patterns of Western Palearctic carabids. *Ecography* 39: 846-857. doi:10.1111/ecog.01570

Sinervo, B., Lively, C.M., 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature Letter* 380: 240-243. doi:10.1038/380240a0

Smith, K.R., Cadena, V., Endler, J.A., Kearney, M.R., Porter, W.P., Stuart-Fox, D., 2016a. Color change for thermoregulation versus camouflage in free-ranging lizards. *The American Naturalist* 188: 668-678. doi:10.1086/688765

Smith, K.R., Cadena, V., Endler, J.A., Porter, W.P., Kearney, M.R., Stuart-Fox, D., 2016b. Colour change on different body regions provides thermal and signalling advantages in bearded dragon lizards. *Proceedings of the Royal Society B* 283: 20160626. doi:10.1098/rspb.2016.0626

Stevens, M., Merilaita, S., 2009. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B* 364: 423-427. doi:10.1098/rstb.2008.0217

Stevens, M., Merilaita, S. eds., 2011. Animal camouflage: mechanisms and function. *University Press*, Cambridge.

Stuart-Fox, D., Moussalli, A., 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London B* 364: 463-470. doi:0.1098/rstb.2008.0254

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65: 13-21. doi:10.1007/s00265-010-1037-6

Tanaka, K., 2005. Thermal aspect of melanistic and striped morphs of the snake *Elaphe quadrivirgata*. *Zoological Science* 22: 1173-1179. doi:10.2108/zsj.22.1173

Tanaka, K., 2007. Thermal biology of a colour-dimorphic snake, *Elaphe quadrivirgata*, in a montane forest: do melanistic snakes enjoy thermal advantages? *Biological Journal of the Linnean Society* 92: 309-322. doi:10.1111/j.1095-8312.2007.00849.x

Tanaka, K., 2009. Some like it cool? Intermorph comparison of preferred body temperature in a colour-dimorphic snake. *Animal Biology* 59: 31-39. doi:10.1163/157075609X417071

Tattersall, G.J., Eterovick, P.C., de Andrade, D.V., 2006. Tribute to R. G. Boutilier: Skin colour and body temperature changes in basking *Bokermannohyla alvarengai* (Bokermann 1956). *The Journal of Experimental Biology* 209: 1185-1196. doi:10.1242/jeb.02038

Towns, D.R., 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. *Pacific Conservation Biology* 2: 286-292. doi:10.1071/PC960286

Towns, D.R., 2002. Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *Journal of Biogeography* 29: 593-607. doi:10.1046/j.1365-2699.2002.00709.x

Towns, D.R., 2011. Eradications of vertebrate pests from islands around New Zealand: what have we delivered and what have we learned?, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 364-371. *IUCN*, Gland, Switzerland.

Uy, J.A.C., Vargas-Castro, L.E., 2015. Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneivenris* of the Solomon Islands. *The Auk* 132: 787-794. doi:10.1642/AUK-14-284.1

Woolbright, L.L., Stewart, M.M., 2008. Spatial and temporal variation in color pattern morphology in the tropical frog, *Eleutherodactylus coqui*. *Copeia* 2008: 431-437. doi:10.1643/CG-06-092

Zapletalová, L., Zapletai, M., Konvička, 2016. Habitat impact on ultraviolet reflectance in moths. *Environmental Entomology* 45: 1300-1305. doi:10.1093/ee/nvw097

CHAPTER 6

DISCUSSION

6 DISCUSSION

I investigated the functional significance of the colouration of a prey species, the shore skink (*Oligosoma smithi*), and the selective processes that maintain its variation within and between populations. In particular, my research focused on the function of colour and colour patterns for crypsis (background-matching) in heterogeneous habitats. I also looked at the potential trade-off between the function for crypsis and two other functions that can affect overall variation:thermoregulation and intraspecific signalling.

6.1 Population colouration in a continuous heterogeneous environment

The degree of disparity between adjacent habitat patches can influence prey populations to either specialise their colouration to match one of the habitat patches, or to become generalists where colour and colour patterns represent a compromise between several habitat patches (Merilaita and Stevens 2011). Here, for the first objective of my thesis, I investigated two external factors that can influence the degree of background-matching: visual habitat characteristics and predator behaviour. I found evidence that variation in colouration of a wild shore skinks population within a continuous spatial vegetation gradient was maintained by selection for background-matching (Chapter 3) and apostatic selection (Chapter 4). These two selective forces are non-mutually exclusive, and differentiating them in natural systems can be challenging (Bond 2007; Bond and Kamil 2006).

6.1.1 Habitat structure, colour and complexity

In Chapter 3, I found that the frequency of body colouration of shore skinks at Tāwharanui Regional Park strongly co-varied with a vegetation gradient. But background-matching was imperfect for colours (i.e. skinks were darker on average than the background at low vegetation cover, and lighter at high vegetation cover), while all four colour pattern types were widely distributed throughout the site. This imperfect matching in colour and colour patterns of the population across spatial habitat supports the views from theoretical modelling and studies using virtual environments for a compromised background-matching strategy (Houston et al. 2007; Merilaita and Dimitrova 2014; Merilaita et al. 2001; Merilaita et al. 1999; Toh and Todd 2017).

6.1.2 Predator behaviour

Despite a clear correlation with skink colouration and background (Chapter 3), certain colour pattern types persisted across the study site, even when they are apparently mismatched with their immediate backgrounds (e.g., higher occurrence of *midspot* than *plain* types at areas of low vegetation cover). The field experiment in Chapter 4 revealed that resident predators at Tāwharanui were twice as likely to attack the more common patterned variants (e,g, *midspot*, *midplain*) than the more rare unpatterned variant, regardless of background type. This result is consistent with apostatic selection, where predators use cognitive search images to find prey, and thus have more success discerning and attacking the most abundant prey types in the population (Bond 2007; Karpestam et al. 2014; Plaisted and Mackintosh 1995; Troscianko et al. 2013).

However, exactly how apostatic selection occurs in the field is often not clear, with many experimental studies describing it as predators targeting only one prey variant at a time (i.e. the most common variant type). As a result, other variants are ignored and therefore, survive in the environment (Bond 2007; Dukas and Kamil 2001; Farkas and Montejo-Kovacevich 2014; Raymond 1984). But there other studies observed predators attacking the most commonly encountered variant as well as other similarly-looking variants. That is, only rare variants distinctly different to the others were overlooked (Allen 1988; Gorbunova 2017; Raymond 1984; Reid and Shettleworth 1992). A simulation study (Bond and Kamil 2002) suggests that the level of crypsis in a prey population can influence how accurately different variants can be detected by predators. The authors found that in a population with low crypsis, all variants were equally detected (i.e. attacked) by predators, while atypical (i.e. distinct) variants were attack the least compared to other variants in a highly cryptic populations. I showed that in the shore skink population at Tāwharanui, it was the rare variant that was attacked the least compared to the other colour patterns, and distinctive difference between these colour patterns was the presence of body patterns, i.e. rare variant (*plain*) did not have any patterning compared to others (i.e. *midplain*, *spot* and *midspot*). Therefore, my field experiment results fitted within the high crypsis populations in the simulations (Bond and Kamil 2002).

6.2 Population colouration in a disjunct heterogeneous habitat

My second thesis objective was to explore how population colouration responds when exposed to a change in habitat visual characteristics. In Chapter 2, I monitored a population of shore skinks that had been translocated from Tāwharanui to a nearby island site consisting of two disjunct habitat types. One year after translocation, the surviving population showed significant changes in colour (i.e. they were darker and less intense in colour on average), and had a lower colour pattern diversity compared to the founder and source populations. Interestingly, body colouration observed in this translocated population was comparable to most other naturally-occurring island populations of shore skinks because other island populations typically are darker and have less colour pattern diversity compared to mainland populations (McCallum 1980, 1982; Towns 1972; Towns and Hayward 1973; also see Chapter 5). Darker colouration, or melanism, in island populations is one of the characteristics for "island syndrome". Island syndrome predicts that island populations have higher population density, are larger in size, have fewer offspring, and have darker colouration compared to their mainland counterparts (Boback and Siefferman 2010; Doutrelant et al. 2016; Novosolov et al. 2013; Runemark et al. 2010).

As has been predicted for distinctly disjunct habitat patches (Houston et al. 2007; Merilaita and Dimitrova 2014; Merilaita et al. 2001; Merilaita et al. 1999), the translocated population of shore skinks were more matched in colour with one background type (i.e. bare rocky stone) over the other (highly vegetated sand). This mismatch in skink colours suggests either a limitation in individual phenotypic flexibility such that individuals can not alter their colour enough to match their immediate background over time (but see Chapter 3), or that the range of variants within the founder population was not sufficient to response to matching of the sand-vegetation substrate at the island (Edelaar et al. 2017; Forsman 2014; Morgans and Ord 2013; Stevens 2016). Additionally, the high amount of vegetation can also provide a means of visual obstruction for predators, so accurate background-matching may not have been as important for skinks' survival in the sand-vegetation substrate.

The documentation of changes in overall colouration in this translocated population highlights the potential implications of translocating cryptic prey species to distinctly different habitats. I emphasised the importance of careful consideration by managers when selecting release sites (habitat characteristics), and when choosing founder individuals to ensure successful translocation and long-term population sustainability (Baling et al. 2016). This is particularly significant as conservation translocations become more common for species conservation management (e.g., Armstrong et al. 2015; Ewen et al. 2012).

