Understanding the drivers and consequences of behavioural variation in coral reef fish under environmental change

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Abstract

Behavioural responses allow organisms to persist under environmental change, maintaining viable populations and shaping ecological communities. My thesis contributes to our understanding of the proximate causes and ultimate consequences of the drivers of behavioural variation, using coral reef fish as a model system. Across four data chapters, I show how multiple aspects of the physical and social environment contribute to variation in the expression of multiple behaviours both between and within populations across two reef fish families.

In **Chapter 1,** I use meta-analytical techniques to explore inconsistencies in animal behavioural responses to environmental change across multiple taxa. In this Chapter, I identify that behavioural variation is driven by a combination of ecological and methodological context-dependent factors. **Chapter 2** investigates how broad-scale variation in nutritional resource availability drives behavioural variation in an obligate corallivore. I show the necessity of considering the co-correlation of multiple behaviours, and the trade-offs between different behaviours in understanding behavioural variation between and within both individuals and populations. **Chapter 3** considers how energy-dependent territorial behaviours can be predicted by the economic defendability of nutritional resources. In this chapter, I provide the first evidence that terrestrial invasive species on remote islands directly impact farmer damselfish territoriality via the disruption of a seabird-derived nutritional pathway. Finally, in **Chapter 4,** I create a mathematical model to further test the applicability of economic defendability theory to territoriality. I confront my model with the empirical data in **Chapter 3** to show how reef fish territoriality is driven by the complex interplay between resource availability, competition intensity and individual state.

Finally, I utilise the outputs from **Chapters 1-4** to place behaviour in an evolutionary context and conceptualise how behaviour can scale up to impact species interactions, community composition and coral reef resilience.

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Author’s declaration

This thesis is my own original work, has not been submitted in part or in full for the award of a higher degree elsewhere, and inputs from co-authors have been acknowledged throughout.

- Rachel L. Gunn, August 2022

Statement of Contributions of Others

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General Introduction

0.1 Environmental change

Environmental change has been occurring naturally for millions of years, but anthropogenic activities have exacerbated the rate and spatial scale of environmental change beyond that which would occur naturally (Wong and Candolin, 2015). Almost all ecosystems, and therefore organisms, have now been subject to Human Induced Rapid Environmental Change (HIREC, Vitousek *et al.*, 1997, Sih, 2013). The impact of HIREC on natural ecosystems is resulting in changes in the sensory environment (Halfwerk and Slabbekoorn, 2015), the size, structure, and connectivity of habitats (Béchet *et al.*, 2004, Shepard *et al.*, 2008), the disruption of physiological processes (Baek *et al.*, 2014, Kroeker and Sanford, 2022), and species interactions (Tylianakis *et al.*, 2008, Thompson *et al.*, 2018). HIREC also has substantial consequences for the abundance, distribution (Ehrlén and Morris, 2015) and diversity (Seehausen *et al.*, 1997) of organisms. Recent research has therefore focussed on how individuals, populations and species can respond to and persist under HIREC (Sih *et al.*, 2011).

0.2 Behavioural responses to environmental change

The increasing temporal rate and spatial scale of HIREC is resulting in rapid environmental changes that occur within the lifetime of organisms, subsequently placing individuals under evolutionarily novel conditions (Sih *et al.*, 2011). As a key mediator between individuals and the environment, behaviour plays a pivotal role in how individuals can adjust to environmental change (Nagelkerken and Munday, 2016). Changes in behaviour can allow individuals to persist under changing conditions, promoting the maintenance of viable populations, and therefore allowing genetic adaptations to new environmental conditions (Tuomainen and Candolin, 2011). Behaviour is therefore a fundamental driver in determining the fitness of an individual in a modified environment (Sih *et al.*, 2011).

Behavioural responses occur most rapidly through plasticity (Tuomainen and Candolin, 2011). Behavioural decisions are then mediated via animal culture, or social learning (Keith and Bull, 2017). Transmission of behaviour between generations may constrain the ability of an individual to respond to change, whilst transmission within generations can facilitate responses to change (Keith and Bull, 2017). The behaviour of one individual can influence the behaviour of others (Dall *et al.*, 2004) and variation in survival between individuals can be explained by individual differences in behaviour (Moiron *et al.,* 2020). Individual behaviour can therefore scale-up to influence population dynamics, with broader community and ecosystem level consequences (Wong and Candolin, 2014). Population-level behavioural responses to environmental change have been well studied and reviewed (Tuomainen and Candolin, 2011). Understanding variation in behavioural responses at the individual level is a relatively recent focal point of research which could have important proximate and ultimate consequences for the persistence of species (Delarue *et al.,* 2015).

0.2.1 Variation in behavioural responses to environmental change

Behavioural plasticity

Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes with variation in environmental conditions (Pigliucci, 2005). Behavioural plasticity is a specialised form of phenotypic plasticity, involving rapid changes in behavioural traits in response to changes in the environment (Komers, 1997, Fox *et al.,* 2019). Behavioural plasticity has been well documented across a spectrum of behaviours (Van-Baaren and Candolin, 2018) including foraging (Karkarey *et al.,* 2017), reproduction (Lampe *et al.,* 2012), activity (Hall and Chalfoun, 2018), interspecific interactions (Keiller *et al.,* 2021), and social behaviour (Ruiz-Gomez *et al.,* 2008). The extent to which an individual or population can display behavioural plasticity is partly dependent upon the degree of heterogeneity present in the environment in which behaviours evolved (Tuomainen and Candolin, 2011). High degrees of behavioural plasticity will be favoured for individuals and populations that persist in fluctuating environments, whereas in stable environments, fixed behaviours are more likely to evolve through directional selection (Pigliucci, 2005, Tuomainen and Candolin, 2011). The ability to display behavioural plasticity is a critical factor in determining the persistence of organisms and the subsequent impact on ecosystem function and stability under rapid environmental change (Ducatez *et al.,* 2020).

Behavioural variation between individuals

Behavioural variation within populations cannot be attributed entirely to behavioural variation *within* individuals, i.e., behavioural plasticity (Wilson, 1998). Meta-analyses have identified that consistent behavioural variation *between* individuals can account for around 35% of behavioural variation within populations (Bell *et al.,* 2009). In behavioural ecology research, consistent behaviours observed over time or across different contexts in an individual are referred to as animal ‘personalities’ or ‘behavioural syndromes’ (Bell *et al.,* 2009, Carter *et al,* 2013). Personality often refers to single behavioural traits, whereas a behavioural syndrome refers to correlations between multiple traits at an individual level (Sih *et al,* 2004a). The presence of consistent behavioural differences between individuals implies that any one individual can express only some of the full range of behavioural trait values within the population (Dingemanse *et al.,* 2010). Animal personalities and behavioural syndromes have been identified across a range of taxa, including mammals (Dammhahn, 2012), birds (Evans *et al.,* 2010), fish (Bell and Sih, 2007), and reptiles (Stapley, 2006). The diverse occurrence of personalities implies that behavioural variation between individuals within populations is a key dimension of intraspecific variation, both ecologically and evolutionarily (Wolf and Weissing, 2012).

The presence of fixed personality traits can seem maladaptive under environmental change, and personality could be considered an evolutionary constraint (Sih *et al.,* 2004b). Nonetheless, personality types can be indicative of different strategies adopted by individuals to cope with environmental change (Sih *et al.,* 2004b). For example, proactive individuals show ‘fast’ exploratory personalities, with high aggression and boldness (Koolhaas *et al.,* 1999, Dingemanse *et al.,* 2004). A proactive personality can be beneficial under certain forms of HIREC, such as urbanisation, whereby bold aggressive individuals are better able to exploit resources in a human dominated environment (Evans *et al.,* 2010, Atwell *et al.,* 2012). However, in other contexts, a reactive personality could be favoured (Verbeek *et al.,* 1994). Reactive, ‘slow’, exploratory individuals are passive and cautious, responding to external environmental stimuli, and are better able to cope in periods of environmental variability (Koolhaas *et al.,* 1999, Sih *et al.,* 2004a). Different behavioural types may therefore be selected for where fitness payoffs depend upon the behavioural history of an individual and the frequency with which different behavioural strategies are present in the population (Dall *et al.,* 2004, Nicolaus *et al.,* 2016).

Behavioural reaction norms

Research often focusses on personality and behavioural plasticity as separate entities, yet individuals within populations have been shown to display inter-individual variation in plasticity (Nussey *et al.,* 2007). The behavioural reaction norm framework combines personality and plasticity to identify their relative contributions (Dingemanse *et al.,* 2010). A behavioural reaction norm refers to the set of behavioural phenotypes produced by an individual across an environmental gradient or a given set of environments. If the relationship between the behavioural phenotype and the environmental gradient is non-horizontal, then there is a degree of behavioural plasticity present (Dingemanse and Wolf, 2013). In other words, the presence of a personality does not imply complete consistency; certain traits could show plasticity (Sih *et al.*, 2004a, Dingemanse *et al.*, 2010, Figure 0.1). For example, individuals within fish populations have been shown to display different behavioural types, or personalities, but the traits associated with these personalities also show flexibility under changing environmental conditions (Frost *et al.*, 2013, Fürtbauer *et al.*, 2015, Barbasch and Buston, 2018). Considering covariance between plasticity and personality allows all possibilities of behavioural variation to be considered within a single framework (Dingemanse *et al.*, 2010, Figure 0.1). Considering behaviour at the level of the individual can therefore reveal potentially adaptive behavioural variation that is not apparent when only population mean level responses are considered (Barbasch and Buston, 2018, see **Chapters 1 and 2**).

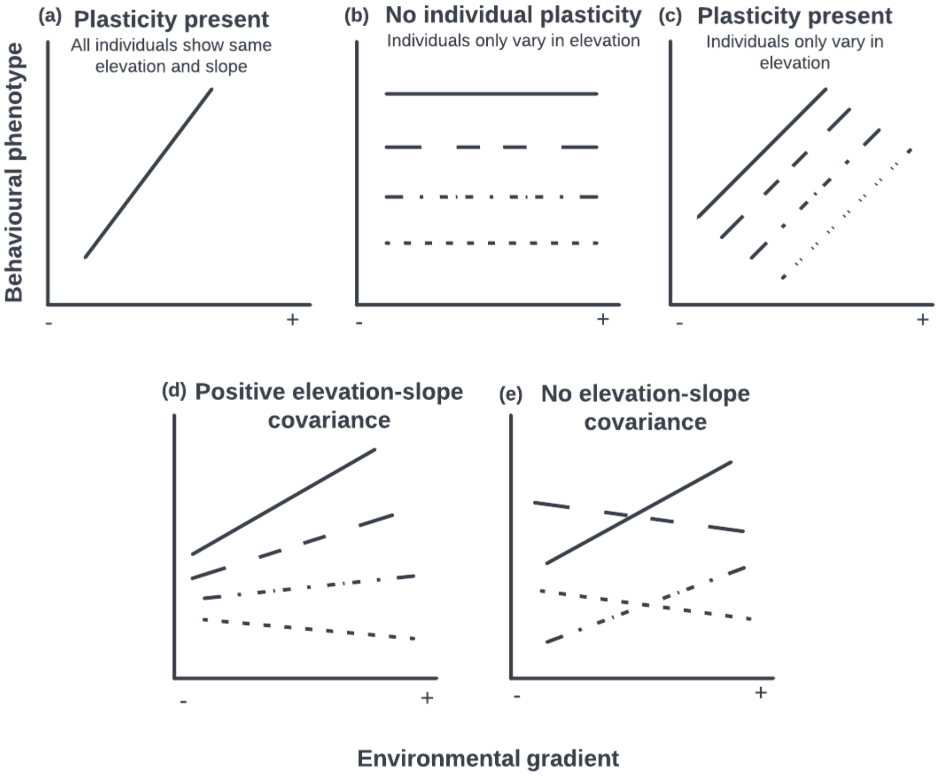

Figure 0.1: Behavioural reaction norm scenarios. Lines represent individuals and multiple lines represent individual variation. Based on Dingemanse *et al.,* 2010.

0.2.2 Evolutionary traps

Organisms often make behavioural and life history decisions using environmental cues to determine habitat quality (Fourcade *et al.,* 2018), evaluate risk (Reader *et al.,* 2006), and select optimal breeding times (Deviche and Davies, 2014). When environmental conditions are stable, these cues correlate with survival and fitness, and cue-based behavioural decisions are adaptive (Williams and Nichols, 1984). However, if environments change rapidly, previously reliable cues may become unreliable and organisms may make maladaptive behavioural/life history decisions (evolutionary traps) or maladaptive habitat choices (ecological traps, Schlaepfer *et al.,* 2002, Sih *et al.,* 2011). Ecological and evolutionary traps may therefore constrain some individuals, populations, or species from displaying appropriate behavioural responses to change (Rubolini *et al.,* 2010). Cue-based responses, behavioural flexibility, and the evolutionary history of an individual and its environment can therefore all contribute to variation in behavioural responses to environmental change (Sih, 2013).

0.2.3 Behavioural correlations and trade-offs

Behavioural responses are complex and often require organisms to produce multi-trait responses to changes in the environment (Sih *et al.*, 2011, Singh *et al.,* 2020). Behavioural correlations often arise due to shared genetic, developmental, or physiological mechanisms (Singh *et al.,* 2020). For example, aggression is often positively correlated with boldness (Pintor *et al.,* 2008, Kendall *et al.*, 2018). Aggression and boldness are both affected by the resources an individual possesses, such as size and resource holding potential (Wolf and Weissing, 2010). There is also evidence that the mechanism underlying correlations between these two traits is genetic (Norton *et al.,* 2011), which can have important evolutionary constraints if individuals are unable to vary levels of boldness/aggression across different contexts (Wong and Candolin, 2014). Time-budgets within a given situation may also give rise to negative behavioural correlations by generating trade-offs between different behaviours (Sih *et al.*, 2004b, Found and St. Clair, 2016). For example, if aggression and foraging behaviours are considered separately, both could be assumed to be maximised to improve fitness (Sih *et al.*, 2004a). However, when considered together, it is clear both behaviours cannot be maximised at the same time and would be expected to be negatively correlated with one another as a result of a trade-off (Sih *et al.*, 2004a). As suites of correlated traits evolve as one, not as individual traits (Sih *et al.*, 2004b), it is necessary to move away from studying behaviours in isolation, and consider the co-correlation of multiple traits, and trade-offs between traits, in order to fully understand the behavioural responses of organisms to environmental change (Gunn *et al.*, 2022, **Chapter 2**).

0.2.4 Territoriality

Territories hold numerous ecological functions, including providing a permanent space for shelter (Gray *et al.,* 2000), reproduction (Nilsson *et al.*, 2019) and defending mates and food resources against conspecifics (Davies and Hartley, 1996). Territoriality, defined as the aggressive defense of resources within a territory, is directly associated with the nutritional resources available for individuals to exploit (Stimson, 1973, Carpenter, 1987). Both the quantity (Keith *et al.,* 2018) and quality (**Chapter 3**) of nutritional resources have been impacted negatively by environmental change (Auer *et al.*, 2020a). Under a threshold model of economic defendability, territoriality is predicted to occur where the net energetic benefits both outweigh the costs (Brown, 1964), and outweigh the benefits of non-territorial behaviour (Peiman and Robinson, 2010). Nutritional declines induced by environmental change could result in the payoff of territoriality becoming negative (Maynard-Smith and Price, 1973) and individuals investing time in territoriality will not be able to meet the minimal energetic requirements for survival (Carpenter and MacMillan, 1976). Subsequently, decreases in territoriality combined with increases in foraging (Gunn *et al.*, 2022, **Chapter 3**) have been documented alongside increases in territory size (Samways, 2005, Sells and Mitchell, 2020) where food resources are low. By affecting growth, resource acquisition and reproductive success, territoriality can also scale up to impact individual fitness (Peiman and Robinson, 2010). By identifying the nutritional thresholds that determine territorially, the persistence and behavioural composition of species under future environmental conditions can be predicted (Delarue *et al.*, 2015, **Chapter 4**).

0.3 Methods in studying animal behaviour

0.3.1 Behavioural repeatability

Behavioural repeatability is the proportion of variation in behaviour attributable to variation between individuals (Lessels and Boag, 1987), and is a common metric used to indicate the presence of different personalities within a population. However, consistency measured via repeatability is only informative on the scale of the behaviour of interest. In other words, repeatability is a statistic of the population, and whilst individuals may display high behavioural repeatability, behavioural variation along the trait of interest may be minimal (Dochtermann and Royaute, 2019). Behavioural repeatability should therefore be complimented with additional measures, such as mean-scaled individual variation, that relates behavioural consistency to the population mean (Dochtermann and Royaute, 2019, Gunn *et al.*, 2022, **Chapter 2**). For example, two populations may display similar levels of behavioural repeatability, but individuals in one population may differ from one another to a greater extent than individuals in the other, and this could be due to differing contributions of genetic (Hansen *et al.*, 2011) and environmental factors (Gunn *et al.*, 2022). The development of quantitative tools that compliment behavioural repeatability estimates allows for more complex causal inferences to be made regarding the magnitude of behavioural variation within populations (**Chapter 2**).

0.3.2 Methodological challenges

The complexity of behavioural responses to environmental change has resulted in challenges arising in behavioural ecology research regarding definitions, methodologies, and analyses of animal behaviour (Beekman and Jordan, 2017, Sánchez-Tójar *et al.,* 2022). For example, the term 'boldness' has been used to define and quantify responses to either risky situations (Réale *et al.,* 2007), or both novel and risky situations (Toms *et al.,* 2010). Discrepancies in definitions such as this can result in multiple behavioural tests being used to measure one trait (Carter *et al.,* 2013). The reverse can also be true: different behavioural traits may be measured using a single behavioural test (Carter *et al.,* 2013), making comparisons across different studies difficult (Beekman and Jordan, 2017). Furthermore, laboratory research often dominates behavioural ecology research (Gunn *et al.,* 2021, **Chapter 1**). Laboratory studies can establish cause and effect by ensuring controlled conditions (Calisi and Bentley, 2009), yet must be complemented by field studies, which are essential to understand behavioural responses in the context of their natural environment (Cuthill, 1991). To accurately predict and understand behavioural responses to HIREC, standardised methods, clear predictions and hypotheses, and a balanced representation of different traits across both field and laboratory studies are necessary (Gunn *et al.,* 2021, **Chapter 1**).

0.4 Coral reef ecosystems

Tropical coral reefs are hugely diverse and productive ecosystems, supporting one third of all marine species within just 1% of the ocean floor (Plaisance *et al.,* 2011). The high diversity within coral reef ecosystems is primarily due to the structure, habitat and food provided by Scleractinian corals and the symbiotic association between corals and zooxanthellae (Rosic *et al.,* 2015). This symbiosis is based on a nutritional exchange, with the photosynthetic products of zooxanthellae providing corals with almost the entirety of their energetic demands, supporting coral growth and the foundation of the coral reef ecosystem (Trench, 1979). However, coral reefs are also one of the most threatened ecosystems on earth. Global and local anthropogenic pressures have placed over one third of coral species at risk of extinction (Carpenter *et al.,* 2008) and a 40% reduction in live coral cover is predicted by 2100 (Sully *et al.,* 2022). Rising sea surface temperatures are increasing the frequency of marine heatwaves (Oliver *et al.,* 2018, Bindoff *et al.,* 2019), which in turn induce mass coral bleaching events (Sully *et al.,* 2022). Prolonged elevated temperatures cause zooxanthellae to be expelled from coral tissues, placing corals at high risk of starvation and death (Hoegh-Guldberg, 1999, Vessaz *et al.,* 2022), whilst also reducing the calcium carbonate production on coral reefs (Lange and Perry, 2019). Combined with additional stressors, such as ocean acidification and eutrophication (Guan *et al.*, 2020), as well as the introduction of invasive species (Albins, 2015, Graham *et al.*, 2018), the structure, function and diversity of coral reef ecosystems are under severe threat as a direct consequence of human-induced environmental change (Pratchett *et al.*, 2008, Darling *et al.*, 2017).

0.4.1 Coral reef fish as model organisms

A vast majority of coral reef fish are directly dependent upon live coral for survival, whether through consuming coral as a food resource (Pratchett *et al.*, 2013), or relying on the structural complexity (Graham and Nash, 2013) of live coral for habitat and shelter. Given the rate at which coral reefs can degrade under environmental change (Sully, 2022), the persistence of reef organisms under future conditions is in part dependent upon the ability of individuals, populations, and species to respond behaviourally (Delarue *et al.*, 2015).

Corallivores

Corallivorous fishes, i.e., species that feed on live coral tissue (Rice *et al.*, 2019), such as butterflyfishes (Chaetodontidae), are good indicators of reef health (Crosby and Reese, 2005). The diet, and subsequently the condition, abundance, and behaviour of corallivores is directly dependent on the availability of live coral (Crosby and Reese, 2005, Graham *et al.*, 2011). Research has shown that butterflyfish territories break down, and aggressive and social behaviours decline, as coral cover decreases (Samways, 2005, Thompson *et al.*, 2019, **Chapter 2**), for example following a severe bleaching event (Keith *et al.*, 2018). The behavioural responses of butterflyfishes to declining coral cover are often associated with foraging strategies, such that declining coral cover can place individuals in a nutritional deficit (Zambre and Arthur, 2018). Nonetheless, few studies explicitly explore a) the role of trade-offs between foraging and other behaviours such as aggression in the behavioural responses to butterflyfishes, and b) the role of behavioural variation between and within individuals that could arise as nutritional resources decline, yet both have potentially important consequences for species persistence (Delarue *et al.*, 2015, **Chapter 2**).

Herbivores

Herbivores are functionally important reef fish species that have the potential to influence coral reef structure and benthic composition (Ceccarelli, 2007). Free roaming herbivores prevent the proliferation of algal communities which would otherwise compete spatially with coral and reduce coral recruitment (Hoey *et al.*, 2011, Adam *et al.*, 2015). Conversely, site-specific farming herbivores hold small, aggressively defended territories that support the growth of turf algae at the expense of other organisms, including certain species of coral (Ceccarelli, 2007, Gordon *et al.*, 2015). Farming damselfish territoriality has also been shown to influence the spatial organisation and social structure of fish communities (Morgan and Kramer, 2004). Algal abundance has been positively correlated with conspecific density and territorial defense and negatively correlated with territory size for the jewel damselfish (*Plectroglyphidodon lacrymatus,* Robles *et al.*, 2018). In remote tropical marine ecosystems, the availability and quality of algal nutritional resources on coral reefs has been impacted by the introduction of black rats (*Rattus rattus*) on islands adjacent to coral reefs (Graham *et al.*, 2018), disrupting a seabird-derived nutrient pathway between terrestrial and marine ecosystems via predation (Graham *et al.*, 2018). The impact of these nutrient disruptions on the behaviour of functionally important reef fish remains unknown but could have substantial consequences for coral reef composition, diversity, and resilience. Site specificity, small territory sizes and high levels of territoriality, make farming damselfish an ideal model organism to understand how fine scale variation in nutrient resource quantity and quality can influence territorial behaviour and subsequently scale up to impact fish communities at higher ecological levels (**Chapters 3 and 4).**

0.5 Thesis overview

The overarching aim of my thesis is to further our understanding of animal behavioural responses to environmental change by bringing together both population and individual level animal behavioural responses across multiple scales (Figure 0.2). By considering the consequences of environmental change on resource availability across both broad and fine scales, my thesis will allow both the proximate drivers and the ultimate consequences of behavioural responses to be better understood.

Throughout the thesis, I will address the following research questions:

1. How do behavioural responses vary across different organisms and with different forms of environmental change, and to what extent is this variation methodological?
2. To what extent does behaviour vary both within and between individuals across areas of high and low food resources?
3. How does fine scale variation in the amount and enrichment of nutrient resources affect energy dependent territorial behaviours?
4. At what critical thresholds do behavioural changes occur, and do these thresholds have the potential to affect species persistence?

I will answer my thesis questions using reef fish on coral reefs as a study system. My thesis will combine empirical field observations, statistical analysis (Frequentist and Bayesian) and mathematical modelling (Figure 0.2). Firstly, I use the current knowledge base and metanalytical models to improve the current understanding of, and identify broad patterns in, the behavioural responses of organisms to HIREC, and identify recommendations for future research (**Chapter 1**). Following these recommendations, I use *in situ* observation methods to evaluate how both population and individual level behaviour varies between high and low resource environments in a corallivorous butterflyfish species (**Chapter 2**). I then address how variation in territoriality in a herbivorous farmer damselfish species is driven by fine-scale variation in the quantity and quality of nutritional resources, by linking the aggression of individual fish to their territory size and nutritional resources (**Chapter 3**). Finally, using mathematical modelling of animal energetics, I quantify and predict critical threshold values that drive changes in behaviour and confront these predictions with empirical data (**Chapter 4**). I use these models to infer how future environmental conditions could impact species persistence.

The four data chapters (**Chapters 1-4**) within this thesis have been written for publication. **Chapter 1** has been published in *Oikos*, and **Chapter 2** has been published in *Behavioural Ecology and Sociobiology.* **Chapter 3** has been formatted for and is under review at *Nature Ecology and Evolution.* **Chapter 4** is in preparation for submission to *Ecology Letters*.

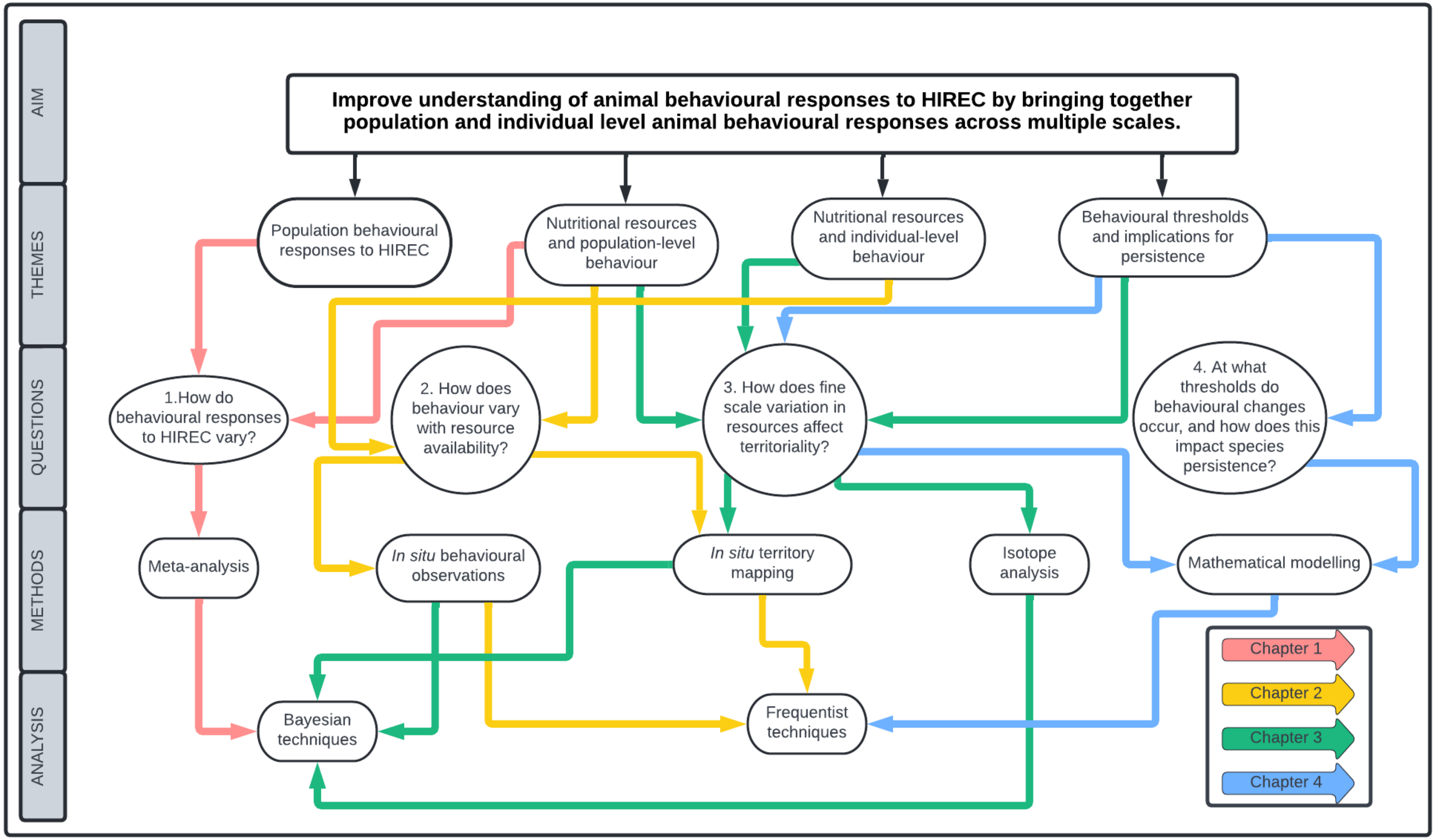

Figure 0.2: Thesis overview, including themes and questions addressed, methods and analysis used, and links between the four data chapters.

Chapter 1

1. Understanding behavioural responses to human-induced rapid environmental change: a meta-analysis

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Contribution of authors

RLG, SAK, IRH and ACA all contributed to the conceptualisation of the work and developed the research questions. RLG performed all data analyses, with assistance from PTN. All authors contributed to manuscript revisions.

Abstract

Behavioural responses are often the first reaction of an organism to human induced rapid environmental change (HIREC), yet current empirical evidence provides no consensus about the main environmental features that animals respond to behaviourally, or which behaviours are responsive to HIREC. To understand how changes in behaviour can be predicted by different forms of HIREC, we conducted a meta-analysis of the existing empirical literature focusing on behavioural responses to five axes of environmental change (climate change, changes in CO_2, direct human impact, changes in nutrients and biotic exchanges) in five behavioural domains (aggression, exploration, activity, boldness, and sociability) across a range of taxa but with a focus on fish and bird species. Our meta-analysis revealed a general absence of directional behavioural responses to HIREC. However, the absolute magnitude of the effect sizes was large. This means that animals have strong behavioural responses to HIREC, but the responses are not clearly in any particular direction. Moreover, absolute magnitude of the effect sizes differed between different behaviours and different forms of HIREC: Exploration responded more strongly than activity, and climate change induced the strongest behavioural responses. Model heterogeneities identified that effect sizes varied primarily because of study design, and the specific sample of individuals used in a study; phylogeny also explains significant variation in our bird model. Based on these results, we make four recommendations to further our understanding: 1) a more balanced representation of laboratory and field studies, 2) consideration of context dependency, 3) standardisation of the methods and definitions used to quantify and study behaviours, and 4) consideration of the role for individual differences in behaviour.

1.1 Introduction

Currently, human induced rapid environmental change (HIREC) is exposing organisms to novel selection pressures that are vastly different from those experienced previously (Lowry *et al.*, 2013). Whilst evolutionary responses to environmental change can occur quickly and buffer the ability of species to persist in a changing environment (Hoffman and Sgro, 2011), behavioural responses are often the initial response of organisms to change (Wong and Candolin, 2014). Moreover, behavioural change can mediate genetic adaptation by allowing time for genetic changes to occur (Tuomainen and Candolin, 2010) or impeding change by shielding organisms from selection pressures (Muñoz and Losos, 2018). Thus, understanding how behaviours are modified by changes in the environment is a crucial step in revealing how human induced environmental changes affect animals.

In response to environmental change, organisms can adapt, relocate and/or acclimatise (Wong and Candolin, 2014). Firstly, populations can respond to changing environments at a genetic level, through evolutionary adaptation resulting from selection (Hoffman and Sgro, 2011). Secondly, organisms can relocate via dispersal into habitats in different geographic spaces in response to environmental factors such as temperature and resource availability (Tesson and Edelaar, 2013). Finally, organisms can acclimate through phenotypic plasticity, which may be physiological, morphological, or behavioural (Noble *et al.*, 2018). Behavioural plasticity allows organisms to respond to a changing environment rapidly by modifying their behaviour to better suit new environmental conditions (Komers, 1997).

Environmental change induces behavioural responses through various pathways, for example, by changing the availability of resources (Berumen and Pratchett, 2006), or through changes in information transmission in the sensory environment (Sih *et al.*, 2010). If an individual has an evolutionary history that has resulted in traits suitable for changing conditions, then short-term behavioural plasticity will be possible (Sih *et al.*, 2010). Where evolutionary history has produced traits allowing for fast evolutionary responses, such as traits with high genetic variation, behavioural adaptations to HIREC could evolve (Hendry *et al.*, 2011). Behavioural responses can occur initially through behavioural plasticity (Wong and Candolin, 2014) that can then be transmitted socially, before evolving over subsequent generations (Tuomainen and Candolin, 2011). Over time, behavioural modifications can therefore promote adaptation; an important process for predicting persistence in a changing environment (Wong and Candolin, 2014).

There are five behavioural domains that have become central in modern behavioural ecology research: aggression, exploration, activity, boldness, and sociability (Reale *et al.,* 2007). These behavioural domains are important since they are related to resource acquisition, dispersal, and many other ecologically important processes, as well as being linked with life-history and physiology (Reale *et al.*, 2010, Dammhahn *et al.*, 2018). A focus on these domains has allowed for a broad scale comparability of behavioural expression across different species, contexts, and time (Koski, 2014). It has also been shown that behaviour scales-up to influence population and community-level processes (Dall *et al.,* 2004, Wilson *et al.,* 2020).

Animal behaviour has been studied in relation to various forms of HIREC, with responses varying within and across taxa. Changes in land use, such as an increase in urbanisation, are associated with increased boldness and exploration in birds (Donaldson *et al.*, 2007, Evans *et al.*, 2010), but led to greater caution in lizards (Lapiedra *et al.,* 2017). In terms of climate change, evidence suggests that increasing air temperatures can alter the phenology of bird species, increasing interspecific competition and associated aggression during breeding seasons (Samplonius and Both, 2019). In fishes, increases in aggression have been associated with warming water (Kvarnemo, 1998) and decreasing water levels associated with drought (Flood and Wong, 2017), but decreases in aggression have been suggested following warming-induced mass coral mortality (Keith *et al.,* 2018). Despite variability in behavioural responses towards changing environments, the same mechanisms have been used to explain both increases and decreases in different behaviours in response to HIREC, such as energetic expenditure (Enzor *et al.,* 2017), resource availability (Gremillet *et al.*, 2012) and fitness consequences (Dingemanse and Reale, 2005). There are, therefore, numerous explanations for behavioural responses to HIREC across different studies, but no consensus.

It is unclear whether inconsistencies in behavioural responses to HIREC reflect different mechanisms operating in different taxa or systems or variation in methodologies across studies. For example, there are multiple methods that can be used to measure a single behaviour, such as boldness, and there are also multiple behaviours (e.g., boldness, exploration, and activity) that can be measured using one test, such as latency tests (Carter *et al.,* 2013). Furthermore, the differences between laboratory and field methods, and the effects of these differences in behavioural expression, are unresolved. Field-based methods allow for observation and/or manipulation under naturally varying conditions (Cuthill, 1991) but are subject to noise from uncontrolled factors (Calisi and Bentley, 2009). Laboratory experiments allow numerous environmental factors to be controlled for, making it easier to establish cause and effect yet lose realism (Cuthill, 1991). Laboratory environments can induce expression of behavioural variation that has not been tested by natural selection (Niemela and Dingemanse, 2014), potentially causing a mismatch between laboratory and field studies.

Here, we explore and quantify the direction and absolute magnitude of behavioural responses to HIREC using meta-analytic tools. Specifically, we focus on the five key behavioural domains (Reale *et al.*, 2007) to determine the extent to which changes in those behaviours can be predicted by different types of HIREC. Moreover, we aim to identify the contributions of different factors influencing behavioural responses, specifically differences between animal taxa and between different methods used to study and quantify behaviour, to provide a deeper understanding of responses to HIREC.

1.2 Methods

1.2.1 Literature search and inclusion criteria

We used the standardised ‘Preferred Reporting Items for Systematic Reviews and Meta-analysis’ (PRISMA) method for selection of studies to include in the analysis (Moher *et al*, 2009, Figure 1.1). We searched the Web of Science core collection database on 5th November 2018 using the following search term: (Animal (Personality OR behav* OR "behav* syndrome") AND ("Environmental change" OR "Climate Change" OR "Global warming” OR "Habitat degradation"). We included terms “Personality” and “behav* syndrome”, in addition to general “behav*”, in our search since research in the field of animal personality has forcefully focused on estimating behavioural responses across different environments (Sih 2013). Moreover, animal personality research also focuses on the key five behavioural domains used in our work (Reale *et al.*, 2007). The Web of Science search identified 974 records, and we collated a further 49 records by searching the reference lists of relevant review papers (Figure 1.1). Following the removal of duplicates, we had a total of 1,023 papers to screen. Titles and abstracts for these 1,023 records were assessed for relevance, and we eliminated a further 658 papers that did not include reference to both “behaviour” and “environmental change”.

The remaining 365 papers were then read in full, and data were extracted for analysis. During this screening, 59 review papers, 52 theoretical modelling papers, 3 method papers, 4 response papers and 21 theoretical papers were excluded as they contained no experimental data. We excluded an additional 64 papers as they did not contain appropriate behavioural data, e.g., they referred to natural seasonal variations in behaviour, or thermoregulatory behaviour. Similarly, 53 papers were removed as they contained behavioural data, but not in relation to environmental change. Five studies that used a repeated measures design were eliminated to avoid issues with calculating sampling error variance. Two papers that had been retracted or were, to our knowledge, being investigated since the initial search were also eliminated. Twelve relevant papers from which we were unable to extract suitable data for quantitative analyses were retained for qualitative analyses. In total, we included 418 data points from 102 studies in qualitative analyses, and 381 data points from 90 studies in quantitative analyses (Table 1.1).

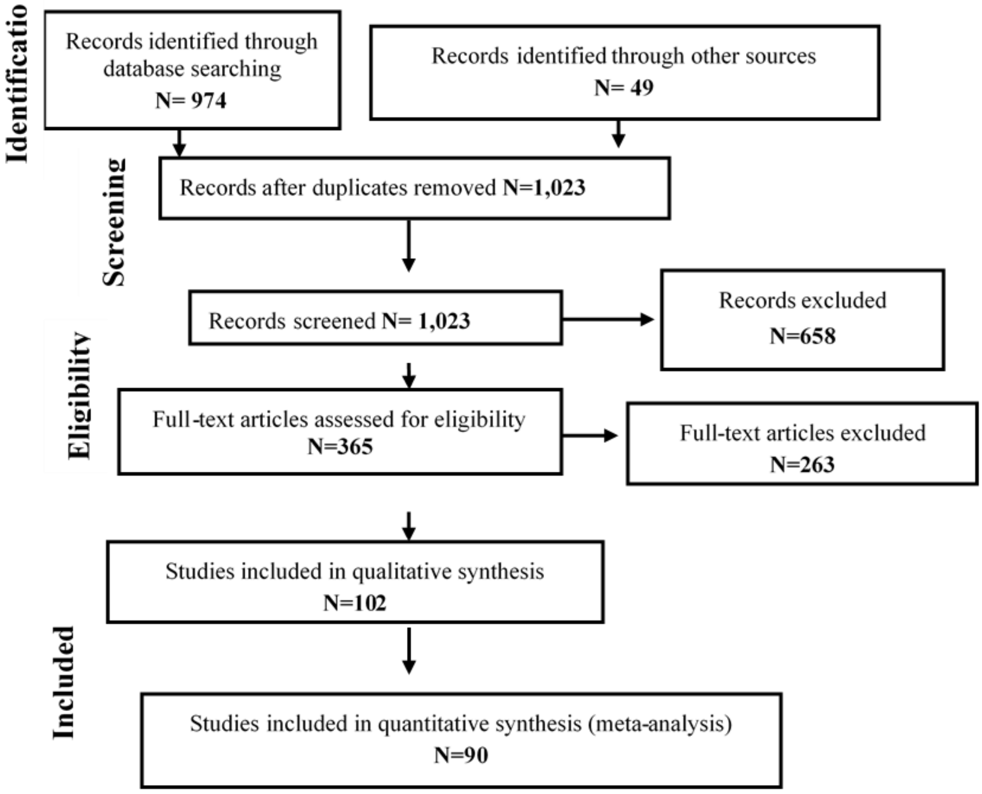

Figure 1.1: Summary of the identification, screening, eligibility, and inclusion process for data included in qualitative and quantitative analyses. Schematic based on the PRISMA methodology (Moher *et al.*, 2009).

1.2.2 Data extraction

Qualitative data

For each paper included in the analysis, we extracted the following information: study taxa (bird, fish, crustacean, mammal, other), study species, study habitat (see appendix A), axis of environmental change, behavioural domain, method of measuring/quantifying behaviour, laboratory or field based, and wild or captive population. For study taxa, ‘other’ grouped poorly represented taxa including amphibians, echinoderms, elasmobranchs, insects, molluscs, and reptiles, which were each included in fewer than 10 papers.

We modified the five axes of HIREC from Sala *et al.* (2000) to broaden their applicability beyond terrestrial systems and assigned all papers to one axis. Direct Human impact (‘Changes in land use’, Sala (2000)) encompassed a wider spectrum of anthropogenic effects including urbanisation, human disturbance, fishing pressures, and anthropogenic noise. Changes in CO_2 concentration (‘Atmospheric CO_2 concentration’, Sala (2000)), encompassed both changes in atmospheric CO_2 and ocean acidification. Changes in Nutrients (‘Nitrogen deposition and acid rain’, Sala (2000)) concerned changes in water column turbidity and eutrophication. Climate change (‘Climate change’, Sala (2000)) encompassed changes in both water and air temperature, and subsequent changes in habitat. Biotic exchanges refer to the impact of invasive species on native populations. In all cases, changes in CO_2 and temperature are unidirectional and refer to increases only.

The five behavioural domains we considered were aggression, exploration, activity, boldness, and sociability (following Reale *et al.*, 2007). There is often a discrepancy in how behaviours are defined (Carter *et al.*, 2013) so for consistency, we used the definitions of Reale *et al.* (2007) to assign behaviours to one of the five domains: aggression is defined as a social contest involving agonistic behaviours; boldness as response to a risky situation (that is not novel); exploration as response to novel situations (which can also be risky); activity as general activity in non-risky and non-novel situations; and sociability as a non-agonistic response to a conspecific. Where focal studies in our data had themselves used Reale *et al.* (2007) as a guideline for defining behaviours, we used the authors definition of behaviour.

We collected multiple effect sizes from the same studies, some of which were on the same sets of animals introducing a source of non-independence that we dealt with in our analysis (see "Analysis" below). We also noted whether studies were laboratory or field-based, and whether study methods were observational or experimental. We then assigned each study to one of the following three study designs: Studies that had taken a single wild population and then used an independent design to measure behaviour across different environmental conditions, such as increased temperature or CO_2 levels, were categorised as ‘experimental manipulations of environmental conditions’. Where behaviour had been measured across two or more populations that exist in different environmental conditions, studies were labelled as ‘cross-sectional’. Finally, studies that considered populations on a temporal scale were marked as ‘longitudinal’. We also noted the precise way in which behaviour was quantified, to account for non-independence in methodologies between different studies. This random effect included a total of 19 methods (appendix A).

Quantitative data

Because dependent variables measured across the studies were highly variable due to a lack of consistency in measuring and defining behaviours, we selected Hedge’s g as an effect size statistic that standardises the dependent variable (Lipsey and Wilson, 2001).

We calculated Hedge’s g with a bias correction and the associated variance based on the standard error, to account for studies with small sample sizes (Table S1.2). Hedges g values were calculated from the control and experimental mean values, sample sizes and standard deviations for each study (appendix A).

For studies that considered a relationship between two continuous variables, we calculated values for the Pearson’s correlation (r) with a Fisher’s z transformation to ensure a normal distribution and converted to Hedge’s g values (Table S1.2). We estimated variance due to sampling error as the standard error of each estimate squared (Hadfield, 2010, Table S1.2). Latency time is often used to measure exploration, boldness, and activity. However, longer periods of time do not always equate to greater levels of boldness/exploration or activity. To ensure our biological interpretations were correct and uniform across estimates, we multiplied effect sizes by -1 for instances where higher values do not equate to greater expressions of behaviour. In other words, we reversed the direction of the behavioural change. This was the case for 60 data points across 26 papers. Following this standardisation, all effect sizes had the same directionality: positive effect size indicates an increase in behaviour, and a negative effect size indicates a decrease in behaviour.

To account for phylogenetic non-independence in our models, we obtained the phylogenies for all species using the NCBI common tree, which is based on molecular phylogenies (Figure S1.2) and was the only available tree with complete species coverage. We produced a single phylogeny for all the species in our dataset. To improve the resolution of this phylogeny, we randomly resolved the polytomies. Our final phylogeny consisted of a tree with 103 tips, and 102 nodes, with a subsequent resolution of 100%. We then computed an inverse phylogenetic matrix that was incorporated into all our models following Moiron *et al.* (2020). To ensure we had controlled for the two sources of among species variation: a shared evolutionary history (i.e., phylogeny) and a shared ecology, we also included a species random effect in all our models (Kruuk and Hadfield, 2007).

1.2.3 Analysis

For all analyses and plots, we used R v3.5.1 (R Core Team, 2019) and the bayesian “MCMCglmm” package (Hadfield, 2010). Phylogenies were produced using the ‘ape’ package (Paradis and Schliep, 2019) and were randomly resolved using the bifurcatr() function in the ‘PDcalc’ package (Nipperness, 2016). To evaluate potential publication bias, we produced funnel plots and ran an Egger’s regression analysis to visually and statistically test if the distributions of effect sizes were symmetrical (Stuck *et al.,* 1998, Figure S1.3). We also calculated Orwin's fail safe N (Orwin, 1983), which uses the ‘trivial’ effect size to determine the number of additional missing studies that would be needed to bring the true effect size under the trivial effect size and render our results non-significant.

Meta-analytic models

We built Bayesian generalised linear mixed effects models (GLMMs) based on Gaussian distributions. In all models, behaviour and environmental axes were fitted as categorical fixed effects. The Hedge’s g sampling variances were also included in all models (Table S1.2). Moreover, we included study identity (i.e., paper reference), the phylogeny, method of measuring behaviour (19 levels, appendix A), and animal group (avian, crustacean, mammal, teleost, other) as random effects in all models. All studies included in our analyses utilised an independent design, such that animals were split and placed in either a control or treatment group. However, for some studies, we extracted multiple effect sizes from the same sample of animals. For example, where studies measured two behaviours, we extracted effect size estimates for each behaviour separately. However, these two estimates would be non-independent since they came from data collected from the same sample of animals. To account for this non-independence, each data point was assigned with an ‘animal sample identity’. In total, our 381 quantitative data points were collected by using 217 different animal samples.

All models were based on two chains, 1,550,000 iterations, with the first 50,000 discarded as a burn in, and a thinning interval of 100 (Table S1.3). Due to model complexity and to ensure convergence, a weakly informative parameter-expanded prior was selected, built on the following parameters: variance matrix, V=1, degree of belief parameter, nu=0.002, prior mean, αmu=0, covariance matrix, α=1000. (Hadfield, 2010). Histograms of fixed and random effect posterior distributions were produced to visually assess the precision of posterior mean estimations. Model convergence and the presence of autocorrelation were analysed visually from trace and density plots (Figure S1.4) and we compared simulated data of 100 models against our data to check the fit of all models (Figure S1.5). We also conducted a Gelman diagnostic analysis (Gelman and Rubin, 1992), to calculate a scale reduction factor and assess the convergence of the two

Markov chain Monte Carlo (MCMC) chains (Table S1.4). A scale reduction factor of 1.01 or less suggests good convergence between MCMC chains (Vehtari *et al.*, 2021).