6.3 Conflicting signals: crypsis versus intraspecific signalling

Visual intraspecific signalling generally promotes conspicuous colouration, which can incur survival costs because conspicuousness can potentially override other functions for colouration such as crypsis (Keren-Rotem et al. 2016; Outomuro et al. 2016). My third thesis objective was to investigate whether there is evidence of a trade-off between colouration for crypsis and intraspecific signalling across a continuous habitat gradient and between biological seasons (Chapter 3). However, I found no evidence that crypsis (background-matching) of shore skinks across vegetation cover was strongly affected by changes of seasons, despite the population showing morphological colour change between breeding and non-breeding seasons.

Nevertheless, the hue and saturation of shore skinks' colours did vary between seasons, from having an intense green-grey dorsal region during the nonbreeding seasons, less intense yellow-grey in the mating seasons, and brown-grey in birthing seasons. Moreover, this temporal variation in dorsal hue did not correspond to seasonal changes in the habitat background colouration. Interestingly, the within-population hue values observed between seasons were similar to the geographical colour variation observed between populations in Chapter 5. In that study, the 17 populations of shore skinks were on average more green-grey dorsally at sites with lower maximum monthly temperatures, while populations at sites of high maximum monthly temperatures were brown-grey (see section "Conflicting signals: crypsis versus thermoregulation" below). So one interesting possibility is that temperature (i.e. thermoregulation) may affect seasonal colour variation at Tāwharanui, because non-breeding seasons for shore skinks typically occur during the cool Austral winter months, mating season during spring, and birthing season in the warm summers.

The lack of change in the degree of background-matching for shore skinks across both the habitat gradient and seasons was likely due to the presence of body colour partitioning, with more conspicuous colouration (i.e. less matched to background) occurring in ventral regions (e.g., Chen et al. 2012; Klomp et al. 2016; Marshall and Stevens 2014; Pérez i de Lanuza and Font 2015; Stuart-Fox et al. 2004). This ventral region also showed differences in colour between age classes (juveniles and adults) and sexes, suggesting an intraspecific signalling function. This study is one of the few studies that have documented the colouration for crypsis and intraspecific signalling in a wild population over both biological seasons and across a spatial habitat gradient.

6.4 Conflicting signals: crypsis versus thermoregulation

My last objective was to evaluate whether geographical colouration of shore skinks vary according to expected trends predicted by two alternative functions: crypsis or thermoregulation. In Chapter 5, I found that the variation in colour across 17 shore skink populations showed patterns consistent with both a thermal melanism function and island syndrome. Population body brightness increased at sites with higher maximum monthly temperatures, supporting the views of other geographical studies on thermal melanism (Azócar et al. 2014; Clusella-Trullas et al. 2007; Harris et al. 2012; Rajabizadeh et al. 2015). Similarly, body hue also co-varied with maximum monthly temperature, where skinks were more brown-grey at sites with higher maximum monthly temperatures.

Additionally, colour pattern diversity varied with latitude. Particularly after controlling for phylogeny, the occurrence of one colour pattern type, *midspot*, decreased as latitude increased. A latitudinal trend is not an uncommon observation for colour polymorphisms, but alternate hypotheses on why colour pattern diversity decreases across latitude is limited (Chapple et al. 2008; Cox and Rabosky 2013; Forsman and Åberg 2008; Forsman et al. 2008; Forsman et al. 2016; Forsman and Shine 1995; McLean and Stuart-Fox 2014). Studies have shown that colour pattern variants can differ in thermoregulatory strategies (e.g., plain darker individual can absorb infrared better than patterned individuals; Castella et al. 2013; Clusella-Trullas et al. 2009; Forsman 1995; Heath 1975) and behavioural traits (e.g., prey with stripes are more active; Allen et al. 2013; Capula and Luiselli 1994; Halperin et al. 2017; Rojas et al. 2014a), so I hypothesise that thermoregulation requirements may play a part in the reduced colour pattern diversity with increasing latitude.

Lastly, the statistical power provided by a high number of island and mainland replicates in this study was large enough to resolve an island effect on colouration (independently of climate or latitude), where skinks were darker and had different colour pattern diversity (i.e. less *midspot* and more *plain*) on islands compared to mainland populations. The increased melanism and reduced colour pattern diversity in this study, and also the translocated shore skink population study in Chapter 2 is consistent with "island syndrome" (Boback and Siefferman 2010; Novosolov et al. 2013; Uy et al. 2016; Uy and Vargas-Castro 2015). However, it is still unclear from this study what the selective processes are that are driving this island syndrome effect on shore skink colouration. Thermal melanism does not seem to apply in this circumstance because large-scale environmental conditions (e.g., monthly maximum temperature, UV index, solar radiation) were not significantly different between island and mainland. However, islands and mainland sites could still differ at a microclimate level, which can strongly influence effective thermoregulation in skinks (Daugherty et al. 1990; Sagonas et al. 2013). The darker colours in island skinks might also result from stronger selection for crypsis, if (avian) predation pressure is higher on islands than the mainland (Graham et al. 2013; Towns 2002, 2011).

6.5 Future research directions

6.5.1 The ability of prey to adapt to the environment

Aspects that stood out from the outcome of this research are a general lack of knowledge on the prey's behaviour and general biology. Such knowledge is necessary to provide further insight into variation in the colouration of shore skinks. In particular, this research suggests the possibility that shore skink variants might have different anti-predator behaviour and thermoregulatory strategies that could affect the maintenance of each variant within the environment. Many studies that use virtual prey or theoretical modelling do not necessarily take these possibilities into account, but instead assume that all colour pattern variants have similar biological characteristics (e.g., Bond and Kamil 1998, 2006; Houston et al. 2007; Nilsson and Ripa 2010;cf. Merilaita et al. 1999).

One question about the behavioural traits of prey in need of increased research is: do prey choose specific backgrounds to optimise their background-matching (Cooper Jr. and Sherbrooke 2012; Gilis 1982; Kang et al. 2013; Karpestam et al. 2012; Merilaita et al. 1999)? Despite the obvious adaptive value of this behaviour, it has only recently generated interest within visual camouflage researchers (e.g., Karpestam et al. 2012; Lovell et al. 2013; Marshall et al. 2016). Experimental studies on crypsis-related behaviour have generally looked at prey choice between two contrasting background types (e.g. light vs. dark), but it is still unknown if colour pattern variants (in a non-physiological colour changing species) will choose to associate with backgrounds based on pattern complexity. Additionally, does background choice differ between variants that are generalists versus specialists in background-matching? Specifically, would specialists choose backgrounds that will accurately match their body colouration, whereas generalists may be less biased in their choice of backgrounds?

Additionally, such choice experiments could be coupled with investigations into alternative anti-predator strategies among colour pattern variants. Particular colour pattern types have been associated with more active foraging and exhibiting rapid escapes (e.g., longitudinal stripes, plain), while other pattern types to be more sedentary (e.g., speckled, blotched patterns) (Allen et al. 2013; Halperin et al. 2017). These differences in behaviours can potentially affect their crypsis and spatial distribution within a heterogeneous habitat. Furthermore, is there plasticity in these prey anti-predator behaviours when exposed to non-camouflaging backgrounds (i.e. fleeing rather than freezing when not cryptic)?

Colour pattern variants are also expected to have different thermoregulatory behavioural strategies that can confer selective advantages at different habitat types. Effective thermoregulation, particularly in ectotherms, is critical for maintenance of other biological processes and behaviours (e.g., digestion, reproduction, mobility). However, studies that link the rate of attaining preferred body temperature (for thermoregulation) to the degree of mobility or escape behaviour (Allen et al. 2013; Capula and Luiselli 1994; Rojas et al. 2014a) and overall fitness (Forsman and Shine 1995; Tanaka 2005, 2007, 2009; Woolbright and Stewart 2008) are lacking.

6.5.2 Predator selection

Many predictions on the effect of predator selection on prey colouration have been derived from theoretical modelling, and laboratory studies of captive or virtual environments that use captive birds or humans as predators (e.g., Bond 2007; Karpestam et al. 2014; Merilaita 2006; Merilaita and Dimitrova 2014; Merilaita and Ruxton 2009; Troscianko et al. 2013; Troscianko et al. 2009). There is therefore a need for more studies testing these predictions in natural systems. My research showed that selective attacks by predators on certain colour pattern variants were consistent with the maintenance of colour variation via crypsis and apostatic selection within a continuous heterogeneous habitat (Bond and Kamil 2006). This experimental approach can be expanded to compare the effect of predator selection on prey colour patterns on several aspects: 1) the degree of disparity in habitat patches (continuous vs. disjunct heterogeneous habitats) to test if apostatic selection is stronger in populations within continuous complex habitats compared to disjunct habitat patches (Bond and Kamil 2002, 2006); 2) different predator densities (e.g., island vs. mainland) to determine if higher predator density reduces strength of apostatic selection and also variation in colour pattern variants (Merilaita 2006); and 3) familiarity with prey (e.g., naturally occurring prey population vs. translocated population) to investigate the effect of predator prior exposure to prey on prey detection (Bond 2007; Troscianko et al. 2013).