We calculated unconditional mean effect sizes for each effect size, using the posterior distributions from each of our models. Unconditional mean effect sizes were calculated using weighted average of each level for our fixed effects, across the different combinations of fixed effects in each model (Tarka *et al*., 2018). For both conditional and unconditional model estimates, we computed 50% and 95% credible intervals. We also calculated the probability of direction (PD) as an index of effect existence (Makowski *et al.*, 2019). The PD is the probability, calculated as a percentage between 50%-100% that the posterior distribution of a model is positive or negative, and is based on posterior mean values. Whilst the PD can correspond with the frequentist *P*-value (Makowski *et al.,* 2019), we include the PD purely as a visual aid to show the extent to which an effect is positive or negative. We used credible intervals to assess the significance of effects in our models. Specifically, we consider an effect to be significant if credible intervals do not overlap zero.

We also calculated the absolute magnitude mean effect sizes for three behaviours (Boldness, Activity and Exploration), three axes of environmental change (climate change, changes in CO_2 and direct human impact), fish data, bird data, field data and laboratory data, using methods based on Moiron *et al.* (2020) and Noble *et al.* (2018). We excluded sociability, aggression, biotic exchanges, changes in nutrients, and longitudinal study design from this analysis, due to small sample sizes in our dataset. The absolute magnitude of the effect size gives additional information compared to the traditional, directional, effect sizes by indicating whether animals do respond to HIREC but are just inconsistent in the direction of the response. We ran separate intercept models for each of the above parameters, and then obtained the absolute values (i.e., without a positive or negative direction) from the model by folding the posterior distribution of the effect size for each intercept model (Morrissey, 2016). As a guide, we considered overall magnitude effect sizes of over 0.8 to indicate a large response to HIREC (Cohen,1992).

Heterogeneity estimates (I^2) were calculated for each random effect in all models (see above), whilst controlling for sampling variance. I^2 is a proportion of total variance in the response variable explained by a focal random effect (Huedo-Medina *et al.*, 2006).

Under the classification by Higgins and Thompson (2002), total sampling variance over 50% is ‘medium’ and over 75% is ‘high’. Furthermore, Senior *et al.* (2016) identified that for meta-analyses, total heterogeneity usually falls between 60 and 90%.

In total, we ran eight separate models (Table S1.3). Initially, we generated a global meta-analytic model based on the full quantitative dataset of 90 studies and 381 data points. Behavioural domain, environmental axes, study design (experimental manipulations of environmental conditions, cross sectional or longitudinal) and data background (laboratory/field) were fitted as categorical fixed effects. Reference categories for the fixed effects were set as exploration (for behavioural domain), climate change (for environmental axes), experimental manipulations of environmental conditions (for study design) and laboratory (for data background), i.e., the best represented categories in the dataset. We ran three sub-models for the three individual environmental axes that dominated our dataset: Climate change, changes in CO_2 and direct human impact, and four additional models based on subsets of the data included in the global model. Specifically, we ran separate models for laboratory and field studies, and separate models for fish and bird studies, using the same reference categories as our initial model.

1.3 Results

1.3.1 Qualitative analyses

In total, 418 data points from 102 studies and 103 species were included in qualitative analyses. ‘Climate change’ and ‘direct human impact’ were the best represented axes of environmental change (135 and 112 incidences respectively). A majority of studies used laboratory-based methods (297 incidences), except for studies on ‘direct human impact’ (Figure 1.2). In terms of behaviour, ‘boldness’ and ‘exploration’ were the most studied (131 and 132 incidences respectively: Figure 1.2). Most research focussed on fish and birds (202 and 68 incidences respectively). For birds, 83% of studies were field based, whereas 87% of fish studies were conducted under laboratory conditions (Figure 1.2).

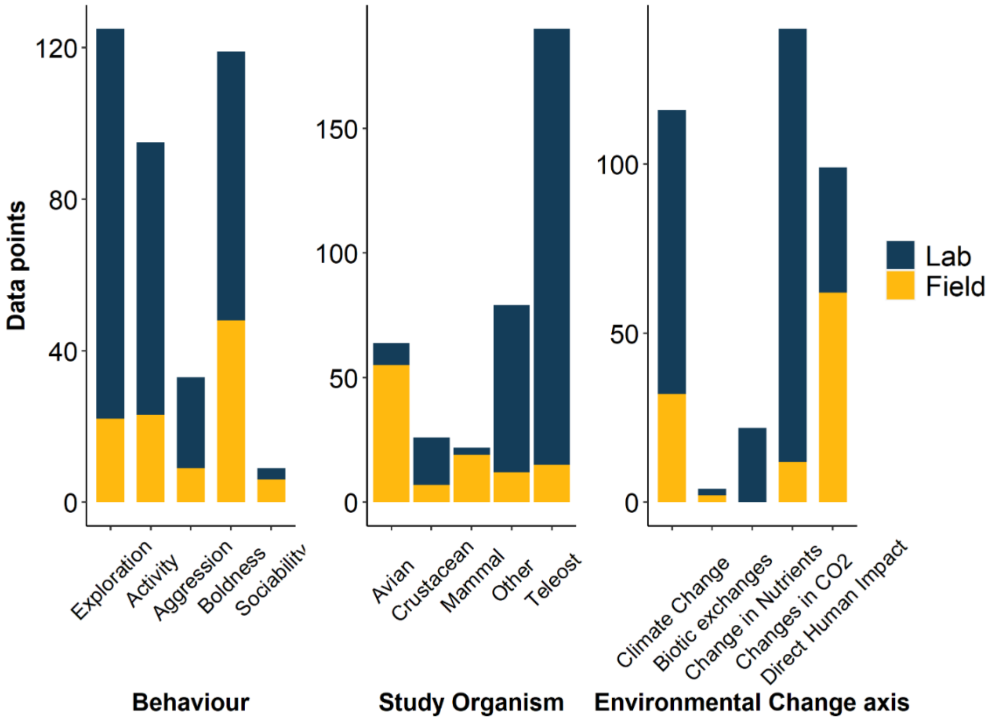

Figure 1.2: Number of data points compiled from studies addressing the effect of environmental change on animal behaviour in terms of axes of environmental change, behaviours, and taxa. Y axis refers to individual data points. Some studies considered more than one axis of behaviour and/or environment and are included in more than one category.

1.3.2 Quantitative analyses

There were 381 data points from 90 studies included in quantitative analyses. Orwin's fail safe number showed that an additional 381 non-significant studies would be required to change the overall effect. The Egger’s regression analyses were also non-significant (*P*=0.14), further supporting a lack of publication bias (Figure S1.2). Conditional estimates for all models are presented in Figure S1.6.

Global model

All parameter distributions had 95% credible intervals that overlapped zero, indicating that there are no clear directional responses to HIREC across all data (Figure 1.3). Nonetheless, in terms of environmental axes, increased behavioural expression to direct human impact, was the most consistent parameter, with an effect size (g) of 0.48 (95% credible intervals: -0.46, 1.41) and probability of direction (PD) of 75.27%. In terms of behaviour, exploration showed the most increase, with an effect size of 0.32 (-0.53, 1.18) and a probability of direction of 79.07%. Sociability showed the most decrease in response to HIREC, with an estimate of -0.82 (-2.93, 1.26) and a PD of 78.13%.

However, for all these estimates, credible intervals overlap zero, and in general, mean estimates are centred around zero.

Environmental axes sub-models

The environmental axes sub-models showed one clear response where credible intervals did not overlap zero: aggression decreased under increased CO_2 conditions, with an effect size of -4.43 (-7.87, -1.30) and a PD of 98.53% (Figure 1.3). However, since this estimate is based on just 6 data points from a single study, our result should be treated with caution. The direct human impact model showed a tendency for consistent responses. Specifically, although credible intervals overlapped zero, the direct human impact model had effect size estimates of 0.62 (-0.41, 1.67) and 0.40 (-0.73, 1.50), with PD values of 89.21% and 76.65% for boldness and exploration, respectively.

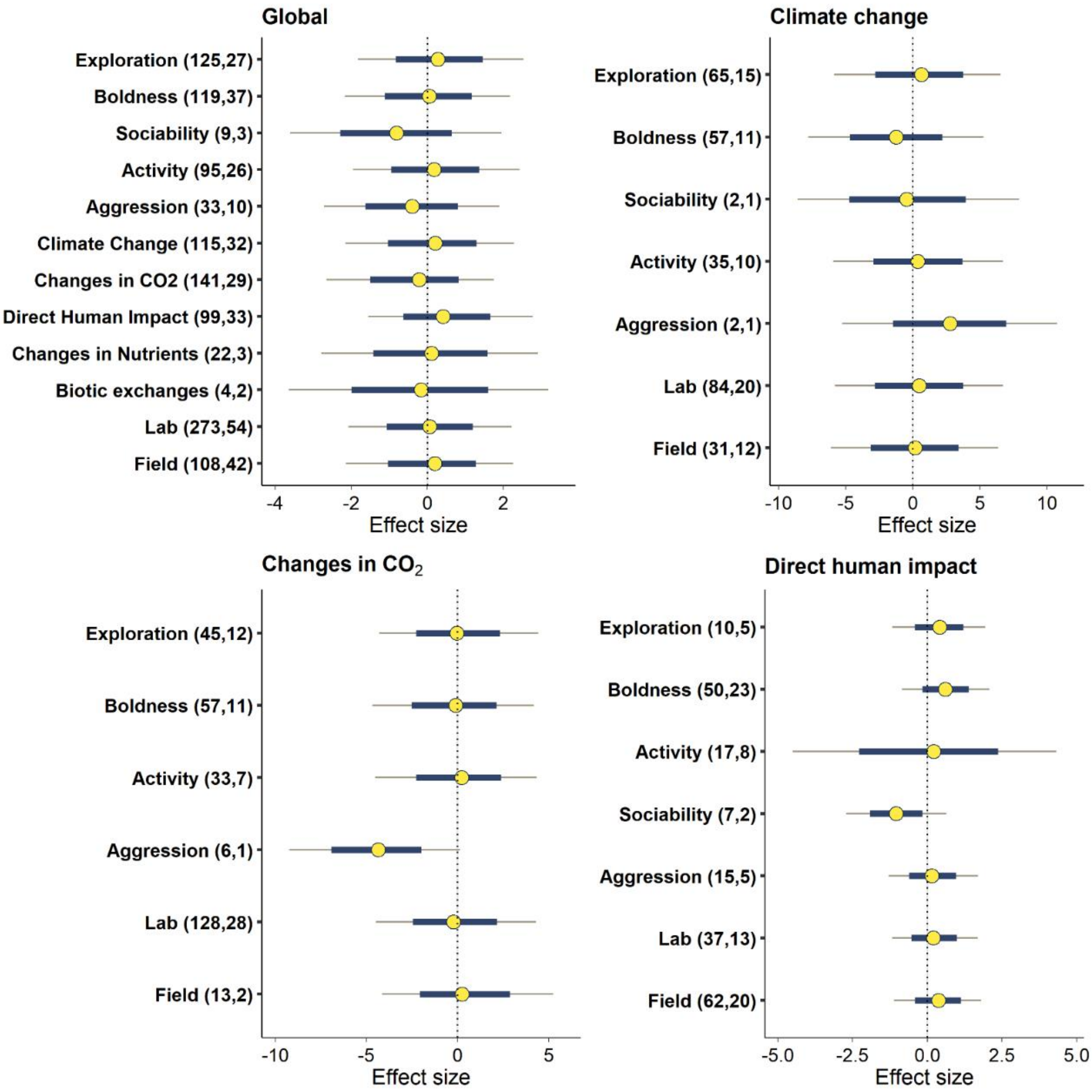

Figure 1.3: Model parameter estimates from our global model and environmental axes models. Points are unconditional posterior mean values. Thick and thin bars represent 50% and 95% credible intervals, respectively. Numbers next to parameters are the number of data points and the number of studies for each parameter, respectively.

Field and laboratory data models

Models ran separately for laboratory and field studies did not yield any parameters with credible intervals not overlapping zero, but there was a general tendency for behavioural responses to be stronger in the field data compared to laboratory data, such that for field data, credible intervals overlap zero to a lesser extent than for laboratory data (Figure 1.4). Specifically, for field data, boldness showed the strongest directional response, with an effect size estimate of 1.46 (-0.02, 2.91) and a PD of 97.44%, compared to an effect size estimate of -0.27 (-1.77, 1.20) and a PD of 65.76% for laboratory data. In terms of axes of environmental change, climate change had the most directional response in field data, with an effect size of 1.01 (-0.26, 2.44) and a PD value of

79.79%, compared to 0.37 (-1.13, 1.81) and 60.30% for laboratory data, although for both, credible intervals did overlap zero. Finally, all three types of study (experimental manipulations of environmental conditions, cross-sectional and longitudinal) showed stronger behavioural responses for field data, with effect sizes and PD estimates of 0.93 (-0.31,2.22), 1.06 (-0.39,2.48), 0.91 (-0.70, 2.55) and 93.77%, 93.47% and 87.58% respectively. For laboratory data, experimental manipulations of environmental conditions, cross-sectional and longitudinal studies had effect sizes and PD estimates of 0.22 (-1.12,1.81), -0.37 (-2.11, 1.24), 0.09 (-2.08,2.54) and 66.14%, 67.83% and 52.69% respectively. Nonetheless, for both models, credible intervals overlapped zero for these parameters.

Taxa specific models

For both the fish and the bird models, there were no effect sizes where credible intervals did not overlap zero, and for most parameters, mean estimates were centred around zero (Figure 1.4). Nonetheless, our model showed a tendency for an increase in exploration in fish, with an effect size of 1.11 (-0.63, 2.90) and a PD of 89.85%, whilst birds showed a tendency for decreased exploration, with an effect size of -0.74 (-3.10, 1.82) and a PD of 75.96%. Furthermore, behavioural responses of birds were generally slightly higher than responses of fish, particularly for boldness and climate change. Specifically, in birds, boldness had mean effect sizes of 1.53 (-0.70, 3.91), and a PD value of 92.79%, compared to -0.42 (-2.02, 1.27) and 70.33% for boldness in fish. Behavioural responses to climate change had a mean effect size of 1.45 (-1.39, 4.19) and a PD value of 87.03% in birds, compared to 0.60 (-1.13, 2.29) and 77.19% in fish.

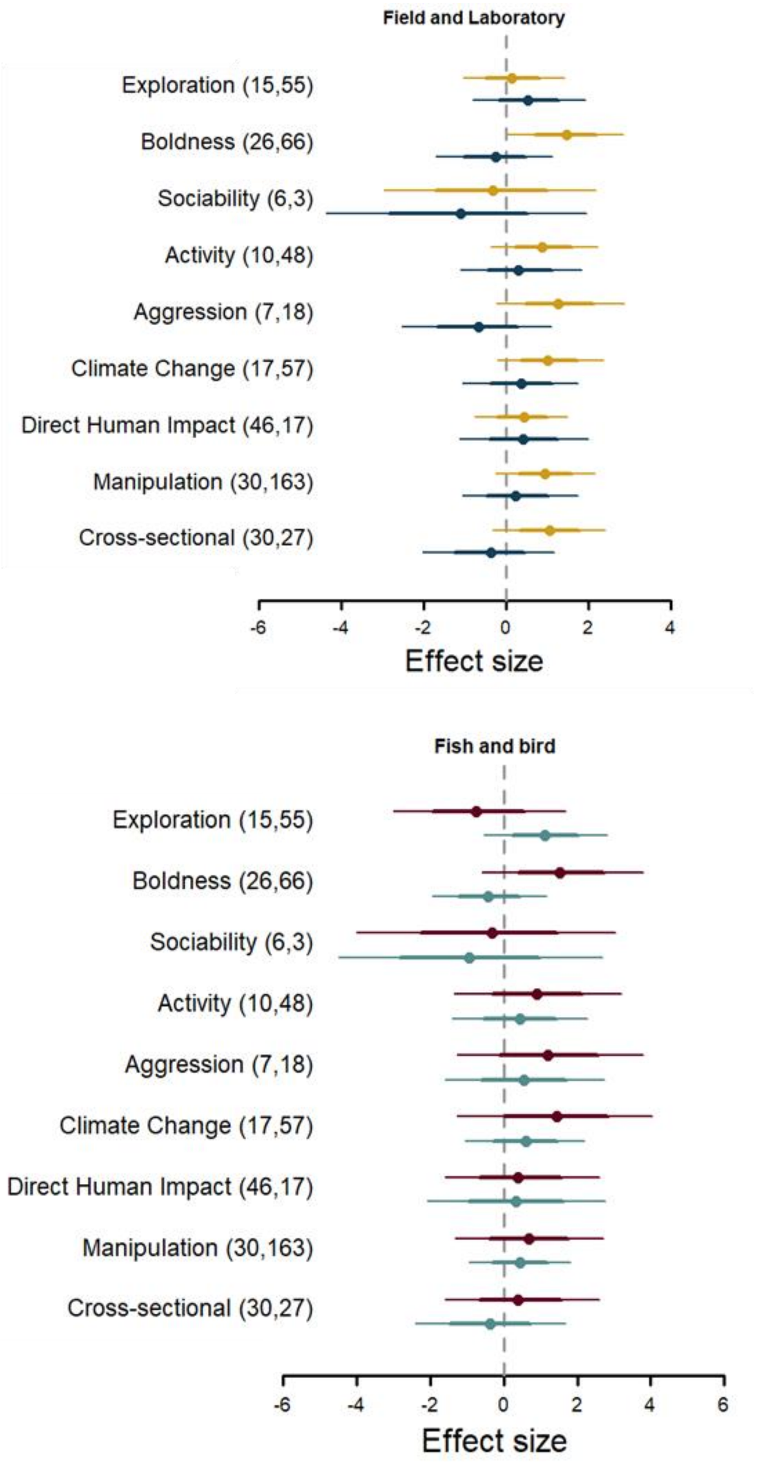

Figure 1.4: Parameter estimates for field (top, yellow) and laboratory (top, blue) models and for bird (bottom, red) and fish (bottom, pale blue) models. Points are unconditional posterior mean values with 50% and 95% credible intervals. Numbers next to parameter labels are the number of data points for field and laboratory (top) and fish and bird data (bottom), respectively.

1.3.3 Absolute magnitude of the effect sizes

Our absolute magnitude effect size estimates were all over 0.8, indicating that when the direction of the effect sizes is ignored, animals show a strong behavioural response to HIREC and significant differences between behaviours and axes of environmental change do occur (Figure 1.5). Furthermore, credible intervals for all parameters are not close to zero, indicating significant responses to HIREC. Exploration showed the strongest overall response to HIREC, with an absolute effect size of 3.63 (2.55, 5.23). Boldness also showed a strong response to HIREC, with an effect size of 2.39 (1.41, 3.60). The responses of both boldness and exploration towards HIREC were significantly higher than that of activity (0.89 (0.45, 1.44)), based on none-overlapping credible intervals for these parameters. Behavioural responses were strongest under climate change (3.70 (2.60, 5.37)), and responses to climate change were significantly greater than responses to direct human impact (1.06 (0.70, 1.50). For study design, overall responses were significantly greater for experimental manipulations of environmental conditions (2.31 (1.93,2.74) than for cross sectional studies (0.64, 1.58). Finally, the overall responses of behaviour in the laboratory (2.51 (1.97, 3.36) were higher than in the field (1.50 (0.79, 2.36), although credible intervals between laboratory and field effect sizes did slightly overlap.

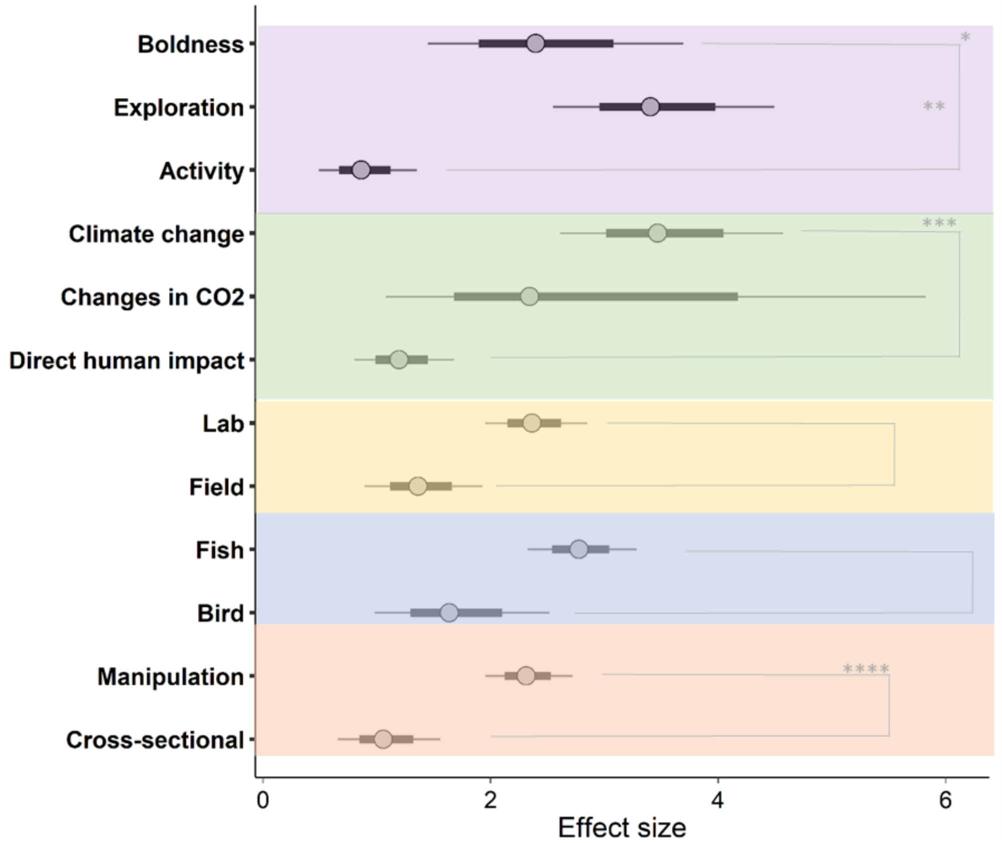

Figure 1.5: Absolute magnitude effect sizes from folded distributions, calculated from individual intercept models. Thick and thin bars represent 50% and 95% credible intervals, respectively. Grey lines and shading group together the levels of behaviour (purple), environmental change (green), study form (yellow), animal group (blue) and study design (orange), and * indicate where there are significant differences between two parameters within these groups.

1.3.4 Model heterogeneities

For all models, total heterogeneity was over 90% (Table 1.1). For the global model, residual heterogeneity was high, at 45%, indicating that effect sizes were variable within each random effect category in our models. Animal sample made up between 26-32% of total model heterogeneity across the global, climate change, direct human impact, laboratory, and fish models. Effect sizes therefore varied more with the specific sample of animals being tested than among individual studies. Phylogenetic heterogeneity was moderate for the field model (11%) and high for the bird model (26%), indicating that there is a substantial phylogenetic signal in behavioural responses to HIREC data collected in the wild and in birds, but not in other data sets. The methods used to measure behaviour made up 48% of model heterogeneity in the direct human impact model, 27% of model heterogeneity the bird model and 32% in the field model. Study design contributed to 20% of heterogeneity in the field and laboratory models. Therefore, effect sizes were variable across different measures of behaviour and study design for the direct human impact model, bird, field, and laboratory models.

Table 1.1: Heterogeneity estimates (I^2) for all Bayesian models. Numbers in brackets are standard deviations. Shading splits the models into environmental axes (green), study form (yellow) and taxa (blue).

	Total	Study	Phylogeny	Species	Animal group	Sample	Method	Residual
Global	0.99 (0.001)	0.17 (0.05)	0.01 (0.02)	0.01 (0.02)	0.04 (0.09)	0.26 (0.06)	0.01 (0.02)	0.45 (0.07)
Climate change	0.99 (0.001)	0.13 (0.09)	0.04 (0.05)	0.02 (0.03)	0.13 (0.18)	0.26 (0.12)	0.03 (0.05)	0.37 (0.12)
Changes in CO2	0.98 (0.01)	0.14 (0.14)	0.05 (0.06)	0.02 (0.03)	0.26 (0.30)	0.04 (0.04)	0.10 (0.11)	0.38 (0.19)
Direct Human Impact	0.97 (0.01)	0.14 (0.14)	0.06 (0.07)	0.07 (0.07)	0.10 (0.14)	0.18 (0.11)	0.48 (0.16)	0.07 (0.07)
Lab	0.99 (0.002)	0.16 (0.07)	0.02 (0.02)	0.20 (0.14)	0.09 (0.14)	0.30 (0.08)	0.02 (0.03)	0.39 (0.09)
Field	0.98 (0.007)	0.17 (0.14)	0.11 (0.14)	0.20 (0.13)	0.14 (0.18)	0.01 (0.012	0.32 (0.15)	0.02 (0.03)
Fish	0.99 (0.001)	0.22 (0.11)	0.04 (0.05)	0.02 (0.03)		0.32 (0.09)	0.03 (0.04)	0.37 (0.08)
Bird	0.99 (0.006)	0.14 (0.14)	0.26 (0.22)	0.10 (0.08)		0.03 (0.04)	0.27 (0.15)	0.08 (0.07)

1.4 Discussion

We have provided insight into the patterns and drivers of behavioural responses to environmental change across a range of taxa. Our results show that animals do have strong absolute behavioural responses to HIREC, and that the magnitude of response varies across behaviours and across different forms of HIREC. Specifically, behavioural responses to climate change were significantly greater than responses to direct human impact. Furthermore, exploration showed a significantly greater response to HIREC than did activity. Animals therefore do respond to HIREC behaviourally, but the direction of the responses are variable, such that behaviour may be upregulated and/or downregulated in response to HIREC. Finally, our results show that study design, methods used to measure behaviour, individual animal samples and phylogeny all contribute to variation, i.e., heterogeneity, in behavioural responses to HIREC.

1.4.1 Global behavioural responses to HIREC

The lack of significant directional responses in our global model could be due to the differences between the types of studies included in the global model. For example, manipulation studies measure intra-generational plastic responses to environmental conditions, whilst cross sectional studies measure differences between two populations, which could reflect intra or inter-generational plastic changes, or evolutionary responses to divergent selection pressures (Kinnison and Hendry, 2001). These differences likely generate a lot of ‘noise’, making it difficult to infer underlying mechanisms behind behavioural responses. Nonetheless, we did find a non-significant tendency for increased behavioural expression under direct human impact, specifically a non-significant tendency for increased expression of boldness under HIREC in field-collected data (see below). As boldness captures responses to risky situations (Reale *et al.,* 2007), our results suggest that animals may start to take more risks in response to increasing HIREC. To persist under conditions of direct human impact, e.g., urbanised areas, risk taking is assumed to be beneficial (Lowry *et al.,* 2013). Thus, increasing boldness might be a general adaptive behavioural response to HIREC, but additional tests are required before this hypothesis can be accepted.

All behaviours expressed strong absolute responses to HIREC, while boldness and exploration showed the strongest response. Furthermore, experimental studies manipulating environmental conditions over a short-term (e.g., Kvarnemo, 1998) seem to induce stronger behavioural responses than cross-sectional studies comparing populations living in different environments (e.g., urban vs. rural; Evans et al., 2010). The lack of overall response in the global model, combined with the high absolute responses for experimental manipulations of environmental conditions studies, and in boldness and exploration, indicates that both substantial increases and decreases in behaviour are present. Organisms may invest in buffering the consequences of environmental change, which could reflect differences in boldness and risk-taking behaviours (Du Plessis *et al.,* 2012). In terms of exploration, organisms might invest in gathering information to reduce uncertainty or invest more in finding food that may have been lost under HIREC (Donaldson *et al.,* 2007), which will likely result in increased exploration (Mathot *et al.,* 2012, Gunn *et al.,* 2022). Alternatively, organisms can become less exploratory to conserve energy and maximise use of the remaining resources (Gremillet *et al,* 2012). Different species, populations and even conspecifics within a population differ in the ecological and environmental characteristics they face, but also on what aspect of the species ecology (e.g., competition, predation pressure), demography (birth rate, death rate) or phenology (timing of reproduction, timing of migration) HIREC is affecting (Wong and Candolin, 2014). For example, a recent review of how organisms respond to HIREC predicts that individuals that have high basal stress levels, display shyness, and have high degrees of plasticity, i.e., have a reactive phenotype, will be more suited to cope with HIREC than individuals with proactive phenotypes (Geoffrey *et al.,* 2020). Therefore, individuals, species and populations could have different optimal behavioural responses to cope with and potentially buffer the effects of environmental change, leading to an absence of clear directional behavioural responses, but the presence of strong absolute behavioural responses in our data.

The strong absolute responses to experimental manipulations of environmental conditions identified in our results compared to cross sectional studies also indicate that length of exposure to HIREC could play a role in determining the optimal responses to HIREC, such that initial, short-term, sometimes extreme behavioural responses may not always be optimal in the longer term (Sih *et al.,* 2011). Furthermore, evolutionary rates have also been shown to decrease with time since the separation of two populations, perhaps because evolution slows as a population reaches a new optimum condition (Kinnison and Hendry, 2001). Short term experimental manipulations of environmental conditions may therefore elicit stronger initial responses than cross sectional studies comparing two different populations that have evolved to their environmental conditions over a long period of time. Here we show that animals respond strongly to HIREC in an absolute sense, but further research is needed to reveal what is causing the variation in direction of those responses.

1.4.2 Behavioural responses to HIREC in the laboratory versus the field

Laboratory and field research provide complementary insights into the behavioural responses of organisms to change. Although our global model indicated no clear difference between field and laboratory collected data, separate models for field and laboratory data generally indicate that the behavioural responses might be stronger in the field-collected data, although this difference is marginal. Research on animal behaviour is particularly sensitive to the environment in which observations occur (Calisi and Bentley, 2009). For example, a meta-analysis on repeatability identified that behaviours measured in the field were more repeatable than behaviours measured in the laboratory. This difference could be because laboratory experiments do not account for contextual information that can enhance behavioural variability within and across individuals, such as the presence of micro-niches (Bell *et al.,* 2009), seasonal variation across different populations (Both *et al.,* 2010), or the presence and state of heterospecific competitors in the field (Lehtonen *et al.,* 2010).

Whilst there was a tendency for greater directional responses in our field data when compared to laboratory data, the absolute magnitude of behavioural responses was greater in laboratory data. Although the difference in absolute effect sizes between the laboratory and field data was not significant (slight overlap in the 95% credible intervals), our result suggests that behaviours may both increase and decrease to a greater extent in response to HIREC when measured in the laboratory compared with in the field. Furthermore, the absolute magnitude of behavioural responses to climate change were higher than responses to direct human impact. Laboratory studies dominate the climate change dataset, whilst the direct human impact dataset is dominated by field studies. It is plausible that a difference in behavioural responses to HIREC between laboratory and field studies is at least partly a driver of this difference in overall magnitude effect sizes. Whilst there are some studies that have used field data to support responses identified in the laboratory (Osborn and Briffa, 2016), our results suggest that there is a need for a balanced combination of field and laboratory studies, across behaviours, forms of HIREC and across different taxa, in order to fully understand the complexity of behavioural responses to HIREC (Campbell *et al.*, 2009).

1.4.3 Taxon specific behavioural responses to HIREC

Our results identified a tendency for higher behavioural responses in birds compared to fish, with research on birds focussed on *in situ* tests of boldness between urban and rural environments. In contrast, behavioural responses in fish were mostly centred around zero, with research focussed on the manipulation of temperature and CO_2 in tanks and monitoring behaviour (Nowicki *et al.*, 2011). This result may reflect differences in the extent of temperature change between terrestrial and marine ecosystems. Long and short-term temperature changes in terrestrial environments are more variable than in marine environments, thus terrestrial organisms may be predicted to have developed responses to cope with short term changes which could in turn buffer the effects of longer-term temperature variability (Steele, 1985). Marine organisms are unlikely to have developed mechanisms to cope with short-term variability, expressing different or weaker responses compared to terrestrial organisms (Steele, 1985). This may also explain why behavioural responses were generally less pronounced in fish than in birds. Evolutionary or developmental history might define how well taxa are equipped to respond behaviourally to HIREC, both now and in the future.

1.4.4 Heterogeneity in behavioural responses to HIREC

One of the issues in understanding behavioural responses to environmental change, and the rationale for this meta-analysis, is that there is apparent inconsistency in responses within taxa (Flood and Wong, 2017), even where the behaviours have been measured across the same axis of environmental change. Our heterogeneity results provide an important insight into the drivers of this inconsistency and variability in behavioural responses to HIREC. In our global model, 45% of model heterogeneity was attributed to residual heterogeneity, such that effect sizes are variable within each model random effect (study, phylogeny, animal group, animal sample, study design, and measure of behaviour). This highlights the importance of accounting for context specific factors that could influence behaviour when analysing behavioural responses to HIREC (Beekman and Jordan, 2017). Furthermore, for all models except for the changes in CO_2, bird and field models, heterogeneity estimates for animal sample were high (between 26% and 32%). The specific sample of animals on which behaviour is measured therefore creates variability in effect sizes. This could be due to inherent differences in behaviour, and in differences in behavioural responses to environmental change, across different individuals, driving variation in group level behavioural expression (Sih, 2013).

The method used to measure behaviour, in the case of the direct human impact, field and bird data, were substantial sources of model heterogeneity. There are numerous different methods in which behaviours can be measured or observed (Cuthill, 1991). For example, ‘boldness’ has been used to define different traits across different studies, which can make inter-study comparisons difficult (Beekman and Jordan, 2017). Whether an individual expresses ‘activity’, ‘exploration’ or ‘boldness’ depends on the environment, context, and the timescale of any environmental change. Exploration refers to movement in a new situation, activity refers to a non-novel, non-risky scenario, and boldness refers to response to a risky situation (Reale *et al.*, 2007). However, under HIREC, behaviours measured via movement could instead be recorded solely as exploration if we assume environmental change places organisms in new or risky situations. To accurately identify behavioural responses to HIREC, clear species-specific hypotheses, definitions and predictions are required.

Heterogeneity estimates for phylogeny were generally small, suggesting that responses to HIREC do not reflect a shared evolutionary history. This result is perhaps to be expected, given that HIREC is a recent phenomenon (Wong and Candolin, 2015), thus there has been little time for evolutionary divergence to occur. However, the role of phylogeny varied across taxa. While fish data had low heterogeneity estimates for phylogeny, bird data estimates for phylogeny were the highest at 26%. As mentioned above, changes in terrestrial environments are more variable than in marine environments (Steele, 1985), so it is possible that birds have had a longer history of exposure to substantial environmental change, resulting in deeper divergence in response, explaining the higher phylogeny heterogeneity estimate. Phylogeny also explain 11% of variation in the field model. However, as fish comprised most of the laboratory data and birds most of the field data, we cannot determine whether there are response differences between taxa or the mode of study.

1.4.5 Future directions

Explaining the behavioural variation observed in our models, and the evolutionary consequences of HIREC, requires greater focus on differences in behaviours at the individual, rather than population level. This shift in focus is because individual variation in behavioural responses expressed within a population can define the strength of selection on behaviours imposed by HIREC (Dall *et al.,* 2004). Moreover, focussing on individual variation expressed under HIREC via repeatability and/or heritability (via additive genetic variation) will allow for the strength of responses to selection to be quantified. Generally, repeatability and heritability of behaviours are moderate (Bell *et al.* 2009, Dochtermann *et al.,* 2020), indicating that behaviours will respond to selection. However, it is unclear whether repeatabilities or heritabilities of behaviours expressed under HIREC differ from those measured under more normal or natural circumstances. Our models are focussed on population mean differences, as it is this level of response that dominates the current literature, so we cannot identify individual differences in responses to HIREC within a population. Understanding differences at an individual level, in terms of both individual differences and the heritability of behaviour (Hansen *et al.,* 2011) would therefore deliver greater insight into the evolutionary ramifications of behavioural responses towards HIREC.

1.5 Conclusions

In conclusion, we have provided an insight into predictors of behavioural responses to HIREC and offer four recommendations that, if addressed, would forward understanding of the mechanisms and drivers behind behavioural responses to HIREC.

Firstly, increasing the representation of field-based research for fish and laboratory-based research for birds is crucial to identify responses to HIREC in a variety of contexts and to pinpoint underlying mechanisms in controlled settings. Secondly, standardisation of methods and study designs used to measure behaviours in both laboratory and field studies. Thirdly, a consideration of context specific factors, such as animal taxa, phylogeny and the specific sample of animal used in studies. Combined, this would greatly assist with identifying generalised responses and aid comparison across contexts. Finally, a greater consideration of individual differences in behaviour would improve understanding of both the evolutionary ramifications and the drivers of behaviour that cannot be fully understood by considering population level responses in isolation. A full understanding of the behavioural responses of organisms to HIREC, as well as the drivers behind these responses, can then be used to accurately predict broader scale population and community level dynamics.

Chapter 2

2. Variation in the behaviour of an obligate corallivore is influenced by resource availability

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Contribution of authors

RLG, IRH, ACA and SAK conceived the ideas. RLG designed the methodology, collected the data with support from NN and analysed the data. RLG led the writing of the manuscript. All authors contributed critically to manuscript revisions.

Abstract

Marine environments are subject to increasing disturbance events, and coral reef ecosystems are particularly vulnerable. During periods of environmental change, organisms respond initially through rapid behavioural modifications. While mean population level modifications to behaviour are well documented, how these shifts vary between individuals, and the relative trade-offs that are induced, are unknown. We test whether the frequency and time invested in different behaviours varies both between and within individuals with varying resource availability. To do this, we quantify differences in four key behavioural categories (aggression, exploration, feeding, and sociability) at two sites of different resource availability, using an obligate corallivore butterflyfish species (*Chaetodon lunulatus*). Individuals on a low resource site held larger territories, invested more time in exploration traded-off by spending less time on aggression, feeding and sociability. Repeatability measures indicated that behavioural differences between sites could plausibly be driven by both plasticity of behaviour within individuals and habitat patchiness within feeding territories. By combining population-level means, the co-correlation of different behaviours, and individual-level analyses, we reveal potential mechanisms behind behavioural variation in *C. lunulatus* due to differences in resource availability.

2.1 Introduction

Behaviour mediates an organism’s complex interactions with both its biotic and abiotic environment. Spatial and temporal variation in the environment can affect various aspects of behaviour, such as predation and competition, which in turn can alter species interactions (Anholt, 1997). Changes in behaviour therefore have the potential to shape ecological communities (Delarue *et al.,* 2015). As a result, behaviour plays a pivotal role in how individuals can adjust to rapid environmental change (Wong and Candolin, 2014, Nagelkerken and Munday, 2016). For example, in marine systems, reef degradation and coral loss can influence reef fish recruitment and settlement (Dixson *et al.,* 2014), predator avoidance and boldness (Böstrom-Einarsson *et al.,* 2018), aggression (Keith *et al.,* 2018) and foraging (Nash *et al.,* 2012). The capacity for a population to acclimate and/or adapt behaviourally to severe environmental change can be determined by factors such as if and how behaviour is transmitted between individuals (Keith and Bull, 2017), geographic variation in biotic interactions (Early and Keith, 2018), and the likelihood that initial acclimation contributes to evolutionary or ecological traps (Schlaepfer *et al.,* 2002). Traps can occur when cues become unreliable under new environmental conditions, leading to maladaptive behaviour and reduced fitness (Schlaepfer *et al.,* 2002). Individuals within a population do not always respond in the same way and can feedback to generate frequencies of alternative strategies within a population (Dall *et al.,* 2004). Individual behaviour can, therefore, scale-up to influence population dynamics, with broader community and ecosystem level consequences (Wong and Candolin, 2014). To understand any potential mechanisms or limitations on adaptation, there is a need to understand the role of individual variation and associated trade-offs in responses to environmental change.

Behavioural responses to environmental change can be measured at three levels: between populations, between individuals within populations and within individuals. Population level behavioural responses to environmental change have been well documented and reviewed (Tuomainen and Candolin, 2011, Wong and Candolin, 2014). Recent research has focused on how individual differences in behaviour affect how organisms respond to change (Mathot *et al.,* 2012, Niemela and Dingemanse, 2018). Behavioural plasticity involves immediate changes in behaviour by individuals in response to the environment (Nussey *et al.,* 2007). Plastic behaviours could allow individuals to buffer the effects of environmental change. For example, butterflyfishes can show flexibility in foraging behaviour following a decline in resource availability (Zambre and Arthur, 2018). Personality refers to repeated correlated suites of behaviours that result in consistent responses by an individual across different behavioural contexts, such as mating or foraging, and across environmental gradients (Sih *et al.*, 2004, Bell *et al.*, 2009). When payoffs are based on the behavioural history of individuals, and the frequency with which different traits and strategies are expressed, these can be shaped over time through natural selection (Dall *et al.*, 2004). Consistent behaviours across multiple contexts are used to indicate the presence of a personality (Hayes and Jenkins, 1997, Bell *et al.*, 2009). This consistency can be measured as behavioural repeatability: the proportion of variation across the population that can be attributed to differences between individuals (Lessells and Boag, 1987). However, because repeatability is a statistic of the population, this measure cannot reveal the extent to which individuals vary in their consistency (Sih *et al.*, 2009). It is therefore also important to account for the magnitude of individual variation around the mean population level (Dochtermann and Royaute, 2019). Considering behaviour on an individual level can, therefore, reveal variation that is not apparent in population mean level responses (Barbasch and Buston, 2018, Gunn *et al.*, 2021).

Evidence suggests that differences in behaviour within and between individuals can constrain the available strategies for coping with environmental change (Koolhaas *et al.*, 1999). For example, less aggressive, but more exploratory individuals could be better able to cope with low resource availability by investing less in territory defense, which is costly where the resource reward is low (Righton *et al.*, 1997). Instead, individuals invest more in exploratory foraging to locate increasingly sparse food resources (Chandler *et al.*, 2016). Exploratory behaviours might be beneficial when individuals experience nutritional deficit, whereas aggressive behaviours are beneficial where resource availability is intermediate (Wyman and Hotaling, 1987). Empirical evidence supports this idea, such that resource availability has been identified as a determinant of territoriality across various taxa. Specifically, territoriality is lower, and territory sizes larger, where resource availability is lower (Justino *et al.*, 2012, Mazzamuto *et al.*, 2020). Individuals that persist in changed environments may do so because they show a high degree of behavioural plasticity, i.e., have shifted their levels of aggression and exploration, and/or because the population of persisting individuals show specific, consistent variation in behaviour, i.e., specific personality types (Kralj-Fiser and Schneider, 2011). To reveal how differences in behaviour within and between individuals can affect responses to environmental change and how that alters the frequency of different behaviours within a population through plasticity or selection, or a combination of both (Dingemanse *et al.,* 2010), we must move beyond exploring behaviours in isolation and consider explicitly how multiple behaviours are correlated, and thus potentially trade-off against one another, in different contexts (Dall *et al.,* 2004, Sih *et al.,* 2004).

Butterflyfishes are an excellent model system to understand the impact of resource levels on behaviour at both the population and individual level. Global declines in live coral cover directly translate to a decline in nutritional resource availability for butterflyfish species. Their diet and, as a result, their abundance, body condition and behaviour, are subsequently influenced directly by the availability and quality of live coral (Graham *et al.,* 2011). Butterflyfish territories have been shown to expand or break down when coral cover is low (Tricas, 1989), especially in specialist obligate corallivores (Pratchett *et al.,* 2014). The underlying mechanism appears to be linked to foraging strategies; reduced food resources lead to a nutritional deficit, so individuals must travel further to locate food and territorial boundaries break down (Zambre *et al.,* 2018). The same mechanisms are also linked to reduced aggression (Berumen and Pratchett, 2006; Keith *et al.,* 2018) and changes in social behaviour (Thompson *et al.,* 2019). As behaviour can influence the survival of individuals (Moiron *et al.,* 2020), understanding variation in behavioural responses between butterflyfish individuals and identifying the drivers of these responses could have important implications for their persistence.

We test the extent to which the frequency of butterflyfish behaviours, and the variation in these behaviours across individuals, are influenced by resource levels (i.e., coral cover), using existing variation in coral cover and an obligate corallivore (*Chaetodon lunulatus*). Specifically, using population and individual level approaches, we (1) test whether territory size is influenced by resource availability such that territories with higher resource availability are smaller; (2) test whether individuals at reefs with high resource availability are more likely to exhibit aggressive behaviours, while those at reefs with low resource availability are more likely to exhibit exploratory behaviours; and (3) calculate both behavioural repeatability estimates and estimates of individual variability around the population mean to determine variation in behaviour between individuals within sites. If behaviours are highly repeatable, then any differences in behaviour between sites are likely a consequence of selection on fixed behavioural types.

2.2 Methods

2.2.1 Study species and field sites

We collected field data using SCUBA between the 15th June and the 7th August 2019. Pilot data from abundance surveys were used to identify a species with strong pair bonding and territory defense behaviour. The most abundant obligate corallivore fitting this criterion was the oval butterflyfish, *Chaetodon lunulatus.* Yabuta and Berumen (2014) characterize *C. lunulatus* as monogamous and territorial with a strong pair bond, allowing us to observe the same breeding pair repeatedly *in situ*, by returning to the same territory on multiple occasions. It was not possible to record data blind because our study involved focal animals in the field.

The Wakatobi Marine National Park (WMNP) is located within the province of Southeast Sulawesi, Indonesia (5°41′S 124°0′E) within the coral triangle. Based on hard coral cover (resource availability), we selected two permanent monitoring sites around Hoga Island: Pak Kasims (PK) and Sampela (SAM, Figure S2.1). The high resource site, PK, was characterized by hard-coral cover of 40-50%, with abundant soft coral (Clifton *et al.,* 2010). In contrast, the low resource site, SAM, consisted of a gently sloping reef with coral cover of 10-20% and various rubble slips (Powell *et al.*, 2015). The sites are similar in terms of wave exposure, reef aspect and depth, with all work conducted between 3 and 10 m across both sites.

2.2.2 Survey methods

Coral cover

We used a long-term reef monitoring programme to obtain coral cover data for 2019. Using permanent transect locations, three replicate 50 m transects were conducted per reef zone (flat, crest and slope) at each of the two sites and benthic composition recorded every 25 cm along each transect. We extracted the percentage of hard coral cover from each transect for analysis.

Territory mapping

We collected intensive behavioural data for ten *C. lunulatus* pairs at each of the two study sites. We mapped the territories for five of these pairs at each of the two sites following the methods in Berumen and Pratchett (2006). We observed a two-minute acclimation period to ensure the behaviour of the focal pair was not influenced by the presence of observers. We then followed the focal pair from a minimum distance of 2 m for 15 minutes. Visual markers (flagging tape attached to fishing weights) were placed at the pair's location every minute. This observation time was based on pilot studies by Berumen and Pratchett (2006) that determined 15-minute observation periods were optimal to accurately estimate *C. lunulatus* territory size. When pairs separated, we followed a single individual for the remainder of the observation period. Following the observation, two 30 x 30 m transects were laid perpendicular to one another outside of the points to provide X, Y axes. We recorded the marker locations as Cartesian coordinates from the transect origin.

Density

We conducted *C. lunulatus* density surveys through an underwater visual census (UVC) using a 50 x 5 m belt transect, which was laid out during counts. We used 10 replicate transects at each of three reef zones (flat, crest and slope) across the two sites, equating to 30 transects and an area of 7,500 m^2 per site. As previous research indicated that territoriality in *C. lunulatus* could be influenced by a dominant competitor, we also recorded the density of *C. baronessa* along the transects (Berumen and Pratchett, 2006).

Behavioural Observations

We recorded 10-minute behavioural observations for 10 pairs at each of the two sites, repeating our observations of each pair five times, resulting in a total of 100 behavioural observations. To keep the time between observations as consistent as possible, we observed individuals at both sites on each survey day, and all individuals were surveyed approximately every 5-7 days. The location of each territory was marked with a weight and flagging tape. Before placing the flagging tape, we observed the chosen breeding pair for approximately five minutes. The flagging tape was then placed within the approximate centre of the territory. Observations were recorded on a waterproof Nikon Coolpix camera from a minimum distance of two meters. As with the territory mapping, we observed a two-minute acclimation period before we began recording behaviour. We also used this acclimation period to observe the pair and ensure that we were following the correct breeding pair, and not a pair from a neighbouring territory. Behaviours were then recorded from video analyses. We selected one individual from each breeding pair as a focal individual and used a continuous sampling method to record the length of time spent exhibiting each behavioural trait. We also identified any species the focal pair interacted with during video analyses. Butterflyfish show minimal sexual dimorphism (Yabuta, 2002), so we were unable to discern between the two individuals within pairs when selecting the focal individual for each behavioural observation. Nonetheless, for *C. lunulatus*, monogamous bonds are long term (Reese, 1975), and pairs have been shown to move throughout the feeding territory in coordination, with both individuals displaying equal levels of aggression (Nowicki *et al.,* 2018). We therefore assumed behaviour to be synonymous between individuals making up a breeding pair.

We assigned observed behaviours to four behavioural categories (aggression, sociability, exploration and feeding), each consisting of one or more discrete behaviours (Table 2.1). Aggression was defined as an intra- or interspecific agonistic interaction initiated by the focal individual. Sociability was defined as the response to the presence of a conspecific (Réale *et al.,* 2007), specifically the amount of time the focal individual spent within 2 m of the breeding partner (Table 2.1). Exploration captured two swimming traits, previously defined by Zambre *et al.* (2018) for butterflyfish: searching for food, defined as when individuals swim slowly, angled towards the benthos between patches, and all other swimming movements, here labelled as travelling. Travelling consisted of faster, streamlined swimming (Zambre *et al.,* 2018). Feeding was defined as when individuals were taking bites out of live coral (Réale *et al.,* 2007). Aggression, sociability, and exploration are three commonly used behavioural categories, all of which have been shown to be repeatable to various extents (Bell *et al.,* 2009; Table 2.1). We assigned the two discrete foraging behaviours (searching and feeding) into separate categories (exploration and feeding respectively), so that the time spent looking for food, and the time spent feeding could be quantified separately. Additional behaviours, specifically the use of cleaning stations and resting were also recorded. However, as these behaviours were observed rarely (< 0.05% of time across all observations), and were not the focal behaviours for this study, they have been excluded from analyses.

Table 2.1: Behaviours recorded during behavioural observations and included in statistical analyses

Behaviour	Definition	Reference	Category
Travelling	Fast moving swimming with directed movement	Zambre *et al.*, 2018	**Exploration**
Feeding	Taking bites from live coral	Zambre *et al.*, 2018	**Feeding**
Searching	Slow, movement over coral, focal individual head inclined down	Zambre *et al.*, 2018	**Exploration**
Aggression	Agonistic reaction to another individual (intra or interspecific). Parallel and fast swimming (rushing)	Reale *et al.*, 2007 Yabuta, 1999	**Aggression**
Sociability	Focal individual in close vicinity to breeding partner	Reale *et al.*, 2007	**Sociability**

2.2.3 Statistical analyses

All our analyses were conducted using R v3.5.1 (R Core Team, 2019). To analyse territory size, we plotted the Cartesian coordinates and calculated the minimum convex polygon to establish the area of each territory. We compared differences in territory size across the two sites using a one-way ANOVA.

Population level

For the population level analyses, we calculated the mean time spent on each behavioural category from the five observations for each breeding pair. We ran a multivariate analysis of variance (MANOVA), with time spent on each behavioural category (Aggression, Sociability, Exploration and Feeding) as the response variables, with site as the predictor variable. We then ran one-way ANOVAs with a Bonferroni correction for multiple comparisons, comparing time spent on each behavioural category separately, to identify which categories were different between the two sites. Based on the output from these tests, we also analysed the amount of time spent on searching, travelling, and feeding using ANOVAs to compare differences between behaviours both within and across the two sites. Due to the small sample size in our study, we also bootstrapped the raw behavioural data and plotted the distributions of the 1000 bootstrap estimates and used non-overlapping confidence intervals to identify significant differences in behaviour between the two sites.

We compared *C. lunulatus* and *C. baronessa* densities across the two sites using basic Gaussian generalised linear models, with abundance as the response variable and site as a fixed effect. We also ran two additional models with reef zone as an additional factor, and then with an interaction between reef zone and species. We used a likelihood ratio test to compare these three models. Furthermore, for *C. lunulatus,* we determined whether aggression was a consequence of abundance by recording both aggressive and non-aggressive interactions between *C. lunulatus* pairs and calculating the probability that any given encounter would result in aggression. The probability was calculated by dividing the number of aggressive interactions by the number of total interactions. We then compared the probability of aggression for each focal individual between the two sites using a generalised linear model with probability of aggression as the response variable and site as the predictor variable.

Individual level

To visualize correlations of behaviours of individual pairs, we used a Principal Component Analysis (PCA) with the Kaiser-Meyer-Olkin (KMO) criterion as a measure of sampling accuracy (Kaiser and Rice, 1974) and Bartlett's test of sphericity (Bartlett, 1951) to ensure our data fit the assumptions of PCA. Kaiser and Rice (1974) suggest that a sampling adequacy of less than 0.5 indicates that the data are not suitable for further PCA analysis. To evaluate differences in traits between pairs within each site, we ran additional MANOVA tests comparing the time spent on each of the four behaviours (Aggression, Feeding, Exploration and Sociability) between the ten pairs within each of the two sites. For these tests, the behavioural traits (Aggression, Searching, Travelling, Feeding and Sociability) were the response variables, with pair ID as the predictor variable. We used two separate MANOVAs, one for each site, rather than a single model with study site as a covariate, because the subsequent outputs from each test were used to calculate behavioural repeatability using an ANOVA approach (see below).

Repeatability estimates

We calculated the repeatability of each behaviour between individuals at each site based on the proportion data using the intraclass correlation coefficient (ICC, Nakagawa and Schielzeth, 2010, Wolak *et al.*, 2012). We took an ANOVA based approach and calculated 1000 bootstrapped ICC estimates using ANOVA variance components in the ICC package (Wolak and Fairbairn 2011), using 2.5 and 97.5% confidence intervals from bootstrapped ICC estimates to identify any significant differences in repeatability between the two sites. To understand the variability of individuals around the population mean, as well as from each other, we used the mean standardization (as defined in Dochtermann and Royauté, 2019) of both the among and within (residual) individual variance (mean scaled individual and mean scaled residual variation) from bootstrapped variance components from the within site MANOVA tests, using equations in Dochtermann and Royauté (2019). Mean scaled individual variation (I_A) calculates the proportion of variation, relative to the mean, that can be explained by differences in the expression of behaviours between individuals. In contrast, mean scaled residual variation (I_W) calculates the proportion of variation, relative to the mean that can be explained by differences in behaviour that are a consequence of unmeasured sources of variation (Dochtermann and Royauté, 2019).

2.3 Results

2.3.1 Coral cover

For 2019, the mean coral cover across the reef flat, crest and slope was 35.69% at PK, the high resource site, compared to 17.67% at SAM, the low resource site. Coral cover was significantly higher at PK than SAM across both 2018 and 2019 (Figure S2.2, ANOVA: $F = 71.01$, $df = 1$, $P \leq 0.001$).

2.3.2 Population level

Territory sizes at the low resource site were significantly larger than those at the high resource site with mean (± standard error) territory sizes of 179.7 ± 35.6 m^2 and 65.0 ± 13.8 m^2 respectively (Figure 2.1, Table S2.1, ANOVA, $F = 9.04$, $df = 1,8$, $P = 0.02$).

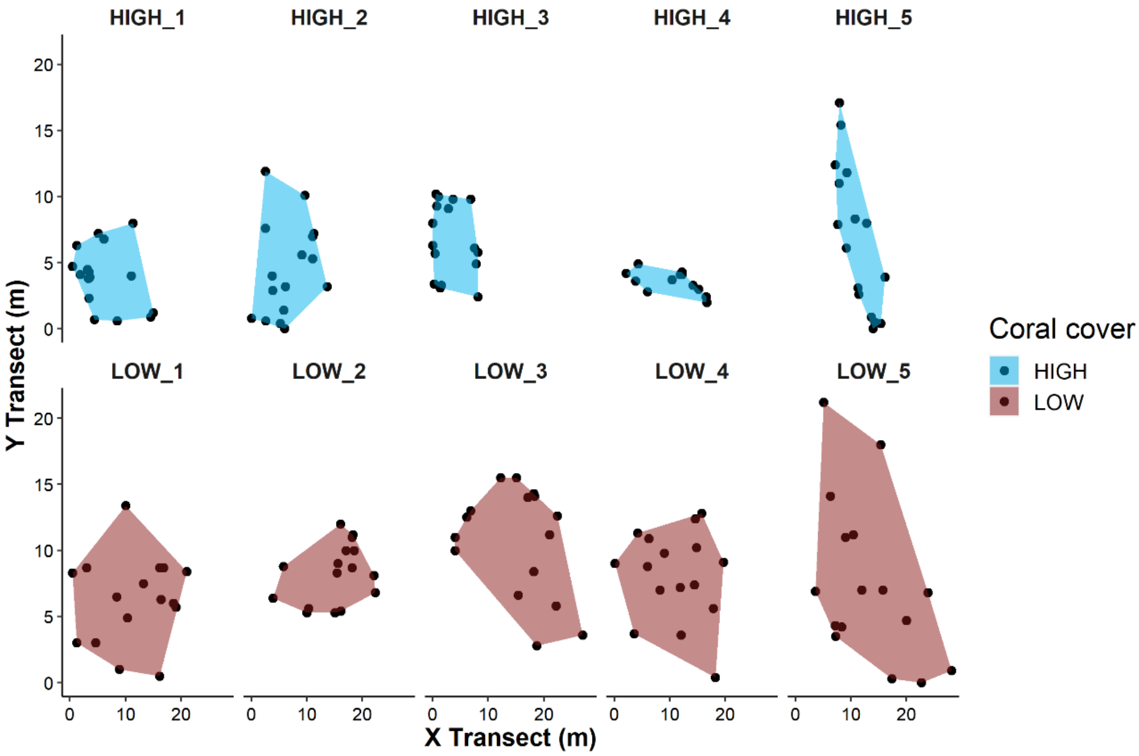


Figure 2.1: *C. lunulatus* territories at a high and low resource site. Points represent the location of the individual markers placed within the territories (n = 5 per site) during 15- minute observations, shaded areas are the minimum convex polygons.

Overall, behaviour also differed significantly between the two sites (Figure 2.2, MANOVA: F = 6.87, df = 3,4, *P* < 0.01). Specifically, individuals at the higher resource site invested more time in aggression (ANOVA: F = 16.67, df = 1,18, *P* < 0.001), sociability (ANOVA: F = 7.87, df = 1,18, *P* = 0.01) and feeding (ANOVA: F = 20.17, df = 1,18, *P* < 0.001) and less time in exploration (ANOVA: F = 24.96, df = 1,18, *P* < 0.001). These differences were also apparent from the 1000 bootstrap estimates, such that confidence intervals for the two sites did not overlap for any of the behaviours (Figure S2.3).

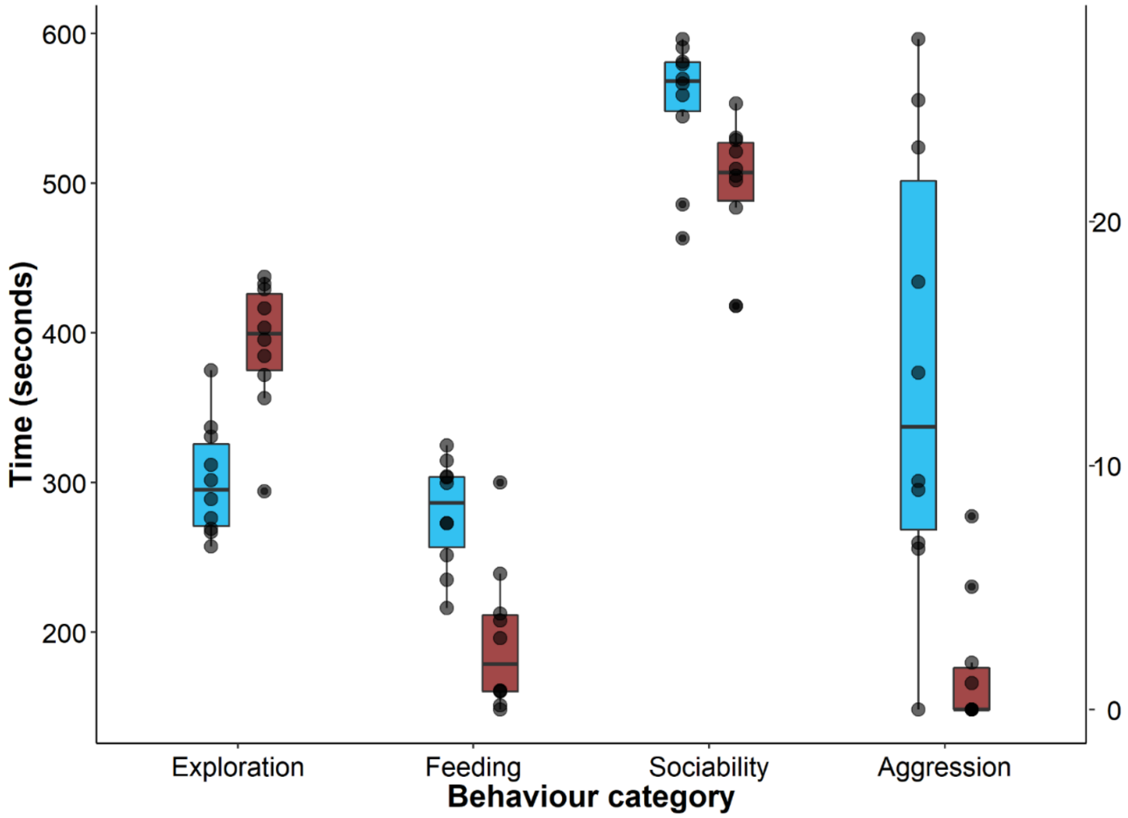


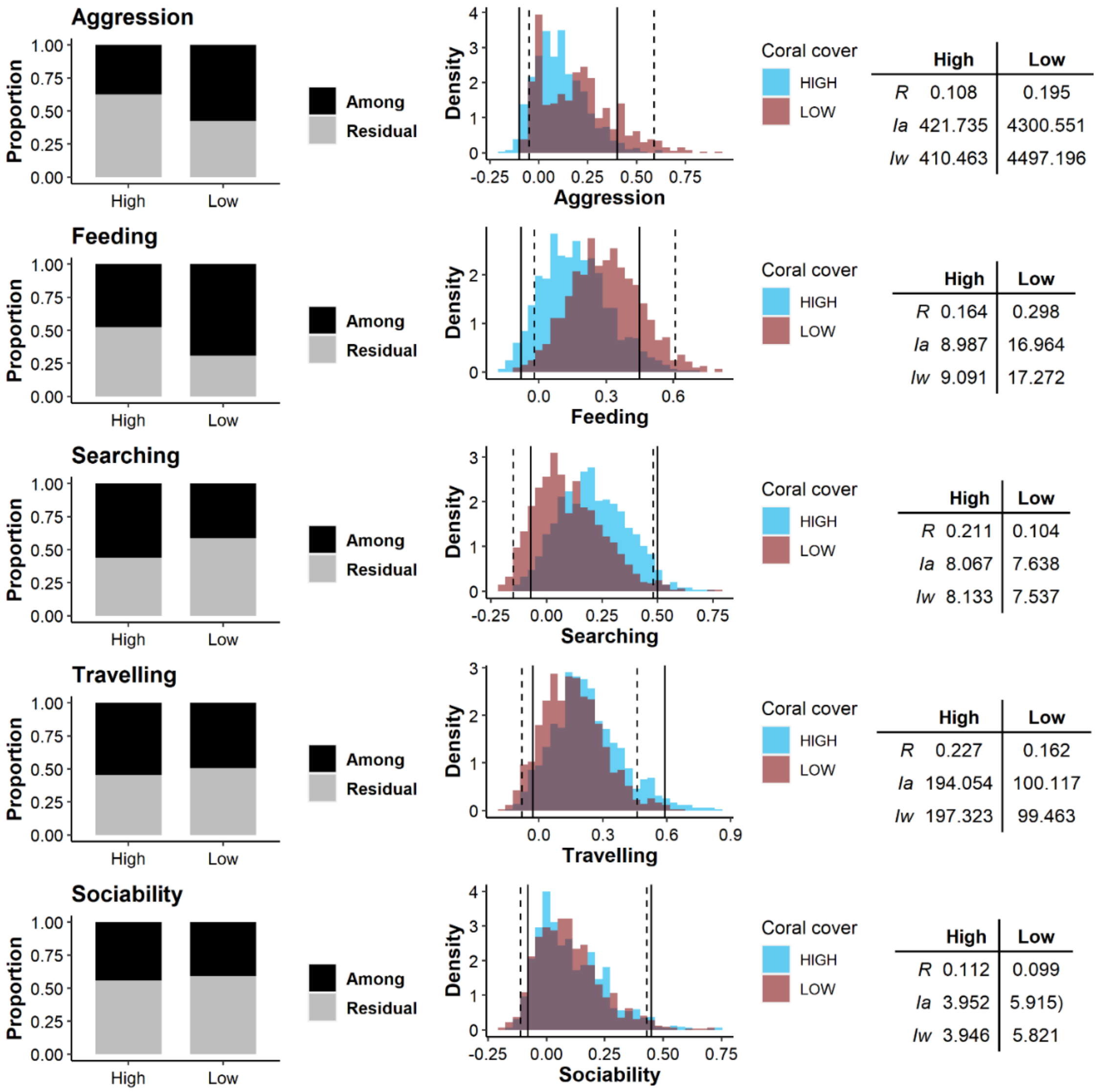
Figure 2.2: *C. lunulatus* behaviour at a high (blue) and low (red) resource site. Behaviours are measured as the time spent on each of the four behavioural categories (left-handed y-axis). N = 10 individuals per site, with five replicate values per individual. Black points represent the mean time spent in each behaviour by an individual such that one point refers to a single individual. Boxplot lines are median values, box lengths represent interquartile ranges and whiskers are 25th and 75th percentiles. A second y-axis is presented for aggression, due to the rarity with which this behaviour occurs.

For comparing *C. lunulatus* density across the two study sites, the likelihood ratio test identified the model with an interaction term for reef zone and site to be the best fit for the data ($\chi^2 = 258.53$, df = 4, $P = < 0.001$). The density of *C. lunulatus* differed significantly between the two sites (Figure S2.4, GLM: t = 7.11, df = 1,58, $P < 0.001$). Despite this difference, conspecific aggression was not influenced by density: the number of encounters between conspecific pairs was the same between the two sites (GLM: t = -1.45, df = 1,58, P = 0.17) yet the probability that an encounter would be aggressive was significantly higher at the higher resource site (GLM: t = -2.30, df = 1,58, $P = 0.03$). Likelihood ratio tests also identified the model with an interaction term for reef zone and study site to be optimal for comparing the density of *C. lunulatus* and *C. baronessa* at both the high ($\chi^2 = 22.16$, df = 4, $P = < 0.001$) and the low ($\chi^2 = 62.49$, df = 4, $P = < 0.001$) resource site. *C. lunulatus* density was greater than *C. baronessa* at the high resource site (Figure S2.5, GLM: t = 4.578, df = 1,58, $P = < 0.001$) but was equivalent at the low resource site (Figure S2.5, GLM: t = 1.633, df = 1,58, $P = 0.108$).

When behaviours within the ‘exploration’ category were analysed separately with feeding behaviour, time spent searching and feeding differed at the two sites (Figure S2.5). Individuals at the higher resource site invested less time in searching (ANOVA: F = 11.3, df = 1,18, $P = 0.003$) and more time in feeding (ANOVA: F = 20.17, df = 1,18, $P < 0.001$) compared to individuals at the lower resource site. Within the higher resource site, there was no significant difference identified between the time spent on searching and feeding (ANOVA: F = 0.25, df = 1,18, $P = 0.63$). In contrast, at the lower resource site, a greater proportion of time was spent searching than feeding (ANOVA: F = 49.39, df = 1,18, $P < 0.001$).

2.2.3 Individual level

At the high resource site, there was no significant variation between individuals in the time spent on any of the four behaviours (MANOVA: F = 0.592, df = 9,40 $P = 0.552$). There was significant variation between individuals at the low resource site in the proportion of time spent feeding (ANOVA: F = 2.23, df = 9, 40 $P = 0.04$). The proportion of variance from the ANOVAs attributed to both within and between individual variation was similar between the two sites, with the exception of feeding, where between individual variation accounted for 70% of total variance at the low resource site. In other words, within the low resource site, individuals varied in the amount of time they invested in feeding (Figure 2.3).



Aggression

	High	Low
R	0.108	0.195
Ia	421.735	4300.551
Iw	410.463	4497.196

Feeding

	High	Low
R	0.164	0.298
Ia	8.987	16.964
Iw	9.091	17.272

Searching

	High	Low
R	0.211	0.104
Ia	8.067	7.638
Iw	8.133	7.537

Travelling

	High	Low
R	0.227	0.162
Ia	194.054	100.117
Iw	197.323	99.463

Sociability

	High	Low
R	0.112	0.099
Ia	3.952	5.915)
Iw	3.946	5.821

Figure 2.3: From left to right: Breakdown of ANOVA variance components from raw data (n = 10 per site, with five replicates per individual), bootstrapped distributions of repeatability estimates, and summary statistics from bootstrapped data for each of the five measured behaviours at the high and low resource site. Summary statistics (mean repeatability (R) mean scaled between individual variation (I_a) and mean scaled residual individual variation (I_w)) were calculated from 1000 bootstrapped estimates of the raw behavioural data and ANOVA variance components. Confidence intervals in the distribution plots (centre) are 2.5 and 97.5% limits of bootstrapped repeatability distributions. Solid and dashed lines are confidence intervals for the high and low resource sites respectively.

Repeatability estimates

Raw repeatability estimates for each trait were small, and most were negative, suggesting a high level of statistical noise. Bootstrapping the raw estimates reduced this statistical noise, and bootstrapped repeatability estimates were all positive, but no estimate exceeded 0.3 (Figure 2.3). Feeding at the low resource site was the most repeatable behavioural trait (R = 0.299). For all traits, confidence intervals for both bootstrapped repeatability (Figure 2.3) and mean scaled between individual variation estimates (Figure S2.7) at each site overlapped, indicating no significant difference in repeatability between the two sites. Although for aggression and feeding, the mean standardization estimate was higher at the low resource site, and by an order of magnitude for aggression, confidence intervals overlapped for all behaviours between the two sites (Figure S2.7). However, mean-scaled residual variation was significantly different for feeding (High: mean = 9.091, 2.5% CI = 9.016, 97.5% CI = 9.165; Low: mean = 17.272, 2.5%CI = 17.117, 97.5% CI = 17.427), such that confidence intervals did not overlap (Figure S2.8). Residual mean standardization estimates were higher at the low resource site.

The PCA is included to visualize the data, with site and individual pairs overlaid as groups (Figure 2.4, Figure S2.9). Although the KMO sampling adequacy criterion produced a low value of 0.48, which is slightly below the acceptance threshold, the Bartlett test of sphericity was significant ($P < 0.05$). We therefore deemed that the PCA would be an acceptable tool to visualize the data. From PCA loading values, PC1 had positive associations with searching and travelling, and a negative association with aggression, feeding and sociability. PC 2 had a strong positive association with aggression. The PCA suggests that sociability and aggression are positively correlated with one another, as are travelling, and searching, whilst feeding is negatively correlated with the exploratory behaviours (travelling and searching).

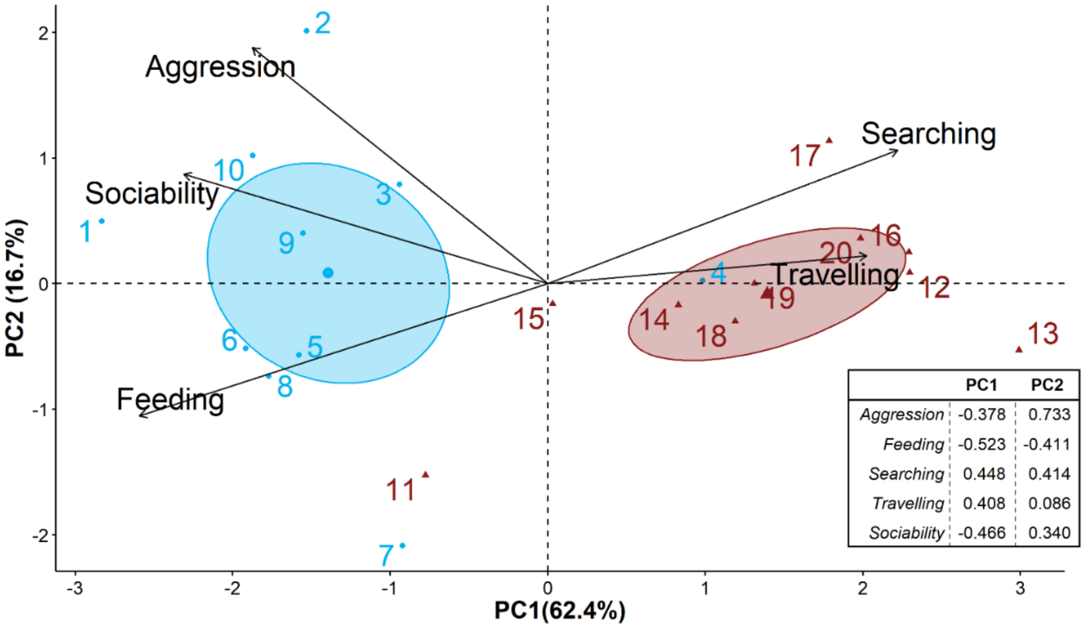


Figure 2.4: The position of each of the 20 (n = 10 per site) breeding pairs in relation to both the principal components, and each behaviour. The two sample sites, (High (blue circles) and Low (red triangles) resource availability) have been overlaid as an additional group. Ellipses around each site mean (larger symbols) are based on 95% confidence limits. PCA loadings for PC1 and PC2 are presented in the inset.

2.4 Discussion

Using an observational approach, we have identified both broad (population level) and fine (individual level) scale differences in the behaviour of *C. lunulatus* between two sites of different resource availabilities. At the population mean level, we have shown that *C. lunulatus* in an area of high resource availability maintain small territories and invest time in aggressive territory defense and feeding. In contrast, *C. lunulatus* in an area of low resource availability held larger territories and spent less time on territory defense and more time invested in searching for food. At the individual level, we identified significant differences in the time spent feeding among individuals at the low resource availability site, and feeding was also the most repeatable behaviour at this site. By considering both population and individual level analyses, combined with a consideration of the co correlation of different behaviours we can provide a deeper insight into the behavioural responses of *C. lunulatus,* than would be possible by considering the population means of individual behaviours in isolation.

Optimal foraging theory predicts that an increase in time spent foraging should yield an increase in food acquisition (MacArthur and Pianka, 1966). One of the assumptions of optimal foraging theory is that all feeding patches are of similar quality, which is not the case for each *C. lunulatus* territory across our two study sites, and it is also possible that within sites, there is variation in patch quality. Although territories were larger and the time invested in searching for food was greater at the low resource site, the time invested in taking bites of coral prey was lower. This suggests that individuals had to invest more time searching, i.e., moving between coral patches, because the available food was more sparsely distributed (Tricas, 1989). The food maintenance hypothesis predicts that territory size is determined according to the food supply needed for short term energetic needs (Stimson, 1973). At the high resource site, food was readily available within a small space, thus the time spent searching prior to being able to take a bite of prey was minimal. Individuals then had the time and energy to invest in territory defence (Davies and Hartley, 1996). At the low resource site, food resources were sparse such that even when time was redistributed from aggression to searching, the nutritional gain was still lower than at the high resource site. A negative correlation between exploratory traits and feeding therefore emerged across both sites. This potential trade-off highlights the need to consider multiple traits together to fully understand the response of individuals to environmental change (Sih *et al.*, 2004).

The differences in territory size that we identified for *C. lunulatus* in sites with different resources differs from previous work, which found territory size decreased with resource availability in the dominant specialist *C. baronessa* but not in generalist corallivores, including *C. lunulatus* (Berumen and Pratchett, 2006). These data were collected in a different region, with different abundances, densities, and diversity of obligate corallivorous butterflyfish, suggesting there is a degree of context specificity in butterflyfish territoriality at the species level. Heterospecific aggression is more prominent in *C. baronessa* than *C. lunulatus* (Berumen and Pratchett, 2006; Blowes *et al.*, 2013). As the density of *C. lunulatus* was greater than that of *C. baronessa* at the high resource site, i.e., where *C. lunulatus* aggression is greater, the presence of more aggressive competitors, such as *C. baronessa*, could therefore be a determinant of territoriality in *C. lunulatus*, along with resource availability.

Differences in aggression and exploration behaviour between our two study sites are consistent with the principles of game theory, specifically the Hawk-Dove game (Maynard-Smith and Price, 1973), and the principles of the model of economic defendability (Wyman and Hotaling, 1988). Under normal (high coral) conditions, aggression within *C. lunulatus* individuals is high. Increasing disturbance to an intermediate level increases the value of the resource (Wyman and Hotaling, 1988), in this case, coral within a *C. lunulatus* territory. In the Hawk-Dove game, if the value of a resource increases, or the ‘odds’ are higher, it pays for an individual to play ‘Hawk’ and act aggressively more often than under the original conditions (Maynard-Smith, 1982). This way, individuals can maximize the use of available resources by feeding on what high quality resources remain (Cole *et al.*, 2008). With additional disturbance, there will be a threshold beyond which aggression will decrease (Peiman and Robinson, 2010; Keith *et al.*, 2018) and exploration will increase, as identified in our study, due to a nutritional deficit and resource availability trade-off (Berumen and Pratchett, 2006). The cost of being aggressive is then outweighed by the benefit of playing ‘dove’, and remaining passive, thus a higher frequency of individuals adopting the low aggression strategy is expected in the population, as seen in our results.

The threshold of behavioural change is likely to be variable across butterflyfish species, locations, and even individuals, such that individual state (e.g., physiological, environmental, morphological) influences the cost-benefit trade-off of aggressive interactions (Dingemanse and Wolf, 2010). This threshold may also be determined by the extent to which behaviours are fixed or plastic within an individual. If behaviours are a result of fixed ‘personalities’, then a frequency change in behaviour can only occur via selection (Dall *et al.*, 2014), whereas if behaviours are plastic, then changes can occur within generations. Identifying the threshold at which behavioural responses occur is important for management efforts, as behavioural modifications have implications to the future distribution and persistence of species (Delarue *et al.*, 2015).

High repeatability between individuals within a population indicates high behavioural consistency, such that within a population, individuals consistently behave differently from one another (Lessells and Boag, 1987). Behavioural repeatability between individuals may be low in two scenarios: either if within individual variation is high, or if between individual variation is low (Nakagawa and Schielzeth, 2010). Our estimates for behavioural repeatability between individuals were all less than 0.5, which tentatively indicates that the measured behaviours show a degree of behavioural plasticity within individuals (Wilson, 2018). Behaviours dependent upon an individual’s physiology or morphology, i.e., their resource allocation (Laskowski *et al.*, 2020), are predicted to be consistent within an individual, but variable between individuals, and therefore repeatable (Bell *et al.*, 2009). Repeatability will be lower for traits dependent on how an individual utilizes the resources in their environment, i.e., on resource acquisition (Laskowski *et al.,* 2020), such as behaviours associated with energetic needs e.g., feeding, and the social environment, e.g., aggression (Bell *et al.,* 2009). Surprisingly, aggression and feeding at the low resource site had the highest repeatability estimates in our study. However, if there is an interaction between an individual and its environment that contributes to between individual variation, for example, if individuals in the low resource site face greater fine-scale variation in the amount of food in their territory compared to individuals in the high resource site, repeatability estimates could be inflated (Nakagawa and Schielzeth, 2010). We identified higher residual (mean-scaled) variation for feeding at the low resource site. There is, therefore, a significant amount of variation in trait expression that is a consequence of unmeasured sources of variation (Dochtermann and Royauté, 2019). If this unmeasured source of variation is environmental, then an interaction between the environment and individuals at the low resource site is plausible. The high degree of unmeasured variation suggests that there is a degree of within territory context specificity that is influencing the behaviour of *C. lunulatus,* that would not have been identified if we had only considered behaviour at the population level.

One potential cause of an interaction between individuals and the environment is habitat patchiness resulting in some individuals having greater access to resources than others. Variation in habitat patchiness can influence the behaviour of individuals to varying extents according to the specific area of habitat they occupy (Catterino *et al.,* 2015, Van Leeuwen *et al.,* 2017). Habitat patchiness may be driving variation in feeding and aggression in our study, masking the amount of variation that can be directly associated with intrinsic differences between individuals at the low resource availability site. It is possible that a preference for specific species of coral as a food source could be driving this variation, rather than habitat patchiness directly. However, we did not quantify the resource availability to the coral species level within each territory due to the temporal scale and design of our study. Nonetheless, the time invested in feeding was significantly different between individuals at the low resource site. As *C. lunulatus* is an obligate corallivore, feeding is directly related to the amount of available live resource, which was significantly lower at the low resource site. A lower nutritional gain at the low resource site also makes energy investment in aggression too costly compared to investing energy in foraging for what little resources are available (Berumen and Pratchett, 2006). Therefore, aggression is also directly linked to the availability of live resource and will also be influenced by habitat patchiness across different territories. *C.lunulatus* individuals at the low resource site may change their behavioural strategy according to the quality of their territory and the distribution of food availability within the territory (Righton and Mills, 2007). An influence from the spatial configuration of habitat would lead to higher consistency within individuals, and therefore the higher-than-expected estimate of repeatability for aggression and feeding at the low resource site.

We have offered insight into how behaviour at both the population and individual level influences the response of *C. lunulatus* individuals to different levels of resource availability, which suggests that loss of cover through environmental disturbance could result in shifts in behaviour at a population level. By looking at behavioural change at both individual and population levels through observation in a natural setting, we have tentatively highlighted the potential for individual behavioural strategies to be masked by mean effects. Our work also highlights the need to both identify the threshold at which behavioural changes occur and identify the relative roles of behavioural plasticity and behavioural consistency, or ‘personalities’. This could be achieved by observing the behaviours of the same individuals across different contexts (varying resource) within sites. To further understand behaviour within sites, our results suggest that context specific factors such as environmental variation within territories, are drivers of behaviour at the individual level, and should be considered and quantified in the future. This will enable a more thorough understanding of the distribution, adaptation, and persistence of important reef indicator species, which in turn can inform future management efforts.

Chapter 3

3. Terrestrial invasive species alter marine vertebrate behaviour

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Contribution of authors

RLG conceived the ideas, collected the data, analysed the data, and led the writing of the manuscript. CEB helped conceive the ideas, supported data collection and analysis and contributed critically to manuscript drafts. NAJG supported data analysis and contributed critically to manuscript drafts. IRH., ACA and SAK. contributed critically to manuscript drafts.

Abstract

Human induced environmental changes, such as the introduction of invasive species, are driving declines in the movement of nutrients across ecosystems with negative consequences for ecosystem function. Declines in nutrient inputs could thus have knock-on effects at higher trophic levels and broader ecological scales, yet these interconnections remain relatively unknown. Here, we show that a terrestrial invasive species (black rats, *Rattus rattus*) disrupts a nutrient pathway provided by seabirds, ultimately altering the territorial behaviour of coral reef fish. In a replicated ecosystem-scale natural experiment, we found that reef fish territories were larger, and the time invested in aggression lower, on reefs adjacent to rat-infested islands, compared to rat-free islands. This response reflected changes in the economic defendability of lower quality resources with reef fish obtaining less nutritional gain per unit foraging effort adjacent to rat-infested islands with low seabird populations. These results provide a novel insight into how the disruption of nutrient flows by invasive species can affect variation in territorial behaviour. Rat eradication as a conservation strategy therefore has the potential to restore species interactions via territoriality, which can scale up to influence populations and communities at higher ecological levels.

3.1 Introduction

The movement of naturally occurring nutrients across habitats and ecosystems is a strong driver of productivity and can influence community dynamics (Polis *et al.,* 1997). Inputs from animals can contribute substantially to the nutrient budget of an ecosystem, but anthropogenic activities have reduced the movement of naturally occurring nutrients between animals to 6% of historic values (Doughty *et al.,* 2016, Burpee and Saros, 2020). Whilst certain aspects of human-induced environmental change can increase the nutrient load to an ecosystem (Gallardo *et al.,* 2016), human-induced declines in the movement of nutrients can negatively impact the resources that organisms are able to exploit (Doughty *et al.,* 2016, Auer *et al.,* 2020a). Organisms initially respond to human-induced environmental change through rapid behavioural modifications that reduce the resource demand of the organism which include changes to foraging behaviour (Van Justino *et al.,* 2012, Overveld *et al.,* 2018), aggression (Keith *et al.,* 2018, Gunn *et al.,* 2022), and territoriality (Davies and Hartley, 1996). Thus, reductions in nutrient inputs are predicted to alter the behaviour of higher trophic-level organisms via cascading effects through food webs, though such connections are untested. As changes in behaviour can influence species interactions and subsequently shape ecological communities (Cahill *et al.,* 2013, Delarue *et al.,* 2015), understanding behavioural responses to change is fundamental to revealing the complex ecological consequences of human-induced nutritional declines.

Nutritional resources are key drivers of territorial behaviour. The food maintenance hypothesis predicts that territory size is primarily determined by the nutritional requirements that allow organisms to meet short-term energetic needs (Stimson, 1973). An inverse relationship between resource availability and territory size (Sells and Mitchell, 2020) is apparent across a range of organisms including mammals (Graf *et al.,* 2016), reptiles (Simon, 1975), birds (Ippi *et al.,* 2018), and fish (Berumen and Pratchett, 2016). Theory proposes that aggression is also largely determined by nutritional resources, such that the aggressive defence of territories, or territoriality, is predicted to occur only where the energetic benefits of territoriality outweigh the costs (Brown, 1964). Under this model of economic defendability, a bell-shaped relationship between territoriality and resource level is predicted, and territoriality is only beneficial when the value of a nutritional resource is above a certain threshold value (Peiman and Robinson, 2010, Grant *et al.,* 2002). When nutritional resources are rare, the energetic cost of territoriality is too high. At intermediate resource levels, positive net benefits for territoriality outweigh the benefits of nonterritorial behaviour, and the net payoff for territorial behaviour reaches a peak (Brown, 1964). Where resources are in excess, the highest net benefit occurs for nonterritorial behaviour, as individuals can obtain resources at low cost without the need for aggression (Peiman and Robinson, 2010). It is plausible that the disruption of nutrient pathways by human induced environmental change lowers the value of nutritional resources, impacting the cost-benefit dynamics of territoriality and the subsequent territorial tendencies of individuals (Davies and Hartley, 1996, Peiman and Robinson 2010). However, the consequences of declines in nutrient transfer on variation in territorial behaviour remains untested.

Seabirds are globally important contributors to nutrient transfer, responsible for a cascade of nutrients through terrestrial (Duda *et al.*, 2020) and marine (Graham *et al.*, 2018) ecosystems by depositing guano on islands after feeding in the open ocean. Invasive species, including black rats (*Rattus rattus*), disrupt this nutrient pathway by driving declines in seabird densities via predation (Jones *et al.*, 2008). Nutrient subsidies from seabirds flowing onto coral reef ecosystems result in higher nitrogen stable isotope quantities ($\delta^{15}N$) in algae and fish (Honig and Mahoney, 2016, Benkwitt *et al.*, 2021) , enhanced coral growth (Savage, 2019) , higher reef fish biomass (Benkwitt *et al.*, 2019), and faster growth rate in herbivorous fishes (Graham *et al.*, 2018, Benkwitt *et al.*, 2021). Furthermore, the presence of invasive rats negatively impacts reef fish diversity and ecosystem function on adjacent coral reefs (Benkwitt *et al.*, 2020). Invasive rats therefore have a substantial bottom-up impact on terrestrial and marine ecosystems. As behaviour is an important mediator between organisms and the environment (Delarue *et al.*, 2015), the behavioural responses of reef organisms could play a mechanistic role in the ecological changes observed on coral reefs adjacent to rat-infested islands.

Here, we use a control-treatment experimental design to provide the first insight into the cascading effects of seabird nutrient subsidies on territorial behaviour and reveal how these effects are disrupted by invasive rats, using the herbivorous farmer damselfish, *Plectroglyphidodon lacrymatus.* We test the model of economic defendability (Brown, 1964) and identify the role of nutritional subsidies in placing the value of resources above the critical threshold value for territoriality. We predict that the nutrient enrichment of resources by seabirds will result in higher aggression and a smaller territory size for *P. lacrymatus* individuals on reefs around rat-free islands compared to individuals on reefs around rat-infested islands. Using *in situ* observations, we link the aggression of individual fish to their territory size, and both the quantity (% cover of turf algal) and nitrogen enrichment of their nutritional resources, to show how a reduction in nutrient subsidies can drive both broad and fine-scale variability in territorial behaviour.

3.2 Results and Discussion

We studied ten islands (n=5 rat-free islands, n=5 rat-infested islands) across three atolls within the Chagos Archipelago, where seabird densities on rat-free islands are up to 720 times higher, and the nitrogen input provided by seabirds is 251 times greater, than around rat-infested islands (Graham *et al.*, 2018). We calculated the area of 60 damselfish territories (n=30 around islands with seabirds, n=30 around islands with rats), and recorded the aggressive behaviour of 57 of these 60 individuals (n=28 around islands with seabirds, n=29 around islands with rats). *P. lacrymatus* is a herbivorous farmer damselfish that feeds on turf algae and aggressively defends small solitary territories (Robles *et al.*, 2018), allowing territorial behaviour to be accurately linked to an individual's nutritional resources.

3.2.1 Nutritional resources

Seabird guano contains high levels of the ^{15}N nitrogen isotope relative to ^{14}N ($\delta^{15}N$). Elevated levels of $\delta^{15}N$ act as an indicator of seabird derived nutrient subsidies and have also been positively associated with reef fish growth rate (Graham *et al.*, 2018), suggesting $\delta^{15}N$ is also an indicator of resource quality. Within *P. lacrymatus* territories adjacent to islands with seabirds, there was a 0.83 posterior probability (PP) that turf algal $\delta^{15}N$ was higher than around islands with rats (Figure 1, slope: 0.53, 95 % credible intervals: -0.46, 1.58, evidence ratio (ER: 4.80)). The posterior probability for this effect is similar to previous estimates of elevated turf algal $\delta^{15}N$ adjacent to islands with seabirds (Graham *et al.*, 2018, Benkwitt *et al.*, 2021). Given the absence of any additional human stressors around the study islands, this isotopic enrichment can be attributed to seabird nutrient subsidies in the absence of invasive rats.

There was no evidence for a difference in turf algal cover with island invasion status (slope: 0.02 (-0.13,0.09), PP: 0.37, ER: 0.59, Figure 3.1), yet the nutritional enrichment of algae was higher within *P. lacrymatus* territories where seabird nutrient subsidies were present. Consequently, in the absence of invasive rats, *P. lacrymatus* achieve greater nutritional gain per unit of foraging effort.

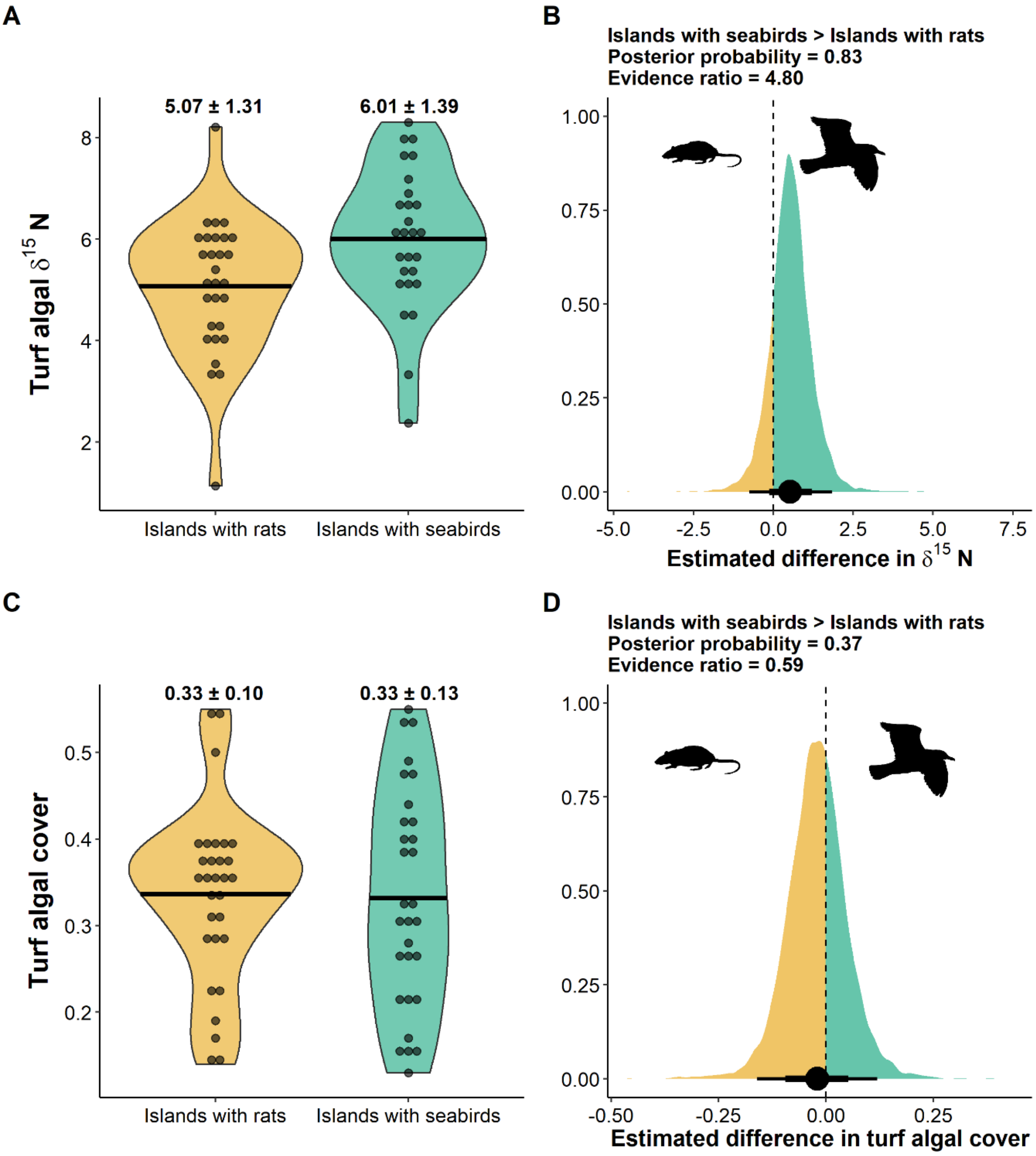

Figure 3.1: Turf algal δ^{15}N and turf algal cover round islands with seabirds and islands with invasive rats within the Chagos Archipelago. Each point on the violin plots (A, C) represents a single *P. lacrymatus* territory. Black bars (A, C) show the mean estimates for turf algal δ^{15}N (A, n=27 around islands with seabirds, n=29 around islands with rats) and for turf algal cover (C, n=20 around islands with seabirds, n=30 around islands with rats). Mean values and standard deviations are presented above each violin plot. Bayesian posterior densities (B, D) show the effect of island invasion status on turf algal δ^{15}N (B) and turf algal cover (D). Points are median estimates with lines representing 75% (thick) and 95% (thin) credible intervals respectively. Posterior probabilities, evidence ratios, and posterior densities in green show the extent to which 1) Nitrogen input (B) and 2) Turf algal cover (D) are higher around islands with seabirds. Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

3.2.2 Territory size

The greater nutritional gain per unit foraging effort available around islands with seabirds resulted in *P. lacrymatus* individuals holding smaller territories compared to individuals around islands with rats (Figure 3.2, slope: -0.21 (-0.34,-0.07), PP: 0.99, ER: 74.47)). The nutritional content of algal resources can shape a trade-off between territory size and quality, with smaller territories yielding higher quality nutritional resources (Catano *et al.*, 2015). Where nutrient subsidies are present, individuals can meet short term energetic demands faster through a higher nutritional gain per unit foraging effort, allowing individuals to hold smaller territories (Wilcox *et al.*, 2021, Gunn *et al.*, 2022). Where seabird nutrient subsidies are absent, *P. lacrymatus* individuals need to consume a greater amount of turf algae to maintain short term energetic demands. As there was no difference in the amount of turf algae available across the study islands, these individuals need to hold larger territories to maximise nutritional gain (Stimson, 1973, Figure 3.2). This observation is also reflected in the association between turf algal cover and turf algal $\delta^{15}N$ around islands with rats, such that territories with the highest turf algal cover had the lowest $\delta^{15}N$ values (Table S3.1B, Figure S3.2). There are, therefore, broad scale differences in *P. lacrymatus* territory size that, given turf algal cover does not vary with invasion status, are most likely driven by the observed differences in turf algal $\delta^{15}N$, which is a direct consequence of the presence or absence of invasive rats.