An additional surprise from the field experiment (Chapter 4) was that body brightness contrast, a common visual cue for predators in other studies (Defrize et al. 2010; Endler 1978; Forsman et al. 2011; Kettlewell 1955; Stevens et al. 2013; Stuart-Fox et al. 2003; Troscianko et al. 2016), was not a prominent factor that elicited predator attacks in shore skinks. I posed one possibility, that this cue is unreliable in open habitats such as a coastal sand dune at Tāwharanui because highly intense lighting condition may affect prey colouration (particularly when body saturation is low) and predators' visual acuity (Endler 1978; Théry 2006). Although there are studies showing lighting conditions affects intraspecific signalling (e.g., Cole and Endler 2016; Gomez and Théry 2004; Klomp et al. 2017; Moyen et al. 2006), visual warning signals (Rojas et al. 2014b) and predator camouflage (Tate et al. 2016), how this affects predation risk for different prey colouration, particularly in bright open habitats, deserves further attention.

6.6 Conclusions

My research has demonstrated how a continuous heterogeneous habitat promotes high intraspecific variance in colouration in a generalist cryptic species within and between populations. The observed patterns for colouration within a population were consistent with both natural selection for background-matching and apostatic selection. When a subpopulation was translocated from a continuous habitat gradient to a disjunct two-patch habitat type, the population responded with reduced colour and colour pattern diversity, with high matching in body colours to only one patch type. Shore skinks showed typical colour division between the body regions, where the ventral regions exhibited age-dependence and sexual dichromatism. The population also showed morphological colour change between non-breeding and breeding seasons, but overall population crypsis across the spatial habitat gradient did not seem to be negatively affected by seasonal variation. Finally, geographic variation in shore skink colouration was related to both thermal melanism and crypsis. There was also a significant island effect on colour patterns for shore skinks, which could be linked to local adaptation and non-selective forces (island syndrome). My thesis provides new insights into how dramatic colouration and patterning of a prey species can be maintained by multiple selective pressures for various biological functions. This work also provides the first quantitative research on colouration in New Zealand reptiles.

6.7 References

Allen, J.A., 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society B* 319: 485-503. doi:10.1098/rstb.1988.0061

Allen, W.L., Baddeley, R., Scott-Samuel, N.E., Cuthill, I.C., 2013. The evolution and function of pattern diversity in snakes. *Behavioral Ecology* 24: 1237-1250. doi:10.1093/beheco/art058

Armstrong, D.P., Hayward, M.W., Moro, D., Seddon, P.J. eds., 2015. Advances in reintroduction biology of Australian and New Zealand fauna. *CSIRO Publishing*, Victoria, Australia.

Azócar, D.L.M., Perotti, M.G., Bonino, M.F., Schulte II, J.A., Abdala, C.S., Cruz, F.B., 2014. Variation in body size and degree of melanism within a lizards clade: is it driven by latitudinal and climatic gradients? *Journal of Zoology* 295: 243-253. doi:10.1111/jzo.12193

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. *Biological Conservation* 203: 298-305. doi:10.1016/j.biocon.2016.10.002

Boback, S.M., Siefferman, L.M., 2010. Variation in color and color change in island and mainland boa constrictor (*Boa constrictor*). *Journal of Herpetology* 44: 506-515. doi:10.1670/09-026.1

Bond, A.B., 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics* 8: 489-514. doi:10.1146/annurev.ecolsys.38.091206.095728

Bond, A.B., Kamil, A.C., 1998. Apostatic selection by blue jays produce balanced polymorphism in virtual prey. *Letters to Nature* 395: 594-596. doi:10.1038/26961

Bond, A.B., Kamil, A.C., 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* 415: 609-613. doi:10.1038/415609a

Bond, A.B., Kamil, A.C., 2006. Spatial heterogeneity, predator cognition, and the evolution fo color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences* 103: 3214-3219. doi:10.1073/pnas.0509963103

Capula, M., Luiselli, L., 1994. Reproductive strategies in alpine adders, *Vipera berus*. The black females bear more often. *Acta Oecologica* 15: 207-214.

Castella, B., Golay, J., Monney, J.-C., Golay, P., Mebert, K., Dubey, S., 2013. Melanism, body condition and elevational distribution in the asp viper. *Journal of Zoology* 290: 273-280. doi:10.1111/jzo.12037

Chapple, D.G., Hutchinson, M.N., Maryan, B., Plivelich, M., Moore, J.A., Keogh, J.S., 2008. Evolution and maintenance of colour pattern polymorphism in *Liopholis* (Squamata : Scincidae). *Australian Journal of Zoology* 56: 103-115. doi:10.1071/zo08040

Chen, I.-P., Stuart-Fox, D., Hugall, A.F., Symonds, M.R.E., 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution* 66: 3605-3614. doi:10.1111/j.1558-5646.2012.01698.x

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2007. Thermal melanism in ectotherms. *Journal of Thermal Biology* 32: 235-245. doi:10.1016/j.jtherbio.2007.01.013

Clusella-Trullas, S., Van Wyk, J.H., Spotila, J.R., 2009. Thermal benefits of melanism in cordylid lizards: a theoretical and field test. *Ecology* 90: 2297-2312.

Cole, G.L., Endler, J.A., 2016. Male courtship decisions are influenced by light environment and female receptivity. *Proceedings of the Royal Society B* 283: 20160861. doi:10.1098/rspb.2016.0861

Cooper Jr., W.E., Sherbrooke, W.C., 2012. Choosing between a rock and a hard place: camouflage in the round-tailed horned lizard *Pherynosoma modestum*. *Current Zoology* 58: 541-548. doi:10.1093/czoolo/58.4.543

Cox, C.L., Rabosky, A.R.D., 2013. Spatial and temporal drivers of phenotypic diversity in polymorphic snakes. *The American Naturalist* 182: E40-E57. doi:0.1086/670988

Daugherty, C.H., Towns, D.R., Atkinson, I.A.E., Gibbs, G.W., 1990. The significance of the biological resources of New Zealand islands for ecological restoration, In Ecological restoration of New Zealand islands. eds D.R. Towns, C.H. Daugherty, I.A.E. Atkinson, pp. 9-21. *Department of Conservation*, Wellington.

Defrize, J., Théry, M., Casas, J., 2010. Background colour matching by a crab spider in the field: a community sensory ecology perspective. *The Journal of Experimental Biology* 213: 1425-1435. doi:10.1242/jeb.039743

Doutrelant, C., Paquet, M., Renoult, J.P., Grégoire, A., Crochet, P.-A., Covas, R., 2016. Worldwide patterns of bird colouration on islands. *Ecology Letters* 19: 537-545. doi:10.1111/ele.12588

Dukas, R., Kamil, A.C., 2001. Limited attention: the constraint underlying search image. *Behavioral Ecology* 12: 192-199. doi:10.1093/beheco/12.2.192

Edelaar, P., Baños-Villalba, A., Escudero, G., Rodríguez-Bernal, C., 2017. Background colour matching increases with risk of predation in a colour-changing grasshopper. *Behavioral Ecology*. doi:10.1093/beheco/arx016

Endler, J.A., 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11: 319-364. doi:10.1007/978-1-4615-6956-5_5

Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J. eds., 2012. Reintroduction Biology: integrating science and management. *Wiley-Blackwell*, UK.

Farkas, T.E., Montejo-Kovacevich, G., 2014. Density-dependent selection closes an eco-evolutionary feedback loop in the stick insect *Timema cristinae*. *Biology Letters* 10: 20140896. doi:10.1098/rsbl.2014.0896

Forsman, A., 1995. Heating rates and body temperature variation in melanistic and zigzag *Vipera berus*: does colour make a difference? . *Annales Zoologici Fennici* 32: 365-374.

Forsman, A., 2014. Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity* 115: 276-284. doi:10.1038/hdy.2014.92

Forsman, A., Åberg, V., 2008. Variable coloration is associated with more northerly geographic range limits and larger range sizes in North American lizards and snakes. *Evolutionary Ecology Research* 10: 1025-1036.

Forsman, A., Ahnesjö, J., Caesar, S., Karlsson, M., 2008. A model of ecological and evolutionary consequences of color polymorphism *Ecology* 89: 34-40. doi:10.1890/07-0572.1

Forsman, A., Betzholtz, P.-E., Franzén, M., 2016. Faster poleward range shifts in moths with more variable colour patterns. *Scientific Reports* 6: 36265. doi:10.1038/srep36265

Forsman, A., Karisson, M., Wennersten, L., Johansson, J., Karpestam, E., 2011. Rapid evolution of fire melanism in replicated populations of pygmy grasshoppers. *Evolution* 65: 2530-2540. doi:10.1111/j.1558-5646.2011.01324.x

Forsman, A., Shine, R., 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of the Linnean Society* 55: 273-291. doi:10.1111/j.1095-8312.1995.tb01066.x

Gilis, J.E., 1982. Substrate color-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn & Hebard). *Animal Behaviour* 30: 113-116. doi:10.1016/S0003-3472(82)80244-3

Gomez, D., Théry, M., 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. *Ecology Letters* 7: 279-284. doi:10.1111/j.1461-0248.2004.00584.x

Gorbunova, E.S., 2017. Perceptual similarity in visual search for multiple targets. *Acta Psychologica* 173: 46-54. doi:10.1016/j.actpsy.2016.11.010

Graham, M., Veitch, D., Aguilar, G., Galbraith, M., 2013. Monitoring terrestrial bird populations on Tiritiri Matangi Island, Hauraki Gulf, New Zealand, 1987–2010. *New Zealand Journal of Ecology* 37: 359-369.