The design of our study allows the relative roles of resource quantity and quality in driving territoriality within and between island invasion status types to be understood. Nutritional resources are predicted to influence territoriality until a point of ‘consumer saturation’, at which point the benefits of territoriality have been maximised (Peiman and Robinson, 2010). *P. lacrymatus* territory size was inversely associated with turf algal cover, providing support for the food maintenance hypothesis (Wilcox *et al.*, 2021, Gunn *et al.*, 2022) with a PP of 0.85 for islands with seabirds and 0.91 for islands with rats (Figure 3.2, slope: -0.50 (-1.31, 0.32), ER: 5.70 around islands with seabirds, slope: -0.71 (-1.59, 0.17), ER: 10.24 around islands with rats). Around islands with seabirds, $\delta^{15}N$ appeared to be at a point of consumer saturation (Peiman and Robinson, 2010), such that the energetic benefits of elevated $\delta^{15}N$ in determining territory size were maximised and fine scale variation in $\delta^{15}N$ had no further effect on *P. lacrymatus* territory size (slope: -0.01 (-0.09, 0.07), PP: 0.59, ER: 1.44, Figure 3.2)). There was also no association between *P. lacrymatus* territory size and turf algal δ^{15}N around islands with rats (slope: 0.01 (-0.06, 0.08), PP: 0.38, ER: 0.60). In the absence of nutrient subsidies, where overall turf algal δ^{15}N is low, slight variation in turf algal δ^{15}N likely yields a lower energetic payoff (Brown, 1964, Peiman and Robinson, 2010) than variation in turf algal cover, indicating a trade-off between resource quality and quantity. As the evidence for both smaller territory sizes (PP = 0.99) and decreasing territory size with increasing turf algal cover ratio (PP = 0.91) for *P. lacrymatus* around islands with rats is relatively strong, resource quantity appears to be the primary determinate of *P. lacrymatus* territory size where nutrient subsidies are absent. These results offer support that nutrient disruption by an invasive terrestrial species has direct consequences on the territoriality of a native marine species.

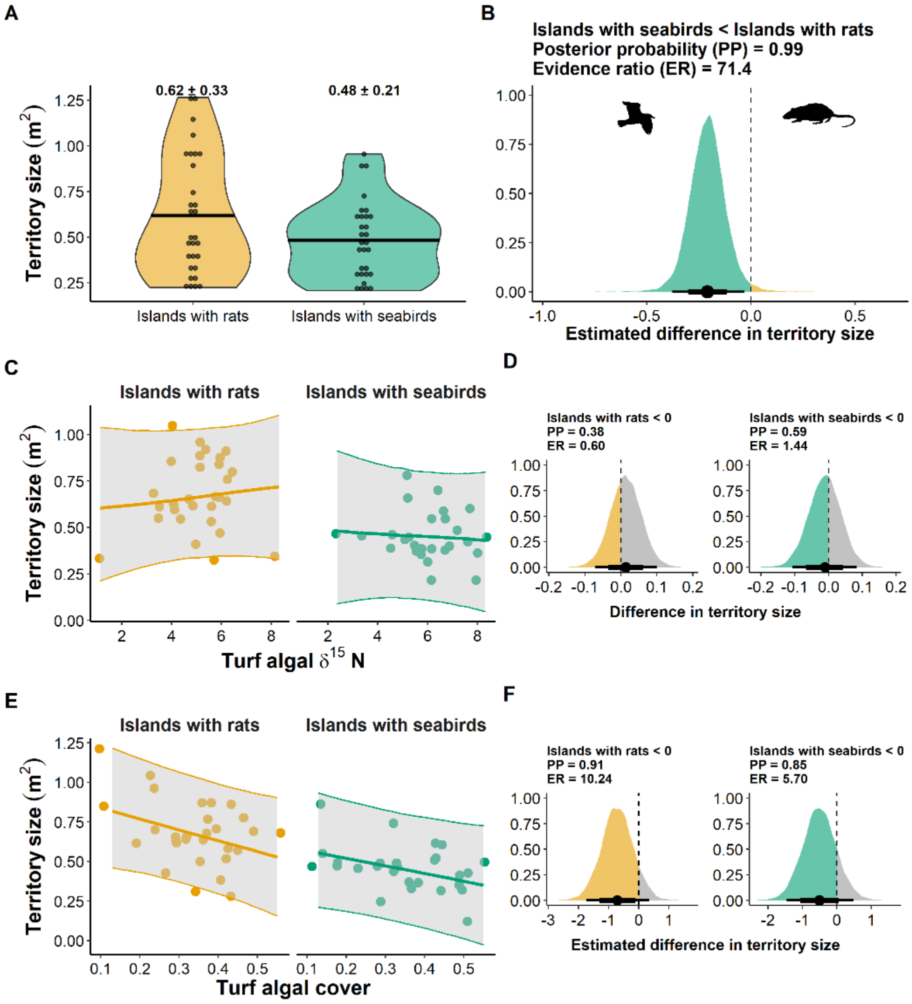

Figure 3.2: Variation in *P. lacrymatus* territory size between and within island invasion status type with Turf algal δ^{15}N and turf algal cover within the Chagos Archipelago. A: raw data showing territory size estimates for *P. lacrymatus* individuals (n = 30 around islands with seabirds, n=30 around islands with rats). Each point represents a single *P. lacrymatus* territory. Black bars show the mean estimates for *P. lacrymatus* territory size, and mean values and standard deviations are also presented above each violin plot. B: Bayesian posterior density showing the effect of island invasion status on *P. lacrymatus* territory size. Points are median estimates with thick and thin lines representing 75% and 95% credible intervals respectively. The posterior probability (PP), evidence ratio (ER), and posterior density in green show the extent to which *P. lacrymatus* territories are smaller around islands with seabirds. C, E: Relationships between turf algal cover (C), turf algal δ^{15}N (E) and *P. lacrymatus* territory size within island invasion status type. Points are partialized residuals extracted from Bayesian models for each *P. lacrymatus* individual. Best fit lines are extracted from Bayesian model conditional effects, with grey shading indicating 75% quantiles. D, F: Posterior density plots showing the strength of the relationships in C and E respectively. Densities right of zero indicate a positive relationship, whilst densities left of zero indicate a negative relationship. Evidence ratios show how much more likely the observed relationship is present over the alternative (grey shading). Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

3.2.3 Aggression

The higher nutritional gain per unit foraging effort available to *P. lacrymatus* adjacent to islands with seabirds provides individuals with the energy to invest more time in aggressive territory defence than individuals adjacent to islands with invasive rats with a PP of 0.85 (Figure 3.3, Slope:0.47 (-0.35, 1.28), ER = 5.47, Davies and Hartley, 1996, Frost and Frost, 1980). Furthermore, this broad scale effect is driven by fine scale variation in turf algae cover and δ^{15}N in *P. lacrymatus* territories within island invasion status. Adjacent to islands with seabirds, the overall elevated turf algal δ^{15}N has maximised the benefits of turf algal δ^{15}N for *P. lacrymatus* aggression, resulting in no relationship between fine scale variation in δ^{15}N and aggression (Figure 3.3 slope: -0.11 (-0.43,0.21), PP: 0.29, ER: 0.41). Variation in aggression is instead driven by turf algal cover within each *P. lacrymatus* individual's territory (Figure 3.3, slope: 2.97 (-0.72, 6.43), PP: 0.91, ER: 10.15). As turf algal cover increases, the value of the territory increases, and the payoff of being aggressive is higher than remaining passive in the presence of nutrient subsidies (Maynard-Smith, 1982, Peiman and Robinson, 2010). It is also possible that variation in aggression is a consequence of *P. lacrymatus* having evolved an inherently lower threshold for aggression in the absence of invasive rats. Aggression is heritable (Dochtermann *et al.,* 2019), and the invasion status of the study islands has been consistent since the introduction of black rats in the 1700s (Sheppard *et al.,* 2012). The short larval duration of *P. lacrymatus* (~23 days, Soeparno *et al.*, 2012), and the prevalence of self-recruitment among reef fish (Green *et al.,* 2015), suggest it is plausible that *P. lacrymatus* individuals adjacent to islands with seabirds only recruit to islands with seabirds and vice-versa. Both the evolutionary history of the economics of territoriality, and the behavioural history of individuals (Dall *et al.,* 2004) can have important consequences for the persistence of species (Delarue *et al*., 2015).

In the presence of invasive rats and the subsequent absence of nutrient subsidies, the costs of aggression (energetic expenditure), appear to outweigh the benefits (energetic gain), even where turf algal cover is high. The resource value of these *P. lacrymatus* territories primarily remains below the threshold where aggression would be beneficial, resulting in no association between either turf algal cover (slope: 0.00 (-3.48, 3.45), PP: 0.50, ER: 1.02) or δ^{15}N (0.09 (-0.26, 0.45), PP: 0.66, ER: 1.98, Figures 3.3&.3.4). The disruption of nutrients by invasive black rats has therefore reduced the aggressive tendencies of *P. lacrymatus* individuals (Figure 3.4).

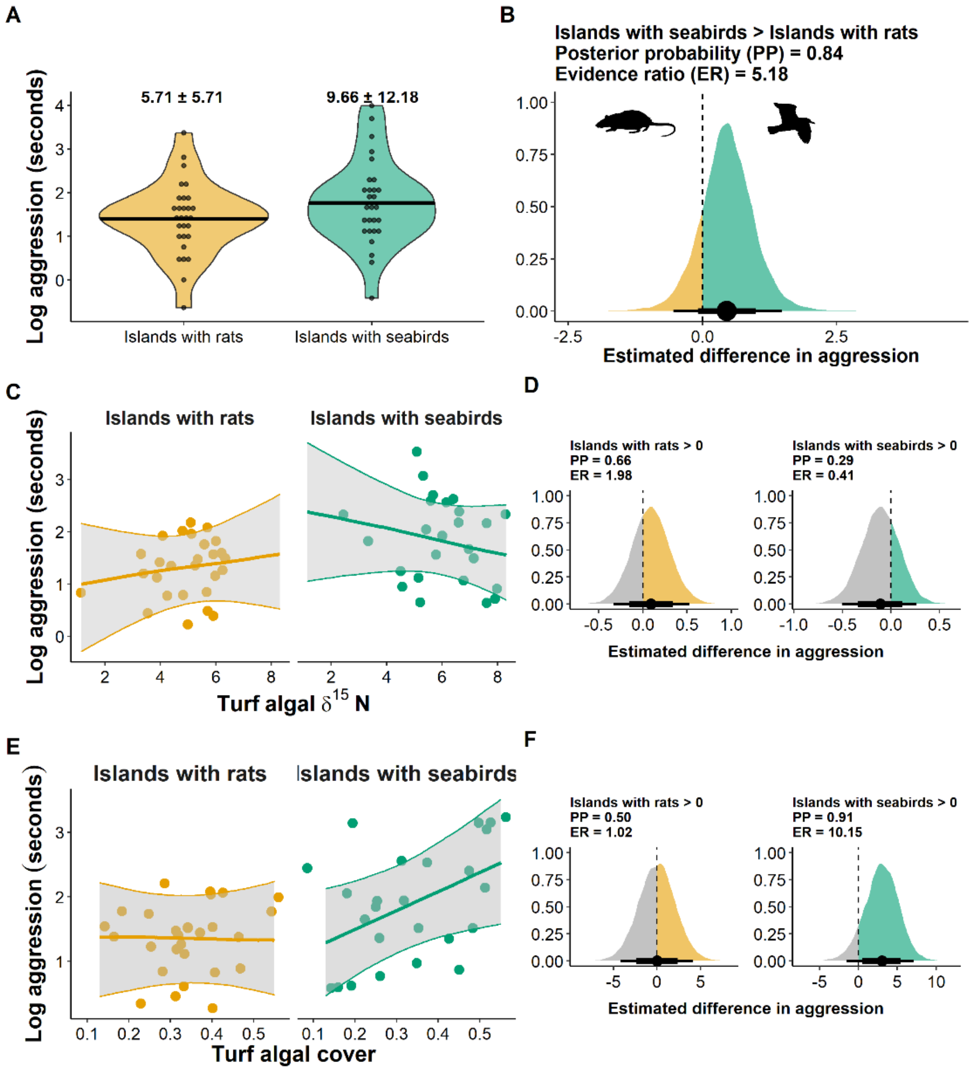

Figure 3.3: *P. lacrymatus* aggression between and within island invasion status type with Turf algal δ^{15}N and cover within the Chagos Archipelago. A: raw aggression estimates for *P. lacrymatus* individuals (n = 28 around islands with seabirds, n=29 around islands with rats). Each point represents a single *P. lacrymatus* territory. Black bars are mean estimates, and mean values and standard deviations are also presented above each violin plot. B: Bayesian posterior density showing the effect of island invasion status on *P. lacrymatus* aggression. Points are median estimates with lines representing 75% and 95% credible intervals respectively. The posterior probability (PP), evidence ratio (ER), and posterior density in green show the extent to which *P. lacrymatus* aggression is higher around islands with seabirds. C, E: Relationships between turf algal cover (C), turf algal δ^{15}N (E) and *P. lacrymatus* aggression within island invasion status type. Points are partialized residuals extracted from Bayesian models, with best fit lines extracted from Bayesian model conditional effects. Grey shading indicates 75% quantiles. D, F: Posterior density plots showing the strength of the relationships in C and E respectively. Densities right of zero indicate a positive relationship, whilst densities left of zero indicate a negative relationship. Evidence ratios show how much more likely the observed relationship is present over the alternative (grey shading). Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

3.2.4 Ecosystem-level consequences

The impact of invasive species in terrestrial ecosystems on the territoriality of reef fish (Appendix A , Figure 3.4, Figure S3.3), could have broader, community level consequences for coral reef ecosystems. *P. lacrymatus* individuals adjacent to rat infested islands display lower growth rates than individuals with access to seabird nutrient subsidies (Graham *et al.*, 2018). This has important consequences for fish biomass and productivity, with faster growing, more aggressive fish adjacent to rat-free islands likely contributing to increased ecosystem function in the presence of seabird nutrient subsidies (Graham *et al.*, 2018, Benkwitt *et al.*, 2020). The influence of invasive rats on *P. lacrymatus* aggression could therefore have indirect bottom-up consequences for reef fish community dynamics.

As a functionally important reef fish (Hoey and Bellwood, 2010), the aggressive nature of *P. lacrymatus* and other territorial damselfish can influence the spatial and social organisation of reef fish communities. For example, space use and foraging areas of butterflyfish (*Chaetodontidae*) are influenced by high levels of interspecific aggression from damselfish (Samways, 2005). The density of surgeonfishes, such as *Acanthurus coeruleus,* are also negatively associated with territorial damselfish density, and damselfish density is a predictor of surgeonfish social mode (Morgan and Kramer, 2005). Furthermore, by driving variation in *P. lacrymatus* territory size, the disruption of nutrients by invasive rats also affects the spatial organisation of territorial damselfish (Figure S3.4, S3.5 & S3.6), which may have broader impacts on the reef community. *P. lacrymatus* have the capacity to influence the composition of both algal and coral communities (Ceccarelli, 2007). Damselfish territories are areas of high algal productivity (Hoey and Bellwood, 2010), but also act as a refuge for some species of coral (Gochfeld, 2010), whilst contributing to the mortality of others (Gordon *et al.,* 2015). The role of invasive rats in altering *P. lacrymatus* territory size could therefore have indirect consequences for coral growth, community composition, and resilience.

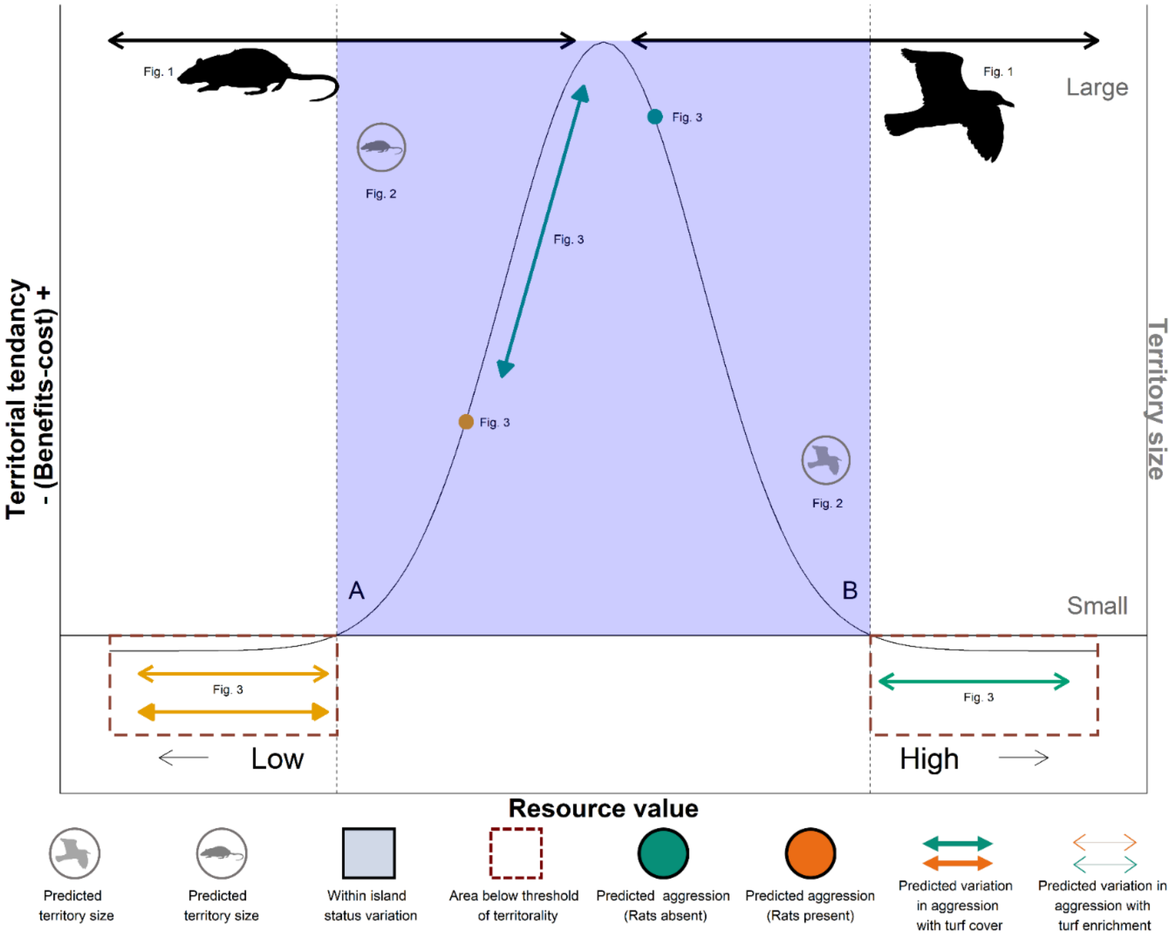

Figure 3.4: Threshold model of economic defendability with results for damselfish territoriality in the presence and absence of seabird nutrient subsidies. Territoriality is predicted to occur where the benefits outweigh the cost (shaded blue area). Below the threshold of territoriality, there is predicted to be no relationship between resource value and territoriality (dashed red boxes). The presence of nutrient subsidies around islands with seabirds is predicted to increase resource value to damselfish, resulting in higher levels of aggression (green point) than around islands with invasive rats (orange point). An inverse relationship between resource value and territory size (secondary y axis) is also predicted, such that territories of higher resource value, i.e., those around islands with seabirds, will be smaller (circular bird icon), than territories with lower resource value, i.e., around islands with invasive rats (circular rat icon). Around islands with rats, resource value is low, and variation in turf algal cover and turf algal δ^{15}N is not enough to place *P. lacrymatus* individuals above the threshold of territoriality (orange arrows). Around islands with seabirds, elevated δ^{15}N is high, placing *P. lacrymatus* territories beyond the threshold of territoriality (green open arrow). Variation in aggression within reefs adjacent to islands with seabirds is instead driven by variation in turf algal cover (green closed arrow). Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

We have provided new insights into how the disruption of cross-ecosystem nutrient subsidies by a terrestrial invasive species can influence territorial behaviour in a reef fish. Given the global decline in the movement of nutrients across ecosystems, understanding the proximate ecological implications of nutritional declines, such as behavioural responses of affected organisms, is a fundamental step in understanding the ultimate consequences of declining nutrient subsidies on species persistence (Delarue *et al.*, 2015). The presence of invasive rats impacts reef fish species interactions via changes in territorial behaviour, impacting benthic and reef fish community composition and biodiversity, and subsequently ecosystem function and resilience (Benkwitt *et al.,* 2020, Benkwitt *et al.,* 2021). Rat eradication therefore has the potential to have multiple, cross-ecosystem benefits, from restoring territoriality in individual reef fish to the subsequent bottom-up effects on populations, communities, and ecosystems.

3.3 Methods

3.3.1 Site and study species

We completed all data collection between the 14th April and 6th May 2021 around the remote northern islands of the Chagos archipelago, part of a large no take marine protected area in the Indian Ocean (Hays *et al.,* 2020). The northern reefs of the archipelago are some of the most pristine in the world, characterised by extremely high fish biomass (Graham *et al.,* 2018). The study area is free of local human stressors, except for invasive rats (Sheppard *et al.,* 2012). In total we surveyed 10 islands across three atolls (Figure S3.1). Five of the islands were infested with black rats (*Rattus rattus*), and five of the islands had high seabird densities and no rat infestations. Seabird densities around rat-free islands have been shown to be 760 times higher than around rat-infested islands (Graham *et al.,* 2018). Otherwise, all islands were similar in terms of environment and size (Hays *et al.,* 2020, Sheppard *et al.,* 2012).

Plectroglyphidodon lacrymatus is categorised as an extensive herbivorous farmer, with both macroalgae and turf algae found within their algal farms (Robles and Martin, 2013). *P. lacrymatus* has also been used in previous studies to quantify nitrogen isotope signals in the presence and absence of invasive rats across the Chagos Archipelago (Graham *et al.,* 2018). Specifically, *P. lacrymatus* around rat-free islands have also been shown to have an elevated nitrogen signature and faster growth rate compared to individuals around rat infested islands in the absence of invasive rats (Graham *et al.,* 2018).

3.3.2 Behavioural observations

At each of the ten islands, we randomly selected six focal *P. lacrymatus* individuals from around sites that were surveyed in 2015 (Graham *et al.,* 2018) and in 2018 (Benkwitt *et al.,* 2019). These survey sites were marked by a GPS in 2015, and the distance of these sites from the island shore was also recorded (Graham *et al.,* 2018). We placed a GoPro camera in the vicinity of the territories of focal *P. lacrymatus* individuals. Cameras were deployed for 20 minutes, with the first 5 minutes disregarded as an acclimation period (Nanninga *et al.*, 2017) to ensure the focal individual was not influenced by the presence of observers or the camera. After 20 minutes, cameras were collected, and videos analysed in the laboratory. We used a continuous sampling approach when conducting video analyses, recording behaviours and the time at which behaviour changed.

We recorded all *P. lacrymatus* aggressive interactions from the behavioural videos using the BORIS software (Friard and Gamba, 2016). Behaviours associated with aggressive interactions included attacking in short, accelerated swimming movements, biting, and butting (Paola *et al.*, 2012). For all aggressive interactions, the encountered species was recorded as either a conspecific or heterospecific. We noted both the number of aggressive interactions and the total length of all aggressive interactions for each individual.

3.3.3 Territory mapping

We mapped the territory of a single individual present at the location of each of the six Go Pro cameras placed for behaviour at each island, using methods similar to Robles *et al.* (2018)**.** We placed a camera on a stand 1 m above the territory of the individual such that the camera had a field of view of 2 x 2 m. A 25 cm scale was visible within the field of view of the camera. Cameras were left for 20 minutes, with the first 9 minutes then discarded as a acclimation period (Nanninga *et al.*, 2017). To calculate territory size, we took 21 screengrabs of the footage, approximately every 30 seconds, across a 10-minute period. We then imported these screengrabs into ImageJ to record the position of the focal individual. We set the frame of the images as an X, Y axes and recorded the individual positions as Cartesian coordinates. We then plotted the Cartesian coordinate positions and calculated the minimum convex polygon of the points for each focal damselfish to estimate territory area.

We also used the territory camera footage to count the number of neighbouring *P. lacrymatus* individuals to estimate *P. lacrymatus* density for each individual patch surveyed within each island. The total length of each focal individual was also estimated from the territory camera footage.

For two of the islands (one rat invested island and one island without rats, and a total of 12 *P. lacrymatus* individuals), territory cameras could not be used due to high currents and wave surge. Instead, we used Go Pro cameras on a photo time-lapse (one photo per second) to take photos of the focal damselfish territory, with a 0.5 x 0.5 m quadrat placed within the territory as a size reference. The photos were then imported into the software programme Agisoft and used to create 3D models of the focal individual territories. To estimate territory size for these individuals, we used the behavioural observation video to mark the location of focal individuals every 30 s for 10 minutes as above, then cross referenced these locations with a screengrab of the 3D model in Image J, using the frame of the image as an X Y axes as above. To estimate the total length of these individuals, we photographed each territory from above, with a 0.5 x 0.5 m quadrat as a size reference, ensuring the focal individual was also within the frame of the photo. These images were then imported into ImageJ and the size of each focal individual was estimated.

3.3.4 Benthic composition

Benthic surveys were conducted using the territory mapping video footage. We took a screengrab of the territory area from the videos and overlaid 100 points onto this image. We recorded the benthos under each of these points to quantify the abundance and percentage cover of algae (turf and macro) within each territory. We used the 3D models for the 12 individuals for which territory cameras could not be used, to conduct the territory benthic surveys using the same methods as above.

3.3.5 Isotope sampling

Following behavioural observations and territory mapping videos, we collected turf algae and macro algae if present (*Halimeda* spp.) from within the territory of each focal individual. All algal samples were dried at 60 ˚C for 24 hours or until dry ahead of nitrogen stable isotope analysis. Dried samples were washed in a 10% hydrochloric acid solution to remove any contaminants and calcareous matter, and then centrifuged at 3000 rpm for six minutes. Samples were washed thoroughly with distilled water between centrifuge cycles. In total, samples were centrifuged four times. Samples were then dried for a final time. Isotope samples were then analysed at Lancaster University (UK). Samples were combusted using an Elementar Vario MICRO cube Elementer Analyser, before being analysed in an Isoprime 100 Isotope Ratio Mass Spectrometer. Samples were analysed with the two international standards IAEA 600 and USGS 41, and a random subset of samples were run in triplicates to ensure readings were accurate. From the analysis, we extracted values for the ratios of the nitrogen isotope N15:14 ($\delta^{15}N$) for both turf and macro algae.

3.3.6 Statistical analysis

All our analyses were conducted using R v4.1.0 (R core team, 2019). We ran Bayesian models using the brms package (Bürkner, 2017) implemented in STAN (Stan development team, 2022). All Bayesian models were run for 10,000 iterations, with a warm-up of 1000 iterations, over four chains. We used weakly informative, normal priors for all models (Hadfield, 2010) and included a nested random intercept for atoll, and the islands within each atoll. As there was no ecological basis to assume variation in slopes between the different islands within each atoll, we did not include random slopes in the models (Graham *et al.*, 2018, Benkwitt *et al.,* 2021). All models assumed a normal likelihood based on distribution plots for each response variable. To check model fit and convergence, we used trace-plots, graphical posterior predictive checks, effective sample sizes (ESS) and the Gelman-Ruban convergence diagnostic (R-hat). We log-transformed the time spent invested in aggression to improve model convergence and remove divergent transitions that were present when we ran the model on untransformed data. A total of 5 models had up to 10 divergent transitions. However, all models had ESS values of over 1000, and R-hat values of less than 1.01, indicating that MCMC chains had converged well (Gelman and Rubin, 1992, Vehtari *et al.,* 2021). To check for heavily weighted, influential data points in our models, we used Pareto smoothed importance-sampling-leave-one-out cross-validation (PSIS_LOO). Where we had pareto-k values of over 0.7, we ran the models with and without the highly influential data points and compared the posterior distributions. We also extracted the conditional effects and partialized residuals from all models. We then used the conditional effects and partialized residuals to determine mean estimates and 75 % uncertainty intervals of the posterior predictive distributions. All of our models comparing between island invasion status therefore had the following basic structure:

Response variable ~ 0 + Invasion status + (1|Atoll/Island)

Our models that compared aspects of nutritional resources and *P. lacrymatus* territoriality within each island invasion status type had the following basic structure:

Response variable ~ 0 + *Explanatory variable(s)*Invasion status* + (1|Atoll/Island)

We then used hypothesis testing to test *a priori* hypotheses for our models. All hypothesis tests were one way, and for each test we calculated the posterior probability (PP) to determine the probability to which our hypotheses were supported, and evidence ratios (ER) to show the extent to which the evidence that our hypotheses is supported is greater than an alternative hypothesis (Extended data Table 1, Table 2). Evidence ratios are transformed posterior probability values such that $ER = \frac{PP}{(1-PP)}$.

Nutritional resources

We compared turf algal δ^{15}N within focal individual territories using a Bayesian model with island invasion status as the explanatory variable. The following hypothesis was then tested, and posterior probabilities and evidence ratios calculated using nonlinear hypothesis testing: δ^{15}N will be higher for *P. lacrymatus* territories around islands where rats are absent.

To compare the proportion of turf algae within focal individual territories between islands with rats absent and islands with rats, we used a Bayesian model with island invasion status (rats absent/rats present) as the explanatory variable. We then used a nonlinear hypothesis test to test the *a priori* hypothesis that there is a higher proportion of turf algae around rat infested islands.

We also ran a model to test for a relationship between resource quality (turf algal δ^{15}N) and quantity (turf algal cover) within *P. lacrymatus* territories, with δ^{15}N as the response variable. We used an interaction term between turf algal cover and island invasion status, as the relationship between resource quality and quantity could be variable between islands with seabirds and islands with rats. We then used nonlinear hypothesis tests to test the strength of the relationship between turf algal δ^{15}N and cover around islands with seabirds and islands with rats, and to see if the relationship was different between the two island types.

To see if turf algal δ^{15}N and cover was influenced by the distance of the territory to shore, we ran two models, with an interaction term between the distances from the GPS marked survey sites to the shore and invasion status, and turf algal δ^{15}N or cover as the response variable. We then tested the following *a priori* hypothesis for both models: Turf algal δ^{15}N/ cover will be higher around sites closest to shore for islands with seabirds.

Territory size and aggression between island type

We tested the effect of island invasion status on *P. lacrymatus* territory size, time spent on aggression, conspecific density, and focal individual total length using Bayesian models with island invasion status (rats absent/rats present) as the explanatory variable.

The length of aggressive interactions was log transformed to improve model fit. We performed non-linear hypothesis tests for four *a priori* hypotheses:

1. *P. lacrymatus* territory sizes will be smaller around islands where rats are absent.
2. *P. lacrymatus* aggression (in terms of the length of aggressive interactions) will be higher around islands where rats are absent.
3. *P. lacrymatus* densities will be higher around islands where rats are absent.
4. *P. lacrymatus* total length will be higher around islands where rats are absent.

We ran a Bayesian model to test the relative roles of resource quality and quantity on *P. lacrymatus* territory size. We ran two models, one with resource quantity (turf algal cover) as the explanatory variable, and one with resource quality (turf algal $\delta^{15}N$) as the explanatory variable. We included an interaction term between the explanatory variable and island invasion status. We then tested two *a priori* hypothesis from each of the two models: Around islands with seabirds (1) and islands with rats (2) territories with a higher turf algal $\delta^{15}N$/ cover will be smaller.

Territory size and aggression within island type

For both aggressive behaviour and territory size, we considered the influence of turf algal $\delta^{15}N$, turf algal cover, conspecific density, and focal individual total length within islands with seabirds and islands with rats, including an interaction term between each explanatory variable and island invasion status. We considered multiple variables in order to determine the strength of the relationship between territoriality and nutritional resources whilst controlling for additional biotic variables (conspecific density and total length). We ran two separate models for territory size and aggression, with all four of the above explanatory variables included in each model. We then ran *a priori* hypothesis tests to determine the strength of relationships between territory size and aggressive behaviour and each of the four explanatory variables.

In addition, we looked at the influence of territory size on aggression with an additional Bayesian model, with aggression as the response variable and territory size as the explanatory variable, with an interaction term between the explanatory variable and islands invasion status also included. We used nonlinear hypothesis tests on this model to test the following *a priori* hypotheses: Around islands with seabirds (1) and islands with rats (2), aggression will be highest for *P. lacrymatus* individuals in the smallest territories, and this relationship will be weaker around islands with rats (3).

Chapter 4

4. Energetic threshold models predict variation in reef fish territoriality

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Contribution of authors

RLG, SAK, IRH and ACA all contributed to the conceptualisation of the work and developed the research questions. RLG developed the mathematical models and performed all data analyses. All authors contributed to manuscript revisions.

Abstract

Human-induced environmental change affects the resources available for organisms to exploit. For example, the introduction of invasive species can interrupt the natural flow of nutrients across ecosystems, directly impacting energy-dependent behaviours such as territoriality. Subsequent changes in species interactions may then scale up to impact species persistence. Here, we use the disruption of a nutrient pathway by invasive rats on remote islands to develop an economic defendability model of feeding territoriality for the farming damselfish, *Plectroglyphidodon lacrymatus* on adjacent coral reefs. We build our model over two scenarios, varying the role of intruder density on the intensity of competition for nutritional resources to determine how both the social and physical environment can drive *P. lacrymatus* territoriality. We show that *P. lacrymatus* territoriality is dependent upon the interplay of nutritional resources, metabolic physiology, and the intensity of competition. By confronting our models with empirical data, we show that variation in *P. lacrymatus* territoriality is driven by variation in intruder density as a result of the presence/absence of nutrient subsidies. We use our models and empirical data to consider the evolutionary ramifications of variation in territoriality and suggest the implications for *P. lacrymatus* persistence under changing resource conditions.

4.1 Introduction

Environmental change impacts the resources available to individuals (Auer *et al.*, 2020a). Changes in resources due to human induced environmental change may place organisms in evolutionarily novel contexts, resulting in a mismatch between the phenotype and the environment (Sih *et al.*, 2011, Maspons *et al.*, 2019). This phenotype-environment mismatch can be reduced by behavioural responses (Komers, 1997, Maspons *et al.*, 2019) such as changes in foraging (Karkarey *et al.*, 2017) and territorial behaviours (Gunn *et al.*, 2022), which can allow organisms to exploit resources that are still available (Stimson, 1973). However, if behavioural choices are made based upon environmental cues that are unreliable under new environmental conditions, behaviours may be maladaptive (Schlaepfer *et al.*, 2002).

Biotic exchanges, i.e., the introduction of non-native species into an ecosystem, are one example of human induced environmental changes that directly impact an organism's resources (Sala, 2000, Sih *et al.*, 2011). Invasive species can have substantial and detrimental effects on ecosystems via multiple pathways, including the disruption of nutrients (Graham *et al.*, 2018). The expression of certain behaviours is directly dependent upon the availability of nutritional resources. For example, altered rates of aggression following a decline in nutritional resource availability have been identified across a range of taxa, including fish (Berumen and Pratchett, 2006, Keith *et al.*, 2018), birds (Golabek *et al.*, 2012, Folz *et al.*, 2015), mammals (Maher, 1994, Maher and Lott, 2000) and amphibians (Pröhl *et al.*, 2019). As species interactions can affect the distribution of species and scale up to impact communities at higher ecological levels (Anholt, 1997, Delarue *et al.*, 2015), changes in nutritional resource availability via human induced impacts such as biotic exchanges, could therefore have substantial ecological implications for individuals, populations, and communities (Gurevitch and Padilla, 2004).

Territoriality is the aggressive defense of resources utilised by an individual (Burt, 1943) and is associated with numerous ecological variables (Maher and Lott, 2000), including food (Gunn *et al.*, 2022), predation and competition (Berestycki and Zilio, 2019), and mating (Carranza *et al.*, 1990). Territorial behaviour often requires significant energy to perform (Gill and Wolf, 1975) and the decision of when to engage in aggressive defence is related to the energy and nutritional resources available to an individual. For example, the Anna Hummingbird (*Calypte anna*) defends breeding territories to maximise reproductive fitness, which is only possible due to a seasonal increase in flower nectar quality during the breeding season (Stiles, 1971). As such, nutritional resource availability and energetic value are predicted to be a driving factor in determining territorial behaviour (Enquist and Leimar, 1986). Where nutritional resources are low, individuals tend to hold larger territories (Davies and Hartley, 1996, Stehle *et al.,* 2017, Gunn et al 2022) and invest time in foraging instead of aggressive defence in order to maintain enough energy for survival (Samways, 2005, Gunn *et al.,* 2022). However, there is also evidence that territoriality ceases where nutritional resource availability is high because individuals can easily obtain sufficient nutritional resources and so territoriality yields no additional benefit (Wyman and Hotaling, 1988, Ostfield, 1990, Justino *et al.,* 2012). Understanding the relationship between nutritional resources and territoriality can provide a valuable insight into the adaptive significance of territoriality and the selection pressures acting upon territorial behaviour (Carpenter and MacMillan, 1987). The impact of environmental change on nutritional resources makes this relationship even more critical.

Territoriality is predicted to evolve where resources are: 1) related directly to fitness, 2) limited and defendable, and 3) are competed for (Hinsch and Komdeur, 2010, Ord, 2021). Theoretical predictions of territoriality are focussed on behavioural economics and energetic cost-benefit analyses (Ha, 2010) such that territoriality is predicted to be adaptive where the benefits outweigh the costs (Brown, 1964, Hinsch and Komdeur, 2010) or where the benefits of territoriality outweigh the benefits of non-territorial behaviour (Wyman and Hotaling, 1988). Carpenter and MacMillan (1976) developed a threshold model of feeding territoriality for the Hawaiian Honeycreeper (*Vestiaria coccinea*) that predicts an upper and a lower threshold of territoriality based on the economic defendability of nutritional resources (Carpenter and MacMillan, 1976). One addition to this model that could improve its potential to predict when territoriality is optimal is the inclusion of environmental heterogeneity. Evidence suggests that patchy resource availability results in higher territory overlap between individuals (Davies and Hartley, 1996), smaller territory sizes (Newsome *et al.,* 2013) and more intensive competition (Rich *et al.,* 2012). Environmental heterogeneity therefore has the potential to affect the energetic thresholds within which territoriality is predicted to occur (Carpenter, 1987). Understanding how territoriality thresholds are influenced by different biotic and abiotic factors could have important implications for species persistence (Delarue *et al.*, 2015). However, few studies have explicitly combined model predictions with empirical evidence to consider how environmental heterogeneity can predict variation in territoriality via variation in economic defendability.

4.1.1 Model study system

Here, we use a model system of nutrient disruption by invasive rats on tropical islands to investigate how the economic defendability of nutritional resources can predict territoriality in a herbivorous reef fish. Seabirds feed in the open ocean and return to islands to roost and breed, depositing nutrients in the form of guano. These seabird-derived, cross-ecosystem nutrient subsidies run off onto adjacent coral reefs, are taken up by coral, algae, and sponges, and are subsequently consumed by reef fish (Graham *et al.,* 2018). Where invasive rats are present on islands, seabird density, biomass and diversity are substantially reduced via predation by the invasive rats, and the nutrient pathway provided by seabirds is disrupted (Graham *et al.*, 2018, Benkwitt *et al.*, 2022). The absence of invasive rats has been shown to have positive effects on the productivity (Graham *et al.*, 2018), structure (Savage, 2019), composition (Benkwitt *et al.*, 2019), and function (Benkwitt *et al.*,2020) of adjacent coral reef ecosystems. The presence of invasive rats on tropical islands therefore has substantial bottom-up implications for coral reef productivity and biodiversity (Benkwitt *et al.,* 2020).

The impact of invasive rats on tropical islands also has important implications for reef fish behaviour. *Plectroglyphidodon lacrymatus* is a site-specific territorial turf algal farming herbivorous fish that is highly abundant within coral reef ecosystems. Individuals hold small territories, cultivating the turf algae they feed upon, and aggressively defend turf algal nutritional resources against conspecifics (Robles *et al.,* 2018). *P. lacrymatus* is highly aggressive, displaying territoriality in the presence of an intruding conspecific with a probability of 84% (Robles *et al.*, 2018). The higher nutrient production on coral reefs adjacent to rat-free islands provides *P, lacrymatus* individuals with a higher nutritional gain per unit foraging effort, resulting in higher territoriality and smaller territories compared to individuals adjacent to rat-infested islands (**Chapter 3**). The presence of invasive rats in terrestrial systems therefore directly impacts the economic defendability of nutritional resources available to *P. lacrymatus* individuals (**Chapter 3**).

Territoriality in reef fish can also be driven by additional biotic variables, such as the density of intruding conspecifics (Zhu *et al.,* 2022). *P.lacrymatus* individuals with neighbouring conspecifics display higher levels of aggressive defense and hold smaller territories than individuals adjacent to heterospecific competitors (Robles *et al.,* 2018). Furthermore, *P. lacrymatus* aggression has been shown to increase with increased abundances of intruding species (**Chapter 3**, Paola *et al.,* 2012). Theoretical and modelling approaches have identified that intruder density, driven by environmental heterogeneity can have a substantial impact on the economic defendability of resources (Carpenter, 1987, Hinsch and Komdeur, 2010). Predicting territoriality and the economic defendability of resources based on both nutritional resource quality and the impact of environmental heterogeneity would allow the proximate causes of territorial behaviour, and the selection pressures acting upon territorial behaviour to be better understood.

4.1.2 Aims and objectives

We test whether economic defendability models of feeding territoriality (Carpenter and MacMillan 1976), extended to include environmental heterogeneity, offer a plausible explanation for the territoriality of the herbivorous farmer damselfish *P. lacrymatus*, in the presence and absence of invasive rats by confronting model predictions with empirical data. We also test the sensitivity of the model to intruder density, competitive intensity, and nutritional resource quality to determine the extent to which different abiotic and biotic variables influence territoriality via economic defendability.

4.2 Methods

4.2.1 Mathematical model

All figures and analyses were produced using R v 4.1.0 (R core team, 2019) and parameters, variables, equations, units, and relevant references are presented in Table S4.1. Relationships between variables are presented in Figure S4.1.

Model summary

Equations 1 & 2 below summarise the threshold model of feeding territoriality proposed by Carpenter and MacMillan (1976). In order for territoriality to occur, the energetic benefits must outweigh both the energetic costs and the benefits of non-territorial behaviour (Brown, 1964). Specifically, the costs of living and the additional costs of territoriality must be less than the energetic yield available to a non-territorial individual:

$$E + T < aP + bP \qquad \textit{(Eq. 1)}$$

where E is the cost of living (J min^{-1}), T is the cost of territoriality (J min^{-1}), P is the productivity of a 1 m^2 area of turf algae (J min^{-1} m^2), a is the proportion of P an individual receives when non-territorial, and b is the additional proportion of P lost to intruders, that would be available to an individual when territorial (Carpenter and MacMillan, 1976).

The model assumes that the additional energetic gain available to an individual when territorial is dependent upon an individual's efficiency at excluding intruders from a territory (Carpenter and MacMillan, 1976). The efficiency (e_T) with which an individual excludes intruders is a determinant of bP, such that:

$$bP = e_T(1 - a)P \qquad \textit{(Eq.2)}$$

As food productivity, P, increases, an individual can meet their energy requirements even if territorial efficiency, e_T, is low. There will therefore be an upper threshold of territoriality where the energetic yield available to non-territorial individuals is greater than the basic energetic requirements for survival (Carpenter,1987).

Model scenarios

The model proposed by Carpenter and MacMillan assumes that intruding competitors recruit proportionately to territories with higher energetic productivity (Carpenter, 1987). However, in heterogeneous patchy environments, the number of intruders may be disproportionately higher where local energetic productivities are high (Sells and Mitchell, 2020). Where intruder recruitment is disproportionately higher in high resource areas, the proportion of food lost to intruders will increase with increasing resource availability, and the proportion of resource available to non-territorial individuals will decrease (Carpenter, 1987). We therefore extended the model of feeding territoriality to account for variation in environmental heterogeneity and varied parameters across the following scenarios (Figure 4.1):

- **Scenario 1: Homogonous environment:** The number of intruders, *D,* is proportional to *P,* and *aP* is constant across all values of *D,* i.e., the relationship between *P* and *D* is linear (Figure S4.1).

- **Scenario 2: Heterogeneous environment:** The number of intruders is disproportionately higher at high values of P, and aP increases with P, i.e., the relationship between P and D is exponential (Figure S4.1).

In addition, each scenario was modelled with two variations to determine how food energy values and energetic costs influence territoriality (Figure 4.1):

- **Variation A:** Multiple values of energy per unit food available.
- **Variation B:** Multiple values of both energy per unit food and varying energetic costs of living.

These model variations capture food nutritional quality differences, which could impact the energetic costs incurred by *P. lacrymatus* individuals (Polunin, 1988).

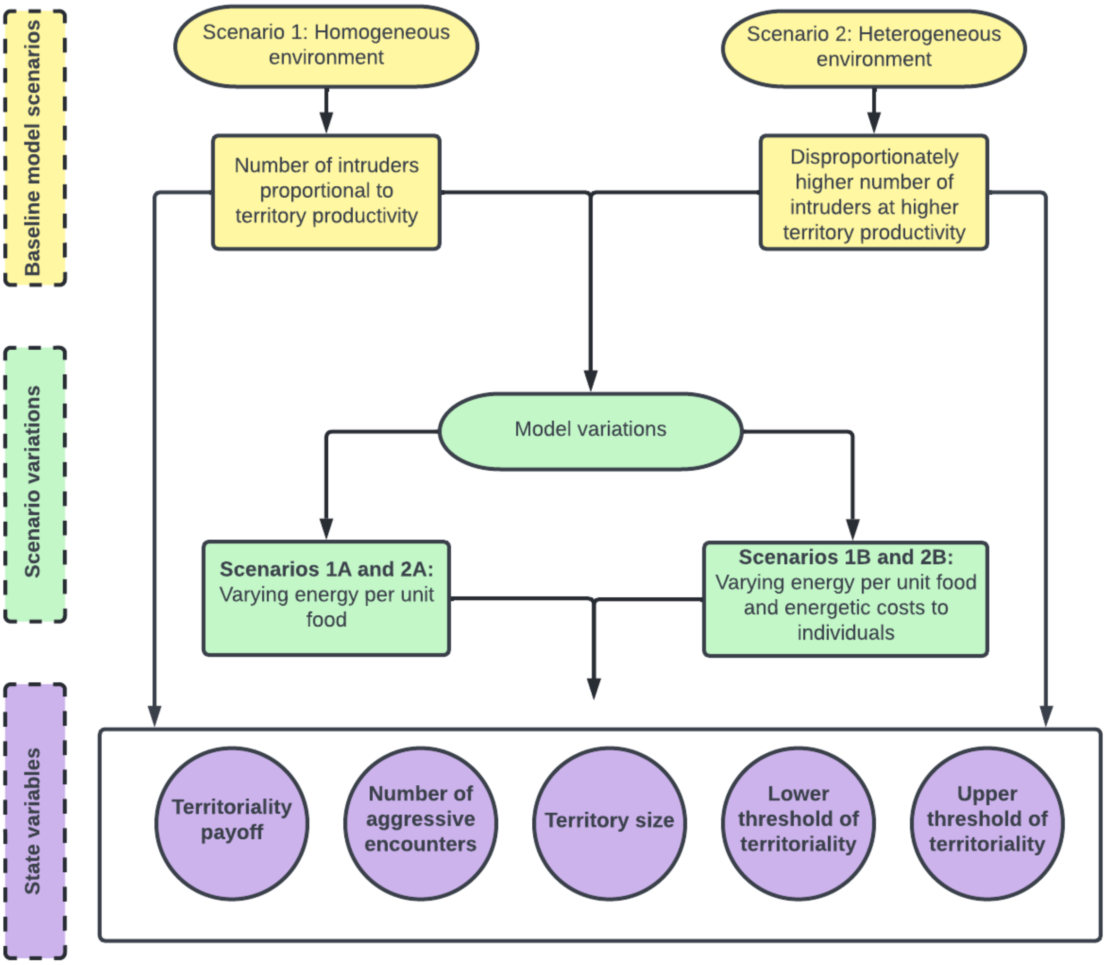


Figure 4.1: Mathematical model summary.

Assumptions

The following assumptions were applied to our mathematical model, following Carpenter and MacMillan (1976): 1) Increased efficiency of territoriality incurs an increased cost of territoriality; 2) cost of living is higher within less productive territories; 3) energetic gain of individuals when non-territorial is associated directly with the number of neighbouring conspecifics (i.e. intruders); 4) below the upper threshold of territoriality, food availability limits non-territorial individuals.

Furthermore, we make the following assumptions for the *P. lacrymatus* study system: 1) turf algae is the defended resource (Jones *et al.*, 2006); 2) territoriality exists to retain and maximise nutritional resources (Paola *et al.*, 2012); 3) behavioural flexibility is adaptive under changing conditions (Carpenter and MacMillan, 1987); 4) Individuals do not invest any excess energy in growth or reproduction (Carpenter and MacMillan, 1987). Whilst we recognise that this final assumption is somewhat unrealistic, we trade-off this issue with maintaining model simplicity as far as possible to ensure that interpretation is clear.

System-specific calculations: Food productivity, P

To apply the model suggested by Carpenter and MacMillan (1987) to our system of *P. lacrymatus* on coral reefs, we added two variables to *Eq. 1* and assume that the energetic yield available to an individual when non-territorial is also dependent upon an individual's territory size and the proportion of time invested in foraging. Territoriality is therefore predicted to occur where:

$$E + T < (aP + bP)SP_f \qquad \textit{(Eq.3)}$$

where the nutritional benefits obtained by an individual are represented by the sum of aP, the proportion of productivity an individual receives when non-territorial, and bP, the additional yield available to individuals when territorial (*Eq. 2*). S refers to territory size and P_f is the proportion of time individuals spend foraging. The product of (aP+bP)S in *Eq. 3* therefore refers to the total productivity of a territory of size S in J min^{-1}.

For the *P. lacrymatus* study system, we assume that food productivity, P, is determined by the energy per unit food ($\mathcal{E}$, J mg^{-1}), the mass of food per unit area (q, mg.min^{-1}m^2), and the proportion coverage of turf algae:

$$P = \mathcal{E}qC \qquad \textit{(Eq.4)}$$

Productivity P therefore represents the energetic yield per m^2 (J min^{-1} m^2, Table S4.1). A baseline value for $\mathcal{E}$ (8.8 J min^{-1}) for turf algae was taken from Leung *et al.* (2019) and a value for q (3.5 mg min $^{-1}$ m^2) was estimated from Polunin (1988). For model scenarios 1A, 1B, 2A and 2B, $\mathcal{E}$ increases between 8 and 11 at increments of 0.75.

System-specific calculations: Number of intruders, D

The number of intruders is calculated as follows for each model scenario:

Scenario 1:

$$D = mP + 1 \qquad \textit{(Eq. 5a)}$$

Equation 5a assumes a positive linear association between territory productivity, P, and the number of intruders, *D*, following the equation of a straight line: $(y = mx + c)$ where *m* represents the gradient, and 1 refers to the y-intercept, *c*. To calculate values for *m* and *c*, we plotted a linear relationship between the minimum and maximum estimated values of *P*, and minimum (1) and maximum (10) assumed values for *D*. This baseline range of values for *D* is in line with conspecific densities observed in the field (**Chapter 3**). For scenarios 1A and 1B, the gradient *m* increases by 0.1 for each increase in Ɛ, to reflect that higher *P* results in an increased number of intruders (Carpenter and MacMillan, 1987).

Scenario 2:

$$D = 1e^{xP} \qquad \textit{(Eq. 5b)}$$

Equation 5b satisfies the assumptions of Scenario 2 by predicting an exponentially increasing relationship between territory productivity, *P*, and the number of intruders, *D*, such that a disproportionate number of intruders coexist at higher values of *P*. For the baseline Scenario 2 model, the multiplier *x* was set at 0.08.

For scenarios 2A and 2B, *x* varies between 0.08 for the lowest value of $\mathcal{E}$ and 0.065 for the highest value of $\mathcal{E}$, to reflect that higher $\mathcal{E}$ results in higher *P*, which demands an increase in *D*.

System-specific calculations: Territorial efficiency, e_T

Territorial efficiency is calculated as a function of either productivity (Scenario 1) or the number of intruders (Scenario 2):

Scenario 1:

$$e_T = -mP + 1 \qquad \textit{(Eq. 6a)}$$

As with Equation 5a, Equation 6a is calculated from the general line equation $(y = mx + c)$, and a negative linear association between territory productivity, *P*, and the costs of territoriality, e_T, is assumed. To calculate values for *m* and *c*, we plotted a linear relationship between the minimum and maximum estimated values of *P*, and minimum (0) and maximum (1) possible values for e_T.

For scenarios 1A and 1B, we assume that increasing $\mathcal{E}$ and therefore *P*, results in increased territorial efficiency due to the additional energy available to individuals when *P* is higher. We therefore decreased values for the gradient *m* from -0.03 (Eq. 9a) by -0.05 for each increasing value of $\mathcal{E}$.

Scenario 2:

$$e_T = e^{-0.05D} \qquad \textit{(Eq. 6b)}$$

e_T is calculated as function of *D* for Scenario 2, as exponentially higher values of *D* at high *P* are assumed to reduce the capacity of *P. lacrymatus* to exclude all intruders. We therefore assume an exponentially decreasing association between *P* and *D.*

System-specific calculations: Non-territorial gain, a

For Scenario 1, *a* is constant across all values of *P,* and is calculated as the slope of the linear function describing the relationship between *P* and *D* (*Eq.7a*). The fraction of *P* obtained by individuals when non-territorial (*a*) is calculated as a function of density for Scenario 2.

Scenario 1:

$$a = \frac{D-1}{P} \qquad \textit{(Eq. 7a)}$$

Scenario 2:

$$a = e^{-0.3D} \qquad \textit{(Eq. 7b)}$$

System-specific calculations: Territorial gain, b

The additional gain when territorial, or the amount lost to intruders when non-territorial, *bP* was then calculated using *Eq. 2.*

System-specific calculations: Cost of living, E

Basic maintenance costs are calculated as the sum of the energy lost when resting and energy lost when foraging:

$$\mathrm{M} = \left(P_f m_f\right) + \left(P_r m_r\right) \qquad \textit{(Eq. 8)}$$

Where P_f is the proportion of time individuals spend foraging, m_f is the energy lost during foraging (J min^{-1}), P_r is the proportion of time spent resting, and m_r is the energy lost during resting (J min^{-1}). A baseline value for m_r of 1.5 J min^{-1} was estimated from standard metabolic rates calculated for *P. lacrymatus* using respirometers (Polunin and Klumpp, 1989), and converted to J min^{-1} using the assumptions of aerobic respiration and approximate conversions of ATP into Joules. m_f was then assumed to be 1.2 m_r. A value of 0.8 for P_f was approximated from **Chapter 3** and Robles *et al.*, (2018). P_r was then assumed to be 0.17, leaving individuals with a maximum of 3% of a 24-hour period to invest in aggressive defense. For model scenarios 1B and 2B, m_r was increased between 1 and 2 at increments of 0.2.

The total cost of living, E is then calculated as follows for each model scenario:

Scenario 1:

$$E = MPe^{-0.2P} \qquad \textit{(Eq.9a)}$$

By using M and the multiplier of P, *Eq. 9a* satisfies model assumptions 2 and 3, that the cost of living increases during territoriality and is higher at lower values of P.

Scenario 2:

$$E = MDe^{-0.08D} \qquad \textit{(Eq. 9b)}$$

In Scenario 2, the number of intruders is predicted to have substantial effects on territoriality. The number of intruders, driven indirectly by food productivity P, is therefore the primary determinate of territoriality in this Scenario. We therefore calculate the cost of living as a function of the number of intruders rather than food productivity directly (*Eq. 9b*).

System-specific calculations: Territoriality costs

The costs of territoriality are determined by territorial efficiency, e_T and the energy lost to aggression (m_a, J min^{-1}), where $ma = 2\,mr$:

$$T = m_a e \qquad \textit{(Eq. 10)}$$

State variables

We used the parameters and variables calculated in Equations 4-10 to calculate the following state variables:

1. Territory size (S, m^2):

$$S = \frac{E+T}{(aP+bP)p_f} \qquad \textit{(Eq. 11)}$$

2. Net payoff of territoriality, (N, J min^{-1}m^2):

$$N = (bP\ x\ S) - T \qquad \textit{(Eq. 12)}$$

The net payoff can then be plotted against productivity P to predict the lower and upper thresholds of territoriality. The thresholds can be identified as the values of P where the net payoff was 0, i.e., where:

$$(bP\ x\ S) - T < \ \mathcal{E}qC \qquad \textit{(Eq. 13a)}$$

therefore

$$\frac{N}{P} = 0 \qquad \textit{(Eq. 13b)}$$

In addition, we use time budget estimates for the proportion of time invested in territoriality by *P. lacrymatus* to calculate the number of aggressive encounters (encounters min^{-1}). First, the overall net energetic gain available to *P. lacrymatus* in a 24-hour period is calculated as:

3. Net energetic gain:

$$G = (aP + bP)S - ET \qquad \textit{(Eq.14)}$$

G is then used to calculate:

4. Number of aggressive encounters (A_n, encounters min^{-1}):

$$A_n = \frac{G}{m_a} * R * 0.03 * 0.84 \qquad \textit{(Eq.15)}$$

Where R is the encounter rate per minute, which we assume to be 40 based on an average of 1.5 seconds per aggressive encounter (**Chapter 3**). A_n is then scaled by the average proportion of time invested in aggression (0.03) and the probability that an encounter will result in aggression, which we assume to be 0.84 (Robles *et al.,* 2018).

4.2.2 Empirical data

The empirical data used to confront the mathematical model was collected from 14th April- 6th May 2021 from coral reefs around remote islands within the Chagos Archipelago. *P. lacrymatus* territory size and aggression were quantified around ten islands across three atolls within the archipelago. Five of these islands had rat infestations and five were rat-free. The empirical dataset consists of values for turf algae cover, C, territory size, S, the number of neighbouring conspecifics (i.e., potential intruders, D), and the number of aggressive encounters (A_n). We converted the empirical values of A_n for the observation periods (~15 minutes) to encounters min^{-1}. The empirical data covers turf algal proportional cover values between 0.12 and 0.55.

4.2.3 Comparison of model and empirical data

To confront our mathematical model predictions with empirical data, we extracted the range of values of turf algal cover (C) for which we also had empirical values, from the mathematical model. In total, we confronted the model estimates with 28 data points from rat-free islands and 29 data points from rat-infested islands.

We generated linear regression models with turf algal cover (C) as the predictor variable to compare the slopes of the model predictions with those of the empirical data. We ran separate models with the dependent variable as either the number of aggressive encounters (A_n) or territory size (S) to identify how effectively our mathematical model could predict two different aspects of territoriality. We generated separate models for empirical data collected from rat-free and rat-infested islands. For territory size, we generated an additional model for Scenario 2 that considered only model predictions beyond the predicted lower threshold of territoriality. All linear regression models included an interaction term between turf algal cover (C) and ‘model’. We extracted the slopes from all linear models and then compared the slopes using post-hoc pairwise comparisons, where an alpha value of $P < 0.05$ shows two slopes were significantly different from one another. We therefore assumed the mathematical model could significantly predict the empirical data where pairwise comparisons between slopes produced a value of $P > 0.05$, indicating the model predictions and empirical data were statistically similar.

4.3 Results

4.3.1 Scenario 1: Homogeneous environment

Under Scenario 1, the number of aggressive encounters was predicted to follow a right-skewed, bell-curve relationship with productivity P (Figure 4.2). Territory size was predicted to be an exponentially decreasing function of territory productivity (Figure 4.2). The territoriality payoffs (N) predicted no lower threshold for aggression but predicted that territoriality should cease at productivity values more than 22.79 J $\text{min}^{-1}\text{m}^2$, equivalent to proportional turf algal cover of ~0.74. A peak territoriality of 0.49 encounters min^{-1} (~35 encounters per hour) was predicted at an energetic productivity of 4.31 J min^{-1}, equivalent to a turf algal cover of 0.14 (Figure 4.2). At the predicted upper threshold for territoriality, territory size was estimated to be 0.16 m^2 (Figure 4.2).

4.3.2 Scenario 2: Heterogeneous environment

Scenario 2 predicts an exponentially increasing relationship between productivity and aggression, with the rate of increase of territoriality starting to slow at the highest productivity levels (Figure 4.2). Territoriality is predicted to occur for territories with a minimum productivity value of 7.70 J $\text{min}^{-1}\text{m}^2$, equivalent to a proportional turf algal cover of ~0.25. This model predicts no upper limit to territoriality. At the highest energetic productivity of 30.49 J min^{-1} and a turf algal cover of 0.99, territoriality was predicted to be 0.79 encounters min^{-1} (~42 encounters per hour). As with Scenario 1, territory size decreased as an exponentially decreasing function of energetic productivity, with a territory size of 0.92 m^2 predicted at the lower threshold of territoriality (Figure 4.2).

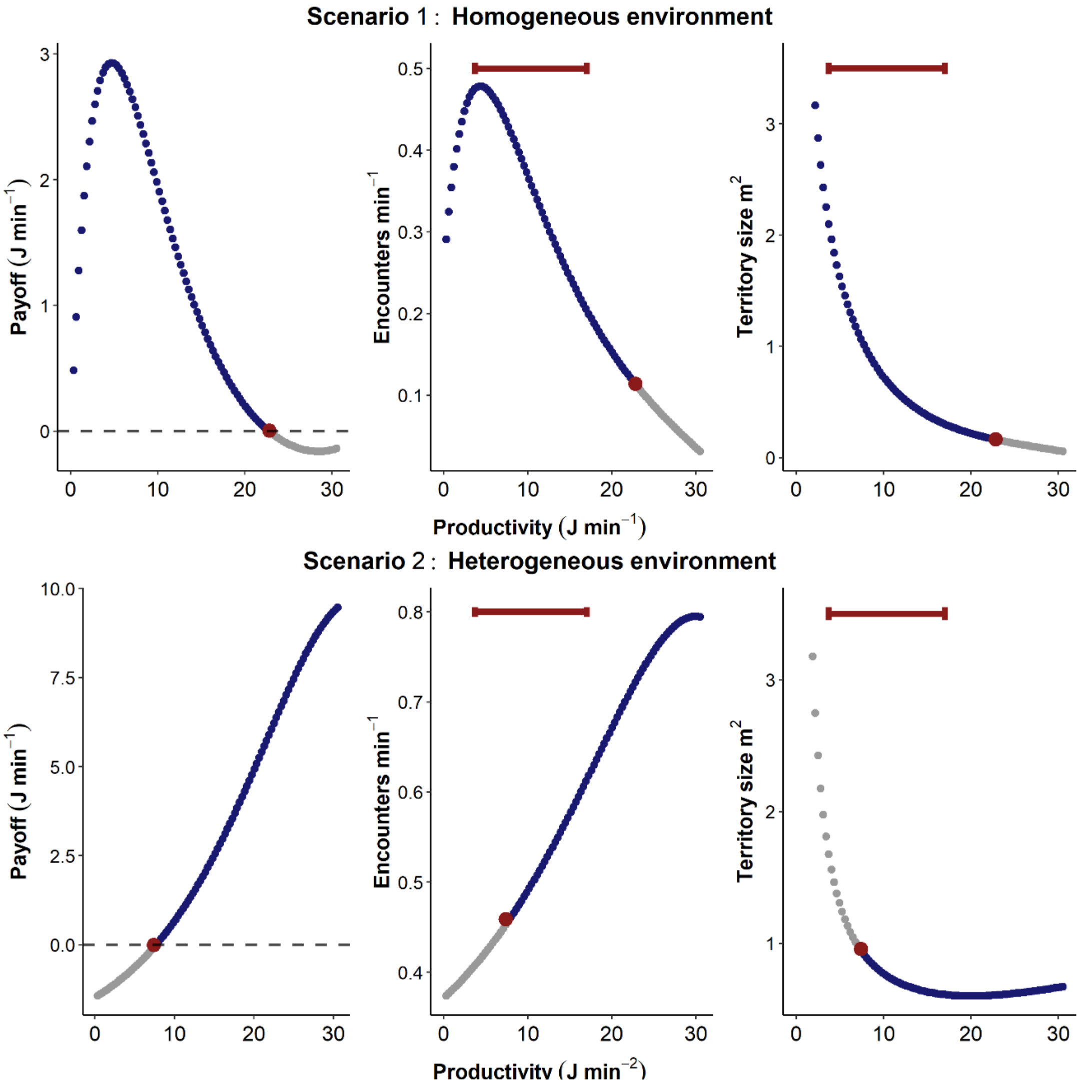


Figure 4.2: Mathematical model predictions for *P. lacrymatus* territoriality and territory size. Dashed lines show where the payoff of territoriality is 0. Red points represent the thresholds of territoriality, calculated as the point at which the payoff of territoriality is equal to 0. Blue points represent territoriality estimates that fall within these thresholds, whilst grey points represent estimates that lie outside of the estimated thresholds. Red bars represent the productivity range captured within our empirical data that we use to confront the mathematical model.

4.3.3 Effect of food energy

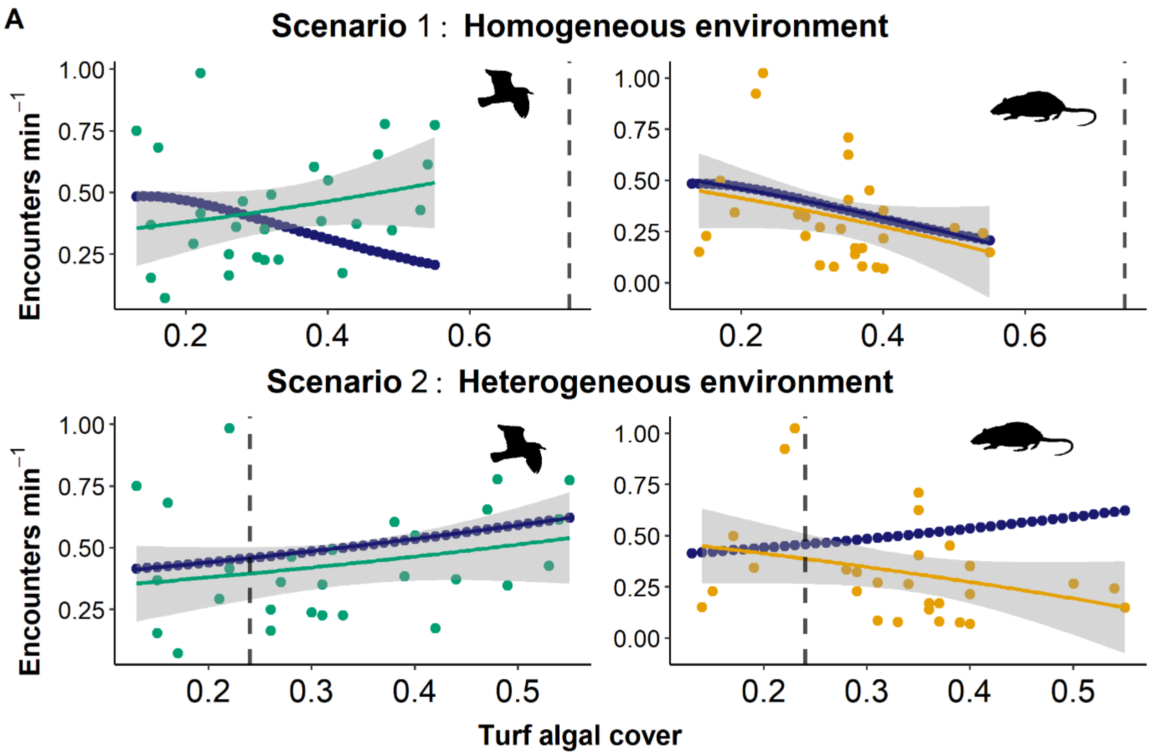
Scenarios 1A and 2A included a range of values for the energy per unit food (Ɛ). Increases in food energy values also had an effect on territoriality estimates and the thresholds within which territoriality was predicted to occur. Specifically, as values for Ɛ increased, the predicted upper threshold of territoriality decreased whilst the lower threshold increased for Scenario 1, with increases in the lower threshold predicted as values of Ɛ increased for Scenario 2 (Table S4.2). Furthermore, no upper thresholds were predicted for any food energy values in Scenario 2. For both Scenarios, territoriality was also predicted to increase slightly with increasing food energy values (Figure S4.2).

4.3.4 Effect of food energy and cost of living

Scenarios 1B and 2B considered how territoriality is influenced by both the energy per unit food, and the energetic costs of living (Figure S4.3). For Scenario 1B, where the food energy values were low and energetic costs were high, there were no thresholds - territoriality was predicted to occur across all values of energetic productivity. Upper thresholds were predicted where both food energy value and energetic costs were high. Furthermore, peaks in territoriality were variable with cost-of-living values, but not with food energy values. (Table S4.2, Figure S4.3). For Scenario 2B, no upper thresholds of territoriality were predicted, regardless of food energy or cost of living values (Table S4.2, Figure S4.3). Lower thresholds of territoriality were variable with variation in cost-of-living values, but not food energy values (Table S4.2). Peak territoriality was highest for high food energy values, regardless of cost-of-living values. Territory sizes were variable with cost-of-living values, with higher cost of living resulting in larger territory sizes (Figure S4.3).

4.3.5 Empirical data

Pairwise comparisons of regression slopes for mathematical model predictions and the empirical data identified that the best fitting model scenario was determined by the invasion status of the islands from which the empirical data were collected. Scenario 1 was able to predict the number of aggressive *P. lacrymatus* encounters for individuals on reefs adjacent to islands where invasive rats were present (Figure 4.3, Table S4.3B and C, Estimate = 0.01, SE = 0.26, $P = 0.99$), whilst Scenario 2 accurately predicted *P. lacrymatus* aggression for individuals adjacent to islands where invasive rats were absent (Figure 4.3, Estimate = 0.09, SE = 0.21, $P = 0.99$). There were significant differences between model and empirical data slopes ($P < 0.05$, Table S4.3B and C, Figure S4.4) for pairwise comparisons between Scenario 1 and empirical data from rat-free islands, and between Scenario 2 and data from rat-present islands for the number of aggressive encounters (Figure 4.3).

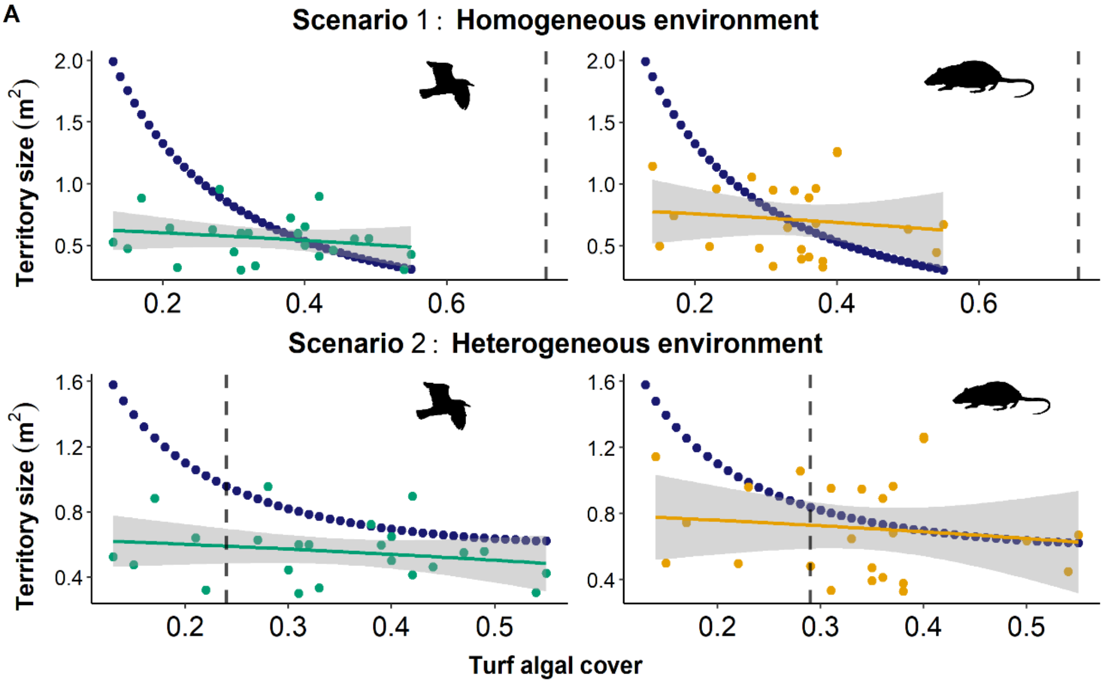


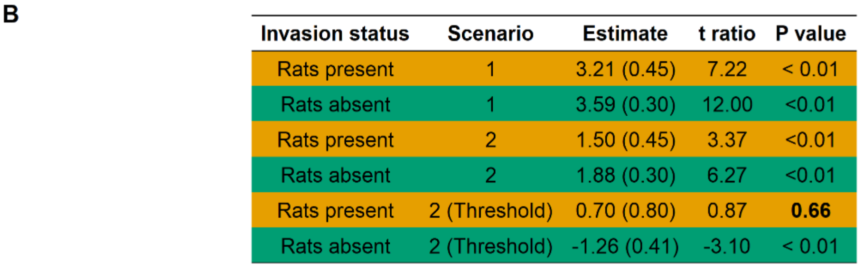
B

Invasion status	Scenario	Estimate	t ratio	P value
Rats present	1	0.01 (0.26)	0.04	**0.99**
Rats absent	1	1.14 (0.21)	5.35	<0.01
Rats present	2	-1.21 (0.26)	-4.72	<0.01
Rats absent	2	0.09 (0.21	-0.41	**0.99**

Figure 4.3: Model predictions and empirical data for *P. lacrymatus* territoriality, measured as the number of aggressive encounters in the presence and absence of invasive rats. A: Points represent raw empirical data for *P. lacrymatus* around islands with rat's present (Orange) and rats absent (Green), presented alongside corresponding best fit lines. Grey shading represents 95 % confidence intervals. Blue points are territoriality predictions from the mathematical model. Dashed lines represent the predicted upper thresholds of territoriality for Scenario 1 and the predicted lower thresholds of territoriality for Scenario 2. B: Summary of pairwise slope comparisons for empirical data where rats are absent (Orange) and where rats are present (Green). Bold *P* values show where *P* > 0.05, i.e., where there is no difference between the mathematical prediction and the empirical data slopes. Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

Our baseline Scenario 1 and Scenario 2 models did not accurately predict *P. lacrymatus* territory size for either the rat-present or the rat absent data (Figure 4.4, Table S4.3B and C, *P* <0.05 for all comparisons). However, baseline Scenario 2 was able to predict *P. lacrymatus* territory size around rat-infested islands where turf algal cover was above 0.30; the predicted turf algal cover at the lower threshold of territoriality (Figure 4.4, Estimate = 0.70, SE = 0.81, *P* = 0.66).





Invasion status	Scenario	Estimate	t ratio	P value
Rats present	1	3.21 (0.45)	7.22	< 0.01
Rats absent	1	3.59 (0.30)	12.00	<0.01
Rats present	2	1.50 (0.45)	3.37	<0.01
Rats absent	2	1.88 (0.30)	6.27	<0.01
Rats present	2 (Threshold)	0.70 (0.80)	0.87	**0.66**
Rats absent	2 (Threshold)	-1.26 (0.41)	-3.10	< 0.01

Figure 4.4: Model predictions and empirical data for *P. lacrymatus* territory size in the presence and absence of invasive rats. A: Points represent raw empirical data for *P. lacrymatus* around islands with rats present (Orange) and rats absent (Green), presented alongside corresponding best fit lines. Grey shading represents 95 % confidence intervals. Blue points are territoriality predictions from the mathematical model. Dashed lines show upper thresholds of territoriality for Scenario 1 and the lower thresholds for Scenario 2. B: summary of pairwise slope comparisons for empirical data where rats are absent (Orange) and where rats are present (Green). Bold *P* values show where *P* > 0.05, i.e., where there is no difference between the mathematical prediction and the empirical data slopes. Comparisons for Scenario 2 specifically for model predictions above the lower threshold, i.e., where turf algal cover ~0.3 have also been included. Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

Model predictions for the number of aggressive encounters for the range of empirical data were not sensitive to food energy values (Estimate = -0.49, SE = 0.07, *P* = 0.99) or cost of living where food energy values were either low (Estimate = -0.11, SE = 0.07, *P* =0.99) or high (Estimate = -0.17, SE = 0.07, *P* = 0.65).

All variations of food energy values and cost-of-living values under Scenario 1 models were equally good fits for empirical data collected adjacent to islands where rats were present, for the number of aggressive encounters (Table S4.3, Figures S4.4 and S4.6, $P > 0.1$ for all values of $\mathcal{E}$ and m_r). The same was true for Scenario 2 and empirical data collected from rat-free islands for the number of aggressive encounters (Table S4.3, Figures S4.5 and S4.7, $P > 0.1$ for all values of $\mathcal{E}$ and m_r). Variation in food energy and cost-of-living values under Scenario 1 were unable to accurately predict *P. lacrymatus* territory size for rat-free empirical data. However, Scenario 2 models were able to accurately predict *P. lacrymatus* territory size adjacent to rat-free islands above the predicted lower threshold of territoriality for all food energy values (Figure S4.5 and S4.7, $P > 0.05$ for all comparisons).

4.4 Discussion

We show that an economic defendability model of feeding territoriality can predict aspects of *P. lacrymatus* territorial behaviour. Furthermore, our different model scenarios are able to capture and predict variation in territoriality arising from the presence of invasive rats. Specifically, adjacent to rat-free islands, *P. lacrymatus* aggressive encounters are best predicted by a heterogeneous environment where territoriality is influenced by both nutritional resources and the intensity of competition, reflecting the importance of both the physical and social environment (Foltz *et al.*, 2015, Kilgour *et al.*, 2020). In contrast, adjacent to rat-infested islands, *P. lacrymatus* aggressive encounters are best predicted by a homogeneous environment where the social environment, in terms of intruder density and competition intensity, is constant. Around rat-free islands, seabird-derived nutrient subsidies drive high levels of territoriality and small territory sizes for *P. lacrymatus* (**Chapter 3**). Our models support this empirical evidence: the heterogeneous environment model (Model Scenario 2) that best predicts *P. lacrymatus* territoriality adjacent to rat-free islands also predicts a higher number of aggressive encounters than the homogeneous environment model (Model Scenario 1). Our two model scenarios are therefore able to capture the relative contributions of the social and physical environment in predicting variation in *P. lacrymatus* territoriality.

Environmental heterogeneity, specifically the impact of intruder density, appears to be a key driver of variation in territoriality between the two model scenarios, and subsequently with the presence and absence of nutrient subsidies for *P. lacrymatus* individuals. When territoriality is considered in terms of the value of the resource under dispute, game theory predicts an evolutionary stable strategy (ESS) whereby individuals should always be aggressive and play ‘Hawk’ where the resource value is below a critical threshold (Houston and McNamara, 1988). This idea is reflective of Model Scenario 1 and *P. lacrymatus* territoriality adjacent to rat-infested islands. *P. lacrymatus* individuals are able to maintain enough energy for survival where nutritional resources are high even if territorial efficiency is low (Brown, 1964, Peiman and Robinson, 2010). Playing an aggressive ‘Hawk’ strategy is also predicted to yield the highest payoff where high population densities increase the risk of starvation as nutritional resources are consumed by intruders (Enquist and Leimar, 1987, Houston and McNamara, 1988). This prediction reflects Model Scenario 2 and *P. lacrymatus* territoriality adjacent to rat-free islands. Disproportionately high intruder recruitment to areas of high nutritional productivity means *P. lacrymatus* individuals invest in territoriality even where nutritional resources are high in order to maintain energy for survival (Carpenter, 1987) and the value of nutritional resources to individuals remains high at high nutritional resource productivities.

The invasion status of the study islands has been constant since the 1700s (Sheppard *et al.,* 2012). Variation in territorial behaviour with island invasion status could therefore be a consequence of variation in fixed behavioural types, or stable strategies that have evolved over time. Organisms that display a ‘fast-explorer’, or proactive behavioural type, display consistently higher aggressive and bold behaviours than individuals adopting a ‘slow explorer’, or reactive behavioural strategy associated with non-aggressive and shy exploratory behaviours (Koolhaas *et al.,* 1999, Dingemanse *et al.,* 2004). Furthermore, selection pressures on these two different behavioural strategies are dependent upon the level of competition. Specifically, fitness has been shown to be higher for proactive individuals where competition is intense, comparable to *P. lacrymatus* individuals adjacent to rat-free islands, whilst selection favours reactive individuals where competition intensity is low, comparable to *P. lacrymatus* individuals adjacent to rat-infested islands (Dingemanse *et al.,* 2004). This association between fitness and competition intensity provides further evidence that *P. lacrymatus* territoriality is predicted by a feeding threshold model that considers the interaction between variation in the social and the physical environment (Foltz *et al.,* 2015). Variation in *P. lacrymatus* territoriality could therefore be driven by different selection pressures acting upon individuals due to the presence and absence of nutritional subsidies.

Organisms can display plasticity in metabolic responses in response to resource availability, and this may reflect strategies that have evolved to maintain energetic demands (Auer *et al.*, 2020a). For example, organisms display higher metabolic rates at warmer temperatures (O'Connor *et al.*, 2009) and lower nutritional resource availabilities (Huey and Kingsolver, 2019). Territoriality is also positively associated with higher metabolic rates (Tremblay *et al.*, 2021). In marine systems, increasing temperatures reduce nutrient availability and constrain primary productivity, which will affect the value of nutritional resources and scale up to impact food web structure (O'Connor *et al.*, 2009). As temperatures increase (Oliver *et al.*, 2018), seabird-derived nutrient subsidies could act as a buffer to any subsequent declines in nutrient availability, maintaining the variation in *P. lacrymatus* territoriality selection pressures with island invasion status indicated by our models.

Species interactions are a proximate cause of local extinctions as nutritional resource availability declines (Cahill *et al.*, 2012) and therefore have important implications for species persistence. Our models and empirical data consider variation in territoriality at the population level with energetic costs and benefits assumed to be constant across all individuals. However, resource use is often dependent upon an individual's specific energy demand, individual state and competitive ability (Auer *et al.*, 2020b). Both metabolic rates (Tremblay *et al.*, 2021) and territoriality (Dochtermann *et al.*, 2019) have been shown to be repeatable and vary consistently between individuals. Metabolic physiology can constrain phenotypic behavioural plasticity (Careau *et al.*, 2008) whilst habitat complexity is a key driver of behavioural flexibility (Delarue *et al.*, 2015). Variation in *P. lacrymatus* territoriality could also be a consequence of different selection pressures acting upon individuals (Dingemanse *et al.*, 2004). Individual variation in both behaviour and metabolic physiology could have important evolutionary consequences (Careau *et al.*, 2008). A deeper understanding of context dependent selection pressures acting on territoriality at the individual level is therefore necessary to better understand the drivers of persistence in functionally important herbivorous fish.

Below the upper threshold of territoriality, individuals are predicted to be unable to survive if they are non-territorial and without access to an additional, non-defended resource to supplement their diet (Carpenter, 1987). However, our models predict *P. lacrymatus* territoriality to be present outside the thresholds predicted by the territoriality payoffs. Our calculation for the territoriality thresholds considers only the energetic cost of territoriality whereas our calculations for territory size and aggressive encounters considers additional energetic costs associated with maintenance and foraging (Carpenter and MacMillan, 1976). The slight mismatch between the territoriality thresholds and predicted number of aggressive encounters is therefore reflective of the additional costs incurred to individuals beyond the costs of territoriality (Carpenter and MacMillan, 1976).

In general, our models did not accurately predict *P. lacrymatus* territory size, although all model scenarios predicted an inverse relationship between territory size and nutritional resource productivity (Stimson, 1973). Density dependent territory size is documented for fish species (Lindeman *et al.*, 2014), including *P. lacrymatus* (Robles *et al.*, 2018). Furthermore, adjacent to rat-infested islands, there is a strong negative relationship between *P. lacrymatus* territory size and conspecific density but increases in conspecific density do not correspond to increases in territoriality (**Chapter 3**). Our territory size calculation does not explicitly include consideration of any interaction between aggressive defense and territory size. *P. lacrymatus* territory size therefore appears to be driven by complex interactions between density dependence, resource availability and territoriality (Perrone *et al.*, 2019) that are beyond the scope of our model predictions.

We have shown that variation in reef fish territoriality is driven by both the physical and the social environment. Furthermore, *P. lacrymatus* territoriality is likely dependent upon the complex interplay between behaviour, energetic metabolism (Norin and Metcalfe, 2019), nutritional resource availability (Auer *et al.*, 2020a), and intruder density (Paola *et al.*, 2012, Yuan *et al.*, 2013). Rat eradication can restore seabird-derived nutrient subsidies to coral reefs (Benkwitt *et al.*, 2021). Our results suggest that the extent to which rat eradication will restore species interactions via the economic defendability of resources will be context-dependent as different selection pressures act on territoriality at both the population and individual level. Overall, the application of economic defendability models to animal territoriality has the potential to provide a valuable insight into the proximate causes and evolutionary ramification of behavioural variation both within and between populations.

General Discussion

My Thesis has added to the understanding of the behavioural ecology of reef fish under environmental change via four main pathways. Firstly, I have identified that the behavioural responses of two reef fish families to variable nutritional resources are consistent at a broad-scale, population level. Secondly, I have demonstrated the importance of context dependency in driving fine-scale variation in behavioural responses to environmental change. Thirdly, I have shown that consideration of individual-level behaviour and the co-correlation of multiple behaviours reveals mechanisms behind potentially adaptive behavioural variation. Finally, by applying economic defendability theory to reef fish behaviour, I have identified nutritional resource availability as a fundamental driver of reef fish territoriality, which can scale up to impact species interactions, community composition and coral reef resilience. My thesis therefore highlights multiple ecological and methodological pathways via which behavioural changes can be driven.

5.1 Consistency in behavioural responses

In **Chapters 2-4,** I identified comparable population-level behavioural responses between two different, functionally important reef fish families (Figure 5.1). Both corallivores **(Chapter 2)** and farming damselfish **(Chapters 3&4)** displayed heightened aggression and smaller territory sizes where nutritional resources were high (Figure 5.1, Gunn *et al.*, 2022, **Chapter 3**). **Chapter 2** also identified that heightened aggression was traded off by decreases in exploratory behaviours (Gunn *et al.*, 2022). The findings in **Chapter 2** strongly indicate that increases in the time invested in one behaviour should be followed by decreases in other behaviours due to constraints within a time-budget (Sih *et al.*, 2004b, Found and St Clair, 2016). Whilst only aggressive behaviour was recorded in **Chapter 3,** it is plausible that high aggression in farmer damselfish (*P. lacrymatus*) is accompanied by a low expression of exploratory behaviours and high feeding in order to maintain energy for territorial behaviour (Gunn *et al.*, 2022). **Chapters 2-4** provide substantial support for economic defendability and optimality theories of behaviour (Brown, 1964, Carpenter and Macmillan, 1976). My thesis therefore provides evidence that broad, population level consistency in behavioural responses between reef fish families could be due to the applicability of economic defendability theory across multiple axes of nutritional resource availability.

In **Chapter 1,** only 4% of variation in behavioural responses was attributed to phylogeny for fish species. As both long and short-term changes in terrestrial environments are more variable than in marine environments, human induced environmental change is a more recent phenomenon for fish species than terrestrial species (Steele, 1985), thus there has been less time for evolutionary divergence of behavioural responses between different fish species to occur (Gunn *et al.,* 2021). Furthermore, the methods used to measure behaviour, and the definitions used to assign traits into behavioural categories, were consistent across both **Chapters 2&3**. The impact of methodology-based context dependency that could drive variation in behavioural responses across the two studies was therefore minimal (Gunn *et al.,* 2021). The similarities in the behavioural responses of corallivores and farming damselfish identified in my thesis could therefore also be explained by the short evolutionary history over which reef fish have been exposed to human-induced changes in resource availability.

5.2 Methodological drivers of behavioural variation

Across **Chapters 1-4,** there is a common theme of the importance of context dependent factors in predicting behavioural responses to environmental change. **Chapter 1** highlights the fundamental role of context dependency in terms of research design, whilst **Chapters 2-4** present the importance of ecological context dependent factors (Figure 5.1). In **Chapter 1,** effect sizes of behavioural responses were generally higher for field studies than for laboratory studies, but the overall magnitude of effect sizes was higher for laboratory studies then field studies (Gunn *et al.,* 2021). Previous meta-analyses have identified that behavioural repeatability is higher for studies conducted in the field (Bell *et al.,* 2009) and boldness is positively associated with survival in the field but not in the laboratory (Moiron *et al.,* 2020). Variation in behaviour between laboratory and field studies could arise because the costs and benefits of the expression of different behaviours in the field may not be transferable to the controlled conditions of laboratory environments (Moiron *et al.,* 2020). Subsequently, the selection pressures individuals are subject to differ between the field and the laboratory (Niemelä and Dingemanse, 2014, Mouchet and Dingemanse, 2021), resulting in differences in the extent to which behaviour facilitates survival (Moiron *et al.,* 2020).

Laboratory experiments are valuable tools for establishing cause and effect, whilst field studies allow organisms to be manipulated and observed under natural conditions

(Cuthill, 1991). Nonetheless, the combined effects of differing selection pressures with different study environments (laboratory vs field) and the methods used to measure behaviour can make the interpretation of behavioural responses complex. Novel environment assays used as proxies for exploration may reflect different behaviours according to the study environment. For example, laboratory tests reflect behaviours associated with fear and exploration, and field tests reflect escape behaviours (Mouchet and Dingemanse, 2021). **Chapter 1** therefore highlights that understanding and controlling for methodological context dependency is necessary to accurately interpret the ecological causes of behavioural variation in response to HIREC.

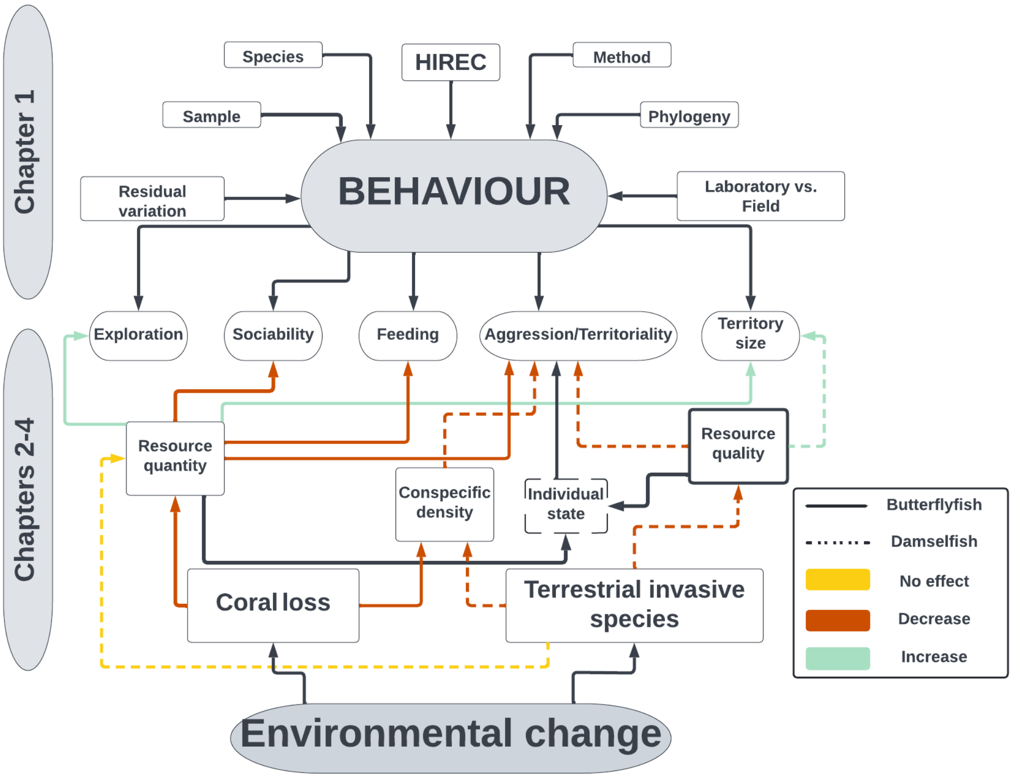


Figure 5.1: The key drivers of behavioural variation in reef fish identified in this thesis. Coloured arrows show the direction of behavioural responses across different traits for both the butterflyfish (solid lines) and damselfish (dotted lines) studied across the four data chapters. Dashed-line boxes refer to aspects not directly measured in this thesis. Black arrows refer to factors that may increase or decrease behavioural expression.