Halperin, T., Carmel, L., Hawlena, D., 2017. Movement correlates of lizards' dorsal pigmentation patterns. *Functional Ecology* 31: 370-376. doi:10.1111/1365-2435.12700

Harris, R., McQuillan, P., Hughes, L., 2012. Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper, *Phaulacridium vittatum*. *Journal of Biogeography* 39: 1450-1461. doi:10.1111/j.1365-2699.2012.02710.x

Heath, D.J., 1975. Colour, sunlight and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia* 19: 29-38. doi:10.1007/BF00377587

Houston, A.I., Stevens, M., Cuthill, I.C., 2007. Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral Ecology* 18: 769-775. doi:10.1093/beheco/arm039

Kang, C.-K., Moon, J.-Y., Lee, S.-I., Jablonski, P.G., 2013. Moths on tree trunks seek out more cryptic positions when their current crypticity is low. *Animal Behaviour* 86: 587-594. doi:10.1016/j.anbehav.2013.06.014

Karpestam, E., Merilaita, S., Foraman, A., 2014. Natural levels of colour polymorphism reduce performance of visual predators searching for camouflaged prey. *Biological Journal of the Linnean Society* 112: 546-555. doi:10.1111/bij.12276

Karpestam, E., Wennersten, L., Forsman, A., 2012. Matching habitat choice by experimentally mismatches phenotypes. *Evolutionary Ecology* 26: 893-907. doi:10.1007/s10682-011-9530-6

Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A., Geffen, E., 2016. Male preference for sexual signalling over crypsis is associated with alternative mating tactics. *Animal Behaviour* 117: 43-49. doi:10.1016/j.anbehav.2016.04.021

Kettlewell, H.B.D., 1955. Selection experiments on industrial melanism in the *Lepidoptera*. *Heredity* 9: 323-342. doi:10.1038/hdy.1955.36

Klomp, D.A., Ord, T.J., Das, I., Diesmos, A., Ahmad, N., Stuart-Fox, D., 2016. Ornament size and colour as alternative strategies for effective communication in gliding lizards. *Journal of Evolutionary Biology* 29: 1689-1700. doi:10.1111/jeb.12908

Klomp, D.A., Stuart-Fox, D., Das, I., Ord, T.J., 2017. Gliding lizards use the position of the sun to enhance social display. *Biology Letters* 13. doi:10.1098/rsbl.2016.0979

Lovell, P.G., Ruxton, G.D., Langridge, K.V., Spencer, K.A., 2013. Egg-laying substrate selection for optimal camouflage by quail. *Current Biology*. doi:dx.doi.org/10.1016/j.cub.2012.12.031

Marshall, K.L.A., Philpot, K.E., Stevens, M., 2016. Microhabitat choice in island lizards enhances camouflage against avian predators. *Scientific Reports* 6: 19815. doi:10.1038/srep19815

Marshall, K.L.A., Stevens, M., 2014. Wall lizards display conspicuous signals to conspecifics and reduce detection by avian predators. *Behavioral Ecology* 25: 1325-1337. doi:10.1093/beheco/aru126

McCallum, J., 1980. Reptiles of the northern Mokohinau Group. *Tane* 26: 53-60.

McCallum, J., 1982. Reptiles of the Hauraki Gulf, New Zealand. *Herpetofauna* 10: 35-41.

McLean, C.A., Stuart-Fox, D., 2014. Geographic variation in animal colour polymorphisms and its role in speciation. *Biological Reviews* 89: 860-873. doi:10.1111/brv.12083

Merilaita, S., 2006. Frequency-dependent predation and maintenance of polymorphism. *Journal of Evolutionary Biology* 19: 2022-2030. doi:10.1111/j.1420-9101.2006.01137.x

Merilaita, S., Dimitrova, M., 2014. Accuracy of background matching and prey detection: predation by blue tits indicates intense selection for highly matching prey colour pattern. *Functional Ecology* 28: 1208-1215. doi:10.1111/1365-2435.12248

Merilaita, S., Lyytinen, A., Mappes, J., 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B* 268: 1925-1929. doi:10.1098/rspb.2001.1747

Merilaita, S., Ruxton, G.D., 2009. Optimal apostatic selection: how should predators adjust to variation in prey frequencies? *Animal Behaviour* 77: 239-245. doi:10.1016/j.anbehav.2008.09.032

Merilaita, S., Stevens, M., 2011. Crypsis through background matching, In Animal camouflage: mechanisms and function. eds M. Stevens, S. Merilaita, pp. 17-33. *University Press*, Cambridge, UK.

Merilaita, S., Tuomi, J., Jormalainen, V., 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* 67: 151-161. doi:10.1111/j.1095-8312.1999.tb01858.x

Morgans, C.L., Ord, T.J., 2013. Natural selection in novel environments: predation selects for background matching in the body colour of a land fish. *Animal Behaviour* 86: 1241–1249. doi:10.1016/j.anbehav.2013.09.027

Moyen, F., Gomez, D., Doutrelant, C., Pierson, J., Théry, M., 2006. Interacting effects of signalling behaviour, ambient light and plumage colour in a temperate bird, the blue tit *Parus caeruleus*. *Revue D Ecologie-La Terre Et La Vie* 61: 367-382.

Nilsson, J., Ripa, J., 2010. The origin of polymorphic crypsis in a heterogenous environment. *Evolution* 64: 1386-1394. doi:10.1111/j.1558-5646.2009.00918.x

Novosolov, M., Raia, P., Meiri, S., 2013. The island syndrome in lizards. *Global Ecology and Biogeography* 22: 184-191. doi:10.1111/j.1466-8238.2012.00791.x

Outomuro, D., Söderquist, L., Johansson, F., Ödeen, A., Nordström, K., 2016. The price of looking sexy: visual ecology of a three level predator-prey system. *Functional Ecology*. doi:10.1111/1365-2435.12769

Pérez i de Lanuza, G., Font, E., 2015. Differences in conspicuousness between alternative color morphs in a polychromatic lizard. *Behavioral Ecology* 26: 1432-1446. doi:10.1093/beheco/arv075

Plaisted, K.C., Mackintosh, N.J., 1995. Visual search for cryptic stimuli in pigeons: implications for the search image and search rate hypotheses. *Animal Behaviour* 50: 1219-1232. doi:10.1016/0003-3472(95)80039-5

Rajabizadeh, M., Adriaens, D., Kaboli, M., Sarafraz, J., Ahmadi, M., 2015. Dorsal colour pattern variation in Eurasian mountain vipers (genus *Montivipera*): a trade-off between thermoregulation and crypsis. *Zoologischer Anzeiger* 257: 1-9. doi:10.1016/j.jcz.2015.03.006

Raymond, D.L., 1984. Wild birds prefer the familiar striped and unstriped artificial prey. *Biological Journal of Linnean Society* 23: 229-235. doi:10.1111/j.1095-8312.1984.tb00141.x

Reid, P.J., Shettleworth, S.J., 1992. Detection of cryptic pey: search image or search rate? *Journal of Experimental Psychology* 18: 273-286. doi:10.1037/0097-7403.18.3.273

Rojas, B., Devillechabrolle, J., Endler, J.A., 2014a. Paradox lost: variable colour-pattern geometry is associated wih differences in movement in aposematic frogs. *Biology Letters* 10: 20140193. doi:10.1098/rsbl.2014.0193

Rojas, B., Rautiala, P., Mappes, J., 2014b. Differential detectability of polymorphic warning signals under varying light environments. *Behavioural Processes* 109: 164-172. doi:10.1016/j.beproc.2014.08.014

Runemark, A., Hansson, B., Pafilis, P., Valakos, E.D., Svensson, E.I., 2010. Island biology and morphological divergence in the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC Evolutionary Biology* 10: 269. doi:10.1186/1471-2148-10-269

Sagonas, K., Valakos, E.D., Pafilis, P., 2013. The impact of insularity on the thermoregulation of a Mediterranean lizard. *Journal of Thermal Biology* 38: 480-486. doi:10.1016/j.jtherbio.2013.08.004

Stevens, M., 2016. Color change, phenotypic plasticity and camouflage. *Frontiers in Ecology and the Environment* 4: 51. doi:10.3389/fevo.2016.00051

Stevens, M., Rong, C.P., Todd, P.A., 2013. Colour change and camouflage in the horned ghost crab *Ocypode ceraphthalamus*. *Biological Journal of Linnean Society* 109: 257-270. doi:10.1111/bij.12039

Stuart-Fox, D.M., Moussalli, A., Johnston, G.R., Owens, I.P.F., 2004. Evolution of color variation in dragon lizards: Quantitative tests of the role of crypsis and local adaptation. *Evolution* 58: 1549-1559. doi:10.1554/03-448

Stuart-Fox, D.M., Moussalli, A., Marshall, N.J., Owens, I.P.F., 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour* 66: 541-550. doi:10.1006/anbe.2003.2235

Tanaka, K., 2005. Thermal aspect of melanistic and striped morphs of the snake *Elaphe quadrivirgata*. *Zoological Science* 22: 1173-1179. doi:10.2108/zsj.22.1173

Tanaka, K., 2007. Thermal biology of a colour-dimorphic snake, *Elaphe quadrivirgata*, in a montane forest: do melanistic snakes enjoy thermal advantages? *Biological Journal of the Linnean Society* 92: 309-322. doi:10.1111/j.1095-8312.2007.00849.x

Tanaka, K., 2009. Some like it cool? Intermorph comparison of preferred body temperature in a colour-dimorphic snake. *Animal Biology* 59: 31-39. doi:10.1163/157075609X417071

Tate, G.J., Bishop, J.M., Amar, A., 2016. Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morph in a polymorphic bird. *Ecology Letters* 19: 679-686. doi:10.1111/ele.12606

Théry, M., 2006. Effects of light environment on color communication, In Bird coloration: mechanisms and measurements. eds G.E. Hill, K.J. McGraw, pp. 148-173. *President and Fellows of Harvard College*, USA.