5.3 Ecological drivers of behavioural variation

5.3.1 Environmental heterogeneity

One source of ecological context-dependency driving the behavioural variation I identified in this thesis is environmental heterogeneity (**Chapters 2&4).** In **Chapter 2,** habitat heterogeneity in terms of nutritional resource patchiness was identified as a potential source of individual-level variation in feeding behaviour. High behavioural repeatability in natural environments is likely due to environmental variation resulting in micro-niches which would allow for between-individual variation in behaviour (Bell *et al.*, 2009). This is reflected in the individual level analysis in **Chapter 2.** Repeatability estimates for feeding and aggressive behaviours at the low coral cover site were higher than expected, with an interaction between butterflyfish individuals and the environment likely inflating repeatability estimates (Gunn *et al.*, 2022). Behavioural variation between individuals within a population could therefore be a consequence of environmental heterogeneity and not the presence of different fixed behavioural types or personalities, or an interplay between the two.

Similarly, **Chapter 3** identified that broad-scale differences in nutritional resource quality, driven by the presence and absence of invasive rats on adjacent islands, drives variation in farmer damselfish territoriality. Furthermore, fine-scale variation in nutritional resources between individual farmer damselfish territories was a driver of territoriality within each island invasion status type. **Chapter 3** considered the percentage cover of nutritional resources within individual territories, and not the density of nutritional resources. However, a combination of resource density, resource distribution and competitor density can determine territorial behaviour (Brown, 1964) and therefore other behaviours, such as foraging and exploration, via behavioural trade-offs (Sih *et al.,* 2004, Gunn *et al.,* 2022). In **Chapter 4,** I incorporated nutritional resource density within the mathematical model of territoriality as a fixed constant, and the model was able to accurately predict the farmer damselfish territoriality observed in **Chapter 3.** My thesis has therefore identified the importance of habitat heterogeneity across multiple scales (reef-level and individual territory level) in predicting fine scale behavioural variation both within and between reef fish populations.

5.3.2 Competition intensity

Competition intensity and the density of competitors often drive aggressive interactions (Blowes *et al.,* 2017). In **Chapter 2,** the density of a behaviourally dominant heterospecific competitor, *C. baronessa* (Blowes *et al.,* 2013), was identified as a potential determinate of *C. lunulatus* aggression (Gunn *et al.,* 2021). The number of conspecific intruders was also a context-dependent factor in predicting variation in farmer damselfish territoriality in **Chapters 3 and 4.** Specifically, adjacent to islands with access to seabird derived nutrient subsidies, the density of conspecific *P. lacrymatus* individuals was higher, and there was a positive association between conspecific density and aggression (**Chapter 3**). This is comparable to previous research that damselfish territoriality can be predicted by conspecific density (Robles *et al.,* 2018) which in turn can be predicted by nutritional resource availability (**Chapter 3**). **Chapter 4** considered how physical environmental heterogeneity can predict heterogeneity in the social environment and drive behavioural variation in territoriality. The models presented in **Chapter 4** predict that the shape of the relationship between nutritional resources and territoriality can be determined by the relationship between nutritional resources and intruder density. The two model scenarios were able to predict farmer damselfish territoriality according to the presence or absence of nutritional subsidies on adjacent islands. The results from **Chapters 2-4** therefore provide substantial evidence that heterogeneity in both the physical and social environment can predict variation in multiple behaviours in response to changing resource availabilities.

5.3.3 Individual state

In **Chapter 1,** I identified that up to 32% of effect size variation in behavioural responses can be attributed to variation between animals within a sample, perhaps due to behavioural variation between individuals (Gunn *et al.*, 2021). **Chapter 2** postulates that the threshold of behavioural change with declining nutritional resources will be variable with individual state, such that environmental heterogeneity and an individual's morphology and physiology may affect the costs and benefits associated with territorial behaviour (Dingemanse and Wolf, 2010, Parthasarathy *et al.*, 2022). In **Chapter 4,** I assumed that all individuals within a model scenario have the same metabolic rates and therefore the same maintenance costs, regardless of nutritional resource availability. However, in actuality, individual variation in resource use is driven by interactions between energy demand and competitive ability (Thomas *et al.*, 2001, Auer *et al.*, 2020b). Organisms can display phenotypic plasticity in metabolic rates (Auer *et al.*, 2020a), so the basic maintenance costs an individual is subject to may also vary with environmental factors such as temperature (O'Connor *et al.*, 2009) and nutritional resource availability (Huey and Kingsolver, 2019). Alternatively, if variation in territoriality is due to different, fixed behavioural types that have evolved in response to different nutritional resource levels, then an individual's metabolism and physiology could be a constraint that promotes the maintenance of behavioural syndromes (Careau *et al.*, 2008). The persistence of species under future resource availabilities could therefore be predicted in part by the mechanism by which individual state drives behavioural variation.

5.4 Macro-ecological consequences of behavioural variation

Variation in nutritional resources within territories results in different individuals receiving different energetic rewards (López-Segoviano *et al.*, 2018). My thesis has shown that the distribution, quantity, quality, and energetic value of nutritional resources can determine the exploratory, foraging, and aggressive behaviours of reef fish (**Chapters 2-4**) via behavioural trade-offs (Gunn *et al.*, 2021). However, behaviour also has the capacity to mediate physiological and morphological trade-offs. For example, high foraging effort promotes rapid growth, but at the cost of increased mortality via predation. A behaviourally mediated trade-off between growth and mortality therefore arises (Biro *et al.,* 2006). In the presence of seabird-derived nutritional subsidies, farmer damselfish obtain a greater nutritional gain per unit foraging effort **(Chapter 3)**, and also display faster growth rates (Graham *et al.,* 2018). In the presence of nutritional subsidies, farmer damselfish may therefore have the capacity to invest in faster growth rates with a lower predation mortality cost. Nonetheless, an increased investment of energy into growth could result in further physiological trade-offs. For example, parrotfish also display faster growth rate in the presence of nutritional subsidies, but at the cost of reduced fecundity (Benkwitt *et al.,* 2021). Behaviourally mediated trade-offs could therefore have substantial impacts on other aspects of reef fish ecology, such as fecundity and growth, that scale-up to impact reef fish biomass and ecosystem function (Benkwitt *et al.,* 2021). Understanding the abundance, demography, and persistence of reef fish in changing environments therefore requires an understanding of both the mechanisms behind behavioural expression, and the consequences of behaviour for reef fish at higher ecological levels (Figure 5.2).

Whilst my thesis shows the importance of context dependency in predicting behavioural expression, one of the overarching contexts of interest; nutritional resources as a driver of territorial behaviours, shows a consistent impact on reef fish behaviour at the population-level **(Chapters 2-4)**. This has important conservation implications as restoring natural nutritional resources to coral reef ecosystems has the potential to restores species interactions across multiple reef fish families (Figure 5.2). In the case of butterflyfishes, behavioural dominance is an increasing function of dietary specialisation (Blowes *et al.,* 2013). **Chapter 2** identified that the density of the focal study species, *C. lunulatus,* was higher than that of the heterospecific dominant competitor, *C. baronessa* (Gunn *et al.,* 2021). *C. baronessa* also has a higher dietary specialisation than *C. lunulatus* (Blowes *et al.,* 2013). If the value of nutritional resources is higher to more specialist species, then heterospecific aggression between butterflyfish species could contribute to resource partitioning and the maintenance of biodiversity (Blowes *et al.,* 2013, Figure 5.2). However, declines in the availability of live coral cover can disrupt these hierarchies through declines in the density of more dominant specialist species (Pratchett *et al.,* 2008, **Chapter 2**), or via plasticity in dietary specialisation which then alters resource partitioning (Semmler *et al.,* 2022).

Recent research addressing the macroecology of reef fish behaviour suggests that interactions between local and evolutionary processes modulate reef fish agonistic behaviour and scale up to structure marine ecological networks (Fontoura *et al.*, 2020). Furthermore, these ecological networks are primarily centred on the Pomacentridae family, of which *P. lacrymatus* (**Chapter 3**) falls under. The aggressive dominance of farmer damselfish can affect the space use and social modes of other reef fish families, including butterflyfishes and surgeonfishes (Morgan and Kramer, 2005, Samways, 2005, Figure 5.2). The behavioural variation identified in my thesis could therefore have substantial macroecological consequences for coral reef ecosystems. Declines in nutritional resources have the potential to disrupt behavioural dominance hierarchies within and between reef fish families which in turn could have bottom-up impacts for coral reef community composition, biodiversity, and resilience (Blowes *et al.*, 2013, Figure 5.2).

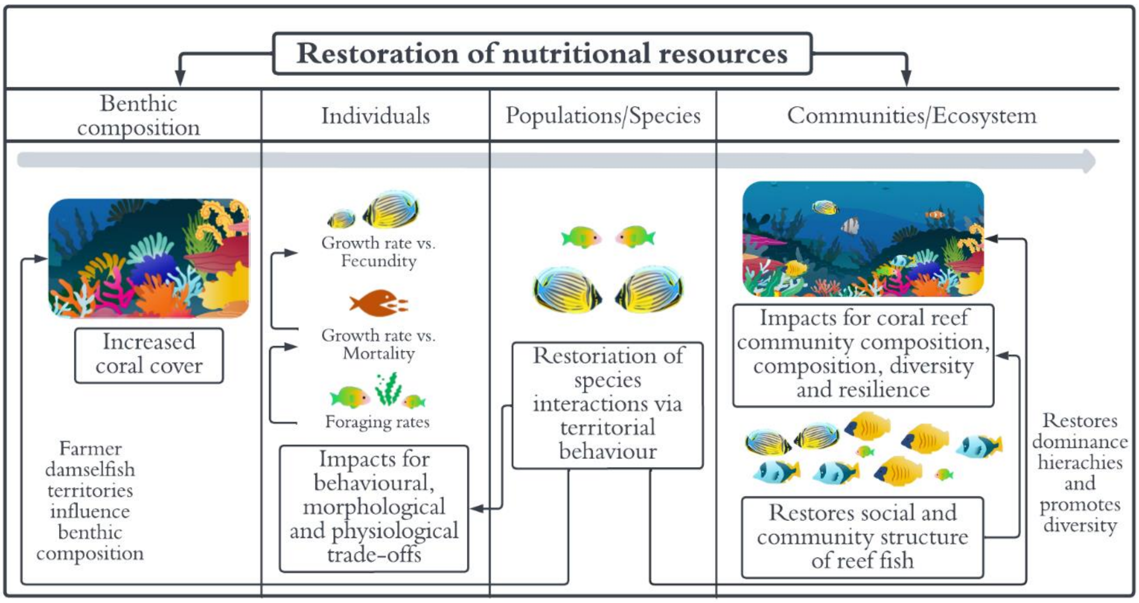


Figure 5.2: Conceptual macro-ecological consequences of restoring nutritional resources for coral reef ecosystems. Reef fish and coral reef images provided by Mair Perkins Ltd. Predation icon provided by Adioma.

5.5 Research directions

In order to fully understand the ecological drivers and consequences of behavioural variation in response to changes in the environment, methodological context dependency needs to be understood and controlled for (Gunn *et al.*, 2021). In **Chapter 1,** I considered five behaviours: aggression, sociability, boldness, exploration, and activity, whilst my remaining chapters (**Chapter 2-4)** focus on four of these behaviours (aggression, sociability, activity, and exploration). Initial behavioural trials for the data collection in **Chapter 2** attempted to quantify boldness *in-situ* using novel object assays, but these tests were unsuccessful due to the topography of the two study sites. However, boldness and aggression are often positively correlated (Kendall *et al.*, 2018) as both behaviours are influenced by the resources an individual possesses (Wolf and Weissing, 2010). My thesis has shown that territorial behaviour is dependent upon nutritional resources and subsequent interactions between the physical and social environment **(Chapters 2-4).** It is therefore plausible that nutritional resources are also a primary driver of variation in bold behaviour, especially given evidence that correlations between aggression and boldness may have a genetic basis (Norton *et al.*, 2011). Furthermore, there are multiple additional behaviours that could be impacted by environmental change not considered in my thesis that may also have important consequences for species persistence. For example, behaviours associated with parental care and mate selection differ consistently between individuals and can be associated with behaviours that have been addressed in this thesis, such as aggression (Koski, 2014). Behaviours that affect multiple aspects of an individual's life history and potentially co-correlate with one another should therefore be considered together in future research in order for the ultimate consequences of behavioural variation in changing environments to be fully understood.

My thesis has provided an insight into the importance of behavioural variation between individuals within a population, with **Chapters 2-4** highlighting that this variation may be driven by the physical **(Chapters 2 and 3)** and social **(Chapters 3 and 4)** environment, as well as individual state **(Chapter 4)**. Nonetheless, further research is required to identify the causal links between individual variation and responses to environmental change, and to quantify the macroecological consequences of individual variation in behaviour (Laskowski *et al.*, 2022). Specifically, the relative roles of behavioural plasticity and fixed behavioural types should be a focal point of future research (Dingemanse *et al.*, 2009). One way to achieve this would be via the manipulation of the resources within the territories of site-specific reef fish and the subsequent monitoring of the behavioural expression of individuals over time *in-situ.* This would also allow the priority of behavioural modifications to be better understood. **Chapter 2** identified a behavioural trade-off between aggression, feeding and exploratory behaviours between two sites (Gunn *et al.*, 2022). However, it was not possible to determine how the differences in behaviour between the two populations arose. If the resource value in a territory decreases, identifying if feeding or aggressive behaviours change first, if at all, would allow the costs and benefits associated with different behaviours, and the subsequent ecological and evolutionary ramifications, to be better understood.

As a population-level statistic (Sih *et al.*, 2004a), behavioural repeatability is unable to capture whether individuals can express large differences in behavioural phenotypes around the population mean (Dochtermann and Royauté, 2019). In **Chapter 2,** I identified habitat heterogeneity as a potential driver of between-individual variation in feeding behaviours by considering mean-scaled metrics of behavioural variation (Dochtermann and Royauté, 2019) alongside classic measures of behavioural repeatability (Lessells and Boag, 1987). Considering only the classic measure of repeatability could have led to incorrect causal inferences regarding the drivers of individual-level variation. Future research considering behavioural variation at the individual level should therefore incorporate metrics that complement repeatability estimates to better understand the extent to which individuals vary around population mean estimates of behavioural expression, and the potential adaptive consequences of this variation.

In conclusion, my thesis has been valuable in identifying methodological and ecological drivers of both behavioural variation and consistency in coral reef fish by considering multiple behaviours at both a population and individual level. By conceptualising how behaviour can scale up to impact species interactions, reef fish community structure and coral reef resilience, my thesis provides evidence that behavioural responses should be a fundamental consideration in measuring the efficacy of coral reef conservation efforts.

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Appendix A: Supplementary material

Chapter 1 Supplementary Material

Table S1.1: Papers included in quantitative and qualitative analyses

Reference	Journal	Taxa	Behaviour	HIREC axis
Aaden *et al.*, 2010	Biology Letters	Crustacea	Boldness	Direct Human Impact
Alenius and Munguia. 2012	Marine and Freshwater Biology and Physiology	Isopoda	Exploration/Boldness	Changes in CO_2
Allan *et al.*, 2013	Proceedings of the Royal Society B	Teleost	Boldness	Changes in CO_2
Almen *et al.*, 2017	Hydrobiologia	Copepod	Boldness	Changes in CO_2
Atwell *et al.*, 2012	Behavioural Ecology	Avian	Exploration and Boldness	Direct Human Impact
Aubret and Shine, 2010	Journal of Experimental Biology	Reptilia	Activity	Climate Change
Barbosa and Mota, 2009	Primates	Mammalia	Activity	Direct Human Impact
Beckmann and Berger, 2003	Journal of Zoology	Mammalia	Activity	Direct Human Impact
Belgrad and Griffen, 2018	Ecology and Evolution	Crustacea	Boldness	Direct Human Impact
Belgrad *et al.*, 2016	Animal Behaviour	Crustacea	Boldness	Direct Human Impact
Beyer *et al.*, 2013	Journal of Applied Ecology	Mammalia	Boldness	Direct Human Impact
Biro *et al.*, 2013	Behaviour	Crustacea	Boldness	Climate Change
Bokony *et al.*, 2012	PLOS One	Avian	Exploration	Direct Human Impact
Borell *et al.*, 2013	Coral Reefs	Teleost	Activity	Changes in CO_2
Boyle *et al.*, 2010	Proceedings of the Royal Society B	Avian	Exploration	Climate Change
Briffa *et al.*, 2016	Current Zoology	Crustacea	Boldness	Climate Change
Burger and Gochfield, 1983	Behavioural Processes	Avian	Boldness	Direct Human Impact
Bzoinovic *et al.*, 2016	Evolutionary Ecology Research	Isopoda	Exploration	Climate Change
Campbell *et al.*, 2010	Proceedings of the Royal Society B	Reptilia	Activity	Climate Change
Candolin *et al.*, 2013	Oecologia	Teleost	Aggression	Change in Nutrients
Cannizzo and Griffen, 2016	Animal Behaviour	Crustacea	Activity	Climate Change
Chapman *et al.*, 2009	Behavioural Ecology and Sociobiology	Teleost	Boldness	Direct Human Impact
Chase *et al.*, 2018	Journal of Fish Biology	Teleost	Exploration	Climate Change
Chivers *et al.*, 2014	Science of the Total Environment	Teleost	Boldness	Changes in CO_2 and Climate Change
Cilento and Jones, 2016	Austral Ornithology	Avian	Aggression	Direct Human Impact
Cosentino and Droney, 2016	Animal Behaviour	Amphibia	Activity	Direct Human Impact
Cripps *et al.*, 2011	PLOS one	Teleost	Exploration	Changes in CO_2

Cunningham *et al.*, 2015	Journal of African Ornithology	Avian	Activity	Climate Change
Davis *et al.*, 2018	Conservation Physiology	Teleost	Boldness	Changes in CO_2
De la Haye *et al.*, 2011	Animal Behaviour	Crustacea	Exploration	Changes in CO_2
Dias *et al.*, 2011	Evolutionary Applications	Isopoda	Exploration	Climate Change
Dixson *et al.*, 2014	Science	Teleost	Exploration	Climate Change
Dodd *et al.*, 2015	Proceedings of the Royal Society B	Crustacea	Activity	Changes in CO_2
Domenici *et al.*, 2014	Journal of Experimental Biology	Teleost	Activity	Climate Change and Changes in CO_2
Domenici *et al.*, 2017	Journal of Experimental Biology	Mollusca	Exploration	Climate Change and Changes in CO_2
Donaldson *et al.*, 2007	Urban Ecosystems	Avian	Boldness/Activity	Direct Human Impact
Du Plessis *et al.*, 2012	Global Change Biology	Avian	Exploration	Climate Change
Duron *et al.*, 2018	Austral Ecology	Avian	Activity	Direct Human Impact
Edwards *et al.*, 2015	Journal of African Ornithology	Avian	Climate Change	Activity
Evans *et al.*, 2010	Ethology	Avian	Aggression	Direct Human Impact
Fernandez and Azkona, 1993	Journal of Wildlife Management	Avian	Sociability	Direct Human Impact
Ferrari *et al.*, 2011	Global Change Biology	Teleost	Boldness	Changes in CO_2
Flood and Wong, 2017	Animal Behaviour	Teleost	Aggression	Climate Change
Frost *et al.*, 2013	Animal Behaviour	Teleost	Boldness	Climate Change and Changes in CO_2
Gracceva *et al.*, 2014	Ethology	Mammalia	Exploration and Boldness	Climate Change
Gremillet *et al.*, 2012	Marine Ecology Progress Series	Avian	Exploration	Climate Change
Hamilton *et al.*, 2015	Biology Letters	Mammalia	Exploration	Climate Change
Harveson *et al.*, 2006	Biological Conservation	Mammalia	Boldness	Direct Human Impact
Heinrich *et al.*, 2016	ICES Journal of Marine Science	Elasmobranch	Activity	Changes in CO_2
Herborn *et al.*, 2014	Behavioural Ecology	Avian	Exploration	Climate Change
Hewes and Chaves-Campos, 2018	Ethology	Crustacea	Boldness	Direct Human Impact
Hewes *et al.*, 2017	Journal of Ethology	Mammalia	Exploration and Activity and Boldness	Direct Human Impact
Hudson *et al.*, 2016	Journal of Crustacean Biology	Crustacea	Activity	Climate Change
Kaiser *et al.*, 2014	Animal Behaviour	Avian	Boldness	Direct Human Impact
Katz *et al.*, 2017	Behavioural Ecology and Sociobiology	Insecta	Exploration	Climate Change
Keiser *et al.*, 2018	Ethology	Crustacea OTHER	Activity	Direct Human Impact
Keith *et al.*, 2018	Nature Climate Change	Teleost	Aggression	Climate Change
Kidawa *et al.*, 2010	Polish Polar Research	Echinoderm	Activity	Climate Change
Kim *et al*, 2016	ICES Journal of Marine Science	Crustacea	Exploration	Changes in CO_2

Kowalczyk *et al.*, 2015	Oecologia	Avian	Exploration	Climate Change
Kvarrnemo, 2010	Ethology, Ecology and Evolution	Teleost	Sociability	Climate Change
Lapiedra *et al.*, 2017	Global Change Biology	Reptilia	Aggression and Boldness	Direct Human Impact
Lefcort and Kotler, 2017	Israel Journal of Ecology and Evolution	Insecta	Exploration	Changes in CO_2
Lehtonen *et al.*, 2016	BMC Ecology	Teleost	Activity	Changes in CO_2
Lienert *et al.*, 2013	Animal Behaviour	Teleost	Activity	Direct Human Impact
Luther and Danner, 2016	American Ornithology	Avian	Boldness	Climate Change
Maulvault *et al.*, 2018	Science of the Total Environment	Teleost	Exploration	Climate Change and Changes in CO_2
McFarland *et al.*, 2014	American Journal of Physical Anthropology	Mammalia	Activity and Sociability	Climate Change
McLaughlin and Kunc, 2012	Biology Letters	Avian	Boldness	Direct Human Impact
Miranda *et al.*, 2013	Global Change Biology	Avian	Boldness	Direct Human Impact
Mitchell *et al.*, 2017	Ecology. Evolution and Organismal Biology	Reptilia	Activity	Climate Change
Montague *et al.*, 2012	Behavioural Ecology	Avian	Boldness	Direct Human Impact
Morris-Drake *et al.*, 2017	Environmental Pollution	Mammalia	Boldness	Direct Human Impact
Munday *et al.*, 2014	Nature Climate Change	Teleost	Exploration and Boldness	Changes in CO_2
Nagelkerken *et al.*, 2015	Nature Climate Change	Teleost	Boldness	Changes in CO_2
Naslund *et al.*, 2015	Marine and Freshwater Research	Teleost	Boldness	Changes in CO_2
Norin *et al.*, 2018	Proceedings of the Royal Society B	Teleost	Activity	Climate Change
Nowicki *et al.*, 2011	Journal of Experimental Marine Biology and Ecology	Teleost	Activity	Climate Change and Changes in CO_2
Pasinelli and Kunc, 2010	The American Naturalist	Avian	Boldness	Direct Human Impact
Pistevos *et al.*, 2015	Nature/Scientific reports	Elasmobranch	Exploration	Climate Change and Changes in CO_2
Poudel *et al.*, 2015	Ecological Research	Mammalia	Boldness	Direct Human Impact
Reynisson and Olasdottir	Journal of Fish Biology	Teleost	Activity and Exploration	Climate Change
Sebastien *et al.*, 2016	Applied Animal Behaviour Science	Teleost	Exploration and Boldness	Direct Human Impact
Sergio, 2003	Animal Behaviour	Avian	Activity	Climate Change
Sloman *et al.*,2000	Animal Behaviour	Teleost	Aggression	Climate Change
Spady *et al.*, 2014	Biology Open	Mollusca	Activity	Changes in CO_2
Spady *et al.*, 2018	Global Change Biology	Cephalopod	Aggression and Boldness	Changes in CO_2
Stahlscmidt *et al.*, 2016	Behavioural Ecology	Reptilia	Boldness	Climate Change
Stawski *et al.*, 2016	Physiology and Behaviour	Mammalia	Activity	Direct Human Impact
Sundin *et al.*, 2010	Ethology	Teleost	Exploration	Direct Human Impact
Thawley and Langkilde, 2017	Animal Behaviour	Reptilia	Exploration and Boldness	Biotic Exchanges

Thomas *et al.*, 2001	Biological Conservation	Avian	Boldness	Direct Human Impact
Tigas *et al.*, 2002	Biological Conservation	Mammalia	Exploration	Direct Human Impact
Tuomainen *et al.*, 2011	Evolutionary Ecology Research	Teleost	Exploration and Activity and Aggression	Change in Nutrients
Underwood *et al.*, 2017	Journal of Animal Ecology	Crustacea	Activity	Direct Human Impact
Voellmy *et al.*, 2014	Animal Behaviour	Teleost	Aggression and Boldness and Sociability	Direct Human Impact
Wale *et al.*, 2013	Animal Behaviour	Crustacea	Exploration and Activity	Direct Human Impact
Watz *et al.*, 2015	Behavioural Ecology	Teleost	Aggression	Direct Human Impact
Wilson *et al.*, 2017	Journal of Experimental Biology	Reptilia	Activity	Climate Change
Wishingrad *et al.*, 2015	Behaviour	Teleost	Activity	Change in Nutrients
Witter *et al.*, 2012	Journal of Animal Ecology	Mammalia	Activity	Biotic Exchanges

Data extraction

Qualitative data

There were 21 different study habitats included in our dataset: Forest, forest trails, deep ocean (>800 m), alpine, aquatic, arctic, beach, coastal, woodland, intertidal, laboratory conditions, marine, reef, river system, rockpool system, reeds and bullrushes, rural, savannah, tundra, waterhole, woodland.

There were 19 different methods used to quantify behaviour in the papers we extracted. These 19 categories were as follows: % time, change in response, complexity scale, distance, height, latency, number of stops, number recaptured, number of items delivered, rate, response, response area, response distance, response duration, response time, score, speed, time, times observed.

The method of quantifying behaviour was categorised as either ‘naturalistic’, ‘observation’ or ‘coding of behaviours’ (Smith and Blumstein, 2008). Study organisms were considered ‘wild’ if individuals were either removed from their natural environment or descended from a wild stock by a single generation, otherwise study organisms were classed as ‘captive’ (Smith and Blumstein, 2008).

Quantitative data

The preferential order of calculating Hedges g from available data was as follows: Raw data - mean values - statistic value - *P* values. Conversions to hedges g values are presented in Table S1.2. We extracted 339 effect sizes from raw or mean data values present in the papers, 19 effect sizes from statistic values, and 23 effect sizes from *P* values. For studies where data showed a non-normal distribution, the assumptions required for the use of Hedges g (SMD) were violated. However, as the bias correction has been utilised for all effect size estimates, Hedges g could still be used (Kelley, 2005).

Typical control/experimental conditions were as follows: ambient/high temperatures and healthy/degraded habitats for ‘climate change’; ambient/high CO_2 levels for ‘changes in CO_2’; undisturbed/disturbed for ‘direct human impact, low/high turbidity for ‘changes in nutrients’, and the absence/presence of invasive species for ‘biotic exchanges’. For both the laboratory and field, control conditions for both temperature and CO_2 were variable across studies, according to regional ambient conditions in the case of field studies, and according to specific protocols in the case of laboratory studies. Where studies had more than one treatment level, we calculated an effect size for each level. This was the case for 14 studies.

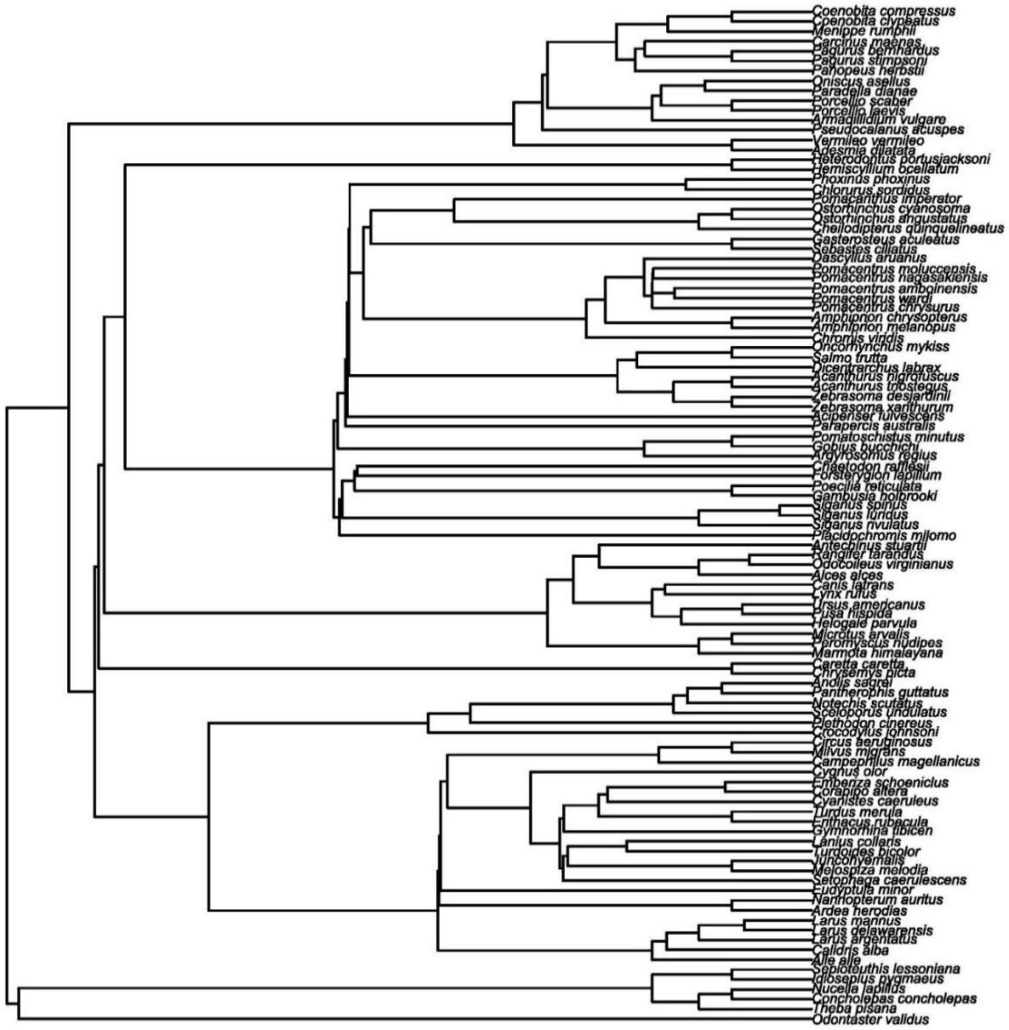

Figure S1.1: Phylogenetic tree for all species included in our dataset.

Analysis

Meta-analytical models

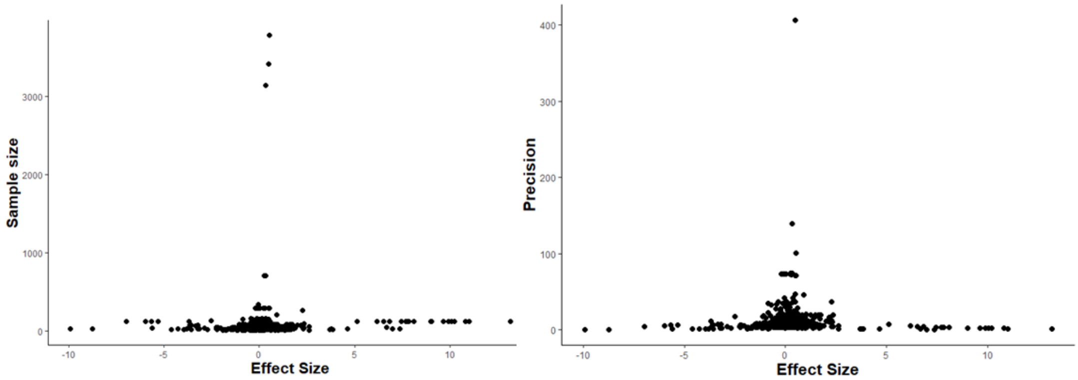

Figure S1.2: Relationship between effect size and sample size, in terms of the number of individuals samples (Left) and effect size and variance (Right), for data points included in the meta-analysis. Plots were used in conjunction with Orwin’s fail safe number and eggers regression analyses to assess for publication bias.

We used 95% credible intervals over the 89% intervals that are sometimes preferred in Bayesian analyses as the effective sample size for all our models were over 10,000 (Table S1.3), the recommended size for using 95% credible intervals (Kruschke, 2014). Secondary model checks were conducted by ensuring the maximum values of the real data fit within a histogram, based on simulated data from 1000 new models (Hadfield 2010/2015).

Table S1.2: Equations used to compute effect sizes and associated variances for the Meta-analyses.

Calculation	Equation	Notation
Standardised mean difference (Hedges g)	$g = \frac{\mathrm{M1} - \mathrm{M2}}{SD_{pooled}}$	M_1: Control mean M_2: Experimental mean SD $_{\text{pooled}}$: Pooled standard deviation
Pooled standard deviation	$SD_{pooled} = \sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}$	SD_1 = standard deviation for control group SD_2 = standard deviation for experimental group
Bias correction (J)	$\frac{N-3}{N-2.25} x \frac{\sqrt{N-2}}{N}$	N= pooled sample size (control+ experimental)
Standard mean difference precision	$W_{sm} = \frac{1}{SE_{sm}^2}$	W_{sm}= Standardised mean difference variance
		SE_{sm}=Standardised mean standard error
Standardised mean difference variance	$V_g = \frac{SD_1^2}{n_1} + \frac{SD_2^2}{n_2}$	V_g== Hedges g variance
Pearson product moment	$r_{xy} = \frac{\Omega_{xy}^2}{\Omega_x \, \Omega_y}$	Ω_x= covariance of X $\Omega_{y=}$ covariance of Y
Pearson product moment effect size (with Fishers z transform	$EZ_{zr} = .5log_r[\frac{1+r}{1-r}]$	EZ_{zr}= Pearson product moment as effect size with fisher Z transform r= Pearson product moment
r from Chi^2 value	$Ø = \sqrt{\frac{x^2(1)}{N}}$	X^2= Chi squared statistic value N=sample size
r from t-test values	$r = \sqrt{\frac{t^2}{t^2} + df}$	t= test statistic df= degrees of freedom
r from ANOVA values	$r = \sqrt{\frac{F\ (1,-)}{F\ (1,-)} + df\ error}$	F= test statistic F(1-)= any F value with df=1 in numerator
r from p level value	$r = \sqrt{\frac{Z^2}{N}}$ or $r = \frac{Z}{\sqrt{N}}$	Z = z value associated with P value (from table of z values) N= sample size

Table S1.3: Structure of nine Bayesian models included in analyses. The thinning interval was set at 100 for all models. Burn-in was set at 50,000 for all models. ESS: Effective sample size.

Model	Random	Reference	Iterations	ESS	Coefficient ESS
Global	Measure Taxa Reference Phylogeny Study type	Exploration Climate change Lab Plasticity	155,000,000	15,000	Intercept: 15,000 Activity: 15,000 Aggression: 14,2394 Boldness: 15,000 Sociability: 15,000 Biotic exchanges: 15,123 Change in nutrients: 15,000 Changes in CO_2: 15,000 Direct Human Impact: 15,000 Field: 15,000 Cross sectional: 15,000 Longitudinal: 15,000
Climate change	Measure Taxa Reference Phylogeny Study type	Exploration Climate change Lab Plasticity	155,000,000	15,000	Intercept: 15,000 Activity: 15,212 Aggression: 14,511 Boldness: 15,596 Sociability: 15,000 Field: 15,000 Cross sectional: 15,000 Longitudinal: 14,941
Changes in CO2	Measure Taxa Reference Phylogeny Study type	Exploration Climate change Lab Plasticity	155,000,000	15,000	Intercept: 14,252 Activity: 14,613 Aggression: 15,000 Boldness: 15,000 Field: 15,000 Cross sectional: 15,000 Longitudinal: 15,000
Direct Human Impact	Measure Taxa Reference Phylogeny Study type	Exploration Climate change Lab Plasticity	155,000,000	15,000	Intercept: 13,748 Activity: 13,586 Aggression: 12,765 Boldness: 12,041 Sociability: 13,096 Field: 15,000 Cross sectional: 15,504 Longitudinal: 14,767
Fish	Measure Reference Study type Phylogeny	Exploration Climate change Plasticity	155,000,000	15,000	Intercept: 15,000 Activity: 16,283 Aggression: 16,366 Boldness: 15,000 Sociability: 15,000 Change in Nutrients: 15,000 Changes in CO_2: 15,000 Direct Human Impact: 15,000 Cross sectional: 15,000 Longitudinal: 15,000
Bird	Measure Reference Phylogeny Study type	Exploration Climate change Plasticity	155,000,000	15,000	Intercept: 15,000 Activity: 15,000 Aggression: 14,462 Boldness: 15,000 Sociability: 15,000 Direct Human Impact: 15,000 Cross sectional: 14,557 Longitudinal: 15,000
Laboratory	Measure Reference Phylogeny Study type	Exploration Climate change Plasticity	155,000,000	15,000	Intercept: 14,637 Activity: 15,000 Aggression: 15,000 Boldness: 15,000 Sociability: 15,000 Biotic Exchanges: 15,000 Change in Nutrients: 15,000 Changes in CO_2: 15,000 Direct Human Impact: 15,000 Cross sectional: 15,000 Longitudinal: 15,367
Field	Measure Reference Phylogeny Study type	Exploration Climate change Plasticity	155,000,000	15,000	Intercept: 13,846 Activity: 14,220 Aggression: 14,196 Boldness: 14,375 Sociability: 15,000 Biotic Exchanges: 15,000 Changes in CO_2: 15,000 Direct Human Impact: 13,293 Cross-sectional: 14,548 Longitudinal: 14,618

Results

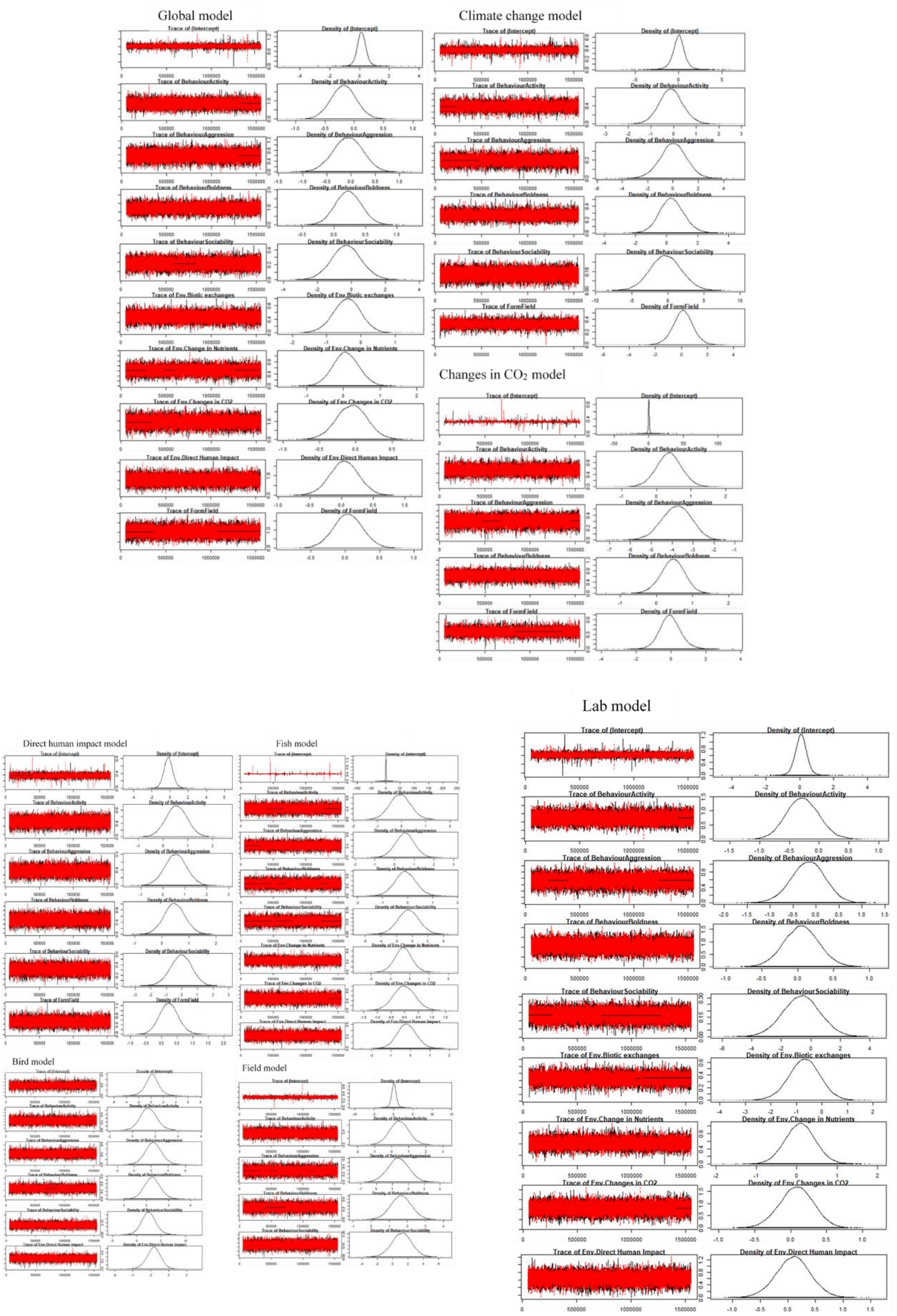

Figure S1.3: Trace plots to assess the convergence of all models, with each model based on two chains (Black and red).

Table S1.4: Summary of the Gelman diagnostic tests used to test chain convergence and autocorrelation. Values of 1.1 or less suggest good chain convergence.

Model	Overall estimate	Coefficients	Estimate	Upper CI
Global	1.06	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Biotic exchanges	1.00	1.00
		Change in nutrients	1.00	1.00
		Changes in CO_2	1.00	1.00
		Direct Human Impact	1.00	1.00
		Field	1.00	1.00
		Cross sectional	1.00	1.00
		Longitudinal	1.00	1.00
Changes in CO2	1.03	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Field	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00
Direct Human Impact	1.02	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Field	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00
Fish	1.03	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Change in Nutrients	1.00	1.00
		Changes in CO_2	1.00	1.00
		Direct Human Impact	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00
Bird	1.02	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Direct Human Impact	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00
Laboratory	1.04	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Biotic Exchanges	1.00	1.00
		Change in Nutrients	1.00	1.00
		Changes in CO_2	1.00	1.00
		Direct Human Impact	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00
Field	1.02	Intercept	1.00	1.00
		Activity	1.00	1.00
		Aggression	1.00	1.00
		Boldness	1.00	1.00
		Sociability	1.00	1.00
		Biotic Exchanges	1.00	1.00
		Changes in CO_2	1.00	1.00
		Direct Human Impact	1.00	1.00
		Cross-sectional	1.00	1.00
		Longitudinal	1.00	1.00

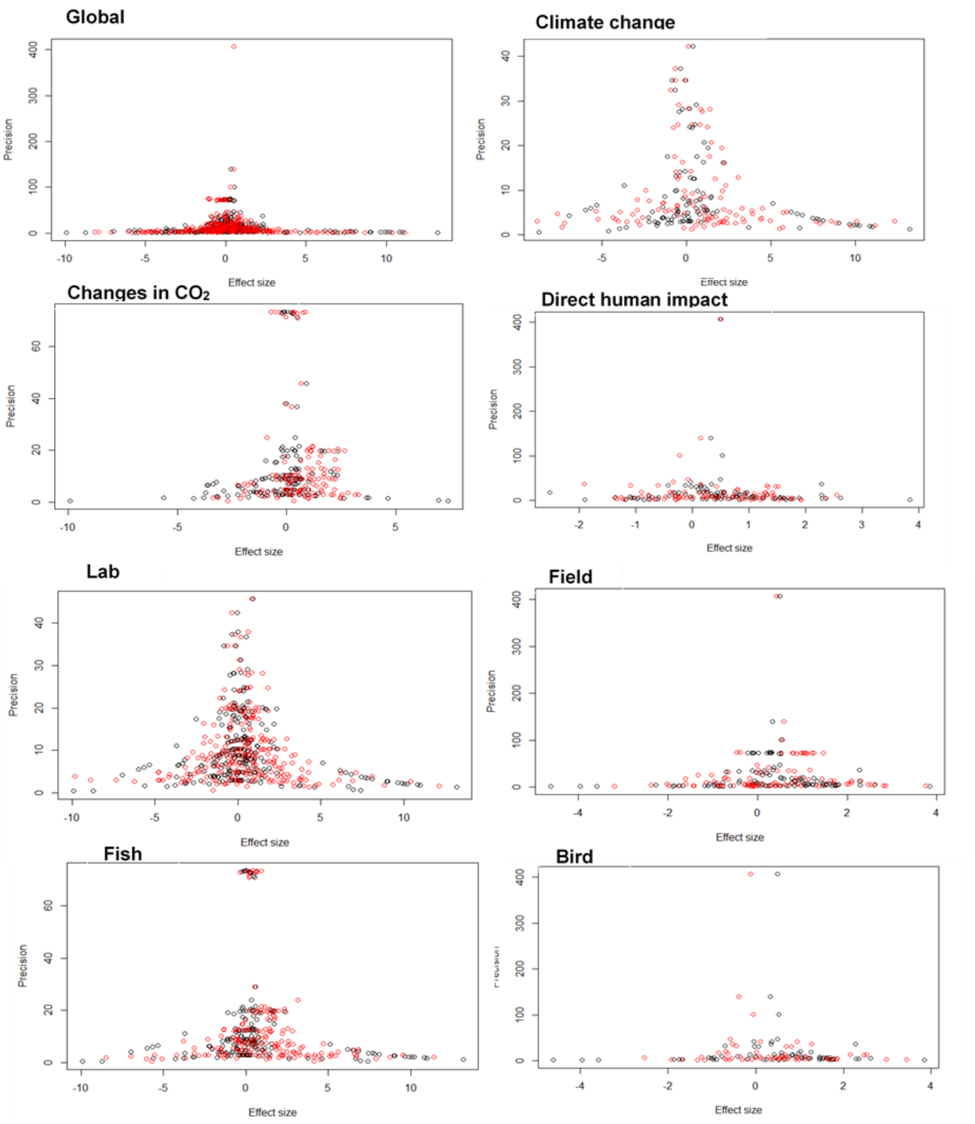

Figure S1.4: Simulated data from 100 models (red) against data used in all models (black) to check model fit.