Toh, K.B., Todd, P., 2017. Camouflage that is spot on! Optimization of spot size in prey-background matching. *Evolutionary Ecology*. doi:10.1007/s10682-017-9886-3

Towns, D.R., 1972. The reptiles of Mercury Island. *Tane* 18: 95-106.

Towns, D.R., 2002. Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *Journal of Biogeography* 29: 593-607. doi:10.1046/j.1365-2699.2002.00709.x

Towns, D.R., 2011. Eradications of vertebrate pests from islands around New Zealand: what have we delivered and what have we learned?, In Island invasives: eradication and management. eds C.R. Veitch, M.N. Clout, D.R. Towns, pp. 364-371. *IUCN*, Gland, Switzerland.

Towns, D.R., Hayward, B.W., 1973. Reptiles of Aldermen Islands. *Tane* 19: 93-104.

Troscianko, J., Lown, A.E., Hughes, A.E., Stevens, M., 2013. Defeating crypsis: detection and learning of camouflage strategies. *PLoS ONE* 8: e73733. doi:10.1371/journal.pone.0073733

Troscianko, J., Wilson-Aggarwal, J., Stevens, M., Spottiswoode, C.N., 2016. Camouflage predicts survival in ground-nesting birds. *Scientific Reports* 6: 19966. doi:10.1038/srep19966

Troscianko, T., Benton, C.P., Lovell P George, Tolhurst, D.J., Pizlo, Z., 2009. Camouflage and visual perception. *Philosophical Transactions of the Royal Society B* 364: 449-461. doi:10.1098/rstb.2008.0218

Uy, J.A.C., Cooper, E.A., Cutie, S., Concannon, M.R., Poelstra, J.W., Moyle, R.G., Filardi, C.E., 2016. Mutations in different pigmentation genes are associated with parallel melanism in island flycatchers. *Proceedings of the Royal Society B* 283: 20160731. doi:10.1098/rspb.2016.0731

Uy, J.A.C., Vargas-Castro, L.E., 2015. Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneivenris* of the Solomon Islands. *The Auk* 132: 787-794. doi:10.1642/AUK-14-284.1

Woolbright, L.L., Stewart, M.M., 2008. Spatial and temporal variation in color pattern morphology in the tropical frog, *Eleutherodactylus coqui*. *Copeia* 2008: 431-437. doi:10.1643/CG-06-092

APPENDICES

7 APPENDICES

7.1 Appendix 1

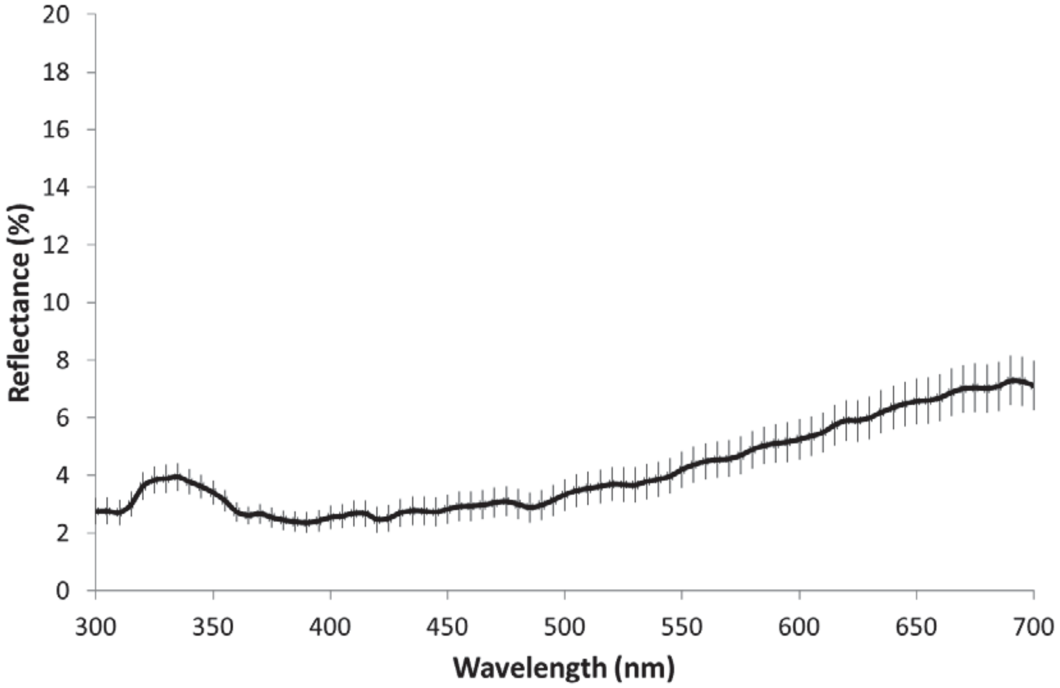


Figure A1. Averaged spectral reflectance (±SE) of 15 shore skinks (*Oligosoma smithi*) from Tāwharanui Regional Park.

7.2 Appendix 2

Standard mean difference of percentage vegetation cover between different dorsal colour patterns of three populations of shore skink: Tāwharanui Regional Park, subset of founders from Tāwharanui, and translocated population at Tiritiri Matangi Island (two different substrates).

Population	**Colour pattern 1**	**Colour pattern 2**	**Effect size, *r* (lower CI, upper CI)**	**$n_{1,2}$**
Tāwharanui	*Plain*	*Midplain*	0.33 (0.132, 0.498) *	19,65
	Midplain	*Spot*	0.02 (-0.175, 0.218)	65, 30
	Spot	*Midspot*	0.20 (0.071, 0.310) *	30, 211
	Midspot	*Midplain*	0.22 (0.109, 0.330) *	211, 65
	Midspot	*Plain*	0.38 (0.265, 0.478) *	211, 19
	Spot	*Plain*	0.36 (0.094, 0.560) *	30, 19
Founder	*Plain*	*Midplain*	0.26 (-0.609, 0.782)	3, 1
	Midplain	*Spot*	0.27 (-0.489, 0.734)	1, 5
	Spot	*Midspot*	0.18 (–0.314, 0.568)	5, 10
	Midspot	*Midplain*	0.35 (-0.242, 0.700)	10, 1
	Midspot	*Plain*	0.26 (-0.283, 0.632)	10, 3
	Spot	*Plain*	0.10 (-0.515, 0.619)	5, 3
Tiri – sand	*Midspot*	*Midplain*	0.13 (-0.358, 0.539)	14, 1
Tiri – rock	*Midspot*	*Midplain*	0.28 (-0.264, 0.642)	1,12
	Spot	*Midspot*	0.73 (0.327, 0.867) *	1,12

* CI's that do not overlap with zero are significantly different at $p < 0.05$.

7.3 Appendix 3

The standard mean differences in colour (brightness and saturation) of three sites occupied by shore skinks: Tāwharanui Regional Park, subset of founders from Tāwharanui and translocated population at Tiritiri Matangi Island (two substrate types).

Sites	**Comparison with site**	**Effect size, r (lower CI, upper CI)**	**n**
Brightness			
Tāwharanui	Founder	0.02 (-0.086, 0.141)	278, 17
	Tiri – sand	0.11 (-0.007, 0.219)	278, 12
	Tiri - rock	0.02 (-0.093, 0.135)	278, 14
Founder	Tiri - sand	0.21 (-0.158, 0.499)	17,12
	Tiri - rock	0.01 (-0.321, 0.343)	17, 14
Tiri - sand	Tiri - rock	0.21 (-0.176, 0.514)	12, 14
Saturation			
Tāwharanui	Founder	0.03 (-0.089, 0.138)	278, 17
	Tiri – sand	0.16 (0.046, 0.268) *	278, 12
	Tiri - rock	0.27 (0.155, 0.373) *	278, 14
Founder	Tiri - sand	0.52 (0.196, 0.705) *	17,12
	Tiri - rock	0.78 (0.602, 0.862) *	17, 14
Tiri - sand	Tiri - rock	0.87 (0.755, 0.924) *	12, 14

* CI's that do not overlap with zero are significantly different at $p < 0.05$.

7.4 Appendix 4

Shore skink model design: We developed a highly realistic skink model using a combination of 3D-printed skink replicas and clay. First, we scanned a dead shore skink specimen using a 3D scanner (SLS-2, DAVID Vision Systems Gmbh, Germany) with software DAVID-LASERSCANNER v3.10.4 (DAVID Vision Systems Gmbh, Germany), and combined all scanned images using Blender 2.70a (Blender Foundation, www.blender.org) to create a digital 3D skink model (available at: www.nzfauna.ac.nz/#!nzfauna---skink). We 3D-printed (Elite P3000, Trump Precision Machinery, China) 240 skink replicas out of nylon powder (Precimid 1170). We tied a clear 0.4 mm fishing line onto the body of each replica, to secure the models to the substrate. We then added soft clay (Sculpey III Hazelnut, Polyform Products Company, USA) to the replicas by hand and painted them using acrylic paint. We used spectral reflectance (Figure A2) of a light and a dark coloured skink from Tāwharanui Regional Park to reproduce paint colours for models.

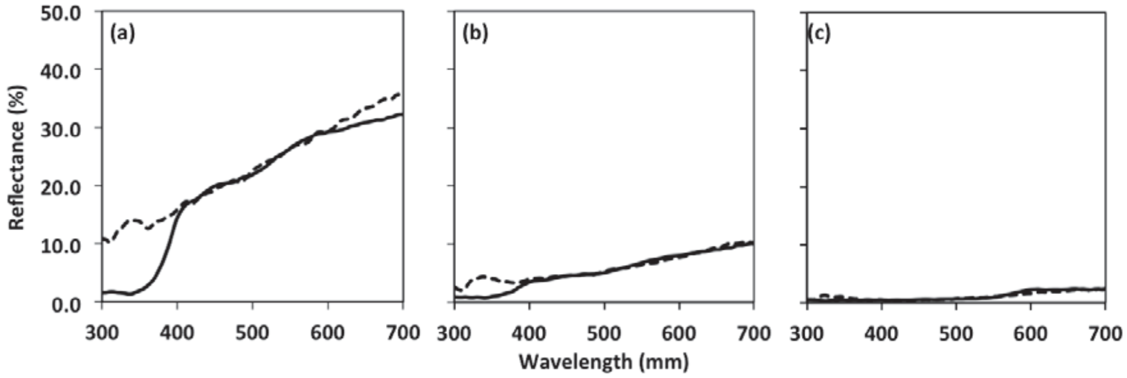


Figure A2. Spectral reflectance of shore skinks, *Oligosoma smithi*, (dotted lines) and acrylic paint mixed (solid lines) to match the reflectance of the skinks. Graph (a) refers to light-coloured skink, (b) is dark-coloured skink, and (c) is black for patterns.

7.5 Appendix 5

Identification of bite marks on models: We identified predation attempts on the models by the presence of small nicks and large bite marks made by either birds or rodents (mice). Bite marks by birds were identified by the presence of small punctures or paired u or v-shaped marks on the body or tail of the models (Figure A3). We recognised rodent predation attempts by the presence of teeth markings on the models (Figure A3). These markings were similar to images of attacked clay models in other studies (Fresnillo et al. 2015; Sato et al. 2014; Watson et al. 2012).

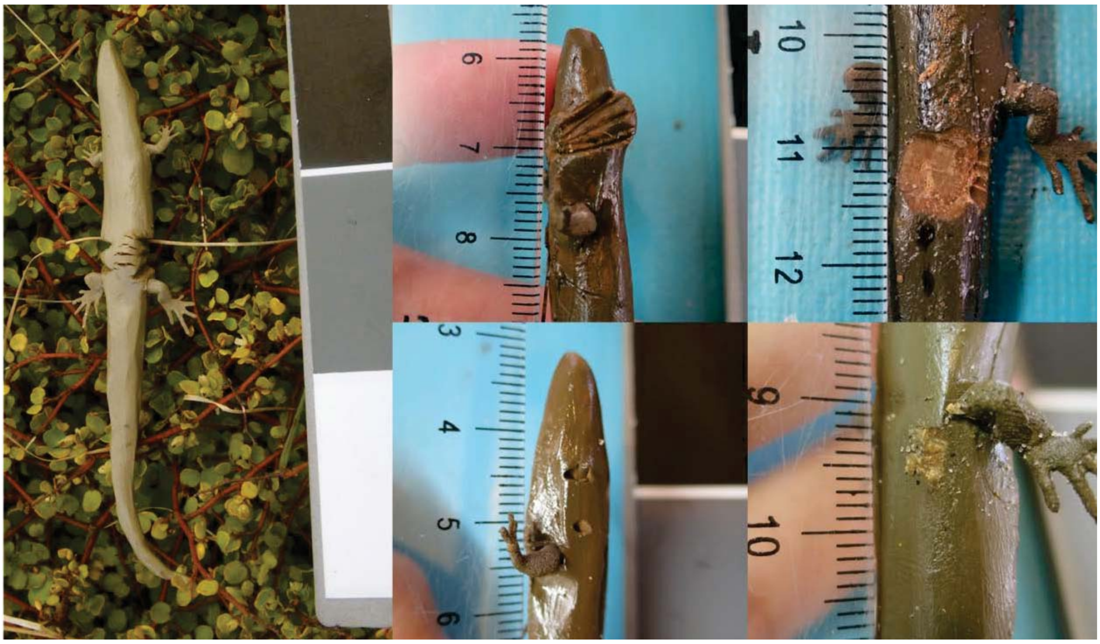


Figure A3. Examples of predator bite marks on the shore skink models. Pictures show large paired v-marks on models (left and middle top), smaller v-marks and puncture wounds (middle bottom), and bite markings of rodents (mice, right).

Supporting references:

Fresnillo, B., Belliure, J., Cuervo, J.J., 2015. Red tails are effective decoys for avian predators. Evolutionary Ecology 29: 123-135. doi:10.1007/s10682-014-9739-2

Sato, C.F., Wood, J.T., Schroder, M., Green, K., Osborne, W.S., Michael, D.R., Lindenmayer, D.B., 2014. An experiment to test key hypotheses of the drivers of reptile distribution in subalpine ski resorts. Journal of Applied Ecology 51: 13-22. doi:0.1111/1365-2664.12168

Watson, C.M., Roelke, C., Pasichnyk, P.N., Cox, C.L., 2012. The fitness consequences of the autotomous blue tail in lizards: an empirical test of predator response using clay models. Zoology 115: 339-344. doi:10.1016/j.zool.2012.04.001

Wedding, C.J., 2007. Aspects of the impacts of mouse (*Mus musculus*) control on skinks in Auckland, New Zealand, In Institute of Natural Sciences. p. 146. Massey University, Auckland.

7.6 Appendix 6

Multiple pairwise comparisons for mixed effects binary logistic regression models with binomial error distribution, testing the effects of background (sand and vegetation), time of day (morning vs. afternoon), and model types (*plain*-light, *plain*-dark, *simple*-dark and *complex*-dark) on the probability of being attacked. Sequential days (days 1 – 7) and grids (Grids 1 - 6) were set as random effects. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Comparisons		**All**			**Vegetation**			**Sand**		
Independent 1	**Independent 2**	**Estimate**	**S.E.**	***p***	**Estimate**	**S.E.**	***p***	**Estimate**	**S.E.**	***p***
All model types										
Plain-light	*Plain*-dark	0.1926	0.3549	0.948	0.1922	0.3516	0.947	-0.7053	1.2343	0.938
	Simple-dark	-0.6237	0.3024	0.164	-0.6213	0.2995	0.160	-1.1228	1.1649	0.763
	Complex-dark	-0.6237	0.3024	0.164	-0.6213	0.2995	0.160	-1.8516	1.0913	0.316
Plain-dark	*Simple*-dark	-0.8163	0.3199	0.052 *	-0.8135	0.3168	0.050 *	-0.4176	0.9258	0.968
	Complex-dark	-0.8163	0.3199	0.052 *	-0.8135	0.3168	0.050 *	-1.1463	0.8311	0.502
Simple-dark	*Complex*-dark	1.003e-05	0.2603	1.000	-2.529e-07	0.2575	1.000	-0.7287	0.7237	0.738
Pattern complexity										
Plain	*Simple*	-0.7158	0.2553	0.014 *	-0.7213	0.2703	0.021 *	-0.7113	0.8273	0.664
	Complex	-0.7159	0.2553	0.014 *	-0.5987	0.2773	0.078	-1.4400	0.7200	0.111
Simple	*Complex*	-6.145e-05	0.2603	1.000	0.1226	0.2833	0.902	-0.7287	0.7237	0.571
Unpatterned vs. Patterned										
Unpatterned	Patterned	-0.7158	0.2196	0.001 **	-0.7132	0.2175	0.001 ***	-1.1343	0.6756	0.093
Brightness										
Light	Dark	-0.4091	0.2665	0.125	-0.3126	0.2789	0.262	-1.331	1.052	0.206
*Background*Time of Day*										
Sand: Morning	Afternoon	-1.2648	0.6529	0.194						
Vegetation: Morning	Afternoon	0.7857	0.2459	0.007 **						
Morning: Vegetation	Sand	3.0834	0.7140	< 0.001 ***						
Afternoon: Vegetation	Sand	1.0329	0.5675	0.243						
Time of Day										
Morning	Afternoon	-1.2650	0.6530	0.052 *	0.5020	0.2178	0.021 *	-1.376	0.714	0.054 *
Background										
Vegetation	Sand	1.0329	0.5676	0.069 *						

7.7 Appendix 7

Correlation between microhabitat types: We conducted a principal component analysis (PCA) on three microhabitat types; rock, vegetation and sand; to identify the variable that explained the most variance in the data (Figure A4). We chose proportion of rock cover as our microhabitat variable as our predictor for our models on pattern types. For skink colour (hue, saturation and brightness), we chose vegetation cover because rock cover is positively correlated to mean monthly maximum temperature (linear regression: $p = 0.04$; $r^2 = 0.195$)