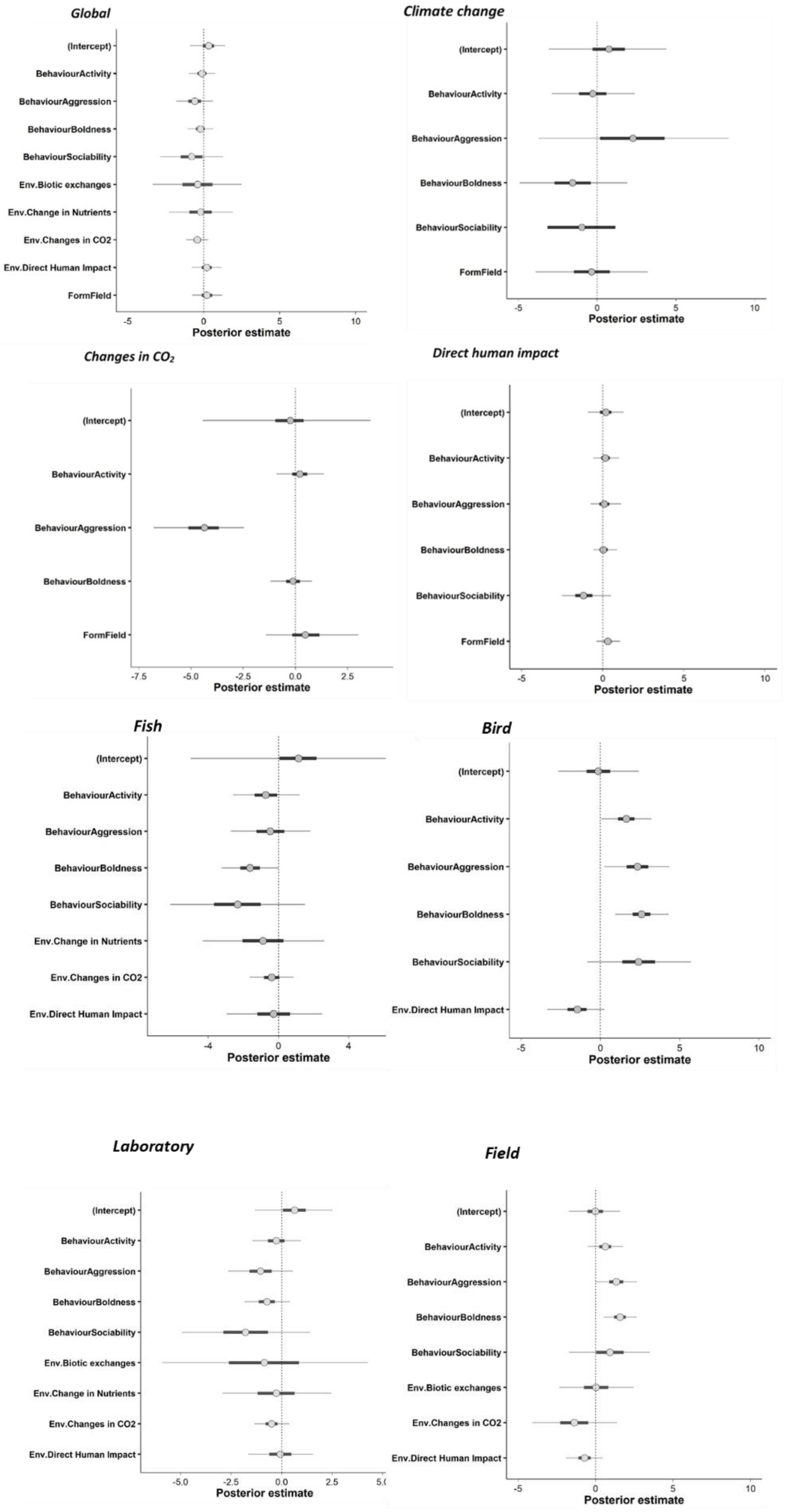

Figure S1.5: Conditional median parameter estimates for seven of the meta-analytical models. Grey shading and distribution tails represent 50% and 95% credible intervals, respectively. Parameters are considered significant where distributions do not overlap zero.

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Chapter 2 Supplementary Material

Methods

Study sites

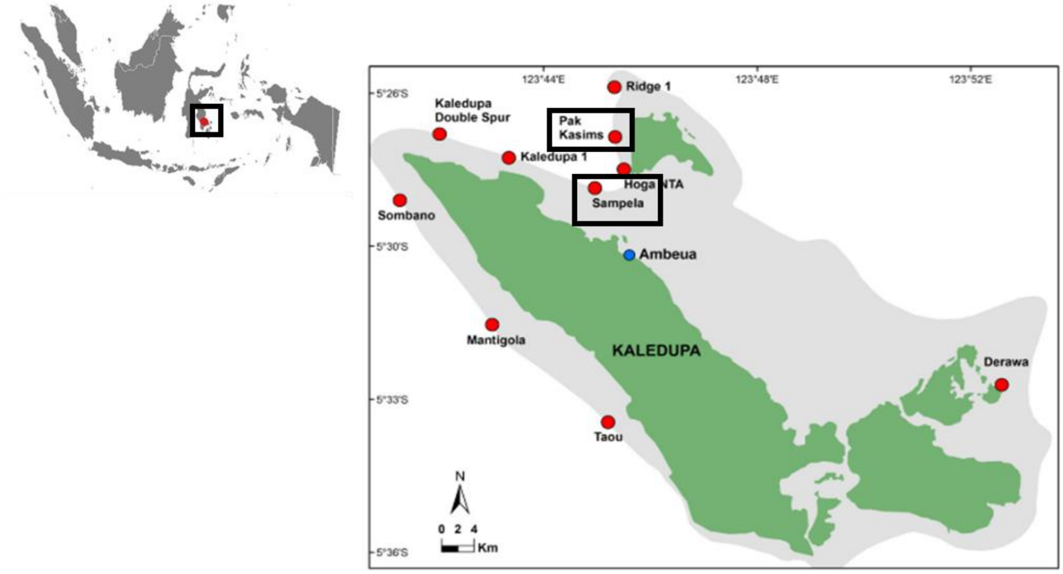

Figure S2.1: Location of the permanent monitoring sites around Hoga Island and Kaledupa. Red points mark the location of the permanent long term monitoring sites. The two sites used for behavioural surveys (Pak Kasims ad Sampela) are shown within bold boxes. Fig. modified from Clifton *et al.*, (2010).

Statistical analysis

Where appropriate, we ran normality, variance, and model fitting tests to ensure model and parametric test assumptions were met. We analysed differences in *C. lunulatus* abundance and differences in coral cover across the two sites using one-way ANOVAs and non-parametric Kruskal-Wallis tests. To visualize the differences between the two sites, we also plotted distributions of the time invested in each behaviour at each site.

Results

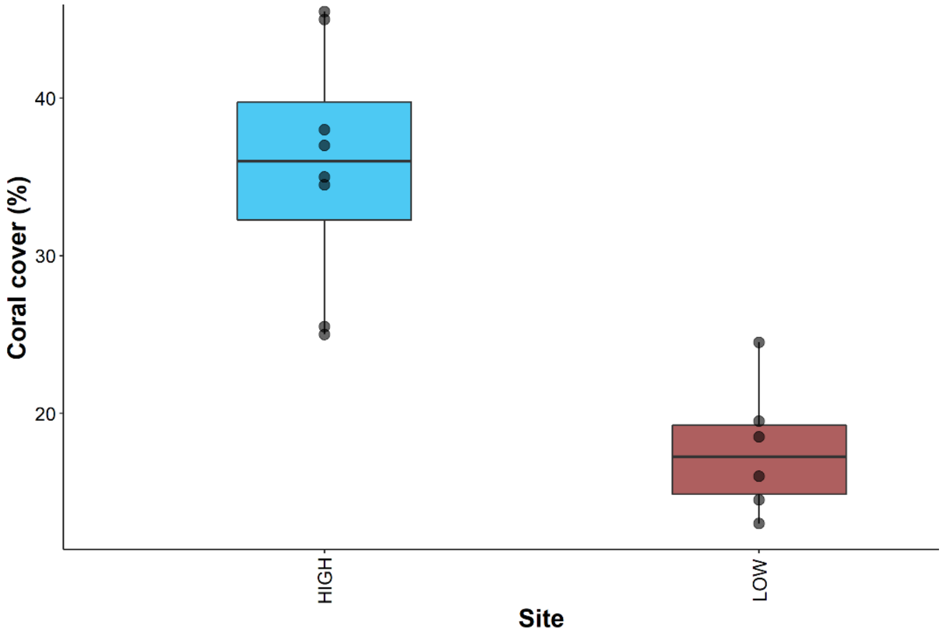

Figure S2.2: Differences in coral cover between the high coral cover site (Blue) and the low coral cover site (Red) in 2019. Lines within the box are median values. Box widths are interquartile ranges. Whiskers represent the minimum and maximum.

Table S2.1: Number of times, seconds, and percentage time *C. lunulatus* invested in behaviours at the two study sites. N=10 breeding pairs per site. Replicates for each breeding pair was summed and then the ten breeding pair values summed to give an overall value for behaviours at each site. Percentages calculated from a total of 30,000 seconds of observation at each site.

Behaviour	Site	Count	Time (S)	Percentage
Aggression	PK	59	693	2.31
	SAM	14	172.2	0. 574
Cleaning	PK	14	181.8	0.606
	SAM	20	279.6	0.932
Feeding	PK	1063	13,665.056	45.55
	SAM	1096	10,235.040	34.117
Searching	PK	1228	13562.100	45.207
	SAM	1419	15,533.580	51.779
Travelling	PK	133	1,492.620	4.975
	SAM	268	3,289.380	10.965
Time with Pair	PK		28,283.400	94.278
	SAM		25,179.600	83.932

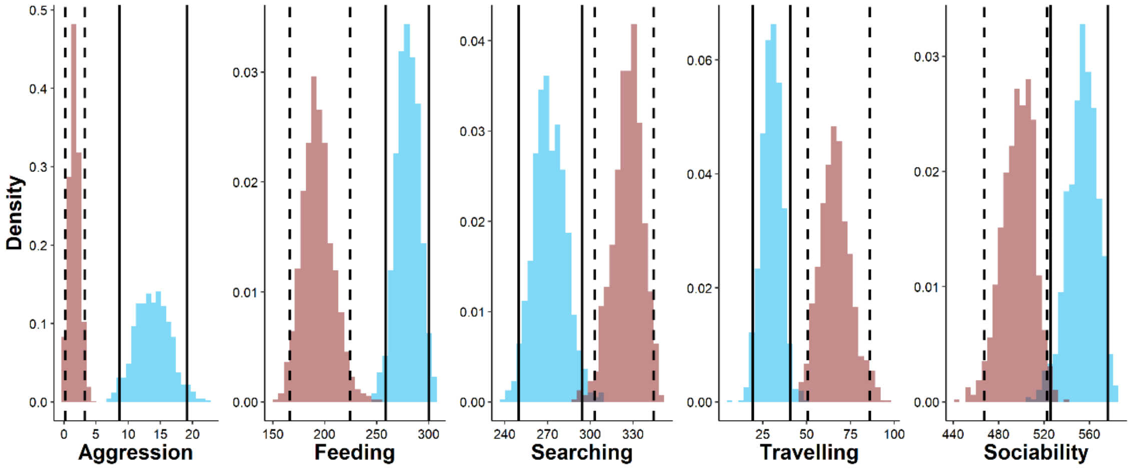

Figure S2.3 Distributions for individual traits based on 1000 bootstrap estimates from raw behavioural data. Solid lines and dashed lines are 2.5% and 97.5% confidence intervals for the high (blue) and low (red) resource site, respectively.

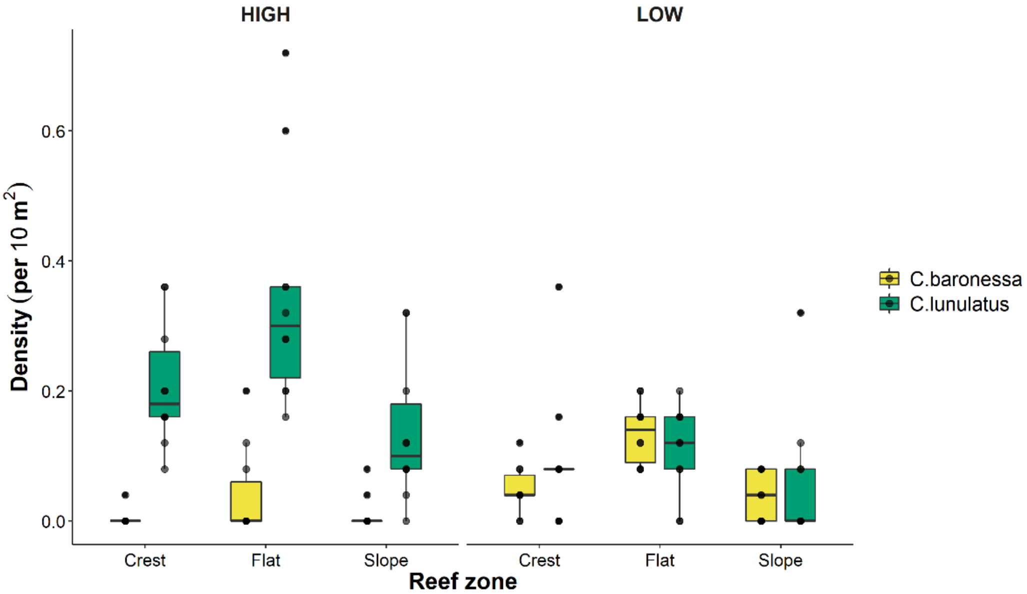

Figure S2.4: Density (per 10m^2) of *C. lunulatus* and C. baronessa at each reef zone across the high and low resource availability sites. Boxplot lines are median values, box lengths represent interquartile ranges and whiskers are minimum and maximum values calculated from the 25th and 75th percentiles. Black points are outliers.

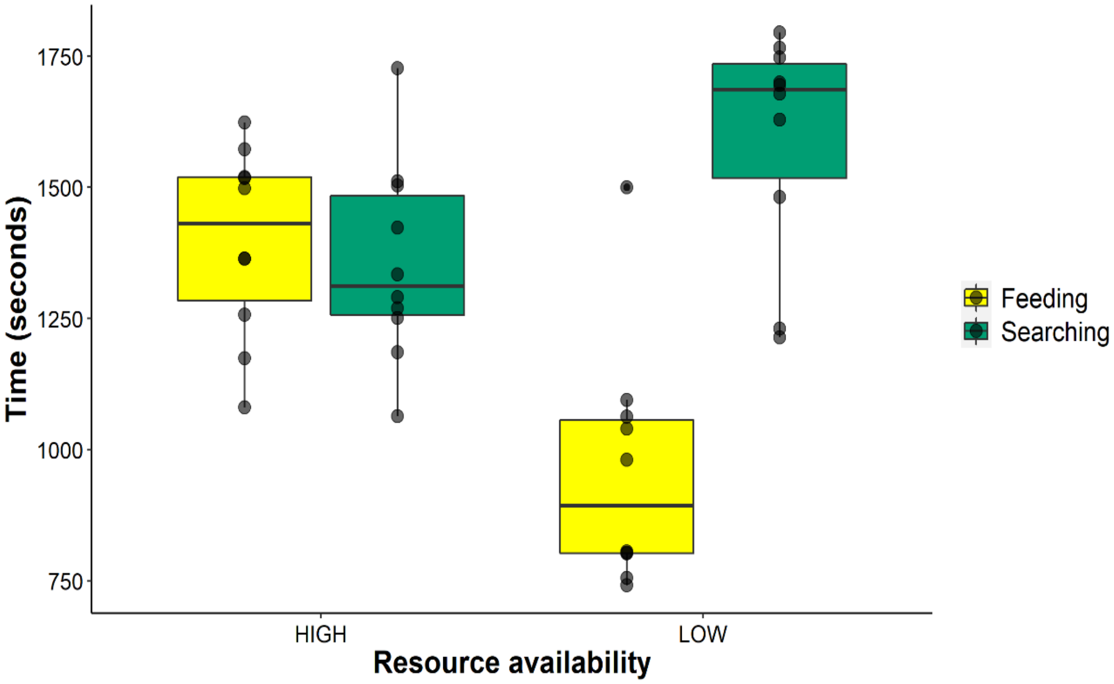

Figure S2.5: Differences in Feeding and searching behaviours between the two sites. Lines within the box are median values. Box widths are interquartile ranges. Whiskers represent the minimum and maximum. Circular points are outliers.

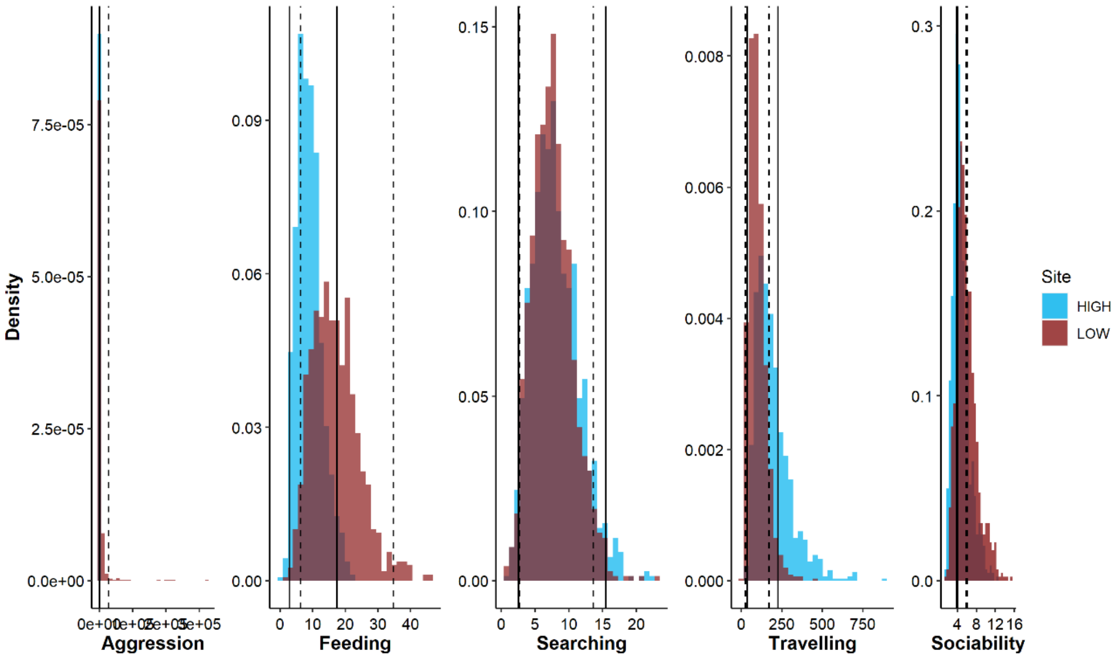

Figure S2.6: Bootstrapped distributions for mean scaled between individual variation of five traits at each of the two study sites. Bold and dashed lines are 2.5% and 97.5% intervals for the high and low coral cover site, respectively.

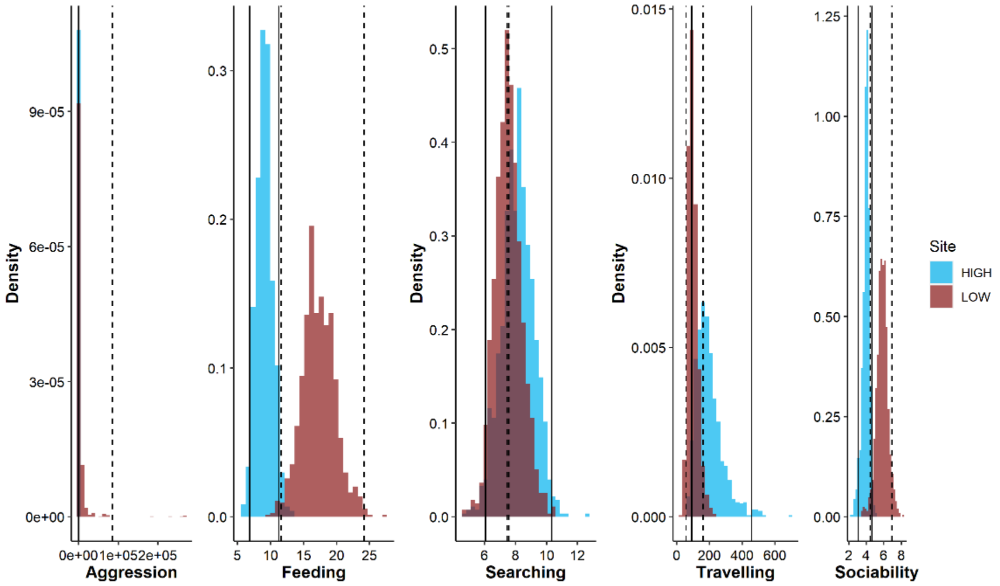

Figure S2.7: Bootstrapped distributions for mean-scaled residual variation of five traits at each of the two study sites. Bold and dashed lines are 2.5% and 97.5% intervals for the high and low coral cover site, respectively. Incidences where confidence intervals do not overlap indicates significant differences between the two sites.

Kaiser's number of eigenvalues and the broken stick model identified PC1 to be significant, but as PC2 still represented around 18% of the variance, both PC1 and PC2 were included in two dimensional plots (Fig. S8).

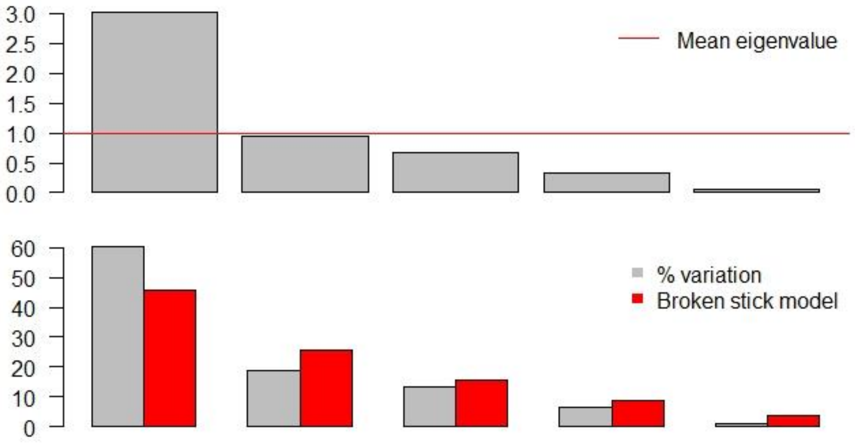

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Figure S2.8: Output from Kaiser eigenvalues (Top) and the broken stick model (Bottom), Values above the mean eigenvalue are significant, as are any values greater than predicted by the broken stick model i.e., where grey bars are greater than the red broken stick model predictions.

Chapter 3 Supplementary Material

Methods

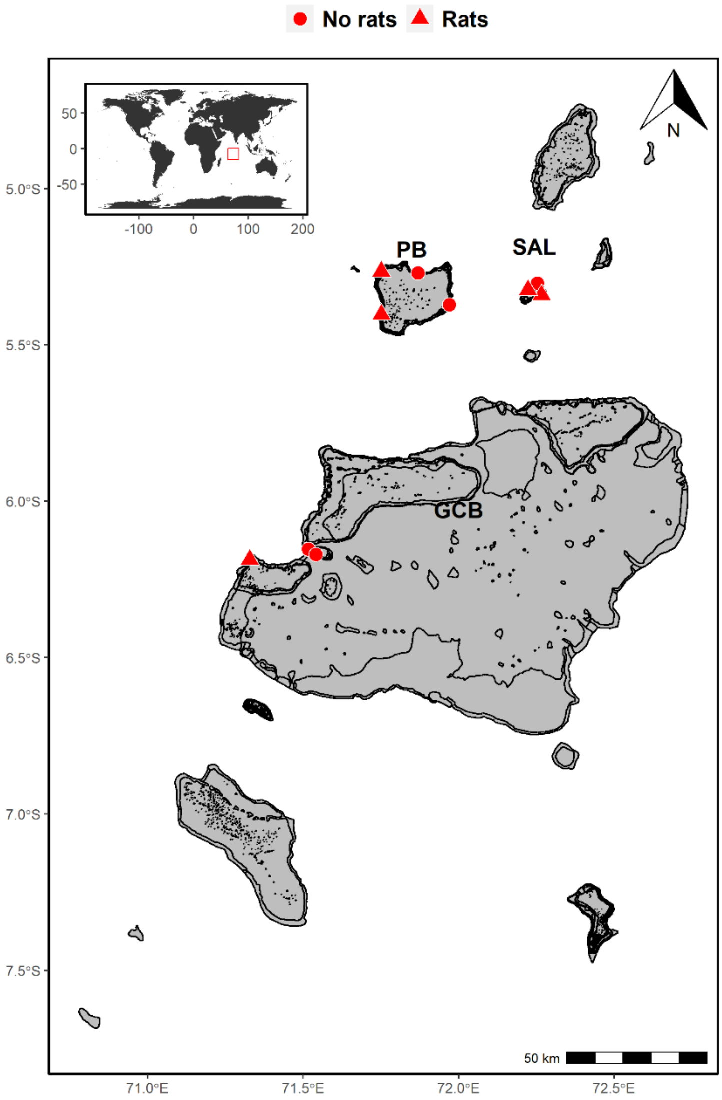

Figure S3.1: The location of study sites around the Chagos Archipelago. The location of the Chagos Archipelago in the Indian ocean is shown in the inset. Surveys were conducted around three atolls: Peros Banhos (PB), Salomon (SAL) and the Great Chagos Bank (GCB). Points represent the locations of the 10 reefs where surveys were conducted.

Statistical analysis

To determine if focal individual total length is driven by density dependence, we modelled *P. lacrymatus* total length as a response variable, with an interaction between islands invasion status and conspecific density as the explanatory variable. We then tested the following hypotheses with nonlinear hypothesis tests: Around islands with seabirds (1) and islands with rats (2) *P. lacrymatus* individuals will be smaller at higher conspecific densities.

Results and discussion

Table S3.1: Summary of Bayesian models and hypothesis tests. A. Summary of models testing the role of island invasion status on nutrients, *P. lacrymatus* territory size, aggression, conspecific density and total length ; B. Summary of models testing the relationship between turf algal $\delta^{15}N$ and turf algal cover within *P. lacrymatus* territories; and C. Summary of models testing the relationship between nutrients (turf algal $\delta^{15}N$ and cover) and two biotic variables (conspecific density and focal individual total length) on *P. lacrymatus* territory size and aggression. All models included a nested random intercept for island within each of the three study atolls.

A.	**Response variable**	**Explanatory variable**	**Bayes R2**	**Hypothesis**	**Median estimate (credible intervals)**	**Posterior probability**	**Evidence ratio**
	$\delta^{15}N$	Invasion status	0.69	Islands with seabirds>Islands with rats	0.53 (-0.48,1.58)	0.83	4.80
	Turf algal cover	Invasion status	0.48	Islands with seabirds>Islands with rats	-0.02 (-0.13,0.09)	0.37	0.59
	Territory size	Invasion status	0.37	Islands with seabirds<Islands with rats	-0.21 (-0.34,-0.07)	0.99	74.47
	Aggression	Invasion status	0.36	Islands with seabirds>Islands with rats	0.47 (-0.35,1.28)	0.85	5.47
	Conspecific density	Invasion status	0.22	Islands with seabirds>Islands with rats	0.18 (-0.16,0.52)	0.82	4.51
	Total length	Invasion status	0.18	Islands with seabirds>Islands with rats	0.11 (-0.99,1.21)	0.57	1.30
B.	$\delta^{15}N$	Turf algal cover* Invasion status	0.70	Islands with seabirds > 0	2.47 (-0.29,5.23)	0.93	13.44
				Islands with rats < 0	-1.55 (-4.83,1.78)	0.78	3.55
				Islands with rats < Islands with seabirds	-4.02 (-8.07,0.12)	0.95	17.31
	$\delta^{15}N$	Distance to shore	0.70	Distance < 0 *(Bird islands only)*	-0.01 (-0.03,0.00)	0.91	10.20

C.

Territory size	Turf algal cover*Invasion status	0.60	Islands with seabirds < 0	-0.50 (-1.31,0.32)	0.85	5.70
			Islands with rats < 0	-0.71 (-1.59,0.17)	0.91	10.24
			Islands with rats < Islands with seabirds	0.21 (-0.95,1.36)	0.62	1.60
Territory size	δ^{15}N*Invasion status	0.60	Islands with seabirds < 0	-0.01 (-0.09,0.07)	0.59	1.44
			Islands with rats < 0	0.01 (-0.06,0.08)	0.38	0.60
			Islands with rats > Islands with seabirds	-0.02 (-0.12,0.07)	0.66	1.97
Territory size	Conspecific density* Invasion status	0.60	Islands with seabirds < 0	0.02 (-0.13,0.17)	0.38	0.62
			Islands with rats < 0	-0.27 (-0.44,-0.09)	0.99	151.38
			Islands with rats > Islands with seabirds	0.29 (0.06,0.52)	0.98	50.28
Territory size	Total length* Invasion status	0.60	Islands with seabirds > 0	0.03 (-0.01,0.07)	0.87	6.76
			Islands with rats > 0	0.05 (-0.01,0.10)	0.91	10.32
			Islands with rats > Islands with seabirds	-0.02 (-0.09,0.05)	0.65	1.84
Aggression	Turf algal cover*Invasion status	0.46	Islands with seabirds > 0	2.97 (-0.72, 6.43)	0.91	10.15
			Islands with rats > 0	0.00 (-3.48,3.45)	0.50	1.02
			Islands with rats < Islands with seabirds	2.97 (-1.99, 7.79)	0.84	5.32
Aggression	δ^{15}N*Invasion status	0.46	Islands with seabirds > 0	-0.11 (-0.43,0.21)	0.29	0.41
			Islands with rats > 0	0.09 (-0.26,0.45)	0.66	1.98
			Islands with rats > Islands with seabirds	-0.20 (-0.65,0.23)	0.23	0.29
Aggression	Conspecific density* Invasion status	0.46	Islands with seabirds > 0	0.31 (-0.32,0.93)	0.79	3.85
			Islands with rats < 0	-0.51 (-1.24, 0.23)	0.87	6.88
			Islands with rats < Islands with seabirds	0.82 (-0.11,1.76)	0.93	12.61
Aggression	Total length* Invasion status	0.46	Islands with seabirds > 0	0.23 (0.03, 0.43)	0.97	30.07
			Islands with rats < 0	0.13 (-0.35,0.08)	0.85	5.84
			Islands with rats < Islands with seabirds	0.37 (0.07,0.66)	0.98	44.33
Aggression	Territory size*Invasion status	0.46	Islands with seabirds < 0	-0.58 (-1.99,0.84)	0.93	12.97
			Islands with rats > 0	0.77 (-0.10,1.64)	0.93	12.97
			Islands with rats > Islands with seabirds	-1.35 (-2.99,0.25)	0.92	10.80

Table S3.2: Summary of supplementary Bayesian models and hypothesis tests. A. Summary of models controlling for the role of nutrients (turf algal $\delta^{15}N$ and percentage cover) on *P. lacrymatus* conspecific density and total length. All models included a nested random intercept for island within each of the three study atolls.

Response variable	Explanatory variable	Bayes R2	Hypothesis	Median estimate (credible intervals)	Posterior probability	Evidence ratio
$\delta^{15}N$	Conspecific density* Invasion status	0.28	Islands with seabirds > 0	0.03 (-0.27, 0.09)	0.59	1.42
			Islands with rats < 0	-0.09 (-0.16, 0.25)	0.79	3.76
			Islands with rats < Islands with seabirds	-0.12 (-0.14,0.41)	0.76	3.15
Turf algal cover	Conspecific density* Invasion status	0.37	Islands with seabirds > 0	2.19 (0.71,3.67)	0.99	113.29
			Islands with rats > 0	2.09 (0.37, 3.82)	0.98	41.33
			Islands with rats < Islands with seabirds	0.10 (-2.07, 2.30)	0.47	0.88
$\delta^{15}N$	Total length*Invasion status	0.22	Islands with seabirds > 0	0.21 (-0.30, 0.73)	0.75	3.05
			Islands with rats > 0	0.07 (-0.43, 0.60)	0.59	1.44
			Islands with rats > Islands with seabirds	-0.14 (-0.55, 0.81)	0.64	1.76
Turf algal cover	Total length* Invasion status	0.21	Islands with seabirds > 0	-1.04 (-5.77, 3.46)	0.36	0.56
			Islands with rats > 0	-1.98 (-6.97, 3.08)	0.26	0.35
			Islands with rats > Islands with seabirds	0.93 (-5.57, 7.24)	0.40	0.40
Total length	Conspecific density* Invasion status	0.32	Islands with seabirds < 0	-1.26 (-2.07,0.45)	0.99	165.67
			Islands with rats < 0	-0.92 (-1.93, 0.11)	0.93	13.11
			Islands with rats > 0	-0.33 (-1.66, 0.98)	0.66	1.98

Nutritional resources

Around islands with seabirds, *P. lacrymatus* territories with high turf algal cover also contained turf algae with the highest $\delta^{15}N$ values (PP=0.93 (2.47 (-0.29,5.23)), Figure S3.2). The input of $\delta^{15}N$ from seabird nutrient subsidies occurs on a gradient, such that $\delta^{15}N$ is highest closer to shore (Benkwitt *et al.*, 2021). The presence of seabird nutrient subsidies has also been shown to enhance algal abundance (Benkwitt *et al.*, 2019) . *P. lacrymatus* territories closer to shore had higher $\delta^{15}N$ values (PP=0.91 evidence ratio=10.20), which is likely driving the positive association between turf algal $\delta^{15}N$ and turf algal cover around islands with seabirds.

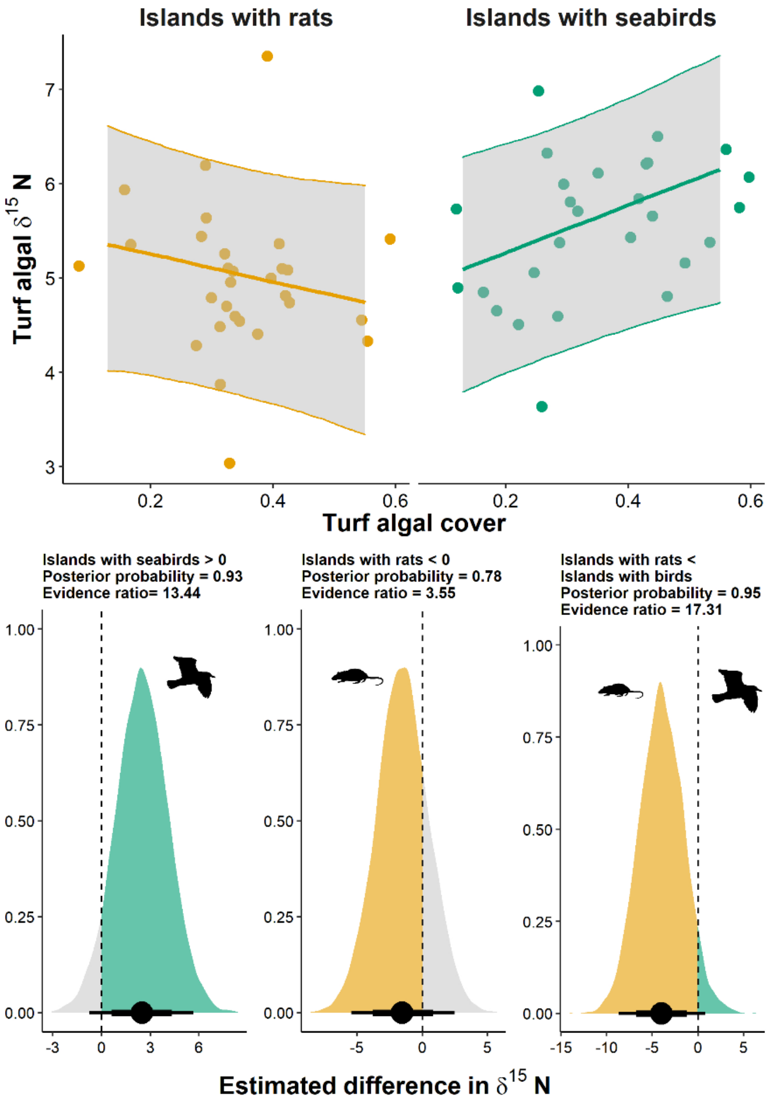

Figure S3.2: The relationship between turf algal cover and δ^{15}N within *P. lacrymatus* territories. Top: Points represent partialized residuals extracted from Bayesian models for each *P. lacrymatus* individual around islands with seabirds (Green) and islands with rats (Yellow). Points are presented alongside best fit lines based on Bayesian model conditional effects, with grey shading indicating 75% quantiles. Bottom: Bayesian posterior densities from non-linear hypothesis tests. Posterior probabilities and evidence ratios show the extent to which 1) a positive relationship is supported around islands with seabirds (Left, green), 2) A negative relationship is supported around islands with rats (Middle, yellow), and 3) The relationship between turf algal cover and δ^{15}N is different (i.e., more negative) for *P. lacrymatus* territories around islands with rats compared to around islands with seabirds (Right, yellow).

Territory size and aggression

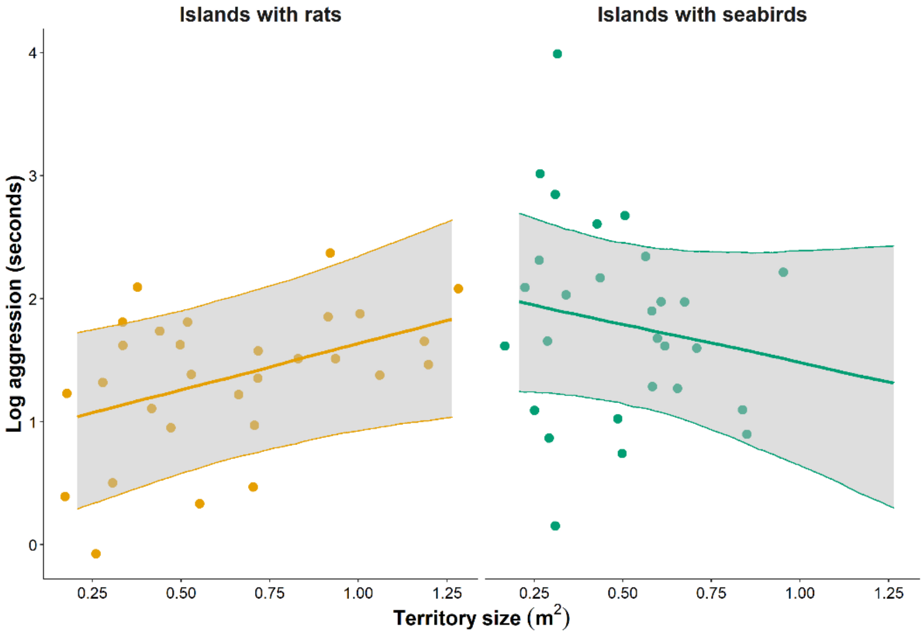

Figure S3.3 The influence of *P. lacrymatus* territory size on aggression around islands with seabirds (Green) and islands with rats (Yellow). Points represent partialized residuals extracted from Bayesian models for each *P. lacrymatus* individual. Best fit lines are extracted from Bayesian model conditional effects, with grey shading indicating 75% quantiles.

Conspecific density and total length

Around islands with seabirds, *P. lacrymatus* density was 1.01 (±0.62) individuals per m^2 compared to 0.89 (±0.42) individuals per m^2 around rat-infested islands. Bayesian models and hypothesis tests showed an 0.82 posterior probability that conspecific density was higher around islands with seabirds than rat-infested islands (0.18 (-0.16, 0.52), Figure S3.4). The mean total length of focal individuals was 9.21 (±1.63) cm around islands with seabirds, compared to 9.15 (± 1.49) cm around islands with rats. There was no evidence to suggest that total length varied with islands invasion status (slope: 0.1 (-0.99, 1.21), PP: 0.57, Figure S3.4). Total length was instead a consequence of density dependence: *P. lacrymatus* individuals in areas of high conspecific densities had smaller total lengths around both islands with seabirds (slope: -1.26 (-2.07, -0.45), PP: 0.99, ER: 165.67) PP = 0.99 (-1.24 (-2.06, 0.41)) and around islands with rats (slope: -0.92 (-1.93, 0.11), PP: 0.93, ER: 13.11).

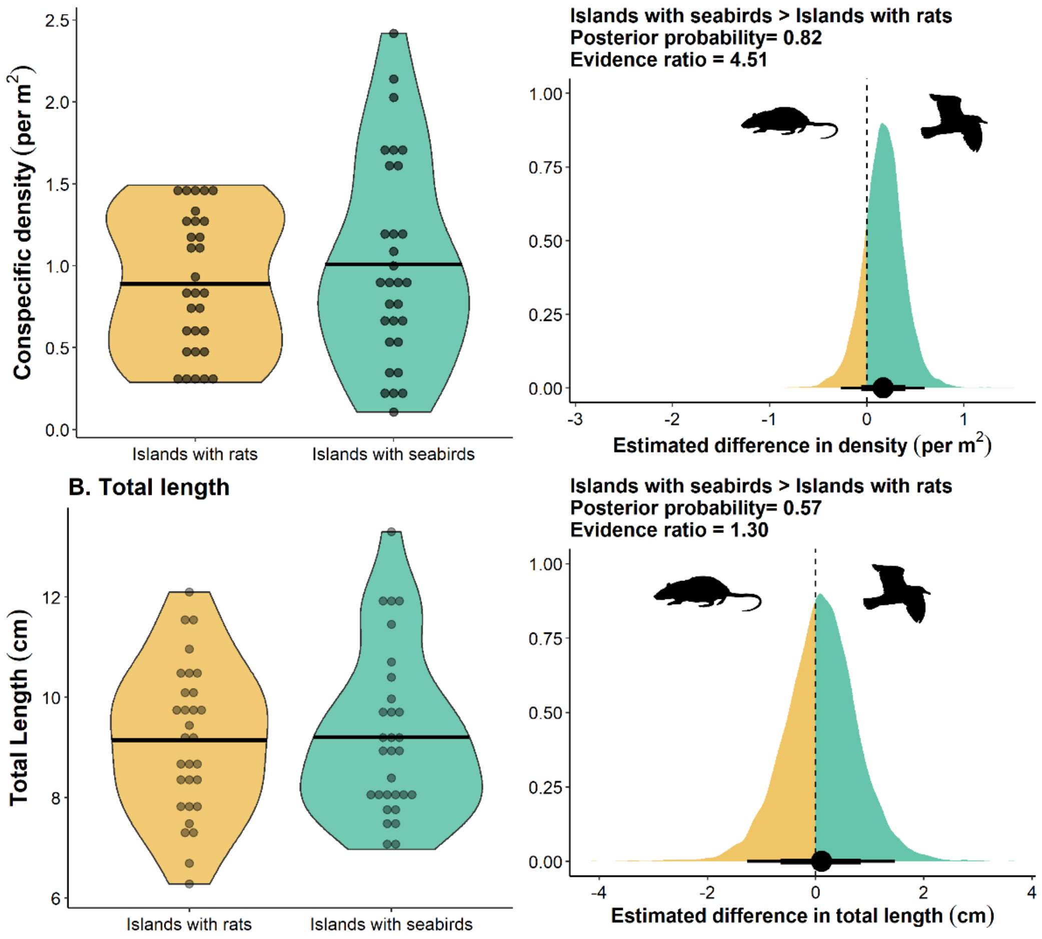

Figure S3.4: *P. lacrymatus* density and focal individual total length around islands with seabirds and islands with invasive rats within the Chagos Archipelago. Each point on the violin plots (left) represents a single *P. lacrymatus* territory. Mean estimates for conspecific density (A, left) around islands with seabirds (n=30) and islands with rats (n=30), and for focal individual total length (B, left) around islands with seabirds (n=30) and islands with rats (n=30) are represented by black bars. Posterior densities (Right) in green show the extent to which the following hypotheses are supported.: 1. Conspecific density (A, right) is higher around islands with seabirds and 2. Focal individual total length (B, right) is higher around islands with seabirds. Evidence ratios show how much more likely these hypotheses are supported over the alternative hypotheses. Rat and seabird graphics from phylopic.org under Public Domain Dedication 1.0 licenses.

Territory size was negatively correlated with conspecific density around islands with rats, such that where conspecific focal individual territories were smaller at higher conspecific densities (Figure S3.5, slope: -0.27 (-0.44,0.09), PP:0.99, ER: 151.38 around islands with rats) but not around islands with seabirds (Figure S3.5, slope: 0.02 (-0.13,0.17), PP: 0.38, ER: 0.62). Around islands with seabirds, conspecific density was weakly positively correlated with length of aggression (slope: 0.31 (-0.32,0.93), PP: 0.79, ER: 3.85). Conversely, around islands with rats, there was a negative relationship between conspecific density and time invested in aggression (slope: -0.51 (-1.24, 0.23) PP: 0.87, ER: 6.88).

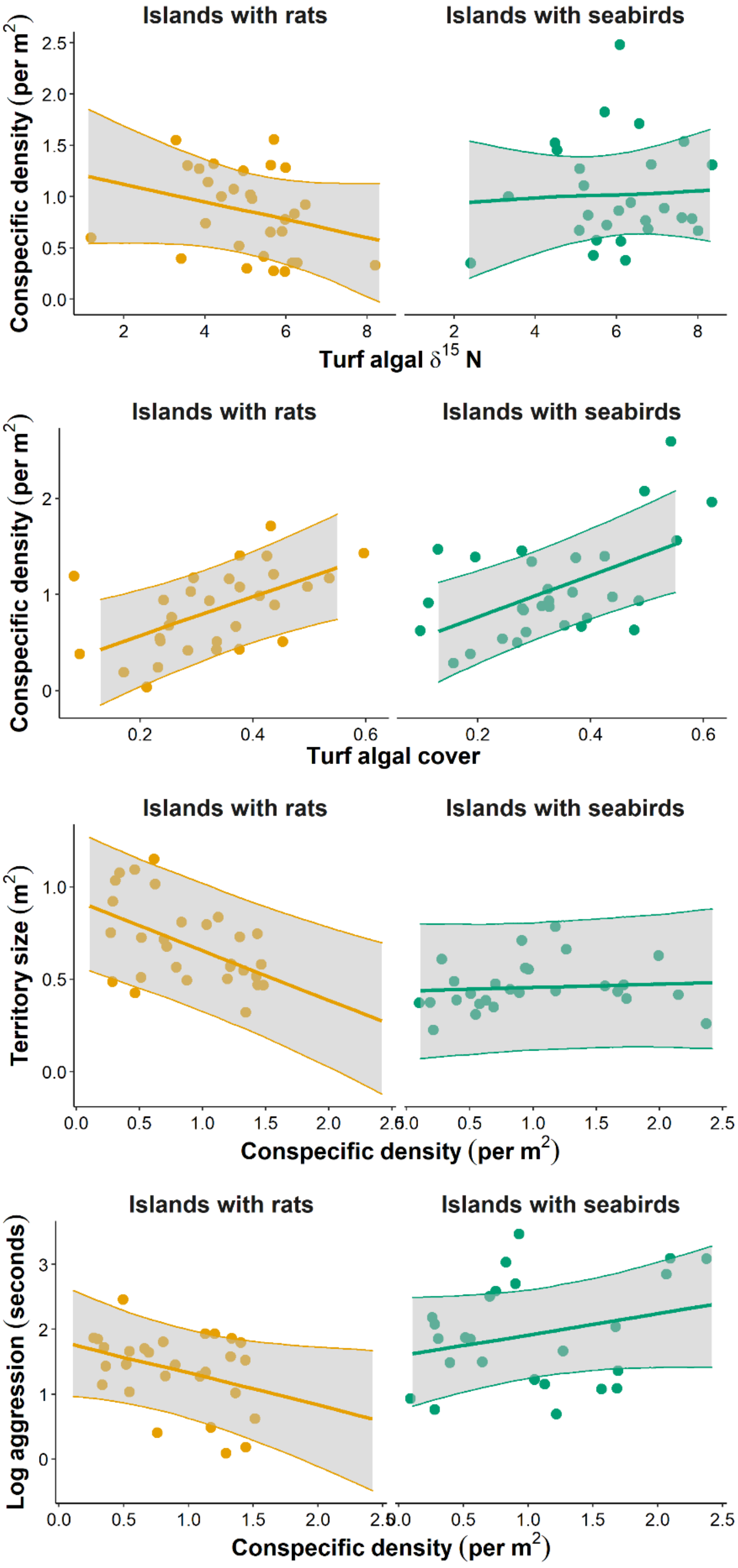

Figure S3.5: *P. lacrymatus* conspecific density, nutritional resources, and territoriality. Points represent partialized residuals extracted from Bayesian models for each *P. lacrymatus* individual around islands with seabirds (Green) and islands with rats (Yellow). Best fit lines are extracted from Bayesian model conditional effects, with grey shading indicating 75% quantiles.