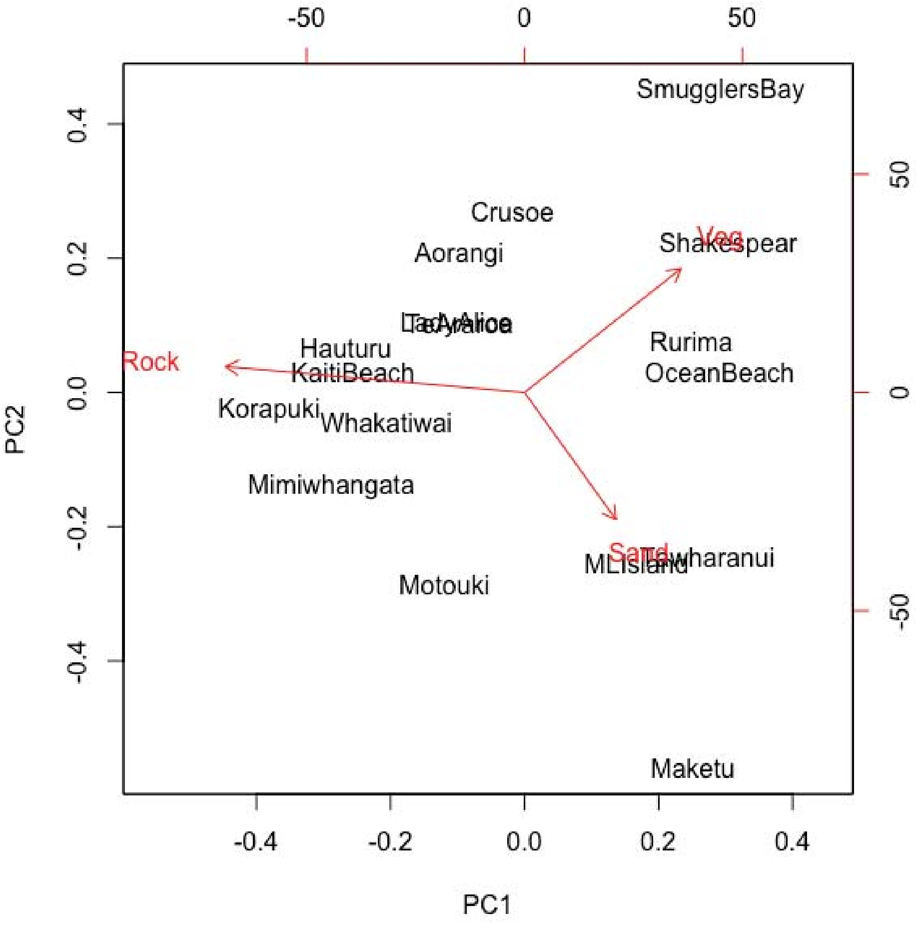


Figure A4. Principal component analysis (PCA) of three micorhabitat types: rock, sand, and vegetation (Veg).

7.8 Appendix 8

Correlation between environmental variables and latitude: Because of the potential collinearity of the environmental variables, we conducted a PCA to identify the variable with most variance in the data (Figure A5). We used: mean monthly temperature, mean monthly maximum temperature, mean solar radiation, mean UV index (UVI), mean maximum UVI, and latitudinal coordinates of each shore skink population. We found that latitudinal cline was positively associated to solar radiation (linear regression: $p < 0.01$, $r^2 = 0.85$) and negatively correlated to monthly temperature (linear regression: $p < 0.01$, $r^2 = 0.73$), UVI (linear regression: $p < 0.01$, $r^2 = 0.95$) and maximum UVI (linear regression: $p < 0.01$, $r^2 = 0.96$). So we chose latitudinal gradient to represent all the correlated variables. Maximum monthly temperature was independent from latitude (linear regression: $p = 0.10$; $r^2 = 0.11$).

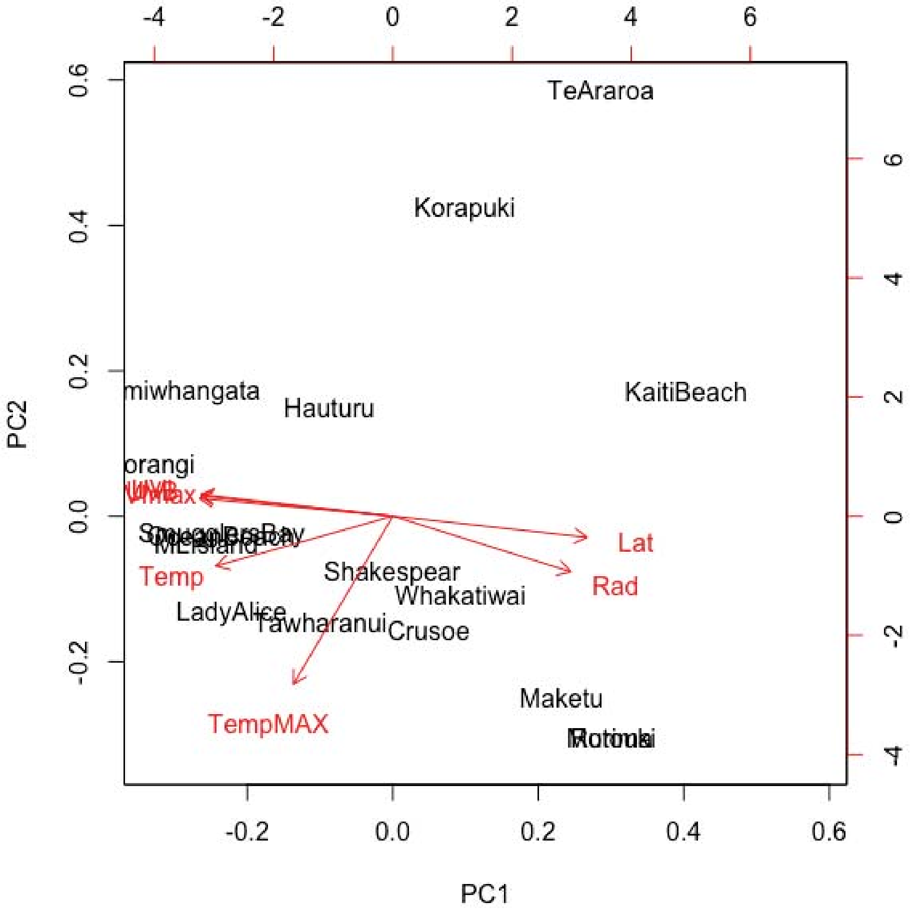


Figure A5. Principal component analysis (PCA) of six variables: Latitudinal cline (Lat), solar radiation (Rad), mean monthly maximum temperature (TempMAX), mean monthly temperature (Temp), UV index (UVI) and mean maximum UV index (UVImax).

7.9 Appendix 9

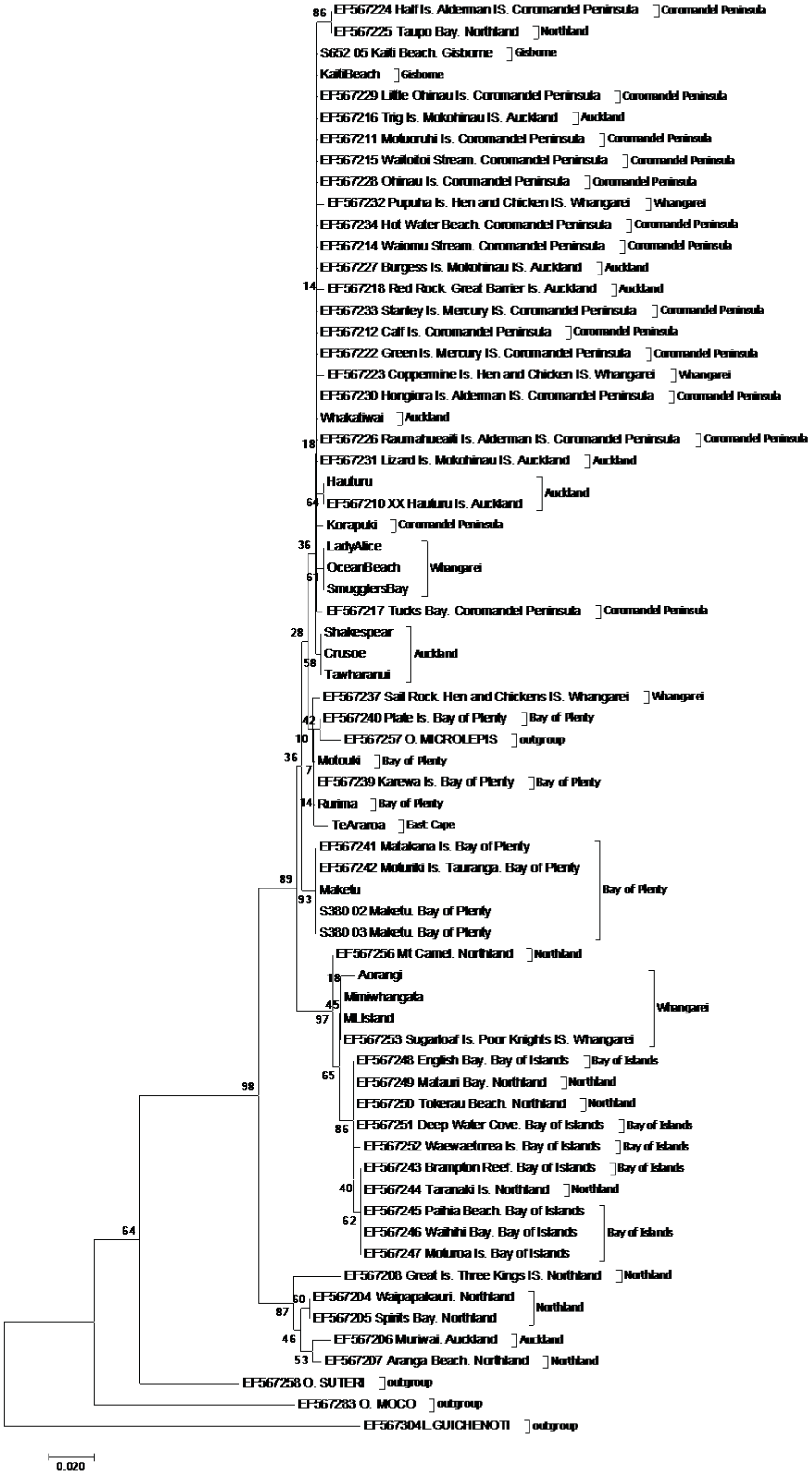


Figure A6. Maximum-Likelihood tree for shore skinks (*Oligosoma smithi*) and four outgroup species (*O. microlepis*, *O. suteri*, *O. moco* and *Lampropholis guichenoti* based on 550 bp of the ND2 mitochondrial gene.