Territory size was positively correlated with focal individual total length such that larger focal individuals held larger territories (Figure S3.6, slope: 0.02 (-0.01, 0.07), PP: 0.87, ER: 6.76 around islands with seabirds, slope: 0.05 (-0.01, 0.10), PP: 0.91, ER: 10.32 around islands with rats). As with conspecific density, the relationship between focal individual total length and aggression was also variable between islands with seabird and islands with rats. Specifically, there was a positive association between total length and aggression around islands with seabirds (slope: 0.23 (0.03,0.43), PP: 0.97, ER: 30.07) and a negative association around islands with rats (slope: 0.13 (-0.35, 0.08), PP: 0.85, ER: 5.84).

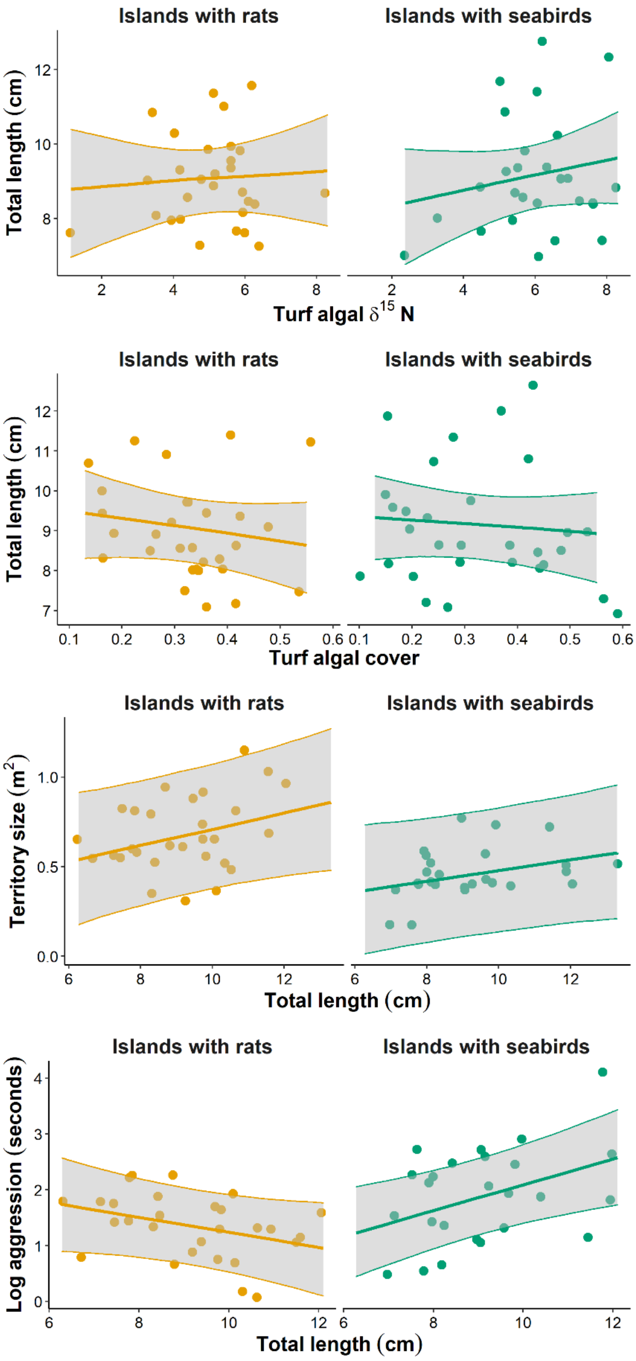

Figure S3.6: *P. lacrymatus* total length, nutritional resources, territoriality. Points represent partialized residuals extracted from Bayesian models for each *P. lacrymatus* individual around islands with seabirds (Green) and islands with rats (Yellow). Best fit lines are extracted from Bayesian model conditional effects, with grey shading indicating 75% quantiles.

Chapter 4 Supplementary Material

Table S4.1: Summary of all model variables and equations.

	Definition	Value	Scenario	Equation	Reference	Unit
	Territoriality prediction			$E + T < aP + bP$ $E + T < (aP + bP)SP_f$	Eq. 1 Eq. 3	
b	Territorial gain			$b = e(1 - a)$	Eq. 2	
$\mathcal{E}$	Energy per unit food	8.8-11				J mg^{-1}
M_r	Energy lost resting	1-2				J min^{-1}
C	Turf algal cover	0-0.99				
q	Mass food per unit area	3.5				mg min^{-1}m^2
P_f	Proportion time foraging	0.8				
P_r	Proportion time resting	0.2				
m_f	Energy lost foraging			$1.2M_r$		J min^{-1}
P	Food productivity			$P = \mathcal{E}qC$	Eq.4	J min^{-1}m^2
D	Number of intruders		**Scenario 1** **Scenario 2**	$D = mP + 1$ $D = 1e^{xP}$	Eq. 5a Eq. 5b	
e_T	Territorial efficiency		**Scenario 1** **Scenario 2**	$e_T = -mP + 1$ $e_T = e^{-0.05D}$	Eq.6a Eq.6b	
a	Non-territorial gain		**Scenario 1** **Scenario 2**	$a = \frac{D - 1}{P}$ $a = e^{-0.3D}$	Eq.7a Eq.7b	
M	Maintenance			$\mathrm{M} = (P_f m_f) + (P_r m_r)$	Eq.8	J min^{-1}
E	Costs of living		**Scenario 1** **Scenario 2**	$E = MPe^{-0.2P}$ $E = MDe^{-0.08D}$	Eq.9a Eq.9b	J min^{-1} J min^{-1}
M_a	Energy lost in aggression			$2M_r$		J min^{-1}
T	Territoriality costs			$T = m_a e_T$	Eq.10	J min^{-1}
S	Territory size			$S = \frac{E + T}{Pp_f}$	Eq.11	m^2
N	Territorial payoff			$N = (bP\ x\ S) - T$	Eq. 12	
	Thresholds			$(bP\ x\ S) - T < \mathcal{E}qC$ $\frac{N}{P} = 0$	Eq.13a Eq.13b	
G	Net energetic gain			$G = (PS - ET)$	Eq.14	J min^{-1}
R	Encounter rate	40				Encounter min^{-1}
A_n	Number of aggressive encounters			$A_n = \frac{G}{m_a} * R * 0.03*0.84$	Eq.15	Encounter min^{-1}

Table S4.2: Summary of predictions from mathematical model variations. $\mathcal{E}$ is energy per unit food, and m_r is energy lost when resting. Thresholds refer to the minimum lower and maximum upper thresholds across all values of territory productivity, *P*.

	Ɛ (J min^{-1})	m_r (J min^{-1})	**Peak Territoriality** (Encounters min^{-1})	**Thresholds** (J min^{-1})	
				Lower	**Upper**
Scenario 1A -Homogeneous environment -Varying Ɛ	8.00	1.50	0.49	NA	NA
	8.75	1.50	0.49	NA	23.89
	9.50	1.50	0.50	NA	19.62
	10.25	1.50	0.50	0.72	15.79
	11.00	1.50	0.51	1.54	11.94
Scenario 2A -Heterogeneous environment -Varying Ɛ	8.00	1.50	0.80	7.56	NA
	8.75	1.50	0.81	7.96	NA
	9.50	1.50	0.81	8.31	NA
	10.25	1.50	0.81	8.97	NA
	11.00	1.50	0.81	9.24	NA
Scenario 1B -Homogeneous environment -Varying Ɛ and m_r	8.00	1.00	0.51	1.40	12.04
	8.00	2.00	0.49	NA	NA
	11.00	1.00	0.51	1.54	11.94
	11.00	2.00	0.49	NA	28.11
Scenario 2B -Heterogeneous environment -Varying Ɛ and m_r	8.00	1.00	0.73	9.24	NA
	8.00	2.00	0.80	7.56	NA
	11.00	1.00	0.81	9.24	NA
	11.00	2.00	0.81	7.70	NA

Table S4.3: Summary of pairwise comparisons between mathematical models (A), mathematical model and empirical data for Model Scenarios 1 (A) and Model scenarios 2 (B). Table 1A: Bold P values indicate where P<0.05 and therefore where two model slopes differ. Numbers in brackets after estimates are standard errors. Tables 1B and 1C: bold P values indicate where P>0.05 and therefore where mathematical model predictions do not differ from empirical data. For models 1A and 2A, numbers in brackets refer to food energy values (Ɛ). For models 1B and 2B, the first number in brackets refers to food energy values, and the second refers to energetic costs (m_r). Adjusted P-values refer to P values following a Bonferroni correction for multiple comparisons.

A

Variable	Treatment	Pair	Estimate	SE	Df	T ratio	P
S	Bird	Empirical-S1	3.59	0.30	110	12.00	<0.01
S	Bird	Empirical-S2	1.88	0.30	110	6.27	<0.01
S	Bird	S1-S2	-1.71	0.27	110	-6.32	<0.01
An	Bird	Empirical-S1	1.142	0.214	108	5.35	<0.001
An	**Bird**	**Empirical-S2**	**0.09**	**0.214**	**108**	**-0.41**	**0.991**
An	Bird	S1-S2	-1.23	0.19	108	-6.42	<0.001
S	Bird	1A (8)-Empirical	-3.98	0.28	784	-14.11	0.00
S	Bird	1A (8.75)-Empirical	-3.73	0.28	784	-13.21	0.00
S	Bird	1A (9.5)-Empirical	-3.46	0.28	784	-12.56	0.00
S	Bird	1A (10.25)-Empirical	-3.20	0.28	784	-11.32	0.00
S	Bird	1A (11)-Empirical	-2.95	0.28	784	-10.45	0.00
An	Bird	1A (8)-Empirical	-1.05	0.08	782	-0.13	0.00
An	Bird	1A (8.75)-Empirical	-1.09	0.08	782	-0.14	0.00
An	Bird	1A (9.5)-Empirical	-1.11	0.08	782	-0.14	0.00
An	Bird	1A (10.25)-Empirical	-1.11	0.08	782	-0.14	0.00
An	Bird	1A (11)-Empirical	-1.09	0.08	781	-0.14	0.00
S	Bird	1B (8,1)-Empirical	-2.60	0.28	784	-9.20	0.00
S	Bird	1B (8,2)-Empirical	-5.30	0.28	784	-18.78	0.00
S	Bird	1B(11,1)- Empirical	-1.98	0.28	784	-7.01	0.00
S	Bird	1B (11,2)-Empirical	-4.20	0.28	784	-14.86	0.00
An	Bird	1B (8,1)-Empirical	-0.90	0.08	782	-0.11	0.00
An	Bird	1B (8,2)-Empirical	-1.04	0.08	782	-0.13	0.00
An	Bird	1B(11,1)- Empirical	-1.09	0.08	782	-0.14	0.00
An	Bird	1B (11,2)-Empirical	-1.29	0.08	782	-0.16	0.00
S	Rat	Empirical-S1	3.21	0.45	110	7.22	<0.01
S	Rat	Empirical-S2	1.50	0.45	110	3.37	<0.01
S	Rat	S1-S2	-1.71	0.35	110	-4.90	<0.01
An	**Rat**	**Empirical-S1**	**0.01**	**0.26**	**109**	**0.04**	**0.99**
An	Rat	Empirical-S2	-1.21	0.26	109	-4.72	<0.01
An	Rat	S1-S2	-1.23	0.20	109	-6.06	<0.01
S	Rat	1A (8)-Empirical	-3.61	0.34	784	-10.54	0.00
S	Rat	1A (8.75)-Empirical	-3.35	0.34	784	-9.79	0.00
S	Rat	1A (9.5)-Empirical	-3.08	0.34	784	-9.00	0.00
S	Rat	1A (10.25)-Empirical	-2.82	0.34	784	-8.23	0.00
S	Rat	1A (11)-Empirical	-2.58	0.34	784	-7.52	0.00
An	Rat	1A (8)-Empirical	**0.08**	**0.10**	**783**	**0.88**	**0.99**
An	Rat	1A (8.75)-Empirical	**0.04**	**0.10**	**783**	**0.46**	**1.00**
An	Rat	1A (9.5)-Empirical	**0.02**	**0.10**	**783**	**0.24**	**1.00**
An	Rat	1A (10.25)-Empirical	**0.02**	**0.10**	**783**	**0.22**	**1.00**
An	Rat	1A (11)-Empirical	**0.04**	**0.10**	**783**	**0.37**	**1.00**
S	Rat	1B (8,1)-Empirical	-2.22	0.34	784	-6.48	<0.01
S	Rat	1B (8,2)-Empirical	-4.93	0.34	784	-14.39	0.00
S	Rat	1B(11,1)- Empirical	-1.60	0.34	784	-4.68	<0.01
S	Rat	1B (11,2)-Empirical	-3.82	0.34	784	-11.16	0.00
An	Rat	1B (8,1)-Empirical	**0.23**	**0.10**	**783**	**2.34**	**0.68**
An	Rat	1B (8,2)-Empirical	**0.08**	**0.10**	**783**	**0.88**	**0.99**
An	Rat	1B(11,1)- Empirical	**0.04**	**0.10**	**783**	**0.37**	**1.00**
An	Rat	1B (11,2)-Empirical	**-0.16**	**0.10**	**783**	**-1.63**	**0.98**

B

Variable	Treatment	Pair	Estimate	SE	Df	T ratio	P
S	Bird	2A (8)-Empirical	-2.27	0.28	784	-8.03	0.00
S	Bird	2A (8.75)-Empirical	-2.05	0.28	784	-7.27	0.00
S	Bird	2A (9.5)-Empirical	-1.87	0.28	784	-6.64	<0.01
S	Bird	2A (10.25)-Empirical	-1.73	0.28	784	-6.11	<0.01
S	Bird	2A (11)-Empirical	-1.60	0.28	784	-5.68	<0.01
An	**Bird**	**2A (8)-Empirical**	**0.02**	**0.08**	**782**	**0.28**	**1.00**
An	**Bird**	**2A (8.75)-Empirical**	**0.05**	**0.08**	**782**	**0.61**	**1.00**
An	**Bird**	**2A (9.5)-Empirical**	**0.07**	**0.08**	**782**	**0.87**	**0.99**
An	**Bird**	**2A (10.25)-Empirical**	**0.09**	**0.08**	**782**	**1.07**	**0.99**
An	**Bird**	**2A (11)-Empirical**	**0.10**	**0.08**	**782**	**1.98**	**0.99**
S	Bird	2B (8,1)-Empirical	-1.59	0.28	784	-5.62	<0.01
S	Bird	2B (8,2)-Empirical	-3.01	0.28	784	-10.67	0.00
S	Bird	2B(11,1)- Empirical	-1.08	0.28	784	-3.82	<0.01
S	Bird	2B (11,2)-Empirical	-1.90	0.28	784	-6.73	0.00
An	**Bird**	**2B (8,1)-Empirical**	**-0.09**	**0.08**	**782**	**-1.09**	**0.99**
An	**Bird**	**2B (8,2)-Empirical**	**0.02**	**0.08**	**782**	**0.28**	**1.00**
An	**Bird**	**2B(11,1)- Empirical**	**0.10**	**0..08**	**782**	**1.20**	**0.99**
An	**Bird**	**2B (11,2)-Empirical**	**0.26**	**0.08**	**7821**	**3.30**	**0.10**
S	Rat	2A (8)-Empirical	-1.89	0.34	784	-5.52	<0.01
S	Rat	2A (8.75)-Empirical	-1.68	0.34	784	-4.89	<0.01
S	Rat	2A (9.5)-Empirical	-1.50	0.34	784	-4.37	<0.01
S	Rat	2A (10.25)-Empirical	-1.34	0.34	784	-3.40	0.01
S	**Rat**	**2A (11)-Empirical**	**-1.23**	**0.34**	**784**	**-3.58**	**0.05**
An	Rat	2A (8)-Empirical	1.15	0.10	783	0.12	0.00
An	Rat	2A (8.75)-Empirical	1.18	0.10	783	1.22	0.00
An	Rat	2A (9.5)-Empirical	1.20	0.10	783	0.12	0.00
An	Rat	2A (10.25)-Empirical	1.22	0.10	783	0.13	0.00
An	Rat	2A (11)-Empirical	1.23	0.10	783	0.13	0.00
S	**Rat**	**2B (8,1)-Empirical**	**-1.21**	**0.34**	**784**	**-3.53**	**0.05**
S	Rat	2B (8,2)-Empirical	-2063	0.34	784	-7.90	0.00
S	**Rat**	**2B(11,1)- Empirical**	**-0.70**	**0.34**	**784**	**-2.05**	**0.86**
S	Rat	2B (11,2)-Empirical	-1.53	0.34	784	-4.46	<0.01
An	Rat	2B (8,1)-Empirical	1.04	0.10	783	0.11	0.00
An	Rat	2B (8,2)-Empirical	1.53	0.10	783	0.12	0.00
An	Rat	2B(11,1)- Empirical	1.23	0.10	783	0.13	0.00
An	Rat	2B (11,2)-Empirical	1.39	0.10	783	0.14	0.00

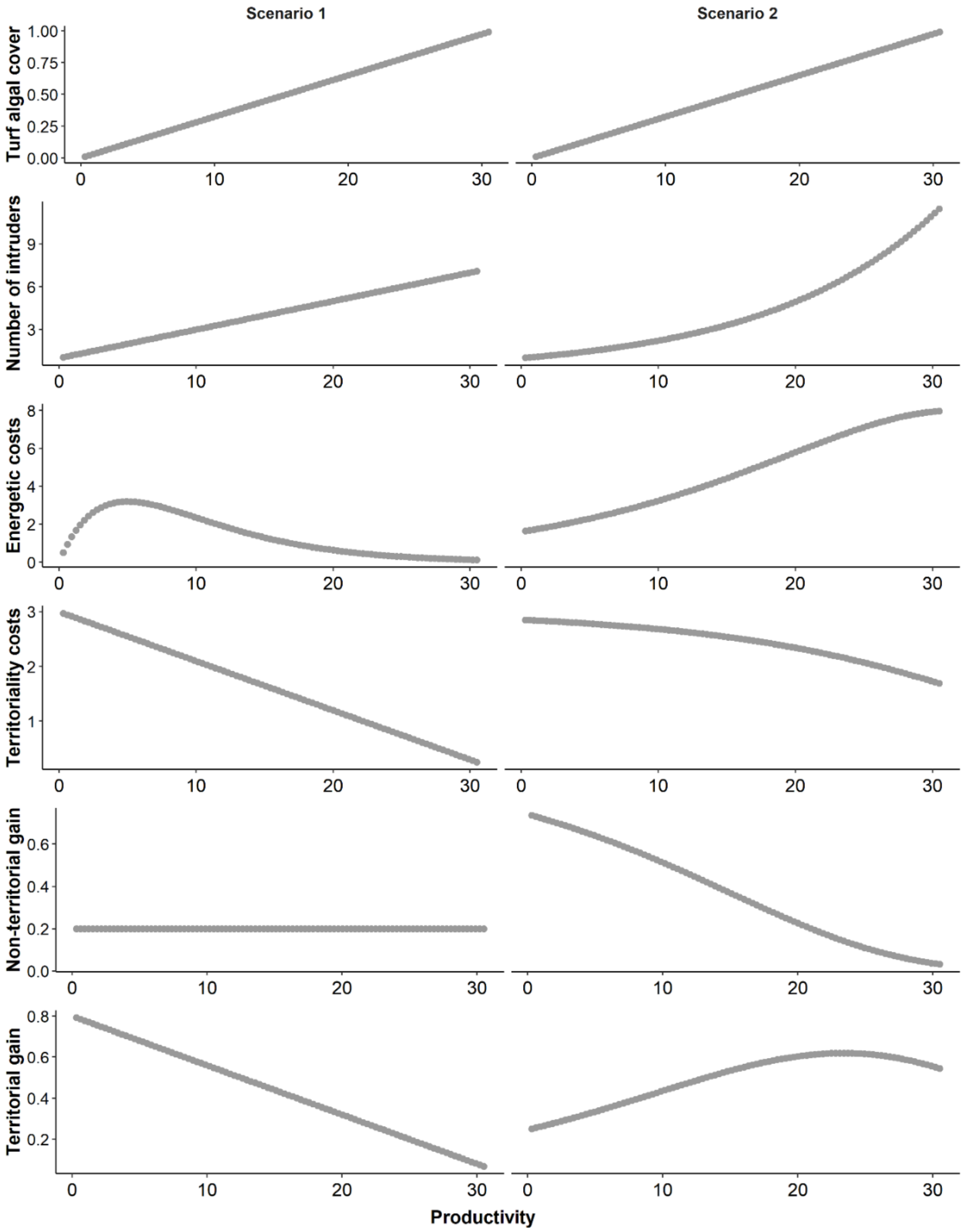

Figure S4.1: Relationship between model variables for Model Scenarios 1 and 2.

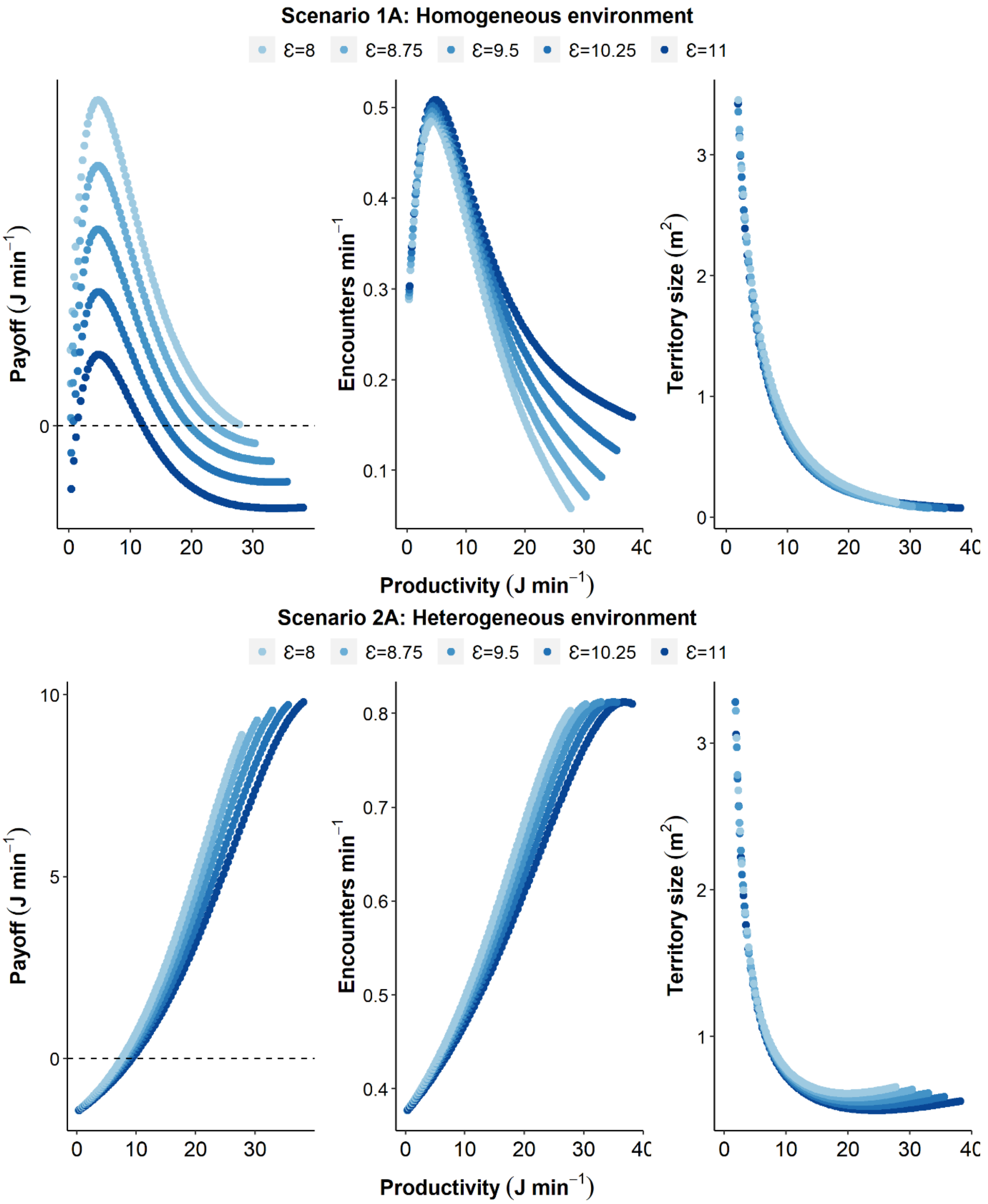

Figure S4. 2: The predicted effect of five food energy values on *P. lacrymatus* territoriality.

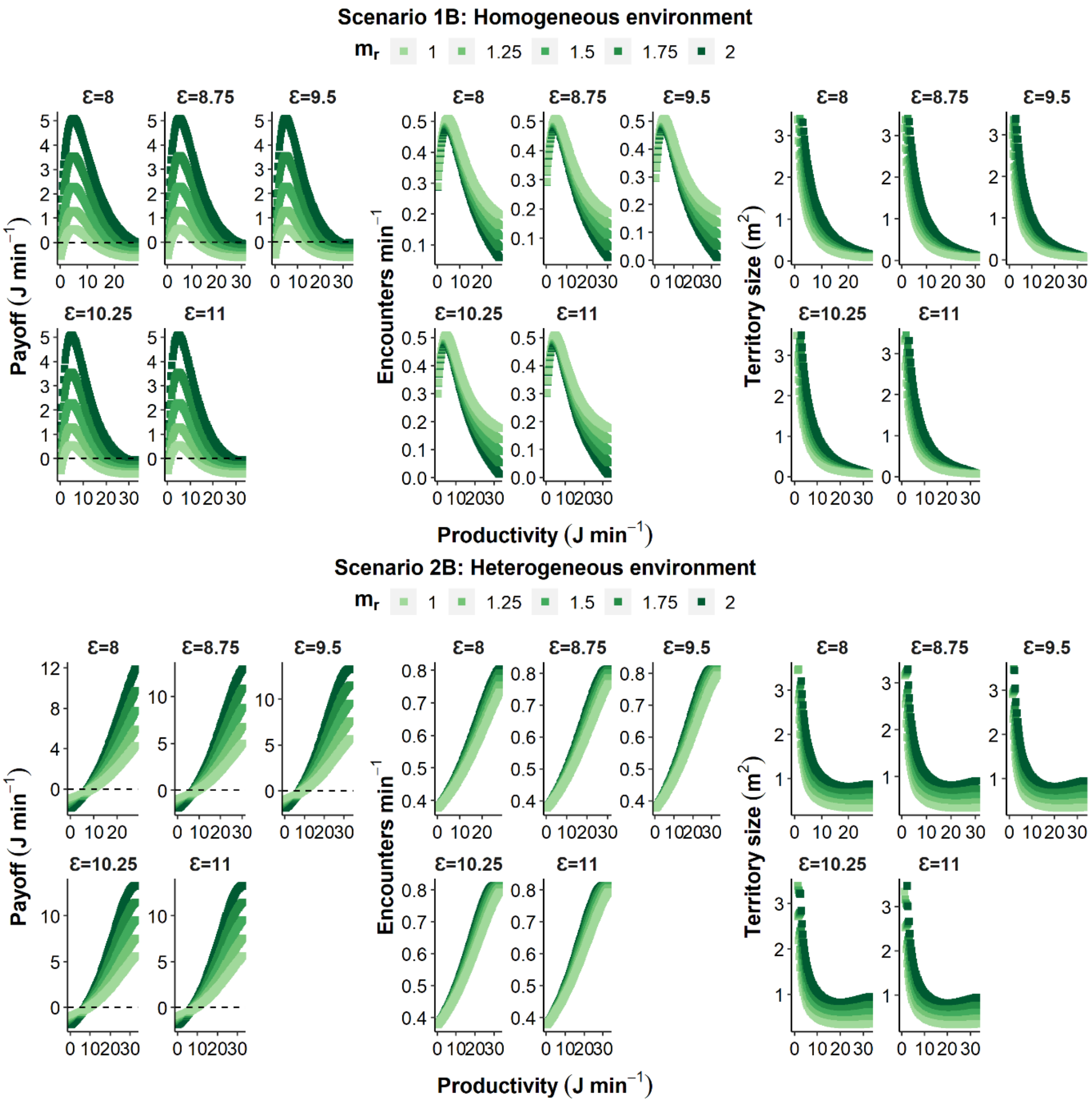

Figure S4 3: The predicted effect of five food energy values and five cost of living values on *P. lacrymatus* territoriality in a homogeneous and heterogeneous environment.

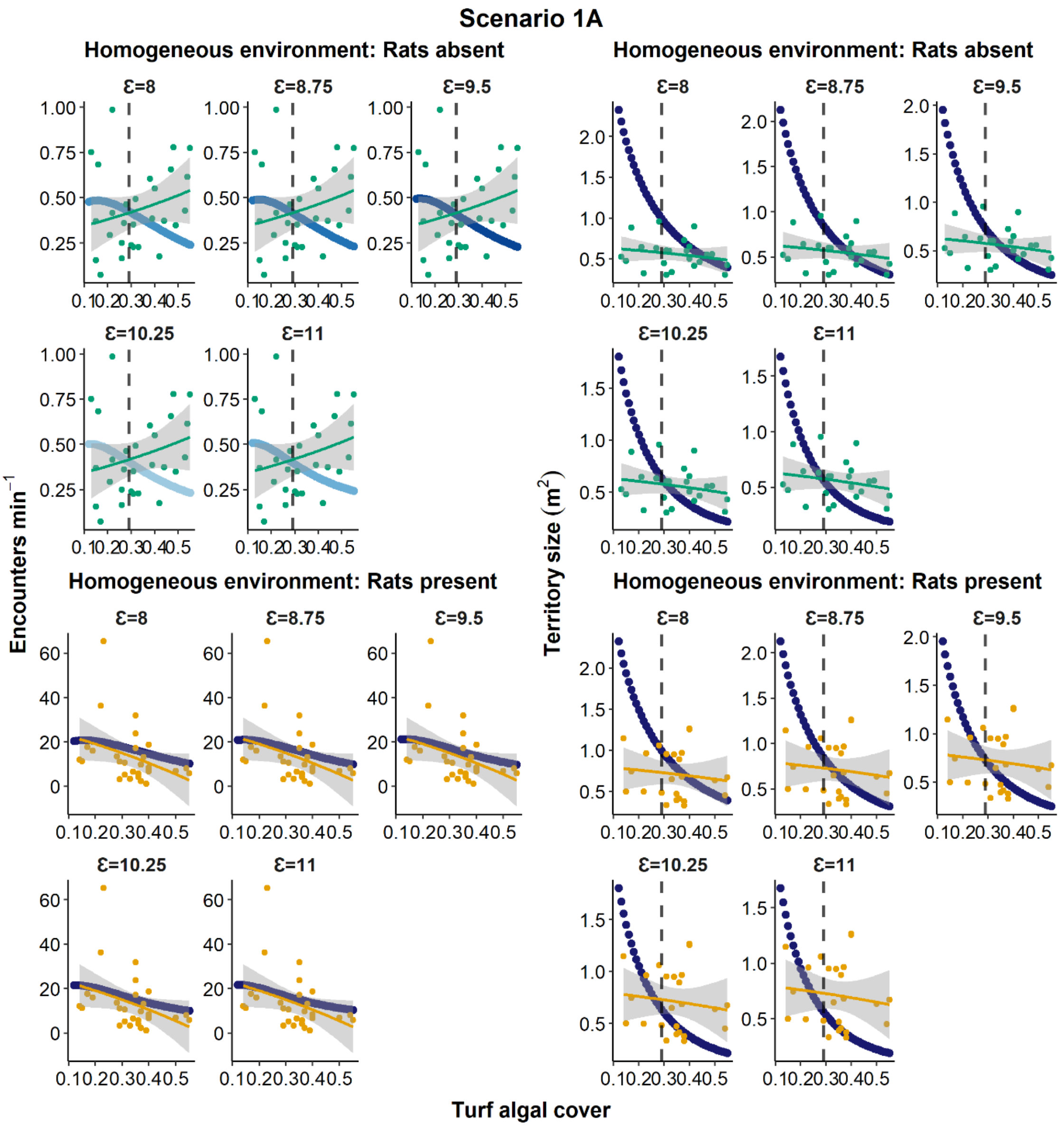

Figure S4.4: Model estimates and empirical data for *P. lacrymatus* territoriality in the presence and absence of invasive rats. Model estimates show the effect of varying food energy values in a homogeneous environment. Points represent raw data for empirical data collected adjacent to islands where rats are absent (Green) and where rats are present (Orange). Green and Orange lines are best fit lines for rat-free and rat-present empirical data respectively. Grey shading represents 95% confidence limits. Dashed lines represent the upper thresholds of territoriality as predicted by our mathematical model.

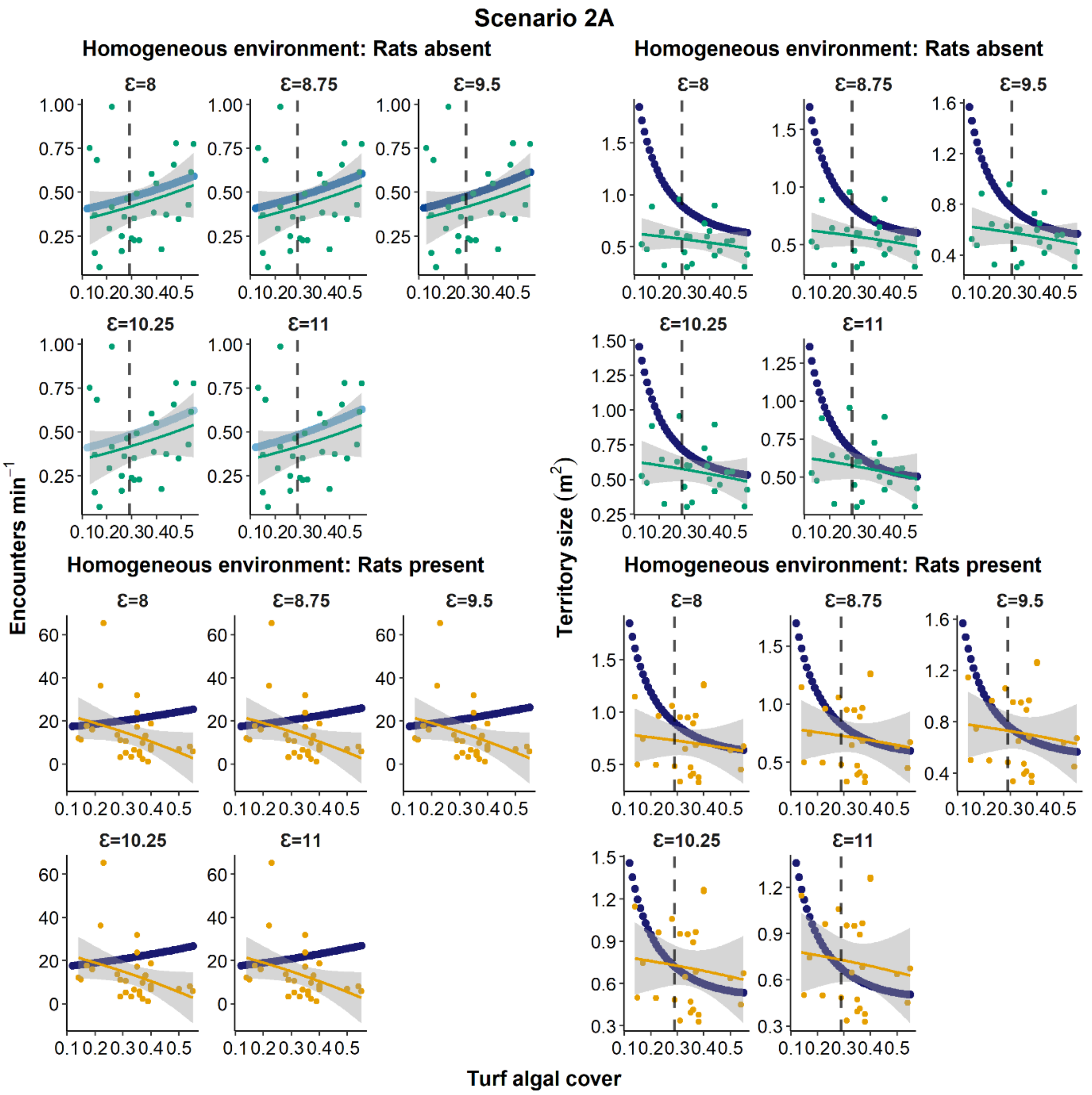

Figure S4.5: Model estimates and empirical data for *P. lacrymatus* territoriality in the presence and absence of invasive rats. Model estimates show the effect of varying food energy values in a heterogeneous environment. Points represent raw data for empirical data collected adjacent to islands where rats are absent (Green) and where rats are present (Orange). Green and Orange lines are best fit lines for rat-free and rat-present empirical data respectively. Grey shading represents 95% confidence limits. Dashed lines represent the lower thresholds of territoriality as predicted by our mathematical model.

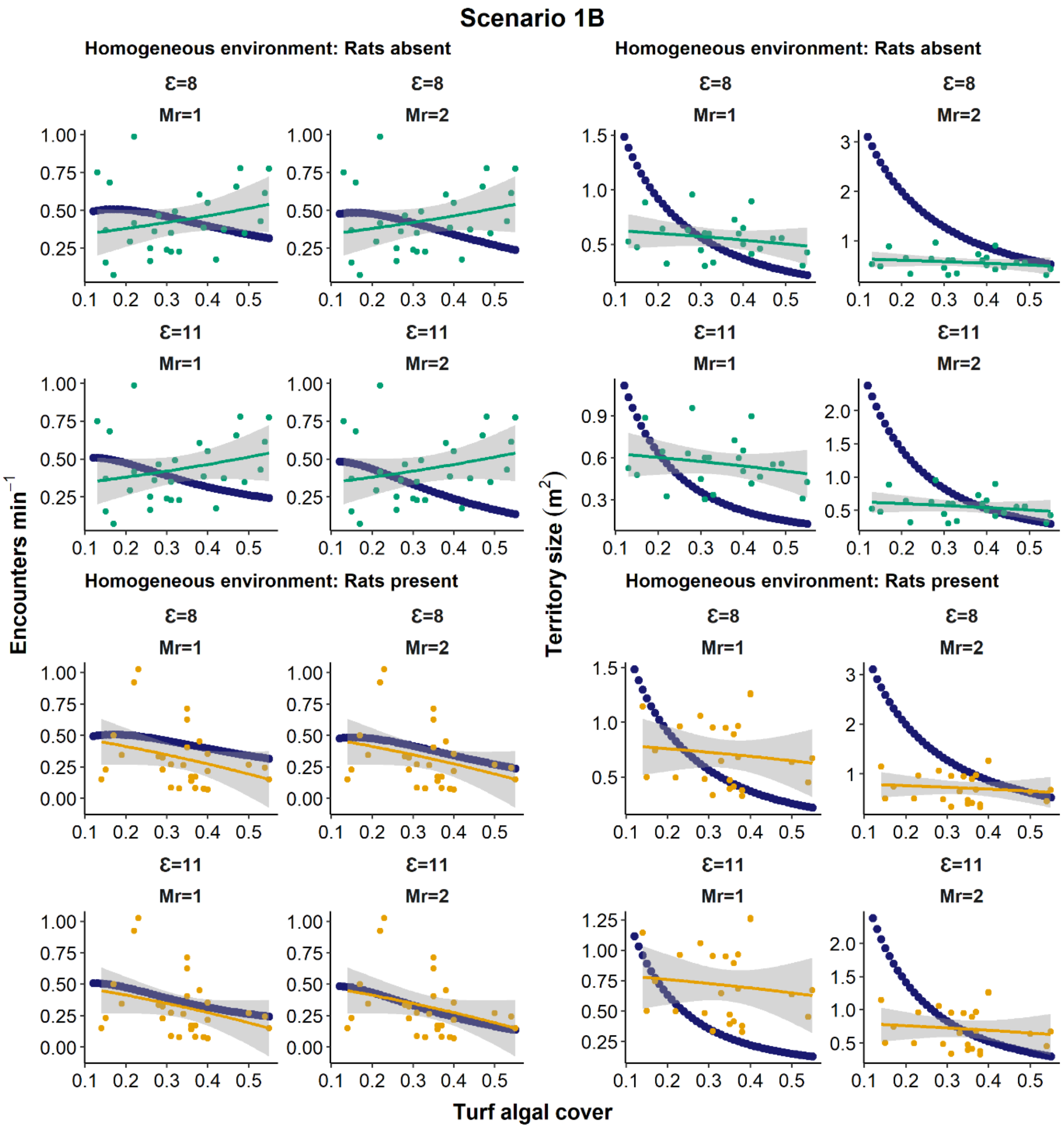

Figure S4.6: Model estimates and empirical data for *P. lacrymatus* territoriality in the presence and absence of invasive rats. Model estimates show the effect of varying food energy and cost-of living values in a homogeneous environment. Points represent raw data for empirical data collected adjacent to islands where rats are absent (Green) and where rats are present (Orange). Green and Orange lines are best fit lines for rat-free and rat-present empirical data respectively. Grey shading represents 95% confidence limits.

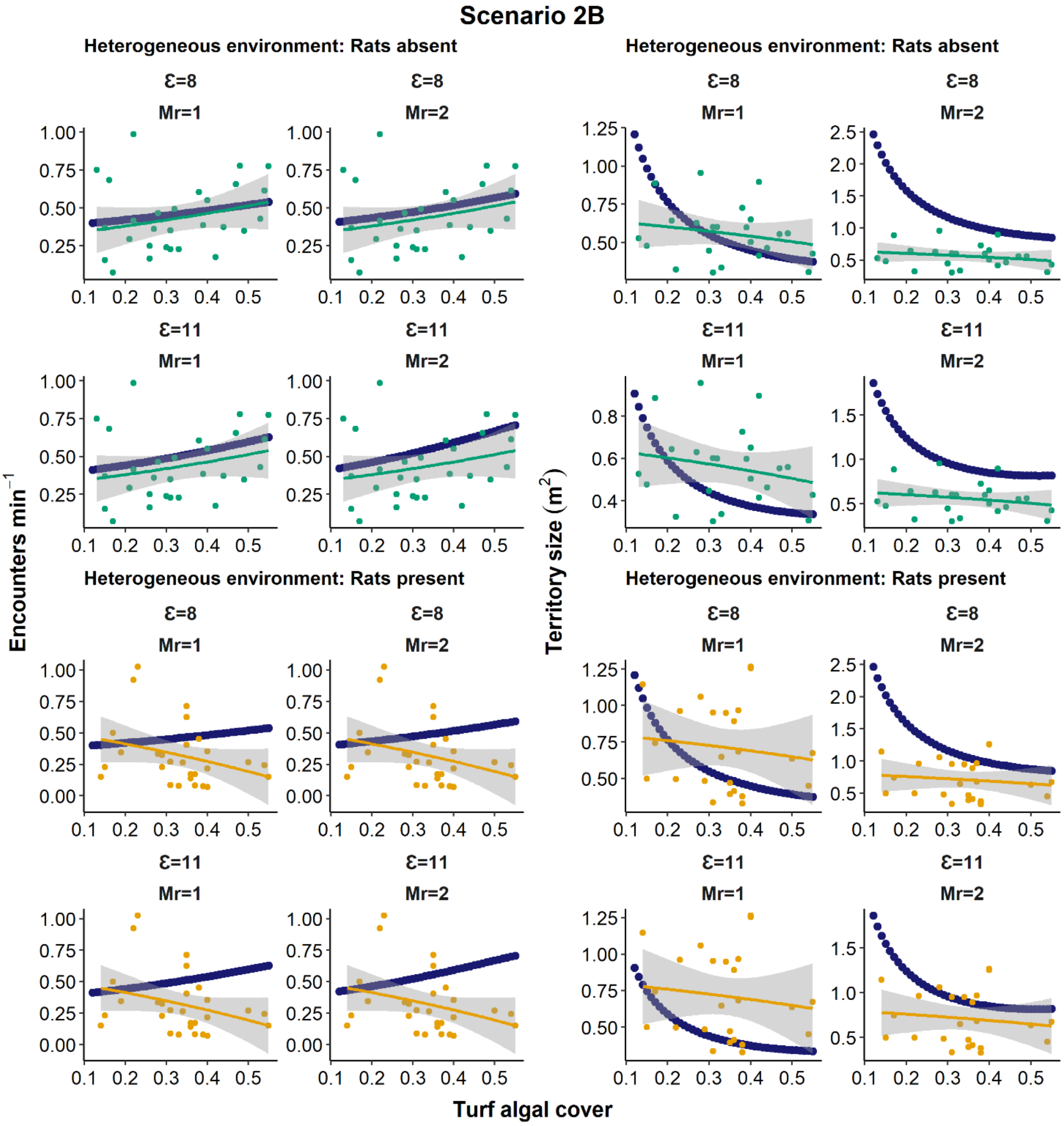

Figure S4.7: Model estimates and empirical data for *P. lacrymatus* territoriality in the presence and absence of invasive rats. Model estimates show the effect of varying food energy and cost-of living values in a heterogeneous environment. Points represent raw data for empirical data collected adjacent to islands where rats are absent (Green) and where rats are present (Orange). Green and Orange lines are best fit lines for rat-free and rat-present empirical data respectively. Grey shading represents 95% confidence limits.

Appendix B: Publications arising from thesis

Gunn, R.L., Hartley, I. R., Algar, A.C., Niemelä, P.T., & Keith, S.A. (2021). Understanding behavioural responses to human-induced rapid environmental change: a meta-analysis. *Oikos*: 1–13. https://doi.org/10.1111/oik.08366

Gunn, R.L., Hartley, I.R., Algar, A.C., Nadiarti, N. & Keith, S.A. (2022). Variation in the behaviour of an obligate corallivore is influenced by resource availability. *Behavioural Ecology and Sociobiology*, 76(2). https://doi.org/10.1007/s00265-022-03132-6