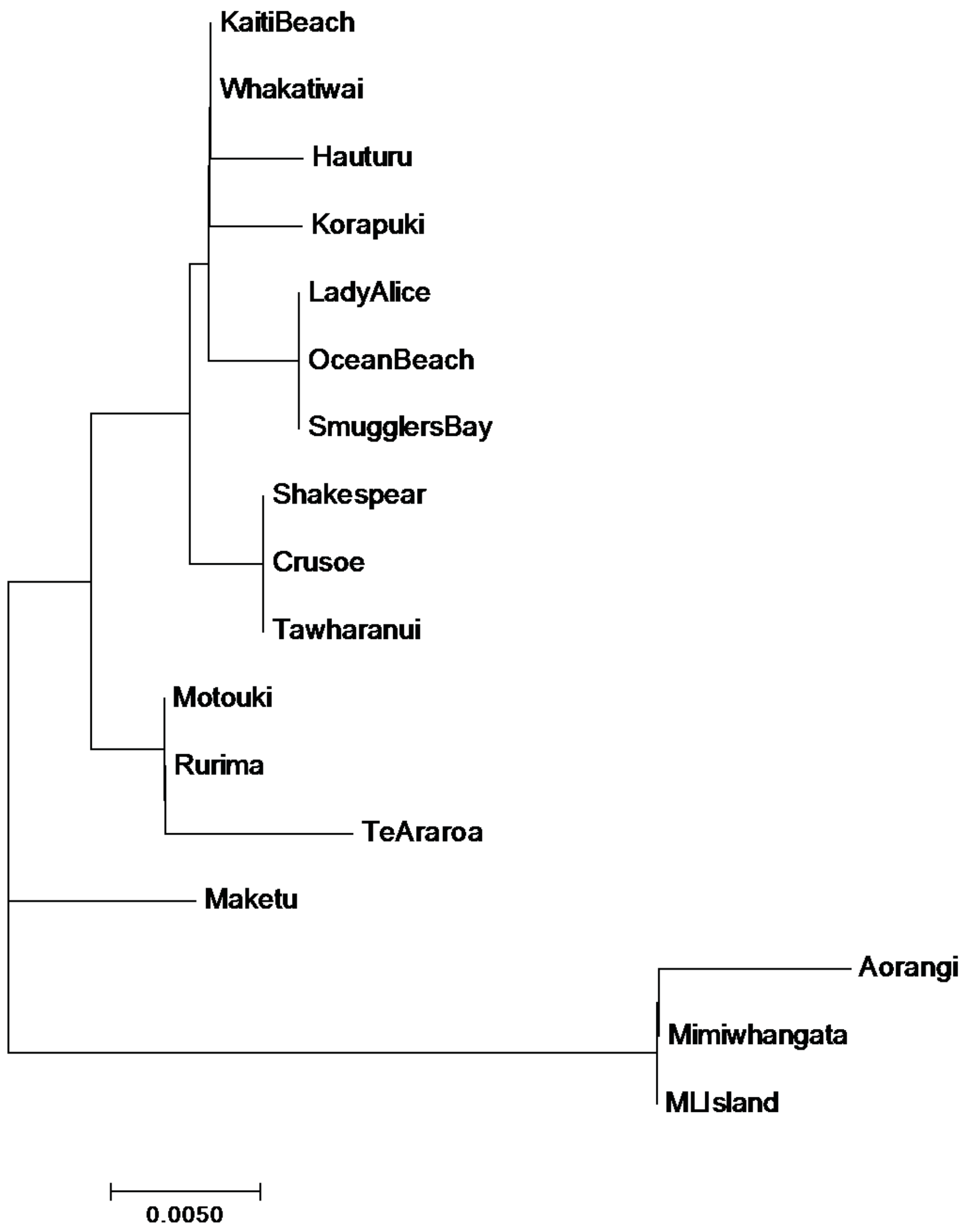
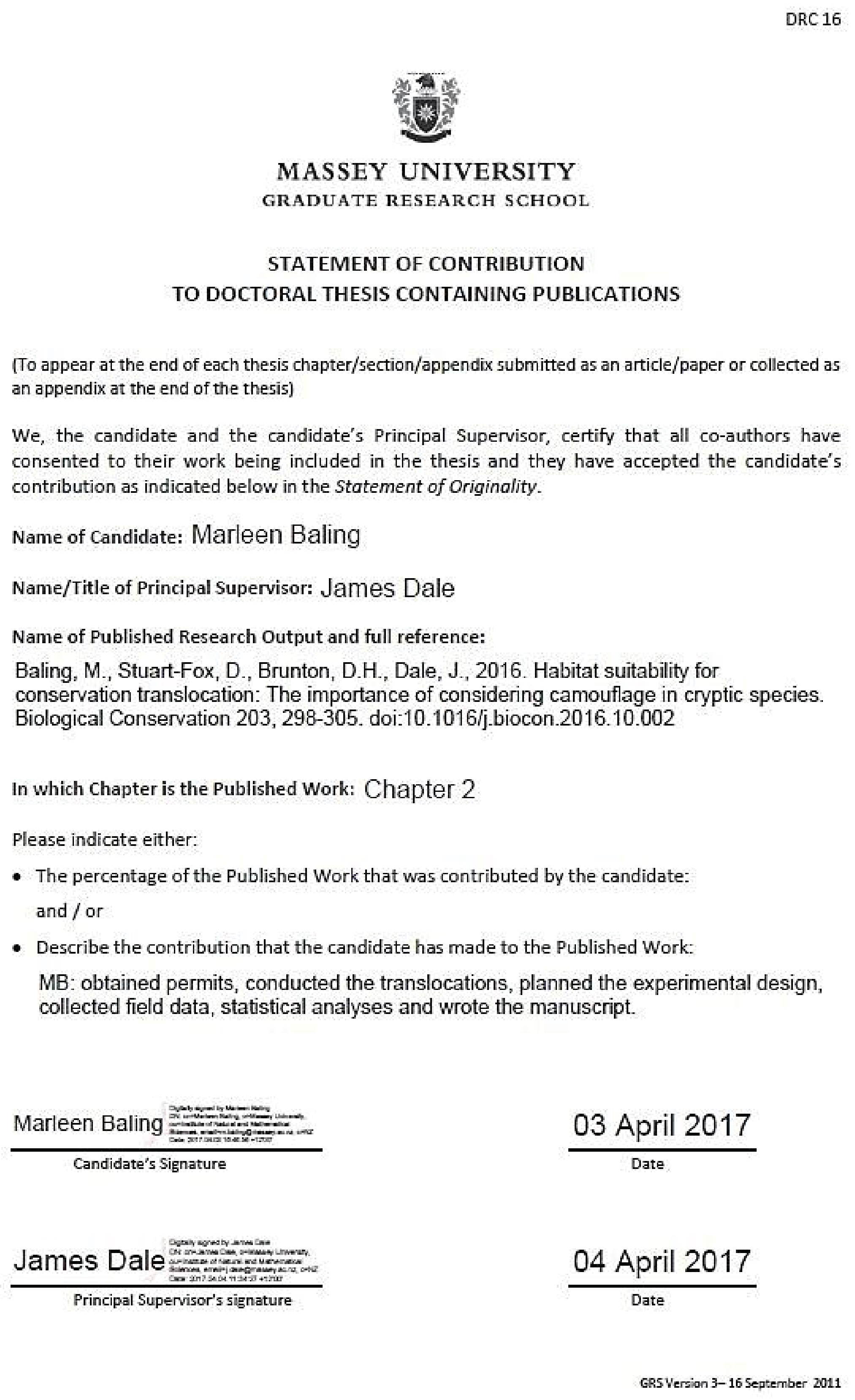


Figure A7. Final maximum likelihood tree for 17 populations of shore skinks, after other populations and outgroups were removed.

7.10 Appendix 10



DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Marleen Baling

Name/Title of Principal Supervisor: James Dale

Name of Published Research Output and full reference:

Baling, M., Stuart-Fox, D., Brunton, D.H., Dale, J., 2016. Habitat suitability for conservation translocation: The importance of considering camouflage in cryptic species. Biological Conservation 203, 298-305. doi:10.1016/j.biocon.2016.10.002

In which Chapter is the Published Work: Chapter 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  MB: obtained permits, conducted the translocations, planned the experimental design, collected field data, statistical analyses and wrote the manuscript.

Marleen Baling
Candidate's Signature

03 April 2017
Date

James Dale
Principal Supervisor's signature

04 April 2017
Date

GRS Version 3– 16 September 2011